



The neuronal basis of on-line visual control in smooth pursuit eye movements



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ABSTRACT

Smooth pursuit eye movements allow us to maintain the image of a moving target on the fovea. Smooth pursuit consists of separate phases such as initiation and steady-state. These two phases are supported by different visual-motor mechanisms in cortical areas including the middle temporal (MT), the medial superior temporal (MST) areas and the frontal eye field (FEF). Retinal motion signals are responsible for beginning the process of pursuit initiation, whereas extraretinal signals play a role in maintaining tracking speed. Smooth pursuit often requires on-line gain adjustments during tracking in response to a sudden change in target motion. For example, a brief sinusoidal perturbation of target motion induces a corresponding perturbation of eye motion. Interestingly, the perturbation ocular response is enhanced when baseline pursuit velocity is higher, even though the stimulus frequency and amplitude are constant. This on-line gain control mechanism is not simply due to visually driven activity of cortical neurons. Visual and pursuit signals are primarily processed in cortical MT/MST and the magnitude of perturbation responses could be regulated by the internal gain parameter in FEF. Furthermore, the magnitude and the gain slope of perturbation responses are altered by smooth pursuit adaptation using repeated trials of a step-ramp tracking with two different velocities (double-velocity paradigm). Therefore, smooth pursuit adaptation, which is attributed to the cerebellar plasticity mechanism, could affect the on-line gain control mechanism.

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1. Introduction

Eye movements are supported by interactions between visual processing and motor control systems. For example, when we precisely track a small moving object, the eye motion should match the target motion to stabilize the image of a moving object on or near the fovea. Such continuous eye movements with an active visual system are called “smooth pursuit”. Smooth pursuit eye movements often require on-line gain adjustments during tracking in response to a sudden change in target motion (perturbation). Previous studies have demonstrated that visuomotor gain during smooth pursuit is regulated by an on-line (dynamic) gain control mechanism (Churchland & Lisberger, 2002, 2005; Nuding et al., 2008; Ono et al., 2010; Schwartz & Lisberger, 1994). The on-line gain control is known to regulate an internal gain parameter in pursuit, where higher target velocities yield higher gains in perturbation responses. Typically in those studies, a single cycle of

sinusoidal motion is introduced during ongoing pursuit to estimate the perturbation ocular response. The advantage of using the sinusoidal motion is to avoid triggering saccadic eye movements during a sudden motion. Our studies and other laboratories have shown perturbation ocular responses without saccadic intrusions. Previous studies have suggested that cortical visual and pursuit systems are involved in the on-line gain regulation (Nuding et al., 2009; Ono et al., 2010; Tanaka & Lisberger, 2001, 2002). Cortical visual processing is necessary for initiating smooth pursuit where visual motion signals are transformed into eye movement commands (Krauzlis, 2004; Lisberger, 2010). Pursuit initiation and steady-state phases are supported by different visuomotor processing. The first 100 ms of pursuit tracking is defined as an open-loop response that occurs before the time of the visual feedback, while steady-state pursuit velocity is maintained by a feedback system (Nuding et al., 2008; Robinson, Gordon, & Gordon, 1986). The initial pursuit phase is driven strongly by retinal error signals carried by cortical neurons. The visual motion-related neuron starts discharging before pursuit onset and the discharge declines once eye velocity reaches the target (Newsome, Wurtz, & Komatsu, 1988). Then, steady-state pursuit velocity is maintained by an extraretinal (non-visual) signal (Ilg & Thier, 2003; Newsome, Wurtz, &

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Komatsu, 1988; Ono & Mustari, 2012). The extraretinal information could be associated with an efference copy of eye motion, volitional pursuit commands or prediction signals. Smooth pursuit is considered as a volitional tracking behavior, whereas the perturbation response to a sudden motion is thought to be different from volitional eye movements. This review focuses on neurophysiological aspects of the on-line visuomotor control to understand how the internal gain parameter is regulated by visual and extraretinal signals. We also argue whether the on-line gain control is influenced by smooth pursuit adaptation associated with plasticity mechanisms in the cerebellum. Understanding of neural mechanisms underlying visuomotor control during ongoing pursuit has advanced significantly in the last decade including how visual and eye motion information is processed at cortico-ponto-cerebellar pathways.

2. Visual processing in the cortical pathway for smooth pursuit

Visual motion signals are processed in the cortical middle temporal (MT) and the medial superior temporal (MST) areas to produce partially formed commands for smooth pursuit (Fig. 1). Early studies have demonstrated that MT neurons with foveal/parafoveal visual receptive fields are modulated during smooth pursuit using a small moving target (Komatsu & Wurtz, 1988; Newsome, Wurtz, & Komatsu, 1988). The response of MT neurons during pursuit is known to be visually contingent, because the neuronal response dropped when retinal image motion is reduced by target stabilization or blinking during pursuit (Newsome, Wurtz, & Komatsu, 1988). The direction selective visual motion signals in MT support pursuit initiation and dynamics in a specific direction (Groh, Born, & Newsome, 1997; Hohl & Lisberger, 2011; Komatsu & Wurtz, 1989; Lisberger & Movshon, 1999; Newsome et al., 1985). The visual motion signals carried in MT also play a role in visual motion perception (Newsome & Pare, 1988; Nichols & Newsome, 2002).

It has been shown that neurons in neighboring area MST are modulated during smooth pursuit. The lateral-anterior part of MST (MSTl) carries mainly visual motion signals, whereas the dorsal-medial part of MST (MSTd) provides extraretinal (non-visual) signals that are related to pursuit eye motion (Ferrera & Lisberger, 1997; Ilg, Schumann, & Thier, 2004; Komatsu & Wurtz, 1988; Kurkin et al., 2011; Newsome, Wurtz, & Komatsu, 1988; Thier & Erickson, 1992). These extraretinal signals carried in MSTd are revealed by extinguishing the target during pursuit when neuronal response continues with pursuit (Newsome, Wurtz, & Komatsu, 1988; Ono & Mustari, 2006, 2012) or when tracking an imaginary target (Ilg & Thier, 2003). These MST neurons also have large visual receptive fields responding to motion in preferred directions. Furthermore, lesions placed in MST/MT produce directional and retinotopic deficits in smooth pursuit eye movements (Dursteler & Wurtz, 1988; Dursteler, Wurtz, & Newsome, 1987).

Fig. 1 illustrates examples of visual motion and smooth pursuit related responses of neurons in MST during step-ramp tracking, showing direction selective activity. Multiple linear-regression modeling allows us to estimate the relative sensitivities of neuronal responses to eye or retinal error motion parameters (position, velocity and acceleration) (Das et al., 2001; Shidara et al., 1993; Sylvestre & Cullen, 1999). Averaged data of step-ramp trials are used to identify coefficients in the eye model, $FR(t + \tau) = A + BE(t) + CE'(t) + DE''(t)$ and the retinal error model, $FR(t + \tau) = A + BR(t) + CR'(t) + DR''(t)$, where $FR(t)$ is the estimated value of the unit spike density function (actual data) at time “ t ,” $E(t)$ denotes the eye motion (position, velocity and acceleration) at time “ t ,” and $R(t)$ denotes the retinal error (position, velocity and acceleration) at time “ t .” Coefficients in the models are

defined by terms A , B , C and D . The latency value of the unit response with respect to target onset or pursuit (eye) onset is represented by the “ τ ” term. Retinal error parameters were calculated as the difference between target and eye motion parameters. Note that target acceleration was assumed as $0^\circ/s^2$, since differentiation of a step in target velocity results in zero target acceleration (Das et al., 2001; Ono & Mustari, 2009; Ono et al., 2005). The goodness of fit is determined by calculating a coefficient of determination (CD) between experimentally observed unit data and model estimated fit. We calculated a set of coefficients (A – D) and estimated coefficients of determination (CD) for a series of latencies (τ). In the final model, we used coefficients that yielded a maximum CD for specific latency values. Retinal error motion variables make the significant contributions to fits for the visual motion response (Fig. 1A), whereas eye movement variables make the significant contributions to fits for the pursuit response (Fig. 1B).

Furthermore, modeling studies have revealed that the visual motion neuron is highly dependent on a retinal error velocity component (REV). In contrast, the pursuit neuron is strongly related to an eye velocity component (Mustari, Ono, & Das, 2009; Ono & Mustari, 2012). The latency of the unit response with respect to target or pursuit onset is obtained from the model with a maximum CD. There is a major difference in the neuronal response latency between visual and pursuit neurons. The visual motion neuron has an early latency that leads pursuit onset (70 ms), whereas the pursuit eye velocity neuron lags behind pursuit onset (50 ms).

Current evidence suggests that the extraretinal (non-visual) signals carried in MSTd are related to volitional smooth pursuit commands rather than proprioceptive or other feedback signals associated with reflex driven eye movements such as vestibulo-ocular reflex (Ono & Mustari, 2006; Ono et al., 2010). Visual motion and pursuit related regions of cortical areas MT and MST must be processed further in the oculomotor regions including the pontine nuclei (Distler, Mustari, & Hoffmann, 2002; Glickstein et al., 1980; May & Andersen, 1986) and the floccular complex (Glickstein et al., 1994; Nagao et al., 1997) and vermal lobules VI and VII (Brodal, 1979, 1982; Langer et al., 1985) in the cerebellum. Here we consider whether cortical regions related to visual motion or extraretinal signals play roles in the on-line visuomotor control in smooth pursuit.

3. On-line gain regulation during smooth pursuit

A sudden change in target motion induces a corresponding perturbation response of eye motion (Churchland & Lisberger, 2002; Ono, 2013; Schwartz & Lisberger, 1994; Tabata et al., 2006). This approach evaluates how the visual input associated with a given speed and direction of image motion on the retina affects the on-line visual control in smooth pursuit eye movements. Fig. 2A illustrates an on-line gain adjustment of smooth pursuit during step-ramp tracking. A brief perturbation using a short-duration single cycle of sinusoidal motion (2.5 Hz, $\pm 10^\circ/s$) was introduced during ongoing pursuit (ramp speed = $10^\circ/s$). Mean eye velocity traces show that the sinusoidal perturbation induces a corresponding change in eye velocity (Fig. 2A). The latency of eye motion with respect to the target perturbation is similar to the pursuit latency (<120 ms). Neuronal activities of MST neurons were recorded to determine whether the perturbation ocular response is attributed to the cortical visuomotor systems. Fig. 2B and C shows typical neuronal responses of MST neurons to the target perturbation. The visual motion related neuron (Fig. 2B) showed a significant modulation in firing rate associated with the perturbation (arrow). In contrast, the pursuit-related neuron (Fig. 2C) carrying an extraretinal signal did not show a corresponding modulation in firing

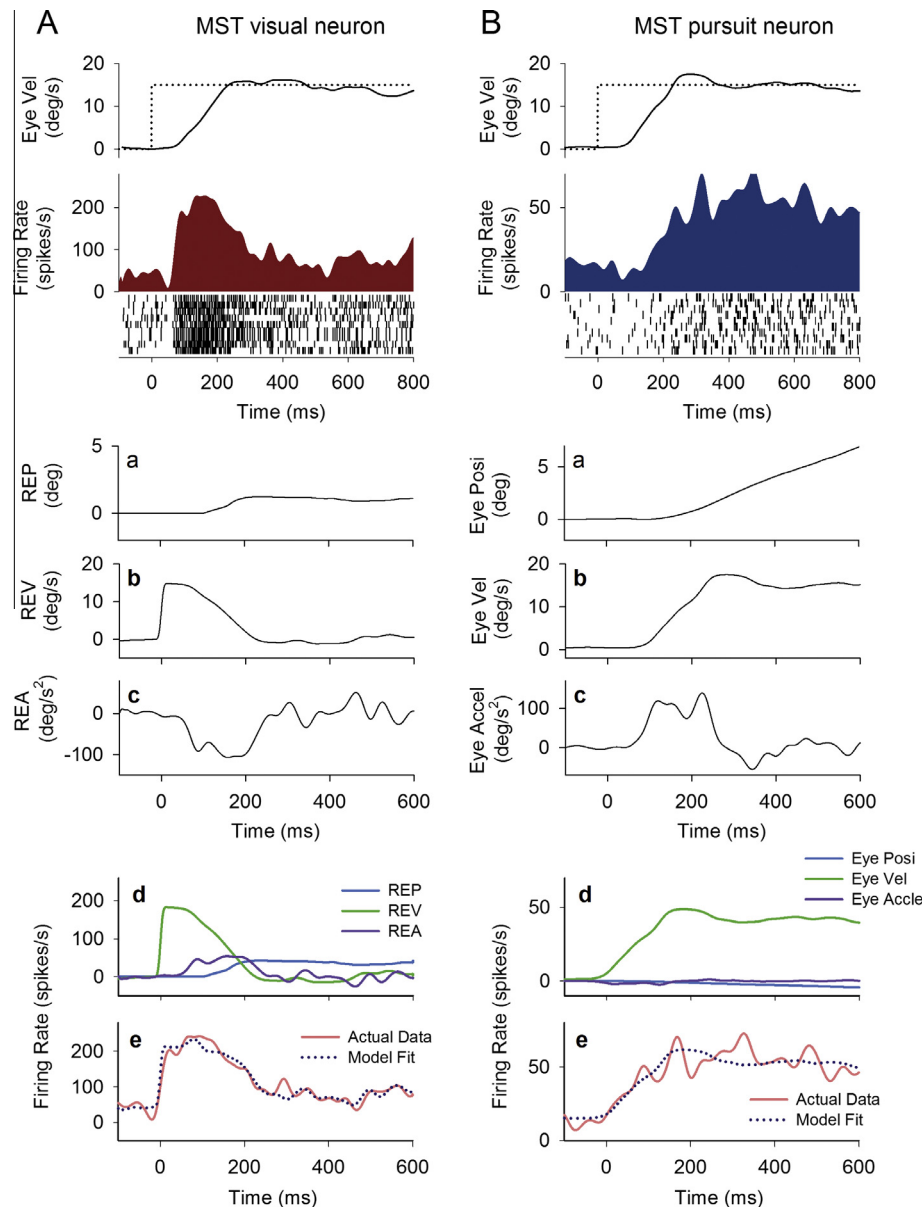


Fig. 1. Response of representative visual motion (A) and smooth pursuit (B) neurons recorded from MST. Averaged data from step-ramp tracking (ramp speed = $15^\circ/\text{s}$). Traces show target and eye velocity, and neuronal activity (spike density and rasters). Curve-fitting procedure used to identify model parameters and estimate coefficient of determination (CD). Individual panels (a–c) show the dynamic values of the components that make up the model. They are retinal error position (A-a), retinal error velocity (A-b), retinal error acceleration (A-c), eye position (B-a), eye velocity (B-b) and eye acceleration (B-c). Panel (d) shows the relative contributions of the components of the model towards the unit response. Panel (e) shows the observed spike density function and the best fit obtained using models. The equation for the fit corresponding to the retina error model (A) is: $FR(t - 70) = 49.9 + 38.0R(t) + 12.3R'(t) - 0.56R''(t)$. The equation for the fit corresponding to the eye motion model (B) is: $FR(t + 50) = 13.9 - 0.52E(t) + 2.64E'(t) - 0.02E''(t)$. We estimated latency related to retinal error or eye motion (τ) as the point that produced the highest CD in our models. The fit obtained from the models had CDs of 0.92 for the retinal error model and 0.83 for the eye motion model.

rate despite prominent changes in eye motion (Ono et al., 2010). Therefore, the on-line gain adjustment to a sudden motion could be associated with visual motion inputs (open-loop control) rather than extraretinal signals. However, the on-line gain control mechanism cannot be explained by only visual motion pathways including MT/MST.

When the perturbation of target motion is applied during smooth pursuit at different target velocities, perturbed eye velocity increases as a function of baseline pursuit velocity (Churchland & Lisberger, 2002; Nuding et al., 2008; Ono, 2013; Ono et al., 2010; Schwartz & Lisberger, 1994). This nonlinear response (gain slope) is thought to be based on the on-line gain control mechanisms in pursuit. Evidence for the on-line gain control was first proposed

by Robinson (Robinson, 1965) as spontaneous oscillations occurred during smooth pursuit tracking but not during fixation of a stationary target. The on-line gain control mechanism is known to regulate an internal gain parameter in pursuit, where higher target velocities yield higher gains in both increasing (toward the pursuit direction) and decreasing (the opposite direction) perturbation responses.

Fig. 3 illustrates representative perturbation responses during ongoing pursuit at different baseline target speeds (5, 10 and $15^\circ/\text{s}$) while the perturbation frequency and amplitude are constant (2.5 Hz , $\pm 10^\circ/\text{s}$). Mean eye velocity traces during step-ramp tracking with a perturbation are shown in Fig. 3B. Perturbed eye velocity is estimated by the difference of the maximum to the

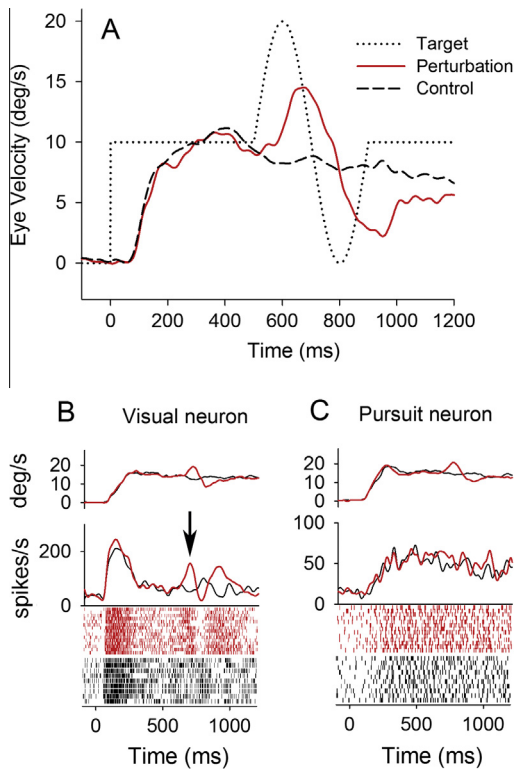


Fig. 2. Perturbation ocular response to a sudden change in target motion during ongoing pursuit. A single cycle of sinusoidal motion (2.5 Hz , $\pm 10^\circ/\text{s}$) is introduced (500 ms after target onset) during step-ramp tracking (A). Eye velocity traces during pursuit with (red line) and without (broken line) the perturbation are shown. Neuronal responses of visual motion (B) and pursuit-related (C) neurons in MST to the target perturbation are shown. The visual response shows a modulation associated with the perturbation, whereas the pursuit neuron shows no change in firing rate despite prominent changes in eye motion during the perturbation (from Ono et al., 2010).

subsequent minimum of eye velocity after target perturbation. Eye velocity traces document that the perturbation response is enhanced when ramp speed is higher. Mean values of perturbed eye velocity and peak acceleration showed significant increases at higher target velocities (Fig. 3D and E). It is important to note that this was the case even though the retinal slip velocity induced by the target perturbation showed no significant change at different target velocities (Fig. 3C). This is because steady-state pursuit eye velocity is nearly the same as the target velocity during step-ramp tracking. Therefore, the nonlinear perturbation response at different target velocities may not be simply due to visual motion signals that constitute the primary input to the pursuit system. The magnitude of perturbation ocular responses could be determined by both retinal slip inputs and internal gain parameters in pursuit. It is possible that the extraretinal (non-visual) signals carried in other cortical areas including the frontal lobe or brainstem/cerebellum could contribute to the on-line gain control (see below).

4. Possible neuronal pathways involving on-line gain control

Fig. 4 illustrates a representative response of a visual motion-related neuron in MST to a target perturbation at 3 different baseline speeds (5 , 10 and $15^\circ/\text{s}$). Despite prominent changes in perturbed eye velocity (Fig. 3), the visual neuron shows little change in firing rate associated with the perturbation (red arrow). Rather, the percentage of responsive data sets tends to decrease with higher target velocities (Ono et al., 2010). This was the case even though the initial firing rate (black arrow) increased with higher

target velocities. Furthermore, our study (Ono et al., 2010) reported that a large proportion of pursuit-related neurons in MSTd did not reflect the perturbation ocular response. Our linear regression analysis showed that the firing rate did not show a correlation with nonlinear ocular responses at 3 different target velocities. The linear regression modeling approach revealed that the neuronal response of MST neurons to the perturbation was not detectable at all stimulus velocities. Therefore, visual motion and pursuit related regions in MST may not have a substantial contribution to the on-line gain control (Churchland & Lisberger, 2005; Ono et al., 2010). However, we cannot exclude the possibility that the on-line gain control results from the interaction between MT/MST and other cortical pursuit-related regions. Komatsu and Wurtz (1989) have shown that electrical stimulation of visual and pursuit related regions in MT and MST increases eye velocity during ipsiversive pursuit. The stimulation of MT/MST is much more effective during ongoing pursuit than during fixation of a stationary target. Similarly, the effect of stimulation is enhanced during higher pursuit velocity, indicating nonlinear responses. Those findings indicate that visual and pursuit signals carried by MST neurons may still be necessary for the on-line gain control. One hypothesis is that MST signals are sent to other cortical or brainstem pursuit areas that could be involved in regulating internal gain parameters.

In fact, at least two cortical structures are involved in the generation of initial pursuit commands. Smooth pursuit is supported by interconnected regions of the parietal (MT and MST) and frontal lobes including the frontal eye field (FEF) and the supplemental eye field (SEF). These cortical areas comprise the cortical visual and pursuit systems (Krauzlis, 2004; Lisberger, 2010), which is responsible for beginning the process of converting visual motion information into motor commands and also more cognitive aspects of pursuit (Fukushima et al., 2002, 2011; Keating, 1993; Mahaffy & Krauzlis, 2011). Although neuronal mechanisms and regions involved in on-line gain control are incompletely understood, it has been suggested that cortical visual and pursuit pathways including FEF play a role in the nonlinear perturbation response (Nuding et al., 2008, 2009; Ono, 2013; Tanaka & Lisberger, 2001, 2002). Tanaka and Lisberger (2001, 2002) have demonstrated that micro-electrical stimulation in FEF enhances the eye motion evoked by a target perturbation. Their results suggest that FEF plays a role in on-line gain control that regulates the visuomotor output even facing same stimulus velocity. A recent study using transcranial magnetic stimulation (TMS) has also shown that disrupting neuronal activity in FEF by TMS alters the perturbation response and attenuates the efficacy of on-line gain control in pursuit (Nuding et al., 2009). Furthermore, electrical stimulation in SEF facilitates eye acceleration and velocity during pursuit initiation (Missal & Heinen, 2001). Therefore, the extraretinal signals (non-visual signals) carried by neurons in FEF or SEF could play a role in the on-line gain control. Taken together, visual motion signals are primarily processed in cortical areas MT/MST to produce formed commands for smooth pursuit. Then, the magnitude of perturbed ocular response during ongoing pursuit is determined by the visual and pursuit signals modulated by the internal gain parameter in the frontal lobes to regulate the feedforward pursuit gain.

5. Altered on-line gain control in pursuit

Previous studies provided abundant evidence that initial pursuit gain, which is based on open-loop control, is highly influenced by the visual properties of target motion (Krauzlis & Lisberger, 1994; Lisberger & Westbrook, 1985; Lisberger et al., 1981; Tychsen & Lisberger, 1986). The visuomotor gain associated with

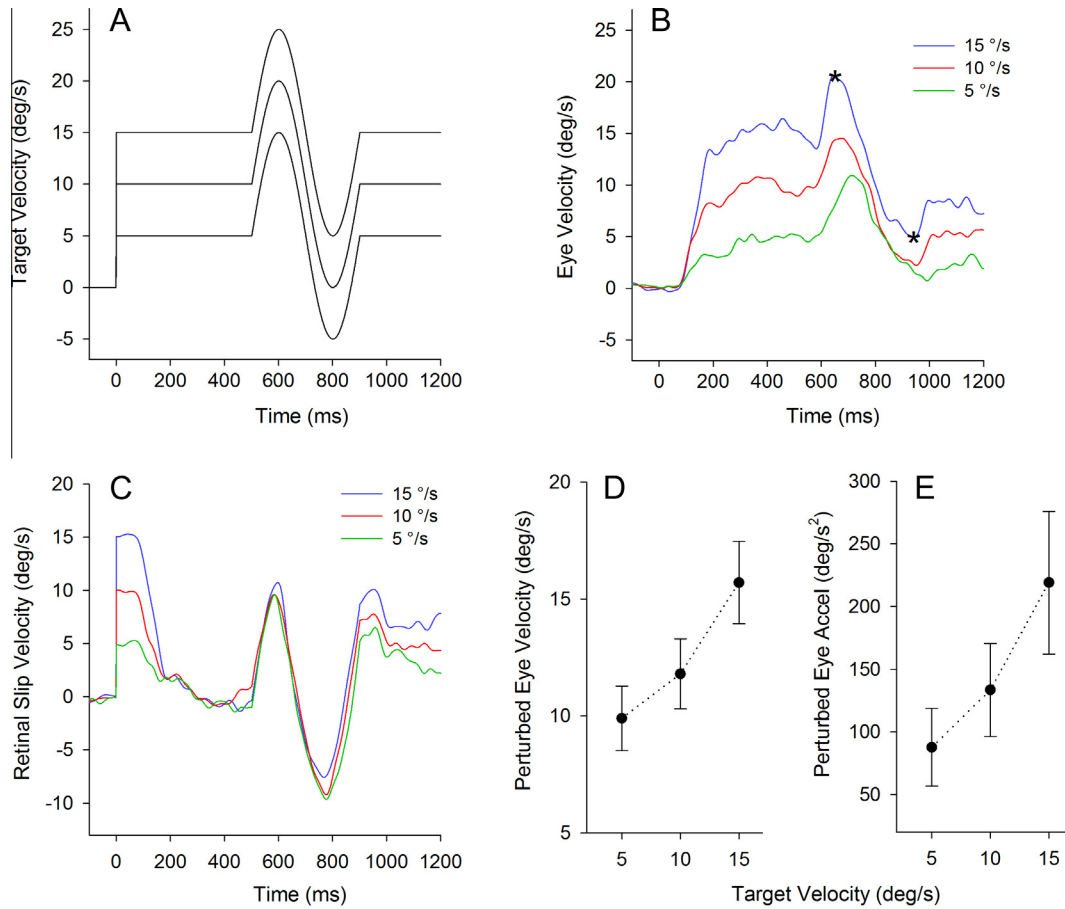


Fig. 3. Enhancement of perturbation responses in accordance with baseline target velocity. (A) perturbation stimulus (2.5 Hz, $\pm 10^\circ/s$) is introduced (500 ms after target onset) during step-ramp tracking at different target velocities (5, 10 and 15°/s). (B) Mean eye velocity traces at 3 different target velocities are shown as a function of time. Asterisks in the eye velocity trace indicate maximum and subsequent minimum of eye velocity following a target perturbation during the tracking velocity of 15°/s. (C) mean retinal slip velocity traces are shown as a function of time. Perturbed retinal slip velocity is estimated by the difference of the maximum to the subsequent minimum of retinal slip velocity during the target perturbation. Mean and standard deviation (SD) values of perturbed eye velocity (D) and peak eye acceleration (E) are shown as a function of target velocity. Increasing target velocities yield a significant increase in the perturbation ocular response even though retinal slip velocity induced by the perturbation is constant, which indicates the on-line gain control (from Ono, 2013).

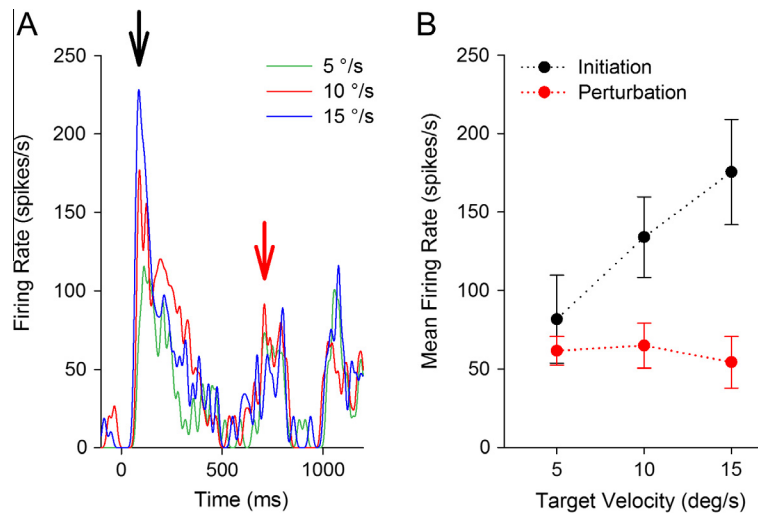


Fig. 4. Response of a visual motion related neuron in MST to the target perturbation during step-ramp tracking at 3 different velocities (5, 10 and 15°/s). The neuronal response to the target onset and perturbation were determined by the time when the response exceeded the mean + 3SD (standard deviation) following the target onset or perturbation. Then mean firing rate was calculated as the average firing rate in the first 100 ms period. Spike density function (A) and mean values of firing rate (B) show that the initial firing rate (black arrow) increases in accordance with target velocity, whereas the response to the perturbation (red arrow) did not show significant changes. This indicates that the on-line gain control is not simply due to the visual response of neurons in MST.

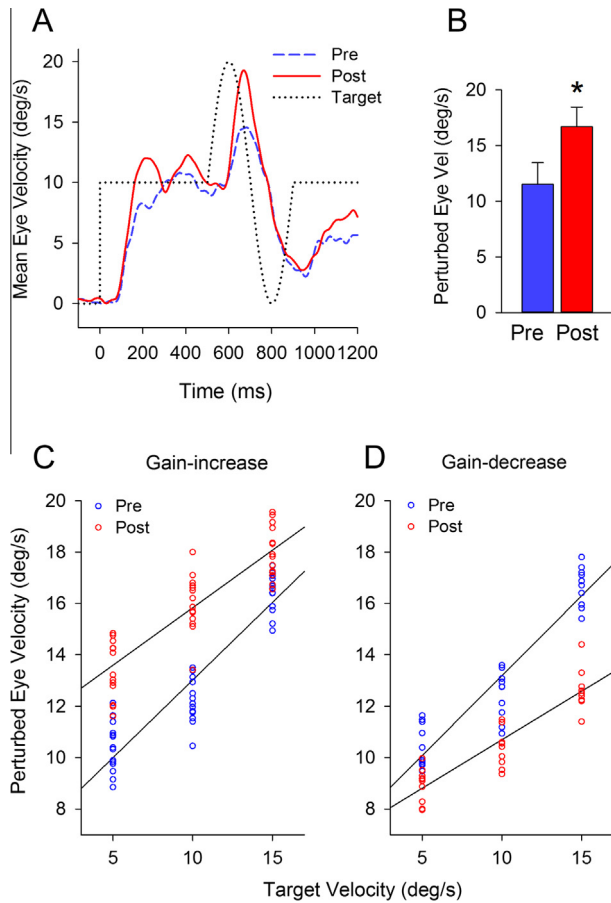


Fig. 5. Effect of smooth pursuit adaptation on the on-line gain control. The perturbation responses during step-ramp tracking pre and post adaptation using gain-increase paradigm are shown (A). Mean eye velocity induced by the perturbation is enhanced in post adaptation (red line) compared with preadapted trials (blue line). Mean values of perturbed eye velocity shows a significantly increase in post adaptation (B). Mean eye velocity of all the perturbation responses at 3 different target velocity conditions (5, 10 and 15°/s) for gain-increase (C) and decrease (D) adaptation. Blue and red circles indicate pre- and post-adaptation, respectively. Straight lines are linear regression fits between perturbed eye velocity and target velocity, indicating that two regression lines of pre- and post-adaptation have different slopes in gain-increase and decrease adaptation (from Ono, 2013).

the initial pursuit is variable, which depends on ongoing behavioral states or cognitive factors (Barnes, 2008; Keating & Pierre, 1996; Krauzlis & Miles, 1996; Tabata, Miura, & Kawano, 2005; Tabata et al., 2006). For example, the initial pursuit response evoked by visual target motion is enhanced when the subjects anticipated the tracking of a moving target. The visuomotor response is related

to the recent experience of pursuit eye movements. Therefore, the on-line gain adjustment could be influenced by not only ongoing pursuit states also pursuit capabilities based on the experience or training factors. Previous studies have demonstrated an adaptive capability of initial pursuit gain using repeated trials of a step-ramp tracking with two different velocities (double-velocity paradigm) in human (Fukushima et al., 1996; Ogawa & Fujita, 1997) and monkeys (Kahlon & Lisberger, 1996; Nagao & Kitazawa, 1998; Ono, 2013; Ono & Mustari, 2012; Takagi, Zee, & Tamargo, 2000). In this paradigm, target speed suddenly changes (increase or decrease) 100 ms after the target onset. Typically, 100–200 sequential trials are used for a double-step paradigm, which alters the gain of visuomotor transmission in pursuit pathways. Here we argue whether the on-line gain control is affected by smooth pursuit adaptation. Fig. 5 shows a representative perturbation response during step-ramp tracking in pre and post-adaptation using a gain-increase paradigm. The perturbed eye velocity increased significantly following adaptation compared with pre-adapted trials. This result indicates that smooth pursuit adaptation affected the magnitude of perturbation responses. Furthermore, the perturbation responses are tested at 3 different target velocity conditions in post-adaptation. Fig. 5C and D shows that smooth pursuit adaptation affected not only the magnitude of perturbation responses also the on-line gain control (nonlinear responses) at different target velocities. Therefore, these findings support the suggestion that smooth pursuit adaptation influences the internal gain parameter in the cortical pursuit areas, which alters the efficacy of the on-line gain control for pursuit (Ono, 2013).

There is strong evidence that plasticity mechanisms in the cerebellum including the floccular complex and oculomotor vermis underlie smooth pursuit adaptation (Dash, Dicke, & Thier, 2013; Kahlon & Lisberger, 2000; Nagao & Kitazawa, 2000; Takagi, Zee, & Tamargo, 2000). The effect of adaptation on the perturbation response is based on the adaptive capability of initial pursuit gain (Ono, 2013). Therefore, the altered gain slope for gain-increase and decrease adaptation could be attributed to cerebellar plasticity. Whether the cerebellar plasticity mechanisms influence cortical visuomotor systems is uncertain. Fig. 6 shows the potential flow of cortico-ponto-cerebellar signals for the on-line gain control in smooth pursuit. Visual motion signals are processed in cortical areas MT/MST and brainstem centers to produce formed commands for smooth pursuit. The cortical visual signal constitutes the primary input to the pursuit system, which is modified by internal gain parameters in FEF to regulate the feedforward pursuit gain. Anatomical studies have shown that FEF receives feedback signals from the cerebellum through the oculomotor thalamus (Huerta, Krubitzer, & Kaas, 1987; Lynch, Hoover, & Strick, 1994; Tian & Lynch, 1997). The FEF and oculomotor thalamus contribute to pursuit initiation that is thought to be an open-loop response for visuomotor control (Fukushima, 2003; Gottlieb, MacAvoy, & Bruce,

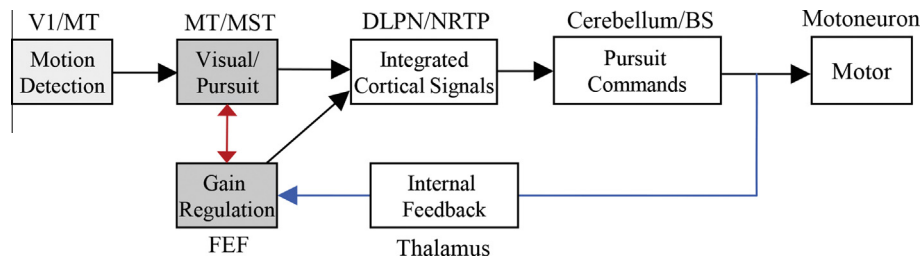


Fig. 6. Simplified diagram to indicate some of the cortico-ponto-cerebellar pathways for smooth pursuit. Cortical area MT provides visual motion information to MST which in turn projects to DLPN. The FEF has reciprocal connections with MT and MST areas (red line), which could play a role in regulation of pursuit gain. The FEF receives feedback signals through the oculomotor thalamus (blue line). The source of pursuit related signals in the thalamus includes the deep cerebellar and vestibular nuclei. BS, brainstem; DLPN, dorsolateral pontine nucleus; FEF, frontal eye field; MST, medial superior temporal cortex; MT, middle temporal cortex; NRTP, nucleus reticularis tegmenti pontis; V1, primary visual cortex. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

1994; Mahaffy & Krauzlis, 2011; Ono & Mustari, 2009; Tanaka, 2005). The source of visual and pursuit signals in the oculomotor thalamus includes the deep cerebellar and the vestibular nuclei (Asanuma, Thach, & Jones, 1983; Kalil, 1981; Lang, Buttner-Ennever, & Buttner, 1979). Taken together, the internal gain parameter in the cortical pursuit system could be modified by the feedback signal derived from the cerebellum to the thalamo-cortical pathway, which alters the efficacy of on-line gain control.

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