

# The effects of preceding moving stimuli on the initial part of smooth pursuit eye movement

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**Abstract** We examined whether there are any adaptive effects on the pursuit initiation after a prolonged exposure to moving visual stimuli. The eye movements of six human subjects were recorded with the scleral search-coil technique or a Dual Purkinje Image Eye-tracker system. A random-dot image appeared on a CRT monitor and moved coherently in one direction (rightward or leftward) at 10 deg/s for 4 s, while the subject fixated on a stationary target (*conditioning stimulus*). The screen was blanked for 0.2 s, and then the target stepped to the right or left of the center and moved 10 deg/s leftward or rightward. We measured change in the eye position over the open-loop period of the pursuit initiation. When the pursuit target moved in the same direction as the preceding visual stimulus, a significant reduction in the initial tracking responses (55.9% decrease on average) was found. We then studied in detail the properties of the motion adaptation in pursuit initiation by varying the visual conditions systematically and obtained the following findings. When the subjects tracked the target that moved at 10 deg/s, the pursuit initiation was affected not only by the conditioning stimulus of the same speed as the target, but

also by those of different speeds. Further, the conditioning stimulus moving at 10 deg/s affected the pursuit initiation not only when the target moved with the same speed but also when it moved at different speeds (more remarkable for slower speeds). The effect of conditioning stimuli on the pursuit initiation was larger when the duration of the conditioning period was longer. The effect of conditioning stimuli decayed as the duration of the blank period became longer. The findings from the present study are consistent with the properties of neurons in the middle temporal area of monkeys.

**Keywords** Motion adaptation · Visual motion · Eye movement · Pursuit · Human

## Introduction

A prolonged viewing of visual motion stimuli causes an adaptation in the visual motion processing (motion adaptation). Psychophysical studies have revealed various perceptual effects of a prolonged viewing of motion: an elevation of the threshold for detecting the moving stimulus, a reduction of the apparent speed of the moving stimulus, a distortion of the appearance of the moving stimulus, an illusory motion of a stationary stimulus in the opposite direction to the preceding motion (motion aftereffect), and so on (see Sekuler (1975); Mather et al. (1998), for reviews).

Barlow and Hill (1963) reported the existence of directionally selective cells in the retina of the rabbit, whose spontaneous activity reduced after a prolonged exposure to stimuli moving in the preferred direction. Similar phenomena have been observed in the primary visual cortex

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of cats (Vautin and Berkley 1977; von der Heydt et al. 1978; Hammond et al. 1986, 1989; Hammond and Mouat 1988; Marlin et al. 1988; Saul and Cynader 1989; Giaschi et al. 1993) and in the middle temporal (MT) area of monkeys (Petersen et al. 1985; Priebe et al. 2002; Priebe and Lisberger 2002; Van Wezel and Britten 2002; Kohn and Movshon 2004; Krekelberg et al. 2006). Functional imaging studies in humans suggest that an adaptation causes a direction-specific reduction in activity in the human area MT<sup>+</sup> (Huk et al. 2001), which is the area homologous to the macaque MT and the medial superior temporal (MST) areas. These neurophysiological findings provide a potential basis underlying the adaptation effect on the visual motion processing.

Smooth pursuit eye movements are used by primates to track small moving objects, allowing them to keep the retinal image of the objects within or near the fovea (Carl and Gellman 1987; Keller and Heinen 1991; Ilg 1997; Lisberger and Movshon 1999). Previous studies have suggested that visually driven smooth pursuit eye movements can be used as a measure when the neural mechanism underlying the visual motion analysis is being investigated. There are evidences that the MT and MST areas are related to driving smooth pursuit (Dursteler and Wurtz 1988; Komatsu and Wurtz 1988; Kawano et al. 1994). Priebe et al. (2001) demonstrated that the eye acceleration of the initial part of smooth pursuit is consistent with the reconstruction of target speed based on the speed tuning of the active population of MT neurons. It suggests that the measurements of the smooth pursuit initiation would reflect the properties of visual motion processing in the MT area. Decreased neural activities in the MT area after a prolonged exposure to visual motion stimuli have been reported in previous studies (Petersen et al. 1985; Priebe et al. 2002; Priebe and Lisberger 2002; Van Wezel and Britten 2002; Kohn and Movshon 2004; Krekelberg et al. 2006), suggesting that the initial part of the smooth pursuit eye movement may show adaptive decrement in metrics in the presence of a prior exposure to visual motion stimuli. Gardner et al. (2004) demonstrated in monkeys that an exposure to small image patches of coherently moving dots for several seconds resulted in marked changes in the direction and speed of the *post-saccadic* part of smooth pursuit eye movements. When the direction of the pursuit target was close to the adapting direction, the direction of the pursuit was repelled from the adapting direction, and the post-saccadic eye speed of the pursuit was depressed relative to that under a no-motion-adaptation condition. However, it remains unclear regarding whether the initial part of smooth pursuit

eye movements shares the properties in the post-saccadic part of smooth pursuit eye movements.

In this study, we studied whether the initial part of smooth pursuit eye movements shows any adaptive effects on human pursuit initiation after a prolonged exposure to moving visual stimuli (conditioning stimuli). Further, we characterized the effects of conditioning stimulus on the pursuit initiation when we varied the experimental parameters systematically.

## Methods

### Subjects

The eye movements were recorded in six subjects (subjects 1–6, five men and one woman), ranging from 28 to 54 years old. Subjects 1, 2, and 3 were authors, and the remaining three were naïve and unaware of the experimental design. Each subject had normal or corrected-to-normal vision, normal visual fields, and clinically normal eye movements. The experiments were performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All subjects gave their informed consent before their inclusion in the study. The experimental procedures were approved in advance by the Kyoto University Graduate School and Faculty of Medicine, Ethics Committee.

### Eye movement recordings

The eye movements of two subjects (subjects 1 and 2) were recorded by means of the electromagnetic search-coil technique (Fuchs and Robinson 1966). This system used an 80 cm diameter field coil system (Enzanshi-Kogyo). The subject sat on a chair so that his or her head was at the center of the field coil and wore an eye coil (Collewijn et al. 1975), which was placed in the right eye following an application of 1 or 2 drops of anesthetic (oxybuprocain hydrochloride); the wearing time was limited to 60 min. The eye movements of the remaining four subjects were recorded with a Dual-Purkinje-Image (DPI) eye-tracking system (Fourward Technologies, generation VI). Viewing was always binocular. The head of the subject was supported by chin and forehead rests so that the eye was 63.4 cm from the CRT monitor on which visual stimuli were presented (see subsequently for the visual stimuli). The signals from the search-coil system were calibrated by having the subject fixate targets at the center of the monitor or 10° up, down, left, or right of the center. Voltage signals encoding the horizontal and vertical components of the eye position were low-pass filtered (200 Hz,

–3 dB) and digitized to a resolution of 12 bits, sampling at 1 kHz.

### Visual stimuli

The visual stimuli were presented on a 19-in. CRT monitor (Eizo FlexScan T766 driven by a PC Radeon 9800 Pro video card). The monitor screen was 360 mm wide and 270 mm high with a resolution of  $1,280 \times 1,024$  pixels (40 pixels/deg) and a vertical refresh rate of 100 Hz. The RGB signals from the video card provided the inputs to an attenuator (Pelli and Zhang 1991), whose output was connected to the “green” input of a video signal splitter (Black Box Corp., AC085A-R2); the three “green” video outputs of the splitter were then connected to the RGB inputs of the monitor. This arrangement allowed the presentation of black and white images with a 12-bit grayscale resolution (Sheliga et al. 2005; Miura et al. 2006). But in our present experiment, we used only black ( $> 0.02$  cd/m<sup>2</sup>) and white (10.5 cd/m<sup>2</sup>) images.

We used two kinds of visual stimuli, a conditioning stimulus and a fixation/pursuit target. The conditioning stimulus was a random-dot pattern consisting of white circular dots (diameter of  $0.1^\circ$ , dot density of 24 dots/deg<sup>2</sup>) on a black background, which was displayed in a fixed region centered on the CRT monitor ( $9 \times 3$  deg,  $360 \times 120$  pixels). The dots in the region were stationary or coherently moving leftward or rightward. The fixation/pursuit target was a white annulus of  $0.3^\circ$  with a  $0.1^\circ$  black dot in the center, so that the subject was able to distinguish them and continue to gaze at the target even when the conditioning stimulus was simultaneously presented.

### Procedures

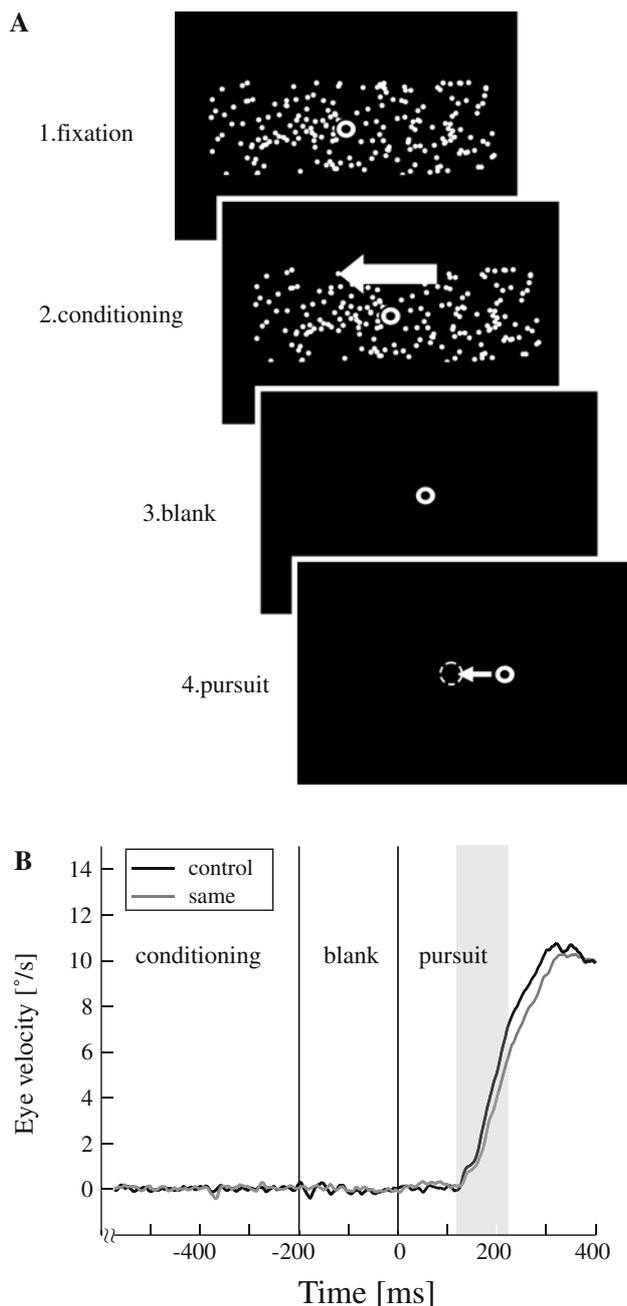
All aspects of the experimental paradigms were controlled by two PCs, which communicated via Ethernet using the TCP/IP protocol (Sheliga et al. 2005; Miura et al. 2006). One of the PCs was running on a Real-time EXperimentation software package (REX) developed by Hays, Richmond and Optican (1982) and provided the overall control of the experimental protocol as well as the acquiring, displaying, and storing of the eye-movement data. The other PC was running Matlab (Mathworks, Natick, MA, USA) subroutines, utilizing the Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997) and generated the visual stimuli upon receiving a start signal from the REX machine.

Figure 1a shows a general sequence of visual stimuli used in the experiments. Each trial consisted of four periods: fixation, conditioning, blank, and pursuit. At the beginning of each trial, a target spot appeared at

the center of the screen together with a stationary random-dot pattern (*fixation period*). One second after the subject’s eye entered within  $2^\circ$  of the central fixation target, the trial proceeded into the *conditioning period*, during which the random-dot pattern moved either leftward or rightward at a constant speed (*conditioning speed*) for a certain period (*conditioning duration*). To obtain no-motion adaptation control, we kept the random-dot pattern stationary during the *conditioning period*. If the subject’s eye moved outside the window ( $2^\circ$  from the fixation target) during this period, the trial was aborted and repeated after the presentation of a uniform black image for 2 s. After this period, the random-dot pattern disappeared. Following a short interval (*blank duration*) in which only the stationary target was presented (*blank period*), the target stepped either left or right of the center and immediately started to move toward the center at a constant speed (*target speed*) (Rashbass 1961). The step size of the pursuit target was varied depending on the target’s speed to reduce the occurrence of a catch-up saccade during pursuit initiation (1, 1, 1.5, 2, or  $4^\circ$  for 0, 2.5, 5, 10, 20, or 40 deg/s, respectively). The motion of the pursuit target lasted for 0.7 s, and the entire image was then replaced by a black homogeneous one, signaling the end of the trial. The inter-trial interval was set at 2 s. The subject was instructed to look at the target spot throughout the trial as best as he or she could.

To characterize the effects of preceding moving stimuli on pursuit initiation, we manipulated four parameters: conditioning speed, target speed, conditioning duration, and blank duration. We then ran four experiments. For Experiment 1, we set the conditioning speed at 10 deg/s, the conditioning duration 4 s, the blank duration 0.2 s, and the target speed 10 deg/s, based on our preliminary experimental results. Thus, the purpose of Experiment 1 was to examine the robustness of the effects of motion adaptation on pursuit initiation, and all six subjects participated. Each experimental block consisted of 6 conditions: 3 conditioning motions (rightward, leftward, stationary)  $\times$  2 target motions (rightward, leftward). The order of these conditions in each block was randomized.

The remaining three experiments were designed to systematically investigate the details of the effect of motion adaptation on the smooth pursuit initiation: the dependence on *the conditioning and target speeds* in Experiment 2, the dependence on *the conditioning duration* in Experiment 3, and the dependence on *the blank duration* in Experiment 4. Two subjects (authors S1 and S2) participated in these experiments. The parameters of the experimental conditions used in individual experiments are summarized in Table 1.



We designed Experiment 2 so that we could examine (1) the effect of conditioning speeds (2.5, 5, 10, 20, or 40 deg/s) on the pursuit of the target moving at a



**Fig. 1** Experimental conditions and an overview of eye movement records. **a** Schematic diagrams of visual stimuli used in the experiments. From *top left to bottom right*, screen shots of visual stimuli in individual steps are shown. Each trial started by presenting a central fixation target and white dots in the region subtending  $3 \times 9$  deg (fixation period). After the subject fixated the target, the white dots moved rightward or leftward at a constant speed within the region (conditioning period). Then the dots disappeared (blank period). After the blank period, the pursuit target stepped left or right from the central fixation spot and immediately moved toward the center (pursuit period). **b** Mean eye velocity profiles of the subject 1 during conditioning, blank and pursuit when the conditioning stimuli are stationary (control, *black line*) and moving in the same direction as the target (same, *gray line*). *Abscissa* indicates time from the onset of the pursuit target. *Upward deflection* indicates a leftward eye movement. The time window used in the quantitative analyses is marked by the *gray shading*

specific speed (10 deg/s), and (2) the effect of conditioning motion at a specific speed (10 deg/s) on the pursuit of the target moving at different speeds (0, 2.5, 5, 10, 20, or 40 deg/s). A single block also involved the control conditions for individual target speeds in which the conditioning stimulus was stationary. The conditioning and blank duration was set to 4 and 0.2 s, respectively. All possible conditions (49) were carried out randomly in each block.

In Experiment 3, the conditioning duration (4 s) was divided into two phases (first the stationary and later the motion) so that the total duration of presenting the conditional stimulus was the same in every trial. The duration of the moving phase was either 0, 1, 2, or 4 s. The conditioning stimulus was stationary or moved either rightward or leftward at 10 deg/s. The blank duration was 0.2 s. The target speed was 10 deg/s. All possible combinations (14) were carried out randomly in each block.

In Experiment 4, the conditioning stimulus was stationary or moved at 10 deg/s. The conditioning duration was 4 s. The blank duration was either 0, 0.1, 0.2, 0.4, 1, or 2 s, and the target speed was 10 deg/s. All possible combinations (36) were carried out in a random order in each block.

**Table 1** Summary of the experimental conditions

	Subjects	Conditioning speed (°/s)	Conditioning duration (motion phase) (s)	Blank period (s)	Target speed (°/s)
Exp 1	1–6	10	4 (4)	0.2	10
2–1	1, 2	0, 2.5, 5, 10, 20, 40	4 (4)	0.2	10
2–2	1, 2	10	4 (4)	0.2	0, 2.5, 5, 10, 20, 40
3	1, 2	10	4 (0, 1, 2, 4)	0.2	10
4	1, 2	10	4 (4)	0, 0.1, 0.2, 0.4, 1, 2	10

## Data analysis

The quantitative analysis of eye movement data was performed on a PC using an interactive computer program based on MATLAB (MathWorks). First, eye position data were smoothed with a digital Butterworth filter (3 poles,  $-3$  dB at 30 Hz). Eye velocity data were then obtained from the smoothed eye position data by using two-points backward differentiation. The eye acceleration data were obtained from the eye velocity data in the same manner. All eye movement data were aligned at the onset of the motion of the pursuit target (the time at which the first motion frame was presented) and sorted according to stimulus conditions. Then, the data that contained saccades during the 220 ms period following the onset of target motion were excluded. The eye velocity and acceleration data were used to identify the occurrence of saccades using velocity and acceleration criteria (eye velocity of more than 20 deg/s and eye acceleration of more than 1,000 deg/s<sup>2</sup>). We subsequently inspected the eye movement data and manually removed the trials containing small saccades that were not detected in the automatic saccade detection process. After this preprocessing, the mean eye velocity profile was computed for each of the different stimulus conditions to peruse the initial part of smooth pursuit.

Figure 1b shows an overview of representative mean eye velocity profiles during the trials obtained in Experiment 1. The black and gray lines indicate the average eye velocity profiles when the conditioning stimulus was moving in the same direction as the pursuit target (leftward) and when it was stationary, respectively. As seen in Fig. 1b, the eye was effectively stationary during the conditioning and blank intervals. In this example, the mean eye velocity ( $\pm$  SD) during the conditioning period (400 ms interval starting from 600 ms before the onset of target motion) was 0.05 ( $\pm$  0.06) deg/s rightward when the conditioning stimulus was moving in the same direction as the pursuit target and 0.03 ( $\pm$  0.05) deg/s rightward when it was stationary. The mean eye velocity ( $\pm$  SD) during the blank period was 0.02 ( $\pm$  0.12) deg/s rightward when the conditioning stimulus was moving in the same direction as the pursuit target and 0.05 ( $\pm$  0.15) deg/s leftward when it was stationary. Thus, the eye movements during the conditioning and blank periods were very small. We examined the fixation quality during the conditioning and blank intervals with the data from the two subjects whose eye movements were recorded using the search coil method. The mean eye velocity during the conditioning and blank intervals for the moving conditioning differed no more than 0.2 deg/s

from those during the stationary conditioning of the corresponding periods, and the differences were not significant in most cases (7/8).

Here, we are interested in eye movement during the open-loop initiation period of pursuit, during which the responses are caused purely by the image motion on the monitor (free of modulation by the subject's own eye movement). To determine the open-loop period, the latency of the pursuit onset was estimated from the mean eye velocity profiles, using a modified method from Carl and Gellman (1987). The pre-response level (offset) was determined by the average of mean eye velocity in 180 ms interval of starting from 100 ms before the onset of target motion. We then searched the earliest time ( $\tau_0$ ) at which the mean eye velocity exceeded 3 SDs of the pre-response level. Then, a regression line was calculated from the mean eye velocity in 40 ms interval starting at  $\tau_0$  and then found the time at which the regression line crossed the pre-response level, giving a latency estimate. The latency estimates were distributed from 117 to 154 ms for the data of two subjects whose eye movements were recorded by means of the scleral search coil method. However, in some cases, the reliable estimates were extremely difficult to obtain with the objective method (and also with other objective methods). Therefore, we did not use the latency estimates to study the effect of the conditioning stimuli. We used the latency estimates only to determine the open-loop interval. Thus, the quantification of pursuit initiation was made by calculating the change in eye position over the 100 ms interval starting 120 ms after the onset of the target motion (referred to as *initial tracking response* hereafter), which provides robust estimates of the initial development of pursuit. The effect of conditioning motion was quantified with the expression:  $100 \times (R_c - R)/R_c$  (referred to as *attenuation index* as in Masson et al. (2001)), where  $R_c$  and  $R$  are the mean initial tracking responses when the conditioning stimulus was stationary and when it was moving (i.e., in the "same" direction or in the "opposite" direction), respectively. For each stimulus condition, data were available for at least 10 trials and generally for more than 20 trials.

## Results

### Experiment 1: motion adaptation on pursuit initiation

Figure 2a shows mean eye velocity profiles when subject 2 tracked the target moving leftward at 10 deg/s after viewing the conditioning stimulus (2 s) that moved at 10 deg/s leftward ("*same*" condition, gray

continuous line), or moved rightward (“*opposite*” condition, black dashed line), or was stationary (“*control*” condition, black continuous line). It is evident that the mean eye velocity during pursuit initiation was slower when the conditioning stimulus moved leftward (“*same*” condition) than when it was stationary (“*control*” condition). On the other hand, when the conditioning stimulus moved in the opposite direction of the pursuit target, the mean eye velocity was larger than that in the control condition.

The magnitudes of the initial tracking responses ( $\pm$  SE) in this subject were  $0.25 \pm 0.013$ ,  $0.31 \pm 0.013$  and  $0.30 \pm 0.011$  deg under the “*same*”, “*opposite*”, and “*control*” conditions, respectively (see [Methods](#) for the definition of the initial tracking response). The results of ANOVA applied to the initial tracking responses showed a significant difference among conditions ( $P < 0.05$ ). A multiple comparison showed a difference between the “*same*” and “*control*” conditions (Tukey-Kramer’s method,  $P < 0.05$ ). To quantify the effect of conditioning motion, the attenuation indices were calculated from the initial tracking responses (see [Methods](#) for the definition). In the case shown in [Fig. 2a](#), the attenuation indices under the “*same*” and “*opposite*” condition were 16.0 and  $-4.3\%$ , respectively. The averages of the attenuation indices for the six subjects were shown in [Fig. 2b](#). The averages of the attenuation indices ( $\pm$  SE) in the “*same*” and “*opposite*” conditions were  $55.9 (\pm 7.5)$  and  $-21.1 (\pm 21.3)$  %. The attenuation index under the “*same*” condition was significantly different from zero ( $t$  test,  $P < 0.05$ ). On the other hand, the attenuation index under the “*opposite*” condition was, on average, negative but was not significantly different from zero. The results suggest that the effect of the moving conditioning stimulus is

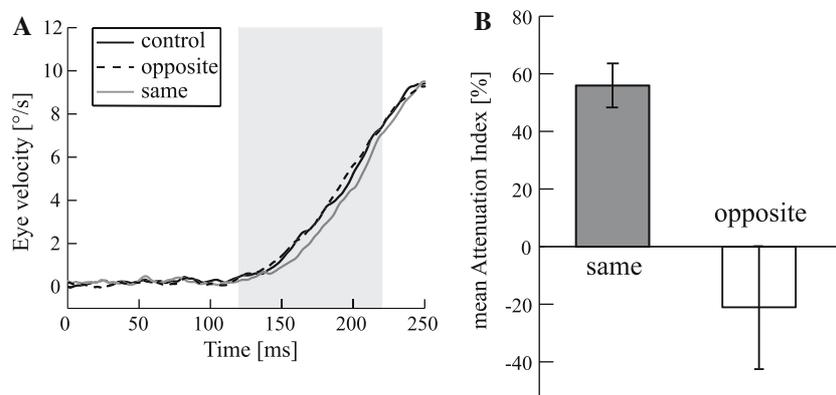
dependent on the direction and are consistent with the effect on motion perception and on the MT neurons.

#### Experiment 2: dependence on the speed of conditioning and test stimuli

In Experiment 2, we examined the effect of conditioning speeds on the pursuit of the target moving at a specific speed (Exp 2–1), and the effect of conditioning motion at a specific speed on the pursuits of the target moving at different speeds (Exp 2–2).

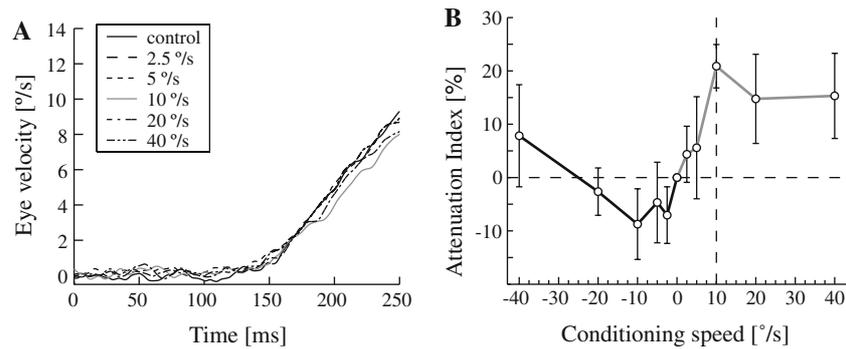
##### Experiment 2–1

[Figure 3a](#) shows mean eye velocity profiles when subject 1 tracked the target moving rightward at 10 deg/s after a prolonged viewing of a visual stimulus (conditioning stimulus) that either moved rightward (“*same*” condition) or was stationary (“*control*” condition, a black continuous line). The speed of the conditioning stimulus was 2.5, 5, 10, 20 or 40 deg/s. The initial pursuit eye velocity in the “*same*” condition was generally smaller than in the “*control*” condition. This property can be confirmed in [Fig. 3b](#), which shows that the attenuation indices averaged for the four cases (two subjects  $\times$  two pursuit directions) as a function of conditioned speeds. The mean attenuation indices in the “*same*” condition were positive except at 2.5 deg/s, and were largest when the conditioning speed was 10 deg/s. All four cases from two subjects showed a broad dependence on the speeds (less clear peak). On the contrary, those in the “*opposite*” condition were in most cases negative, and were the smallest when the conditioning speed was 10 deg/s.



**Fig. 2** Effects of conditioning stimulus on initial pursuit responses. **a** Mean eye velocity profiles of smooth pursuit when subject 2 tracked a target moving at 10 deg/s. *Upward deflection* indicates leftward eye movement. The time window used in the quantitative

analyses is marked by the *gray shading*. **b** Attenuation indices of the initial tracking response averaged over all subjects. The *gray and white bars* indicate the mean attenuation indices in the “*same*” and “*opposite*” conditions, respectively. *Error bars* are 1 SE



**Fig. 3** Dependence on speeds of the conditioning stimulus. **a** Mean eye velocity traces when subject 1 tracked the pursuit target moving at 10 deg/s after exposures of a stimulus moving in the same direction at 0 (black continuous line), 2.5 (black wide dashed line), 5 (black narrow dashed line), 10 (gray continuous line), 20 (black chain line) and 40 deg/s (black chain-double-dashed line). An upward deflection of the traces indicates rightward eye move-

### Experiment 2–2

Here, we compared the effect of conditioning stimulus moving at 10 deg/s on the pursuit of the target moving at different speeds. Figure 4a–f shows mean eye velocity profiles when subject 2 tracked the target which was stationary (i.e., 0 deg/s) or moved leftward at 2.5, 5, 10, 20 or 40 deg/s after viewing of a conditioning stimulus that moved at 10 deg/s leftward (“same” condition, gray continuous line), rightward (“opposite” condition, black dashed line), or was stationary (“control” condition, black continuous line), respectively. When the target was stationary, the eye did not move irrespective of whether the conditional stimulus was stationary or moving (Fig. 4a). When the target moved, the eye velocity at the pursuit initiation was always slower under the “same” condition than under the “opposite” or “control” conditions (Fig. 4b–f). Figure 5a shows group means of the normalized initial tracking responses under the “same” (circles connected by a gray continuous line), “control” (squares connected by a black continuous line) and “opposite” (triangles connected by a black dashed line) conditions. The normalization in each case was performed by dividing the initial tracking responses of a given condition by the response when the target moved at 10 deg/s under the “control” condition. The attenuation indices averaged over 4 cases were shown in Fig. 5b. Under the “same” condition, the attenuation index was the smallest at 10 deg/s, and was larger especially when the speed of the target was slower than that of the conditioning stimulus. Significant effects of the conditioning ( $t$  test,  $P < 0.05$ ) were found at all the speeds under the “same” condition. Under the “opposite” condition, significant effects of the conditioning were found at 2.5 and 20 deg/s ( $t$  test,  $P < 0.05$ ).

ment. **b** Group mean of the attenuation indices of the initial tracking response (four cases: two subjects  $\times$  two directions) plotted as a function of conditioning speeds. Positive conditioning speeds indicate that the direction of the conditioning stimulus were the same as that of the pursuit. Vertical dashed line indicates the speed of the target. Error bars are 1 SE

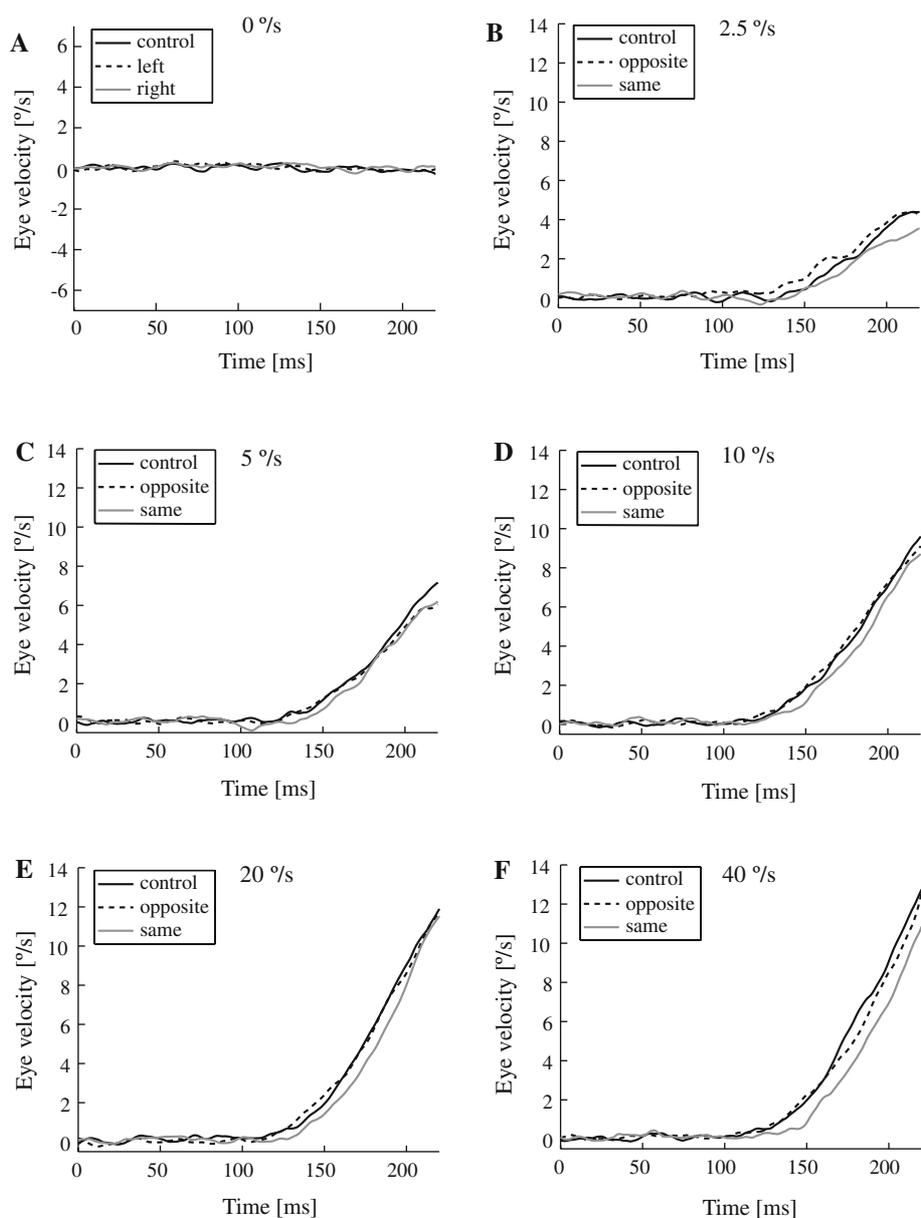
### Experiment 3: dependence on the conditioning duration

We examined the dependence on duration of the conditioning stimulus in motion. Figure 6a shows mean eye velocity profiles when subject 1 tracked the target moving at 10 deg/s in the same direction as the conditioning stimulus, which moved at 10 deg/s for one of the three durations: 0 s (control condition, thick black continuous line), 1 s (thin black dashed line), 2 s (thin black continuous line), or 4 s (gray continuous line). The attenuation indices averaged for the four cases under the “same” condition were monotonically decreased as the duration of the conditioning motion increased. The average attenuation indices fit well with a single exponential function of the duration of the conditioning motion ( $t$ ):  $k \times (1 - \exp(-t/\tau))$ , where  $k$  is the asymptotic level,  $\tau$  is the time constant of the decay. The best-fit  $k$  and  $\tau$  obtained from the averaged data shown in Fig. 6b were 0.45 and 1.7 s, respectively ( $R^2 = 0.993$ ). The mean best-fit  $k$  and  $\tau$  obtained from individual cases ( $R^2 > 0.960$ ) were  $0.49 (\pm 0.14)$  and  $2.1 (\pm 0.66)$  s, respectively. The effect of duration of the conditioning stimulus in motion in the “opposite” condition was not significant (not shown).

### Experiment 4: dependence on blank duration

This experiment was designed to characterize a recovery from adaptation on the pursuit initiation. Before we described about this point, we should notice that the smooth pursuit initiation was quite sensitive to the blank duration. Figure 7 shows average eye velocity profiles under the control (a), the same (b) and the opposite (c) conditions. In any conditions, we can see

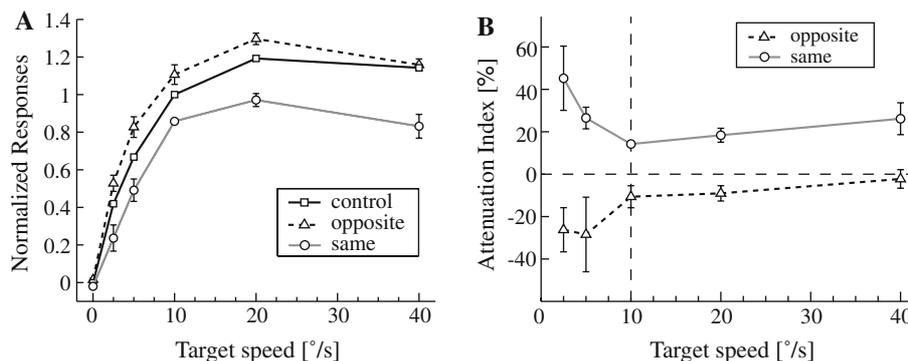
**Fig. 4** Mean eye velocity profiles when subject 2 fixated a stationary target or tracked the target moving leftward at different speeds after an exposure of conditioning stimuli (**a** 0 deg/s, **b** 2.5 deg/s, **c** 5 deg/s, **d** 10 deg/s, **e** 20 deg/s, **f** 40 deg/s). In all panels, an upward deflection indicates a leftward eye movement. Black continuous line, black dashed line and gray continuous line indicate mean eye velocities after exposures of the stimuli which were stationary, and moved rightward and leftward at 10 deg/s, respectively



that the initiation of smooth pursuit delayed when there was no blank period (black continuous line). When the blank interval was 0.1 s, the smooth pursuit developed earlier than the no-blank condition. The smooth pursuit initiation was best developed when the blank duration was 0.2 s (gray lines). Further increase in the blank duration resulted in slower developments of smooth pursuit. This anomalous effect of the blank duration might be due to a sudden offset of a bright conditioning stimulus. This may give a technically important suggestion when one studies the effect of conditioning stimulus on the pursuit initiation (see the next section for further discussion about this effect).

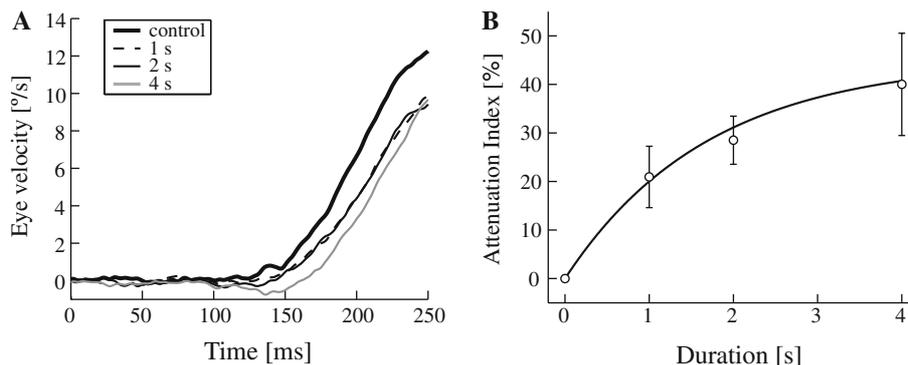
Even with this anomalous property of the pursuit initiation, effects that were attributable to moving con-

ditioning stimuli could be extracted from the data. Figure 8a summarizes the initial tracking responses as a function of the blank duration. The initial tracking responses were generally decreased when the conditioning stimulus moved in the same direction as the tracking target (circles, gray continuous line). The results of ANOVA applied to the initial tracking responses for individual blank duration showed a significant difference among conditioning motion when the blank duration was 200 ms ( $P < 0.05$ ). A multiple comparison among the responses at this blank duration showed that the responses in the “same” condition was significantly different from those both in the “control” or “opposite” conditions (Tukey-Kramer’s method,  $P < 0.05$ ).



**Fig. 5** Effect of conditioning motion (10 deg/s) on the pursuit of the target moving at different speeds. **a** The group means of normalized initial tracking responses when the subjects tracked the pursuit target are plotted with error bars (1SE) against target speed. For individual cases (two subjects  $\times$  two directions), the normalized responses were calculated by dividing the mean initial tracking responses for individual speeds by the mean responses for the target speed of 10 deg/s under the control condition. **b** The group means of the attenuation indices of the initial tracking

response plotted as a function of target speeds (four cases: two subjects  $\times$  two directions). *Circles and triangles* indicate the normalized responses in the “same” and “opposite” conditions, respectively. The *error bars* are 1 SE. *Positive target speed* indicates that the direction of the adaptation stimulus was the same as that of the conditioning stimulus. *Vertical dashed line* indicates the speed of the conditioning motion. Notice that when the target speed was 0 deg/s, the attenuation index is not defined



**Fig. 6** Effects of the duration of the motion phase of conditioning stimulus on initial tracking responses. **a** Mean eye velocity traces when subject 1 tracked the pursuit target moving at 10 deg/s in the same direction as the conditioning stimulus, whose durations of the motion phase were 0, 1, 2, or 4 s. An *upward deflection of the*

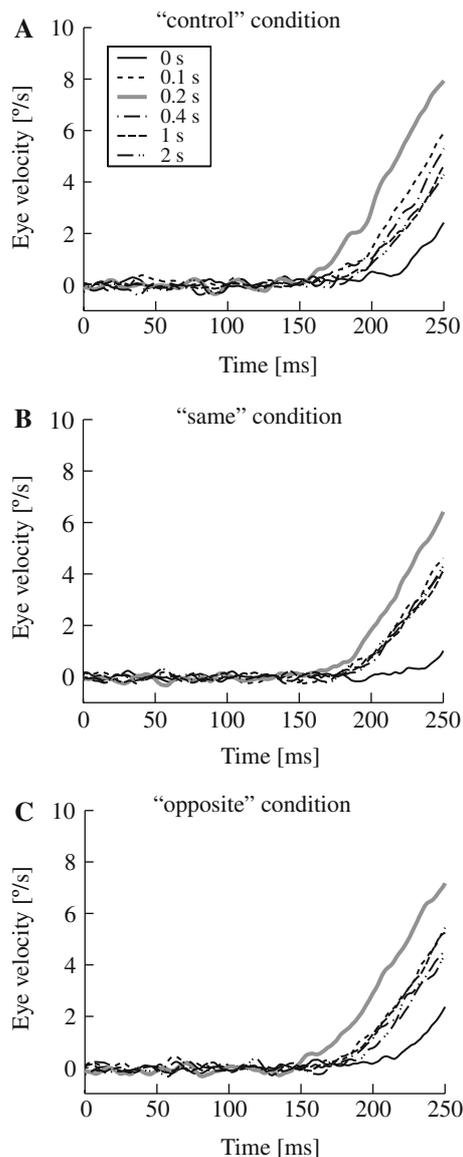
*traces* indicates rightward eye movement. **b** The group means of attenuation indices are plotted as a function of stimulus durations (four cases: two subjects  $\times$  two directions). The *error bars* are 1 SE. A *continuous line* indicates the best-fit curve with a single exponential function:  $0.45 \times (1 - e^{-t/1.7})$

Figure 8b shows attenuation indices averaged for the four cases. Under the “same” conditions, the mean attenuation indices were decreased as the duration of the blank period increased, while those under “opposite” condition tended to be closer to 0. This result suggests the time course of recovery from motion adaptation such that the effect of motion adaptation on the initial tracking responses decays monotonically over time. We attempted to fit the mean attenuation indices under the “same” condition with a single exponential:  $k \times \exp(-t/\tau)$ , where  $k$  and  $\tau$  are constants. The best-fit  $k$  and  $\tau$  for the single exponential function obtained from the averaged data shown in Fig. 7b were 0.68 and 0.21 s, respectively ( $R^2 = 0.897$ ). The mean best-fit  $k$  and  $\tau$  obtained from individual cases

( $R^2 > 0.625$ ) were  $0.70 (\pm 0.22)$  and  $0.39 (\pm 0.18)$ , respectively. We also attempted to fit the mean attenuation indices under the “same” condition with a double exponential function:  $k_1 \times \exp(-t/\tau_1) + k_2 \times \exp(-t/\tau_2)$ , and found that a slightly better fit than using a single exponential function ( $R^2 = 0.964$ ). The best-fit values were  $k_1 = 0.36$ ,  $k_2 = 0.37$ ,  $\tau_1 = 0.0042$ , and  $\tau_2 = 0.59$ .

**Discussion**

In this study, we examined the effect of a prolonged viewing of the preceding moving stimuli on the pursuit initiation. In Experiment 1, we found that the eye velocity in the pursuit initiation decreased when the



**Fig. 7** Mean eye velocity profiles of subject 1 for different blank periods (no blank: *black continuous line*; 0.1 s: *black narrow dashed line*; 0.2 s: *gray continuous line*; 0.4 s: *black chain line*; 1 s: *black wide dashed line*; 2 s: *black chain-double-dashed line*), under the “control” (a), “same” (b) and “opposite” (c) conditions. In all panels, an *upward deflection* indicates a rightward eye movement

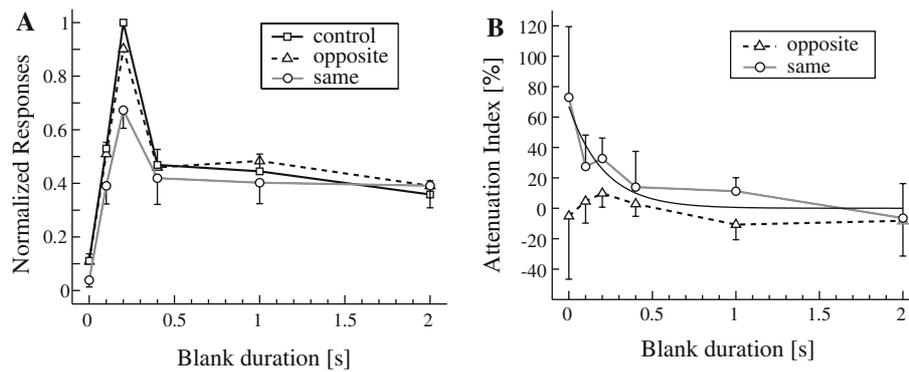
pursuit target moved in the same direction as the preceding visual stimulus. On the other hand, the responses were not affected or increased when the conditioning stimulus moved in the opposite direction to the target. In Experiment 2, we found that the preceding moving stimulus affected a wide range of combinations in speeds of the conditioning stimulus and target. We further found that the effect of the conditioning stimulus on the pursuit initiation was larger as the duration of the conditioning was longer (Experiment 3),

and that the effect of the conditioning stimulus was quickly decayed to about 10% by 0.4 s after the end of the conditioning (Experiment 4).

#### A technical issue

As shown in Figs. 7 and 8a, the pursuit initiation was dependent on the duration of the blank period in an anomalous way. Several mechanisms other than motion adaptation might underlie this phenomenon, because the entire form of this dependence was independent of the type of the conditioning stimuli. The smallest initial tracking responses under no-blank condition may be related to the visual masking. Richards (1969), for example, reported that the thresholds obtained during steady fixation are slightly elevated near the lighting and extinction of the background field and discussed that these transient effects reflect the underlying “on” and “off” bursts of neural activity (Boynton 1958; Ratliff et al. 1963). In our experiments, a sudden offset of conditioning stimuli might mask the following displacement of the fixation/pursuit target. Kawano and Miles (1986) reported a similar suppression of the ocular following responses by using saccade-like movements of the visual scene. They showed that a suppression of the responses was observed when the conditioning and test stimuli were confined to the peripheral and central retina, respectively, and discussed that this suppression is due to the shift effect or masking effect, which have been described previously (shift effect: Fischer et al., (1975); masking effect: see Breitmeyer and Ganz (1976), for review). Further, they showed that the responses were enhanced after the suppression period (peaked at 0.06 s). In the present study, we observed the largest enhanced pursuit responses when the target started moving at 0.2 s after the conditioning stimuli.

Although the mechanism underlying this effect is unclear, this finding might provide a technically important suggestion. To effectively observe the effect of the conditioning stimuli on smooth pursuit initiation, one must carefully choose the blank duration to have a better S/N. Under the blank duration of 0.2 s, the amount of changes may involve an interaction between the adaptation effect and the effect of sudden offset of the conditioning stimulus. The adaptation effect might be magnified by the sudden offset of the conditioning stimulus. We would emphasize here that, under this situation, the attenuation index (percent reduction measure) would provide an effective and fair measure to characterize the effect of moving conditioning stimuli on the pursuit initiation.



**Fig. 8** Effects of a blank period on initial tracking responses and motion adaptation. **a** The group means of normalized initial tracking responses are plotted against the blank duration (four cases: two subjects  $\times$  two directions). For individual cases (two subjects  $\times$  two directions), the normalized responses were calculated by dividing the initial tracking responses for individual blank durations by the responses when the blank duration was

0.2 s under the control condition. The *error bars* are 1 SE. **b** The group means of the attenuation indices of the initial tracking responses (four cases: two subjects  $\times$  two directions) are plotted as a function of blank durations. The *error bars* are 1 SE. A *black continuous line* indicates the best-fit curve with a single exponential function:  $0.68 e^{-t/0.21}$

## Comparisons with previous findings

### *Dependence on directions and speeds*

Van Wezel and Britten (2002) demonstrated the effects of motion adaptation on neural activities in the middle temporal (MT) area of monkeys. The responses of neurons in the MT area to subsequent test patterns given after the presentation of a moving random-dot pattern in the preferred direction were reduced by an average of 26% compared to those after the presentation of a static pattern. On the other hand, no significant reduction was found in the responses after the stimulation with the pattern in the null direction. A similar directional selectivity predicted from their findings was observed in the pursuit initiation in the present study. This point is consistent with the idea that neurons in the human brain region that correspond to the monkey MT area may be adapted in a similar manner after a prolonged viewing of moving visual stimuli. Although we rarely found the statistical significance, the initial tracking responses tended to be larger than the stationary control. Van Wezel and Britten (2002) reported that, in MT, adaptation only systematically affected responses of neurons tuned to the adaptation direction. Thus, the effect of the conditioning motion in the opposite direction to the pursuit target may reflect the properties of the downstream of the MT area in the pursuit pathway. Further, neurophysiological and behavioral studies are needed to determine the detailed mechanism underlying this effect.

Krekelberg et al. (2006) examined the responses of MT neurons of monkeys to test stimuli moving at various speeds after a presentation of a conditioning stimu-

lus moving at each neuron's preferred speed. They demonstrated that the effect of the conditioning stimulus was the least when the motion of the target and conditioning stimulus matched and was larger, especially when the target was moving in the same direction and with slower speeds than the conditioning one. We here obtained a consistent finding with this (see Fig. 5b).

Figures 3b and 5b indicate that the effects of conditioning stimuli were observed even when the speeds of the target and conditioning stimuli did not match. However, the effect of the conditioning stimulus on the tracking of the target that moved at 10 deg/s was fairly small when the speed of the conditioning stimulus was 2.5 or 5 deg/s (see Fig. 3b). We consider that this property might reflect a temporal property of the development of motion adaptation. Previous psychophysical studies demonstrated that the development (the temporal property) of motion adaptation depends highly on the conditioning speeds (Hammett et al. 2000, 2005). Hammett et al. (2000) reported the time constants of the reduction in perceived speeds as a function of conditioning (adaptation) duration. The time constants were 15.9 and 1.9 s for the adaptation with the conditioning stimulus moving at 2 and 12 deg/s, respectively. Thus, a longer duration is necessary to fully develop an adaptation-effect of a slower conditioning stimulus. In the present study, we used the conditioning duration of 4 s for all the conditioning speeds in Experiment 2. The small effects of the conditioning stimulus observed when the conditioning stimulus was 2.5 or 5 deg/s (in Fig. 3b) may result from the insufficient conditioning duration we had adopted.

Priebe et al. (2002) demonstrated that the responses of MT neurons to a test stimulus moving at their preferred

speed (which is determined under no conditioning) were affected by the conditioning motion of various speeds (conditioning duration of 64 ms). In approximately half of the MT neurons, the largest reduction in the firing rate occurred when the conditioning speed matched each neuron's preferred speed, while this was not the case in the remaining neurons. This allowed us to predict a broadly tuned dependence on the conditioning speeds when the conditioning duration was constant as in Fig. 3b. Unfortunately, detailed comparisons are not feasible because of the differences between their experimental conditions and ours (e.g., their conditioning duration was 64 ms); hence further behavioral and neurophysiological experiments are needed.

### *Temporal properties*

Previous studies reported that the perceived speed of a constantly moving stimulus decreased exponentially as a function of the conditioning duration to a steady level (Clifford and Langley 1996; Hammett et al. 2000), although the time constant of the development of motion adaptation depends on speeds of conditioning stimuli, faster for faster speeds (Hammett et al. 2000). Hammett et al. (2000) reported that the time constant of decay was 1.9 s for the adaptation with the conditioning stimulus moving at 12 deg/s. In our case (target speed of 10 deg/s, see Fig. 6), the best-fit time constant estimated from individual cases was similar and was on an average 1.5 s.

Hammett et al. (2000) also reported the time constants of recovery from motion adaptation. The estimated time constants were 11.8 and 30 s for adaptation stimuli moving slower (2 deg/s) and faster (12 deg/s). On the other hand, the time constant estimated in this study is much shorter than the ones estimated in the previous studies. In their study, the conditioning motion lasted 64 s, while ours is 4 s. This difference in experimental conditions may underlie the difference in the property of the recovery from adaptation.

Recently, Kanai and Verstraten (2005) examined a bias in the perceived direction of the test pattern presented after conditioning motion in one direction, and its dependence on the temporal separation (the duration of blank period) between the end of conditioning period and the onset of the test period. They demonstrated that the perceptual bias in the opposite direction of conditioning occurred when the conditioning duration was 320 or 640 ms (they referred this effect to as a rapid MAE: rMAE). They also reported that the rMAE decayed completely after a blank period of 2–3 s. This time course is similar to our data. Further, they pointed out that the mecha-

nism underlying the rMAE induced by this short conditioning is different from the one underlying the classical MAE that is caused by long duration of the conditioning stimulus. Our finding on the smooth pursuit initiation may be related to the mechanism underlying the rMAE.

Unfortunately, there is no available neurophysiological finding for the temporal properties of motion adaptation under similar experimental parameters. However, there may be a few findings that would be worth to mention. A rapid recovery from (short-term) adaptation was observed in the MT neurons in monkeys (Priebe et al. 2002). They demonstrated that a temporal separation for 256 ms between the offset of conditioning motion and the onset of test motion resulted in almost no effect of conditioning. Our data (Fig. 8) show an initial rapid decay of the effect of motion adaptation. This rapid decay may reflect the rapid decay found in the MT neurons. However, the property of this short-term adaptation found by Priebe et al. does not fully explain our behavioral data (Fig. 8b). This discrepancy may be due to the different conditioning durations between ours (4 s) and the previous studies (64 ms).

### *Comparisons with post-saccadic eye velocity*

Gardner et al. (2004) demonstrated in monkeys that an exposure to small image patches of coherently moving dots for several seconds resulted in direction-dependent changes on the post-saccadic smooth pursuit. This property is consistent with that of the initial part of smooth pursuit (see Fig. 2).

They also reported that the post-saccadic eye speed was on average 91.7% of the control when the pursuit target moved at the same speed as the conditioning stimulus. The decreases in the post-saccadic eye speed of the smooth pursuit became either greater or smaller when the pursuit targets moved slower or faster than the adapting speed. This finding is similar to ours. However, the effect of conditioning speeds on the pursuit at a specific speed was not investigated in their study. Thus, the consistency in the entire dependence remains unclear.

There is a difference between the finding of Gardner et al and ours. They reported the effects of motion adaptation under shorter (1–1.5 s) and under longer (7–7.5 s) were not different in the extent of the adaptation of pursuit speed, which averaged 84.1 and 85.2% of the control response for the short- and long-duration adapting stimuli, respectively. On the other hand, our data predict that a difference in the effect of adaptation can be seen in this range of conditioning duration (see

Fig. 6). This difference suggests that the visual motion analysis reflected in the initial pursuit responses may be different from that reflected in the post-saccadic eye velocity of smooth pursuit.

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