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Citation	Experimental Brain Research, 168(3), 427-435 https://doi.org/10.1007/s00221-005-0102-2
Issue Date	2006-01
Doc URL	http://hdl.handle.net/2115/5979
Rights	The original publication is available at www.springerlink.com
Type	article (author version)
File Information	EBR168_3.pdf



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Prediction in the timing of pursuit eye movement initiation revealed by cross-axis vestibular-pursuit training in monkeys

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Abstract Words: 285

Text pages (including cover, abstract, references, figure legends and figures): 25

Figures: 6

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ACKNOWLEDGMENTS: We thank Dr. C.R.S. Kaneko for his valuable comments on this manuscript.

This research was supported by grants from Japanese Ministry of Education, Culture, Science, Sports and Technology (16650087,16300128, 16015203), Marna Cosmetics, and Toyota Riken

Abstract

The smooth-pursuit system interacts with the vestibular system to maintain the image of a moving target on the fovea. Efficient tracking performance requires information about the velocity and the initiation of target motion. Previous studies in monkeys have shown that training with orthogonal pursuit and whole body rotation results in adapted eye movement direction during chair rotation. In addition, the latency of pursuit shortens and initial eye velocity increases in a task-dependent manner. To examine whether these adapted eye movements are predictive pursuit, we studied whether our monkeys could predict the timing of smooth eye movement initiation during chair rotation. Two young Japanese monkeys were rotated horizontally in a trapezoidal waveform ($20^\circ/\text{s}$, $\pm 10^\circ$) with random inter-trial intervals. A laser spot was moved vertically with the same trajectory at a constant delay ranging from 100 to 700 ms after the onset of chair motion. The monkeys were required to pursue the spot. After this training, the latencies of pursuit eye movements following the onset of chair motion were examined in the presence of the target motion. The target was also briefly (for 500-700 ms) extinguished at 80 ms after the onset of chair rotation. Pursuit eye movements after training were initiated before the onset of target motion and the latencies were proportional to the delays used for training. The latencies and response magnitudes of pursuit with or without target blanking were similar. The auditory-pursuit training did not induce an initial pursuit response similar to that induced by vestibular-pursuit training. These results indicate that smooth eye movements during the chair rotation after the vestibular-pursuit training included a predictive pursuit component. The monkeys' estimate of the delays revealed by the latencies of pursuit was shorter by 22-36 % than the actual delays.

Key Words: Adaptive change – Smooth-pursuit - Prediction - Timing - Latency

Introduction

The smooth-pursuit system interacts with the vestibular system to maintain the image of moving visual targets on the fovea during head movement (see review by Leigh and Zee 1999). Because of the long latencies (~100 ms) between changes in target movement and the initiation of changes in pursuit eye movements, prediction must compensate for these delays that are due to processing the visual motion information and/or delays in generating the eye velocity commands (e.g., Barnes 1993). To accomplish this, the information about the target velocity and the information about the timing of onset of the movement are necessary (Robinson 1981; Barnes and Donelan 1999).

Previous studies in monkeys have indicated that pursuit training with orthogonal whole body rotation results in adapted smooth eye movements in response to chair rotation (Fukushima et al. 1996; Walker and Zee 2002). A normally absent, low-gain component of smooth eye movement develops in the direction orthogonal to the rotation, even when tested in complete darkness without a target. In addition, in the presence of a tracking target that moves orthogonal to the direction of chair rotation, the latencies of pursuit are shorter and initial eye velocities increase in a task-dependent manner (Fukushima et al. 2001a). Moreover, if a new target velocity is presented during identical chair rotation after training, initial eye velocities with latencies as short as 50 ms are modulated immediately within a few trials. These latencies are too short for a visual feedback that requires about 100 ms and too early for new adaptive changes to develop, suggesting that initial smooth eye movements induced by cross-axis vestibular-pursuit training are predictive pursuit induced by the vestibular stimulation (Fukushima et al. 2001a). The prediction-related modulation of the smooth-pursuit has been demonstrated in humans (Wells and Barnes 1998; Jarrett and Barnes 2001). To further examine the properties of initial smooth eye movements during a cross-axis pursuit and to determine whether they

are indeed predictive pursuit, we studied whether our monkeys could predict the timing of eye movement initiation during the chair rotation that required memory of the time delay between the onset of chair rotation and target motion onset. We demonstrate that our monkeys predicted the timing of pursuit initiation effectively in a task-dependent manner during the chair rotation. Some of these results have been presented in preliminary form (Tsubuku et al. 2004).

Materials and Methods

A total of three young, Japanese monkeys (H, K, S, *Macaca fuscata*, 4.8-6.0 kg) were used. All experiments were performed in strict compliance with the *Guide for the Care and Use of Laboratory Animals* (1997). Our protocols were approved by the Animal Care and Use Committee of Hokkaido University School of Medicine. Our methods for animal preparation, training, recording and data analysis are described in detail previously (Fukushima et al. 2001a). Briefly, each monkey was sedated with ketamine hydrochloride (5 mg/kg, i.m.), and then anesthetized with pentobarbital sodium (25 mg/kg, i.p.). Under aseptic conditions, head-holders were installed to restrain the head firmly in the primate chair in the stereotaxic plane during recording sessions. Vertical and horizontal components of eye movement were recorded by the scleral search coil method (Fuchs and Robinson 1966).

Analgesics and antibiotics were administered post-surgically to reduce pain and prevent infection.

Following a week of recovery, the monkeys were trained, for a reward of apple juice, to track a laser spot (0.2° in diameter) that was back-projected onto a tangent screen 75 cm in front of the animals' eyes in an otherwise completely dark room. The monkeys' heads were firmly restrained in a primate chair in the stereotaxic plane. The inter-aural midpoint of the animals' head was brought close to the axis of horizontal (yaw) rotation. All monkeys were initially exposed to cross-axis vestibular-pursuit training with a reward of apple juice using sinusoidal chair and target movement (Fukushima et al.

2001a, b).

Figure 1 near here

Figure 1A shows the trapezoidal trajectory used in this study. Two monkeys (H, K) were rotated in the yaw plane at $20^\circ/\text{s}$ for 1s towards either right or left. The chair remained stationary during the random-duration inter-trial interval (1-3s). The target moved with the chair in the same trajectory but in the orthogonal (i.e., vertical) plane after a delay ranging from 100 to 700 ms following the onset of the chair motion (Fig. 1A). The target was visible prior to any vertical target motion in normal circumstances. Target position was controlled by a servomotor/mirror combination using the position signal derived from the horizontal motion of the chair. As a control, the vertical pursuit was tested using the target motion alone without the chair rotation. Because the velocity trajectory of target motion using the actual chair position signal was not a perfect trapezoid (Fig. 1C, top trace), we moved the target by using the recorded chair position signal to drive the spot when vestibular stimulation was not applied (Fig. 1B). Daily training lasted for 0.5-1 h in 15 min blocks in each training session 4 days a week. One hour training contained an average of 1,000 trials (i.e., 500 trials for each direction). Training effects were examined by comparing the ocular tracking performance induced by the identical target motion without chair rotation before training and with chair rotation 30 and 60 min after training started for each recording session, each for ~5 min. To examine the effects of different delay periods, only one delay condition was tested in a recording session and other delay conditions were tested on different days for each monkey.

To examine the effects of target presence on initial pursuit eye movements after training (see Results), the target was briefly extinguished (“target blanked”) at 80 ms after the onset of chair rotation. The duration of the blanking period was 500 ms for delays of 100-500 ms. For the 700 ms delay, the target was extinguished for 700 ms.

To examine how specific chair rotation was for inducing smooth eye movement responses in the orthogonal direction, in monkey S we applied auditory stimuli (instead of chair rotation) while the target moved vertically in the same trapezoidal trajectory (at $20^\circ/\text{s}$ for 1s) as used for the chair rotation but without a delay. A speaker was positioned on the monkey's right and a 1,000 Hz beep was given for 1s. The monkey was trained to pursue the spot combined with the auditory stimuli for 1 h per day for four consecutive days, and the training effects were compared with those using horizontal chair rotation combined with vertical target motion (Fukushima et al. 2001a).

Eye, target and chair velocity signals were obtained by analog differentiation (DC-100 Hz, -12 dB/octave) to obtain velocity. All signals were digitized at 1 kHz. Saccades were marked with a cursor on eye velocity traces and removed using our interactive computer program as described previously (Fukushima et al. 2000a). Traces in which saccades appeared within 200 ms of the onset of chair motion were omitted. More than 20 traces were superimposed and aligned with the onset of chair motion. In the absence of vestibular stimulation, traces were aligned with the onset of target motion. These traces were then averaged to obtain means and standard deviation (SD) for each session for each monkey for rotation at different delays. SD values were typically $\sim 1.3^\circ/\text{s}$ and in most cases $< 2.0^\circ/\text{s}$. Latencies of eye movement responses were measured as the time at which the mean oppositely directed (i.e., upward/ downward) eye velocities diverged as described earlier (Fukushima et al. 2001a).

Figures 2 and 3 near here

Results

Change in the latency and the magnitude of pursuit eye movements after cross-axis vestibular-pursuit interaction training with different delay conditions

Figure 1B, C compares representative vertical eye velocity traces to vertical target motion without (Fig. 1B) and with horizontal chair rotation after 60 min of training (Fig. 1C). The target moved with a delay of 300 ms after the onset of chair motion (Fig. 1C). Upward and downward eye/target velocities associated with rightward and leftward chair motion are superimposed. As reported in our previous study (Fukushima et al. 2001a), the latency of the eye movement response at the beginning of training was comparable to that of smooth-pursuit without chair rotation (Fig. 1B). However, after training, smooth eye movements started before the onset of target motion with chair rotation (Fig. 1C), and these eye movement responses increased velocity at 119 ms after the onset of target motion (dashed lines, Fig. 1C). Because this latency was similar to the normal smooth-pursuit latency in this monkey (Fig. 1B, 115 ms), these eye movements are presumably smooth-pursuit induced by target motion.

Figure 1C shows that with training, the initial smooth-pursuit eye velocities were significantly larger compared to the velocities with target motion alone because of the preceding eye movement responses (Fig. 1C vs Fig. 1B following second dashed line). The mean eye velocities at 115 ms after the onset of target motion for the two conditions were 3.0 and 0.2°/s, respectively ($p < 0.05$, Student's t-test, Fig. 1B vs Fig. 1C). Such adaptive eye movement changes were observed in about 30 min (~250 trials) after training started in each session as illustrated in Fig. 2. This figure plots vertical eye velocity after the onset of target motion with the target motion delay of 500 ms against the trial number for the first day of training; Fig. 2A plots upward eye velocity associated with rightward chair rotation, and Fig. 2B plots downward eye velocity associated with leftward chair rotation. Average eye velocities

(*open circles*) gradually increased during 200 trials (~ 30 min). However, once the monkeys adapted to a particular delay condition, it took only a few minutes for them to adapt to that delay during trials on succeeding days, suggesting that there were both short-term and long-term training effects as we observed previously (Fukushima et al. 2001a).

Figure 3 shows representative records of the effects of changing delays in one monkey (K) during yaw rotation combined with vertical target motion. Vertical eye velocities without (Fig. 3A) and with removing saccades (mean \pm SD, Fig. 3B) are shown for comparison. Changing the delays of the onset of target motion after the onset of chair motion (Fig. 3B, indicated by *rightward arrows with vertical bars*) clearly affected the latencies of smooth eye movements relative to the onset of chair motion (Fig. 3B, *upward arrows*). When the delay was 100 ms, smooth eye movements started almost simultaneously with the onset of the target motion. However, with longer delays of 300-700 ms, smooth eye movements started clearly before the onset of the target motion and the latencies (Fig. 3B, *upward arrows*) were delayed in parallel with the actual delays of target motion (Fig. 3B, *vertical bars*).

Figure 4A summarizes the mean (\pm SD) latencies of smooth vertical eye movements after training in two monkeys (H, K) plotted against the delay in the onset of the target motion following the onset of chair rotation (*filled circles* connected by *straight lines*). Although there was a slight difference in latency for the two monkeys, in both monkeys latencies were significantly correlated with the delay and were shorter than the actual delay especially with the delays \geq 300 ms. Regression slopes calculated for the two monkeys were 0.57 and 0.67 (Fig. 4A) with the mean of 0.64, and the intersection with y axis (i.e. estimated latency at the delay 0 ms) was 25-34 ms which was similar to the actual latencies observed previously (Fukushima et al. 2001a, see Discussion).

To compare the magnitudes of initial eye movement responses, Fig. 5 (A, B, D, E) shows the average vertical smooth eye velocity trajectories with different delays (shown by *keys*). Upward (Fig. 5A, B) and downward (Fig. 5D, E) eye velocity traces are aligned with the onset of target motion (0 ms) for the two monkeys (Fig. 5A, D vs Fig. 5B, E). Their trajectories are similar. To quantify the response magnitudes, mean (\pm SD) velocities at 100 ms after the onset of target motion are plotted for upward and downward components in Fig. 5 (C, F) for the two monkeys. In all delays we tested (100-700 ms), vertical eye velocities at 100 ms after the onset of the target motion after training were significantly larger than those before training (one-way ANOVA, $p < 0.01$, post-hoc Scheffe's F test). In addition, the response magnitudes were largest at the shortest delay (100 ms) and gradually decreased as the delay increased. Barnes and Asselman (1991) reported that the magnitudes of predictive pursuit velocity in humans decay exponentially. We estimated time constants for these decays by fitting an exponential function for each direction for each monkey. In all four cases, the time constants were similar between 6.5 and 7.0 s with the overall mean of 6.8 s, and the intersection with y-axis (i.e. estimated velocity at the delay 0 ms) was 5.5-9.7°/s.

Figures 4 and 5 near here

Effects of target disappearance after training

Our results show that, after training, smooth eye movements were initiated before the onset of the target motion (Fig. 3) and that latencies and initial magnitudes of these eye movements did not depend on target motion. However, they do not exclude the possibility that the presence of the tracking target, even though it was stationary, affected initial smooth eye movement responses, because it has been shown that anticipatory and smooth-pursuit eye accelerations are influenced by the presence of a stationary foveal target (Morrow and Lamb 1996). To examine whether the presence of the tracking

target affected initial smooth eye movements during chair rotation after the cross-axis pursuit training, we extinguished the target for 500-700 ms at 80 ms after the onset of the chair rotation (see Methods).

Figure 4B illustrates mean \pm SD vertical eye velocity during target blanking in one monkey (K). As expected, smooth eye movements started during the blanking period. Latencies to the onset of chair motion paralleled the actual delays that had been used for training despite the fact that the target was not shown during initiation of smooth eye movements (*upward arrows*, Fig. 4B). Figure 4A (*open diamonds* connected by *dashed lines*) summarizes the latencies of smooth eye movements after training during target blanking in the two monkeys. Latencies with or without blanking were basically similar ($p > 0.1$ for each delay condition, Student's *t*-test) except at the longest delay (700 ms) in monkey H. The other monkey also showed a similar tendency at the longest delay (monkey K). Regression slopes calculated for the two monkeys were 0.72 and 0.83 with the mean of 0.78 (not shown). We also compared the difference in mean eye velocities at 100 ms after the onset of the target motion between the two conditions. They were similar between the two conditions ($p > 0.1$). These results suggest that the mere absence of the target shortly before and during its motion (Fig. 4B) did not affect the initiation or initial magnitude of smooth eye movements after training.

Auditory-pursuit interaction

To examine how specific chair rotation was for inducing predictive smooth-pursuit, in monkey S we applied auditory stimuli for 1s (instead of chair rotation) while the target moved vertically without delay. The training effects were compared with those using chair rotation (see Methods). Figure 6 illustrates an example. As expected, latencies of vertical smooth-pursuit during chair rotation were shortened after vestibular-pursuit training (Fig. 6B) compared to the latencies induced by the target motion alone (Fig. 6A). However, even after 4 days of pursuit training combined with the auditory

stimuli, the latencies of vertical pursuit were similar to those induced by the target motion alone (Fig. 6C vs 6A, $p>0.1$). We also applied auditory stimuli briefly for 0.5 s at the onset of the chair rotation combined with vertical target motion for three consecutive days in another monkey. The latencies of vertical pursuit in this condition were shortened during the chair rotation similar to the record shown in Fig. 6B. However, when the monkey was tested for the effects of the auditory stimuli combined with the vertical target motion but without chair rotation, latencies of vertical pursuit were longer compared to those during chair rotation (not shown), and were still similar to those induced by target motion alone (e.g. Fig. 6A). These results suggest that auditory-pursuit interactions are not as effective as vestibular-pursuit interactions in our task conditions (see Discussion).

As reported earlier (Fukushima et al. 2001a), smooth-pursuit to vertical target motion without chair rotation after training was similar to pursuit before training in both monkeys. The horizontal vestibulo-ocular reflex (VOR) induced by yaw rotation in complete darkness showed no consistent changes before and after cross-axis vestibular-pursuit interaction training, indicating that adaptive changes were specifically induced in vertical eye movements by yaw rotation, consistent with the training task conditions.

Figure 6 near here

Discussion

In the present study, the smooth eye movements that appeared after vestibular-pursuit interaction training have properties similar to adaptive pursuit eye movements described earlier, namely their short latencies and their development within 30 min of training (Fig. 2, also Fukushima et al. 2001a).

Initiation of smooth eye movement in the present study required memory of the time delay between the onset of chair rotation and the onset of target motion. Our results show that the monkey effectively

learned the timing of smooth eye movement initiation during chair rotation (Figs. 3, 4, 5). These results indicate that the initial smooth eye movements were induced predictively. Pursuit neurons in the frontal eye fields (FEF, McAvoy et al. 1991) discharge in association with the adaptive smooth eye movements during cross-axis pursuit (see Discussion of Fukushima et al. 2001a). We, therefore, think that smooth eye movements in the present study are predictive pursuit eye movements.

The present results indicate that our monkeys' estimate of the delays revealed by the latencies of pursuit was shorter by 22-36 % than the actual delays (Figs. 3, 4). Such an under estimation has also been reported in human subjects performing predictive smooth-pursuit (Lekwuwa and Barnes 1996). Previously, our laboratory reported that adaptive smooth eye movements were induced by cross-axis vestibular-pursuit training in a task-dependent manner, and because these eye movements were induced by vestibular stimulation alone in complete darkness after training, they were called cross-axis VOR (Fukushima et al. 1996, 2000a, 2001b; Sato et al. 1999; cf. Walker and Zee 2002). However, the present results demonstrate that pursuit eye movement initiation with appropriate delays were basically similar with or without the presence of the tracking target (Figs. 3, 4). Moreover, the estimated latencies and eye velocities at the delay 0 ms in the present study (Figs. 4, 5) are similar to those when the target motion and chair rotation were applied simultaneously (Fukushima et al. 2001a). In some trials, we also completely extinguished the tracking target for a few cycles, but pursuit eye movements were still initiated similarly (Tsubuku et al. unpublished observations), consistent with our previous study (Fukushima et al. 2001a). These results suggest that the cross-axis VOR contains a predictive pursuit component as suggested earlier (Fukushima et al. 2001a). Consistent with this interpretation are our previous results showing that: (1) cross-axis VOR was induced by sequentially flashed (10 μ s) targets minimizing retinal image slip during orthogonal chair rotation (Fukushima et al. 2001b); (2) eye

velocity sensitivity of gaze velocity Purkinje cells of the cerebellar floccular region tested was similar between smooth-pursuit and cross-axis VOR (Fukushima et al. 2000b, 2001b).

Further similarity in the predictive pursuit between monkeys and human is the decay in the magnitudes of predictive responses (Fig. 5C, F). Wells and Barnes (1998) reported that anticipatory pursuit velocity, measured at 100 ms after the onset of the target motion, decreases with increasing interval (also Barnes and Asselman 1991; Chakraborti et al. 2002). However, there is a difference in the way that predictive pursuit was learned between humans and monkeys. Barnes and Donelan (1999) demonstrated in human subjects that anticipatory smooth pursuit is elicited by auditory, visual or tactile cues with similar magnitudes, although the response to the visual cue is significantly delayed. A question arises whether the onset of head movement in the present study was simply acting as a cue for conditioning in the same way that was demonstrated for humans. However, our results show that the auditory stimuli combined with vertical pursuit did not significantly shorten the latencies of pursuit even after extensive training for four consecutive days despite the fact that latencies were effectively shortened during chair rotation (Fig. 6). This indicates a clear difference in our monkeys to learn predictive pursuit between vestibular-pursuit interactions and auditory-pursuit interactions. We do not exclude the possibility that further training may have induced some adaptive changes. We think that vestibular signals induced by chair rotation in our monkeys not only provide information about the timing of movement onset, but also provide driving signals for predictive pursuit eye movements after vestibular-pursuit interaction training.

Previous studies also indicated that vergence tracking combined with pitch rotation resulted in adaptive changes during chair rotation; latencies of vergence eye movements shortened and initial vergence eye velocities increased in a task-dependent manner (Akao et al. 2004; also Sato et al. 2004).

Prediction may have contributed to the initial depth pursuit responses as well.

The neural substrates for the timing of predictive pursuit initiation during chair rotation observed in the present study are unknown. Although the involvement of the supplementary eye fields (SEF) and FEF in predictive pursuit is suggested (Heinen and Liu 1997; McAvoy et al. 2000; Fukushima et al. 2002), it is still unknown how timing signals are generated in the vestibular-pursuit interaction conditions. In fact, pursuit neurons in both FEF and SEF receive robust vestibular inputs (Fukushima et al. 2000a; Ebata et al. 2004; Fukushima et al. 2004). Because predictive smooth-pursuit in humans is reported to be largely preserved even after large cortical lesions including the frontal cortex (Lekwuwa and Barnes 1996), predictive pursuit functions including target velocity and timing estimation must be distributed in multiple circuits including those frontal cortical structures and feedback circuits possibly from the cerebellum (see Fukushima 2003 for review). Single neuron studies in behaving monkeys will be necessary to elucidate the neural mechanisms for timing signals in pursuit eye movements.

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Figure legends

Fig. 1. Stimulus trajectory for cross-axis vestibular-pursuit training and representative vertical pursuit eye movements before and after training. A, stimulus trajectory. Inter-trial intervals for chair motion were random (*top trace*). The chair was rotated in the yaw plane at 20°/s for 1s. the delay between the onset of chair motion and the onset of target motion is marked by *vertical dashed lines*. B, vertical eye movements induced by target motion alone without chair rotation before training. C, vertical eye movements induced by combination of yaw rotation (*top trace*) and vertical target motion with delay of 300 ms after 60 min of training. In B and C, saccade velocities are clipped and all traces (upward and downward target and eye velocity, leftward and rightward chair velocity) are superimposed with respect to the onset. The bottom traces in B and C are de-saccaded mean \pm SD vertical eye velocity. Mean \pm SD were obtained from 20 trials.

Fig. 2. Time course of adaptive eye velocity induced by vestibular-pursuit interaction on the first day of training. The target moved after a delay of 500 ms following the onset of chair motion. Eye velocity

measured at 100 ms after the onset of target motion is plotted against trial number for upward eye velocity associated with rightward chair rotation (A) and downward eye velocity associated with leftward chair rotation (B). Averages of consecutive 20 trials are plotted as *open circles*.

Fig. 3. Representative records of vertical eye velocity after 30 min of cross-axis training with the delay indicated. Saccade velocities are clipped in A. B shows de-saccaded mean \pm SD vertical eye velocity. Mean \pm SD were obtained from 20 trials. *Dashed lines* in A and B indicate the onset of chair motion. *Vertical bars* with rightward arrows in B indicate the onset of actual target motion with different delays. *Upward arrows* in B indicate onset of vertical smooth eye movements. All traces are superimposed with respect to the onset of chair motion.

Fig. 4. Latencies of vertical smooth eye movements induced by horizontal chair rotation after training and effects of target blanking on pursuit initiation. A plots mean \pm SD latencies against the delays between the onset of chair motion and the onset of target motion for cross-axis training in two monkeys. *Open diamonds* and *filled circles* are values with and without blanking the target, respectively. Seven to ten different recording sessions were combined to calculate mean and SD which was smaller than the symbol size in most cases. Only one plus SD is shown for means with blanking and one minus SD is shown for means without blanking. Linear regressions are shown for *filled circles* (i.e., without blanking). B, representative records of de-saccaded mean \pm SD vertical eye velocity after 30 min of cross-axis training with target blanking. Mean \pm SD were obtained from 20 trials. *Dashed line* in B indicates the onset of chair motion. *Vertical lines* with *rightward arrows* indicate the onset of target motion with different delays that had been used for training. The *thick bars* above each delay indicate the period the tracking spot was extinguished. *Upward arrows* in B indicate onset of vertical smooth eye movements. All traces in B are superimposed with respect to the onset of chair motion.

Fig. 5. Comparison of initial eye velocity trajectories before and after vestibular-pursuit training with different delays. Upward (A and B) and downward (D and E) smooth eye velocities associated with rightward and leftward horizontal rotation, respectively, are aligned with the onset of target motion (0 ms). Eye velocity before training is shown with *thick lines*. Eye velocity at different delays are shown by *keys*. C and F plot mean \pm SD upward (C) and downward (F) eye velocity for the two monkeys (*keys*) at 100 ms after the onset of target motion.

Fig. 6. Comparison of vestibular-pursuit and auditory-pursuit training effects. Upward and downward eye velocities are superimposed with respect to the onset of vertical target motion at $20^\circ/s$ for 1s (*dashed line*). A, Vertical eye movements induced by target motion alone. B, Vertical eye movements induced by upward and downward target motion combined with rightward and leftward chair rotation, respectively (at $20^\circ/s$ for 1s). Chair rotation was applied simultaneously with the onset of target motion. C, Vertical eye movements induced by upward and downward target motion combined with auditory stimulus (1000Hz for 1 s). The latter was applied simultaneously with target motion onset. *Upward arrows* indicate onset of vertical pursuit.

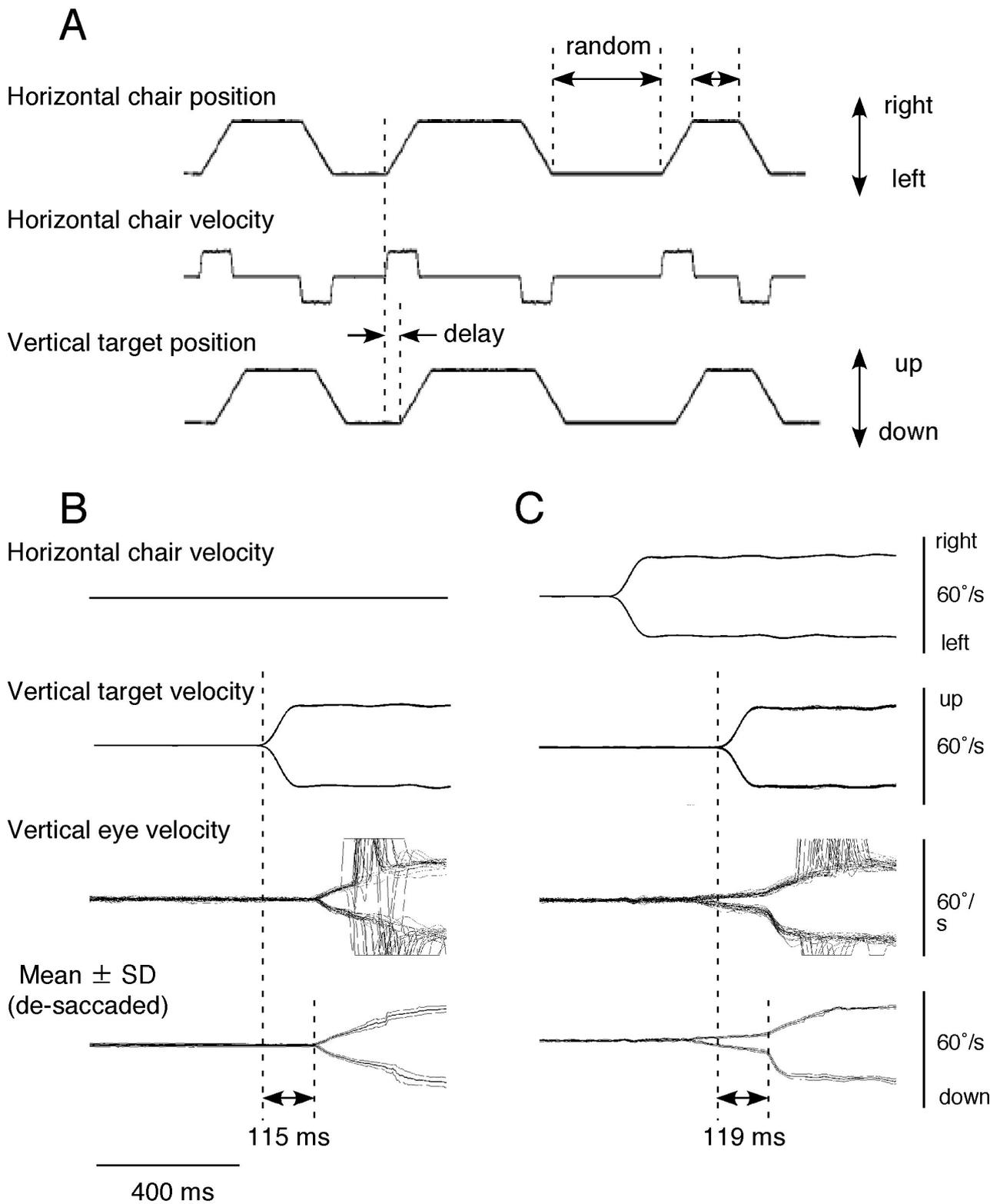


Fig. 1

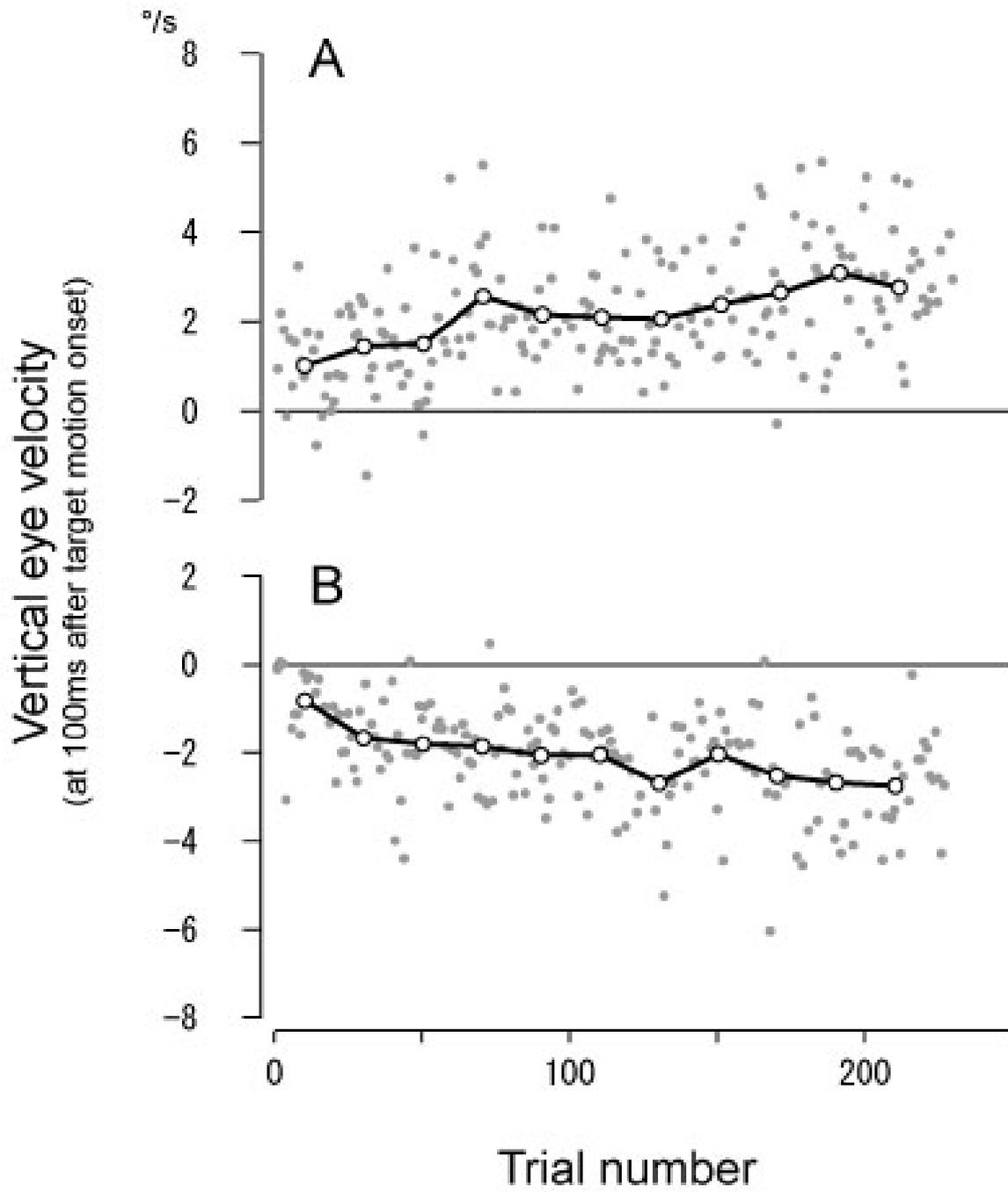


Fig. 2

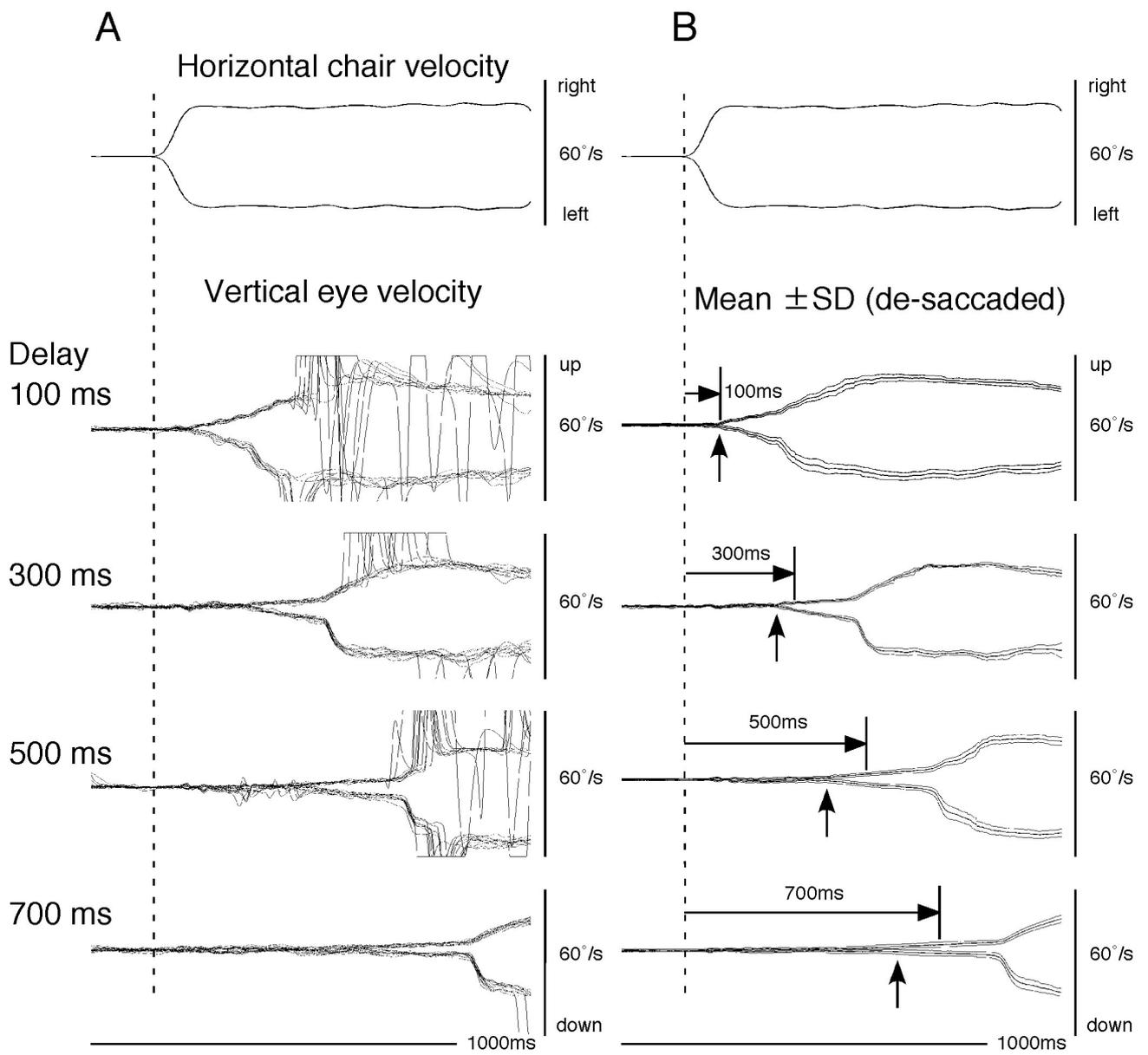


Fig. 3

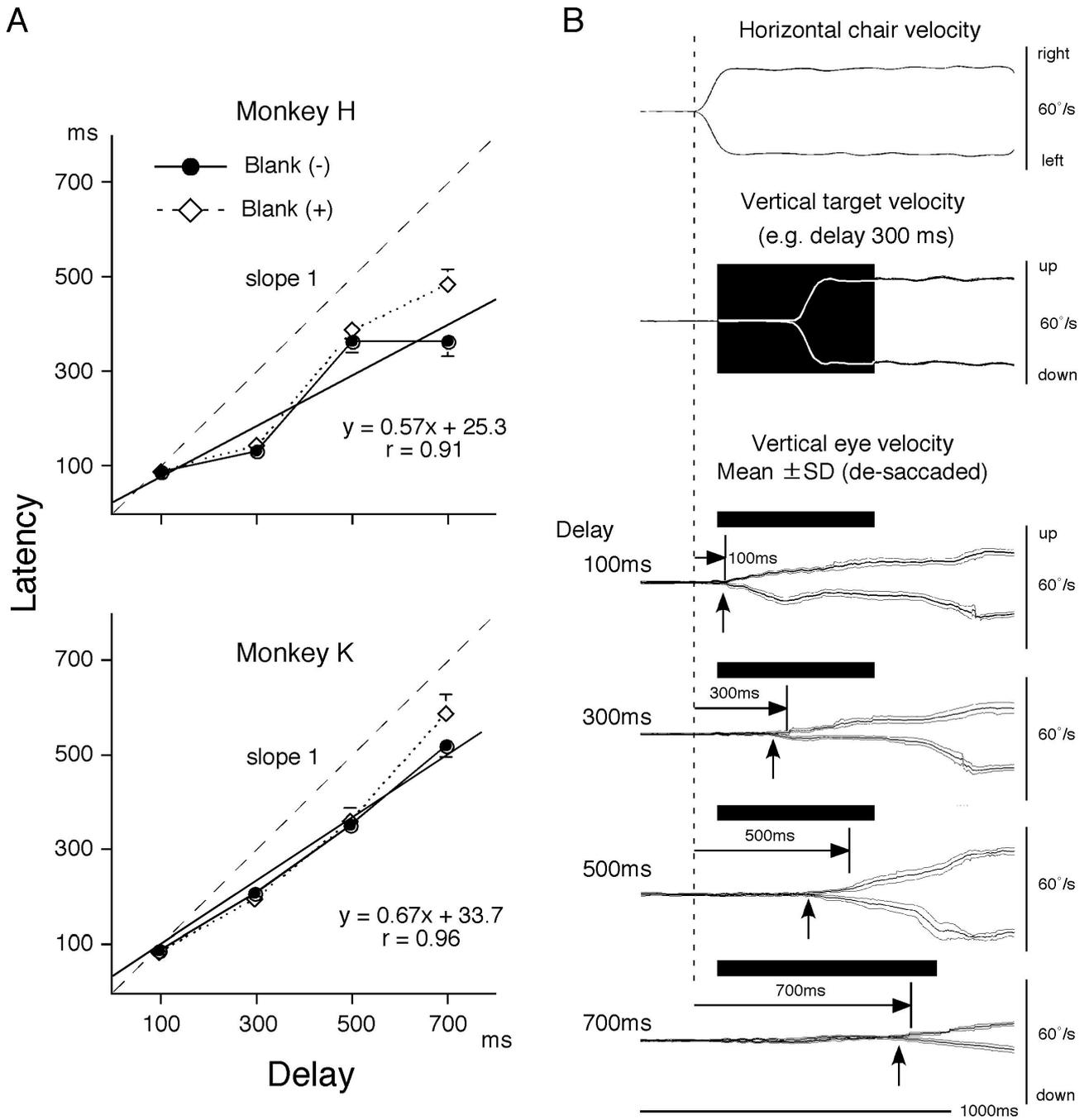


Fig. 4

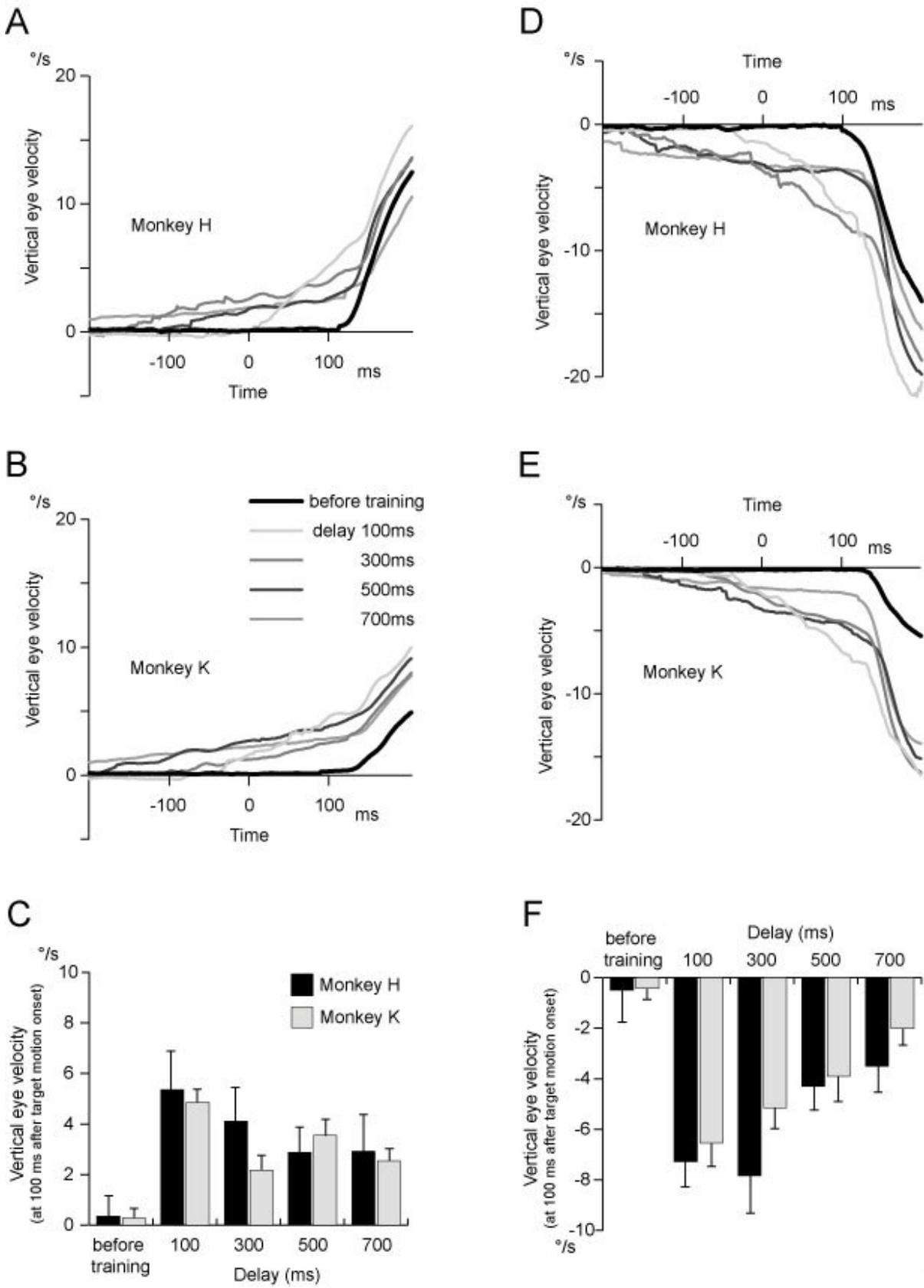


Fig. 5

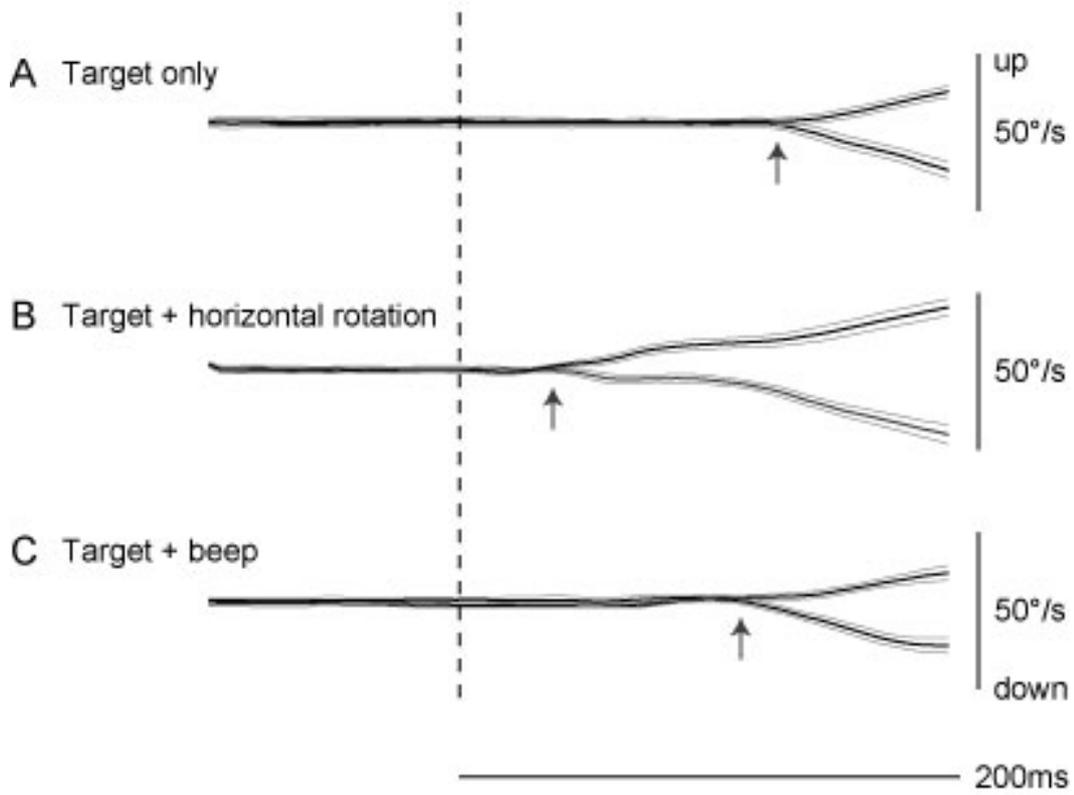


Fig. 6