

Adaptive feedback control models of the vestibulocerebellum and spinocerebellum

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Abstract. We extend the cerebellar learning model proposed by Kawato and Gomi (1992) to the case where a specific region of the cerebellum executes adaptive feedback control as well as feedforward control. The model is still based on the feedback-error-learning scheme. The proposed adaptive feedback control model is developed in detail as a specific neural circuit model for three different regions of the cerebellum and the learning of the corresponding representative movements: (i) the flocculus and adaptive modification of the vestibulo-ocular reflex and optokinetic eye-movement responses, (ii) the vermis and adaptive posture control, and (iii) the intermediate zones of the hemisphere and adaptive control of locomotion. As a representative example, simultaneous adaptation of the vestibulo-ocular reflex and the optokinetic eye-movement response was successfully simulated while the Purkinje cells receive copies of motor commands through recurrent neural connections as well as vestibular and retinal-slip parallel-fiber inputs.

1 Introduction

Although the Marr-Albus model of the cerebellum (Marr 1969; Albus 1971) provides a formal framework for understanding how the heterosynaptic of plasticity Purkinje cells might be used for motor learning, the physiological details remain largely an enigma. Developments in computational neuroscience and artificial neural networks applied to real control problems were essential to fully understanding how the work-space error information associated with movement performance can be converted into motor-command errors, and how these errors can be used as one kind of synaptic input by motor learning algorithms that are based on biologically plausible heterosynaptic plasticity rules (Kawato et al. 1987; Kawato 1990). Kawato and

Gomi (1992) proposed a computationally coherent model of the cerebellum based on the feedback-error-learning scheme. It mainly treated computational principles of feedforward control, however. The spinocerebellum, for example, receives direct feedback information from the periphery, unlike the lateral cerebellum. Many parts of the cerebellum are involved in movements which require feedback rather than feedforward control, such as posture control, the optokinetic eye-movement response and smooth pursuit. Thus, in order to deal coherently with learning in different regions of the cerebellum, we need to extend our computational model from the purely feedforward case to general situations which include adaptive feedback control as well. In this paper, we develop a computational theory and neural circuit models of the cerebellum for adaptive feedback control. As a representative example, simultaneous adaptation of the vestibulo-ocular reflex and the optokinetic eye movement response was successfully simulated while assuming that the Purkinje cells receive motor-command feedback signals through recurrent neural connections as well as from the vestibular and retinal-slip parallel-fiber inputs.

2 Adaptive closed-loop control by feedback-error learning

We proposed the closed-loop control system shown in Fig. 1 based on the feedback-error-learning scheme (Gomi and Kawato 1990) by extending the basic feedback-error learning scheme for purely feedforward control. The state of the controlled object θ obeys the following nonlinear differential equation.

$$d^2\theta/dt^2 = f(d\theta/dt, \theta, \tau). \quad (2.1)$$

Here, f is an n -dimensional nonlinear vector function. The motor command τ fed to the controlled object is the summation of the motor command τ_c generated by the conventional feedback controller and the motor command τ_n calculated by the nonlinear adaptive feed

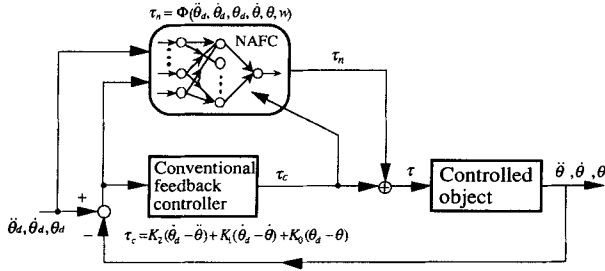


Fig. 1. Control structure of closed-loop feedback-error learning

back controller (NAFC in Fig. 1). τ_n is given as follows.

$$\tau_n = \Phi(d^2\theta_d/dt^2, d\theta_d/dt, \theta_d, d\theta/dt, \theta, w). \quad (2.2)$$

It is noted that the NAFC receives the feedback information about the state of the controlled object and its velocity but not its acceleration. The conventional feedback controller can be nonlinear, but here we explain the simple linear case, where it calculates the motor command according to the following equation.

$$\tau_c = K_2 d^2(\theta_d - \theta)/dt^2 + K_1 d(\theta_d - \theta)/dt + K_0(\theta_d - \theta). \quad (2.3)$$

Here, this is a PDA (Proportional, Derivative, and Acceleration) feedback controller. The synaptic modification equation is exactly the same as that in the open-loop system (2.2) of Kawato and Gomi (1992).

$$dw/dt = (\partial\tau_n/\partial w)^T \tau_c. \quad (2.4)$$

As learning proceeds, the motor command generated by the conventional feedback controller decreases. It can be mathematically shown that, based on this learning equation, NAFC acquires the inverse dynamics of the controlled object plus the nonlinear PD feedback controller which uses the error and its first derivative. Ultimately, the overall system dynamics obeys the following differential equation.

$$K_2 d^2(\theta_d - \theta)/dt^2 + K_1 d(\theta_d - \theta)/dt + K_0(\theta_d - \theta) = 0. \quad (2.5)$$

That is, the behavior of the total system is determined by the reference model prescribed by the conventional feedback controller.

In this scheme, the conventional feedback controller plays three roles. First, it converts the trajectory error into the motor-command error as a linear approximation of the inverse model of the controlled object. Second, like a typical feedback controller, it guarantees global trajectory stability. Third, it defined an inverse reference model for the model-reference-adaptive control as shown in (2.5). In the framework of the model-reference-adaptive control which has a long history, the reference model determines the ideal response of the controlled object, then the control law is changed according to an adaptation law based on the discrepancy between the desired response defined by the reference model and the realized response. The final objective of this adaptation is to achieve the ideal response. There

are at least two different points between the conventional model-reference-adaptive control and our scheme. In the former scheme a forward reference model is used whereas the inverse reference model is used in the latter. Second, in most conventional schemes, only a linear controller was investigated, whereas ours is a fully nonlinear scheme.

For example, suppose that we prepare a PDA feedback controller in the Cartesian space as the conventional feedback controller. Then it defines the mechanical impedance of the hand tip in the Cartesian space. In this case, K_2 determines the virtual inertia, K_1 viscosity, and K_0 stiffness. Thus after learning is completed, the total system including the conventional feedback controller, NAFC and the controlled object behaves like a point mass system with the mass K_2 , the viscosity K_1 , and the stiffness K_0 .

If we simply feed a motor-command error to the adaptive feedback controller without summation with its derivative and acceleration, a difficult problem of gain explosion occurs. This is an inherent problem in an adaptive feedback controller. In feedback control, in order to decrease the motor error simply to zero, one needs to increase the feedback gain infinitely. This is not only impractical but also very dangerous regarding system stability because feedback delay is always present. Our main proposition is to use a conventional feedback controller which outputs zero even when the trajectory error is not zero. This is an intuitive explanation of the inverse reference model.

3 Vestibulocerebellum

3.1 Interpretation of VOR/OKR circuit by feedback-error learning

Cerebellar motor learning has been most intensively studied in the vestibulocerebellum using the vestibulo-ocular reflex (VOR). The vestibulocerebellum occupies the flocculonodular lobe. During head turns, the VOR normally acts to stabilize retinal images by generating smooth eye movements that are equal and opposite to the rotary head movements. During experimental manipulations of retinal slips using magnifying spectacles, inversion prisms, or rotating visual screens, the VOR gain (the ratio of eye and head movements) changes. Such VOR adaptation is abolished in cats, rabbits, and monkeys when the flocculus is destroyed, or in rabbits when only the visual climbing fiber pathway is destroyed (see Ito and Nagao 1991 for review). The site of motor learning in primates is still in dispute and will be discussed later. Here we review the model for rabbits. Fujita (1982a, b) expanded the basic Marr-Albus model to incorporate dynamic responses, proposing that the cerebellum is an adaptive filter that can learn to compensate for dynamical characteristics of the oculomotor plant. He simulated adaptive modification of the VOR based on both long-term depression (LTD) and the hypothesis proposed by Ito (1970, 1984, 1989) that the parallel-fiber/Purkinje-cell synapses of the cerebellar flocculus are the site of modification. Climbing-fiber

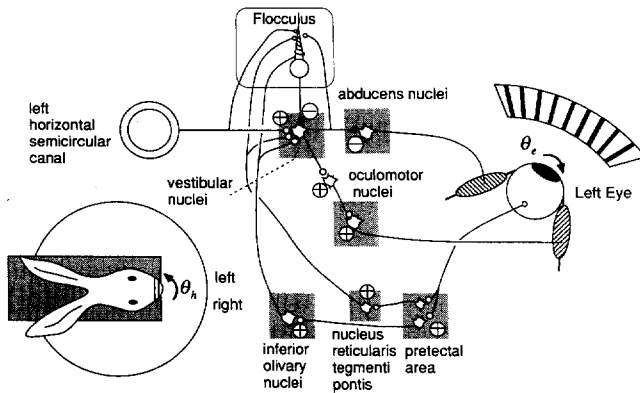


Fig. 2. Schematic diagram of the neural circuit for the horizontal vestibulo-ocular reflex and optokinetic response

activities are assumed to reflect motor-performance error information conveyed by the retinal slip velocity (Maekawa and Simpson 1973).

The horizontal VOR is regulated by a three neuron reflex arc as well as by the microzone of the flocculus called the H-zone (Ito 1984), which also participates in control of the optokinetic eye movement response (OKR). The OKR moves the eye in the direction of the visual field motion to stabilize the retinal image, and shares major neural mechanisms with VOR. A schematic diagram of the neural circuitry for the VOR and OKR is shown in Fig. 2. When the head is rotated to the left, the semicircular canal sends the head rotational velocity to the vestibular nucleus and the flocculus, and the eye is rotated to the right. If the VOR is not perfect, images move on the retina, and retinal slip information is sent back to both the vestibular nucleus and the flocculus by the climbing and mossy fibers. This retinal slip information is the sensory input used by the OKR. In additional examination of the eye-velocity components in simple spikes of Purkinje cells revealed that the corollary discharge of the motor command forms a positive feedback loop through Purkinje cells and the vestibular nucleus (Stone and Lisberger 1990; Nagao 1991). Thus, the Purkinje cells of the flocculus receive three kinds of synaptic inputs via parallel fibers: the head-velocity signal measured by the vestibular organ, the retinal-slip signal measured by motion detectors in the retina and sent from the nucleus reticularis tegmenti pontis, and a copy of the motor command (mainly the eye-velocity signal). Retinal-slip velocity, conveyed by the climbing fibers to Purkinje cells, is the error signal in LTD and is essential for adaptation of the OKR as well as the VOR (Nagao 1988).

Figure 3 is a block diagram of the neural circuit. This is a model of only that microzone of the flocculus (the H-zone) which is related to the horizontal VOR and OKR. Here, θ_h , θ_e and θ_{ext} denote the head rotation angle, the eye-rotation angle and the rotation angle of the external world, while u is the motor command sent to the muscles. Superscripts w , r , c and m indicate variables represented in the world, retinal, canal, and muscle coordinates. s indicates the Laplace operator and $1/s$ corresponds to integration. T_{wc} and T_{wr} repre-

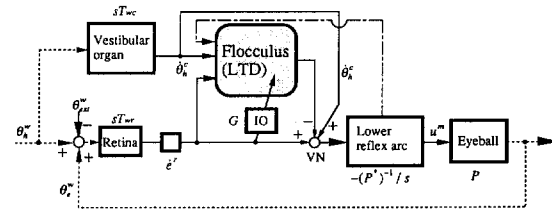


Fig. 3. Block diagram of adaptive modification of the vestibulo-ocular reflex and optokinetic response by the flocculus H-zone. VN is the vestibular nucleus and IO is the inferior olive nucleus

sent coordinate transformations from the world frame to the canal frame and to the retinal frame, respectively. The vestibular organ sends the head-rotation velocity in the canal coordinates, $d\theta_h^c/dt$, to the vestibular nucleus and the flocculus. The forward dynamics of the eyeball are represented by the operator P . Because some portion of the VOR is left even when the flocculus is destroyed, the lower reflex arc should provide the integrated negative of the approximated inverse of the controlled object $-(P^*)^{-1}/s$. This is because the transfer function of the main reflex arc should be roughly $-1 : s \rightarrow -(P^*)^{-1}/s \cdot P \sim -1$.

Simpson and Alley (1974) showed that the visual system, which provides climbing-fiber input, senses the retinal-slip velocity de^r/dt . Figure 3 shows that, if the external world is stationary, the retinal slip is the summation of the head and eyeball velocities: $d(\theta_h + \theta_e)/dt$. The eyeball velocity required to stabilize the retinal image is then the negative of the head velocity: $-d\theta_h/dt$. The time derivative of the error between the desired and actual eye velocity is sent to the vestibular nuclei and the flocculus via the visual climbing fiber and the OKR feedback pathways: $de/dt = d(\theta_h + \theta_e)/dt = -d(\theta_{ed} - \theta_e)/dt$. The minus sign in the third equation is canceled if one considers the three sign inversions, namely, LTD, the inhibitory action of the Purkinje cells, and the minus sign of the lower reflex arc. Thus, the OKR closed loop constitutes a derivative-type negative feedback controller, with its activity monitored as the error signal by the climbing fibers, and the VOR constitutes purely feedforward control. If one compares Fig. 3 with the block diagram in Fig. 1, the adaptive function of the flocculus can be understood on the basis of our feedback-error-learning scheme. Because the combined dynamics of the lower reflex arc and the eye can be approximated by the negative of the integration, this derivative-type negative feedback controller corresponds well to the approximated inverse dynamics of this combined system. In this scheme, the cerebellar flocculus and the basic three-neuron VOR arc can together be interpreted as a neural network able to acquire the inverse dynamics model of the oculomotor plant.

3.2 Simulation of simultaneous adaptation of VOR and OKR

We assume that the outputs of the VOR and OKR systems are summed linearly at the vestibular nucleus (Robinson 1977). The flocculus is responsible for simultaneous adaptation of the VOR and OKR (Nagao

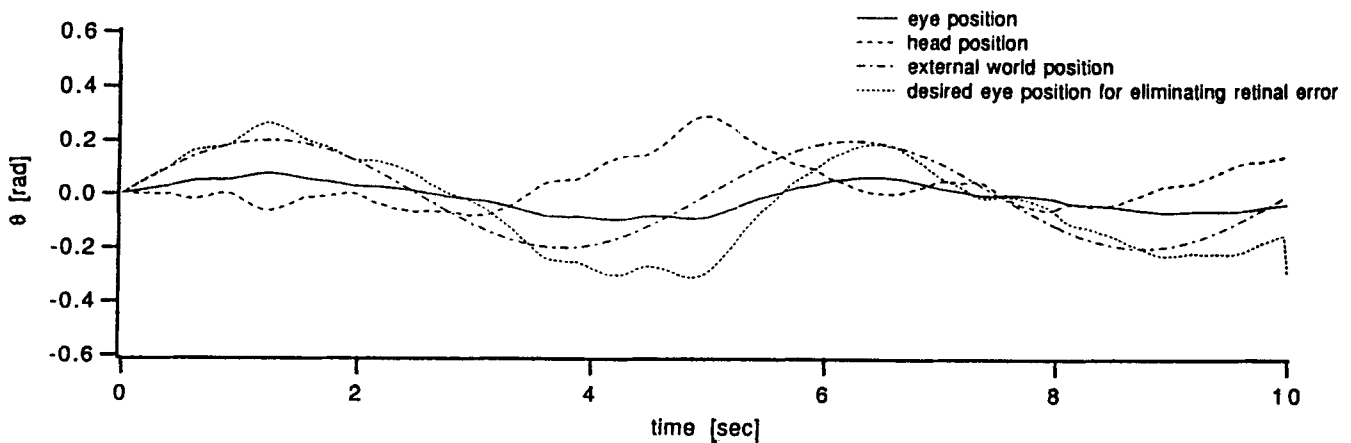
1988). As mentioned above, the flocculus receives three kinds of synaptic inputs via parallel fibers: the head-velocity signal $d\theta_h^c/dt$, the retinal-slip signal $d(\theta_h^r + \theta_e^r - \theta_{ext}^r)/dt$, and the eye-velocity signal $d\theta_e^w/dt$ which is a copy of the motor command. The VOR input to the flocculus in Fig. 3 corresponds to feedforward input of the desired trajectory to the NAFC in Fig. 1, whereas the OKR input to the flocculus corresponds to the closed-loop feedback signal to the NAFC. For both inputs, the direct arc from the retina to the vestibular nucleus acts as a conventional feedback controller.

We simulated simultaneous adaptation of the VOR and OKR based on the block diagram in Fig. 3. The experimental design of the simulations is outlined in Fig. 2. The animal is fixed on a rotating table which elicits head rotation to stimulate the VOR. OKR is induced by visual stimulus on a rotating drum. There are three reasons for adopting this experimental setting. First, Ito and his colleagues used this experimental paradigm extensively for rabbits and monkeys (see, for example, Ito and Nagao 1991; Nagao 1988, 1991). Second, it is similar to natural environments in the sense that the head and the visual world can rotate independently. The third and most important reason is that we

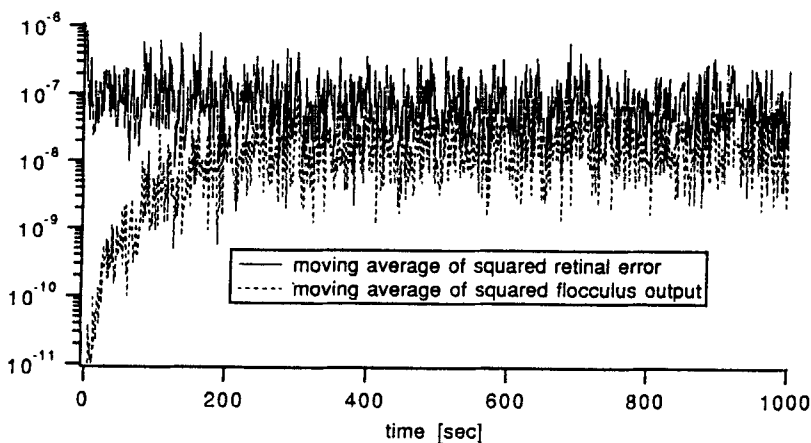
can estimate the pure VOR and OKR gains before and after adaptation.

A delay of 10 ms was assumed for the motor-command feedback to the flocculus. 20-ms feedback delay was used for calculation of the retinal slip. The dynamics of the eyeball were modeled by taking into account its mass, viscosity, and stiffness. Numerical integration was done with a 0.2 ms time increment which is shorter than the natural frequency of the eyeball. The initial synaptic efficacies of the three inputs to the flocculus, the vestibular input, the retinal-error input, and the motor command feedback were all assumed to be zero. Thus, the VOR and OKR were executed only by the fixed feedback loop at the beginning of the simulation. G is the transfer function from the retinal slip velocity to the climbing-fiber responses. Actually, we assumed that the inferior olive sends a linear combination of the retinal-slip position, velocity, and acceleration but experimental data indicated that the velocity term was dominant and thus simulated (Simpson and Alley 1974; Nagao 1988).

The simulation results are shown in Fig. 4. Graph a shows the eye, head, external world, and desired eye positions during the first 10 s of the total 1000-s training period. The screen was rotated sinusoidally at

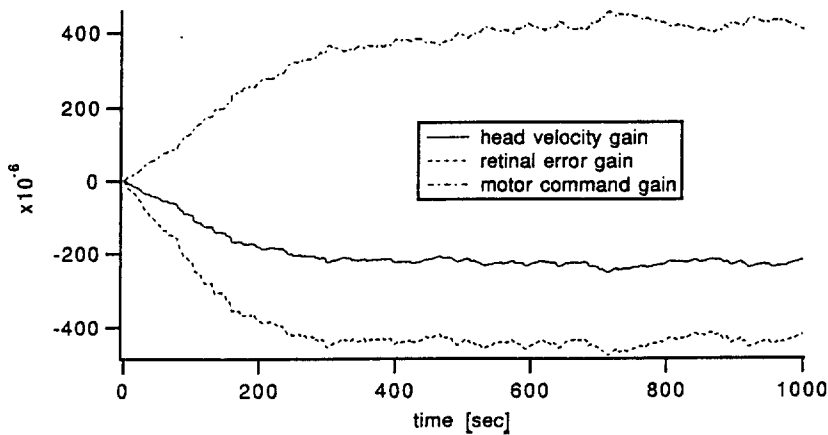


(a)

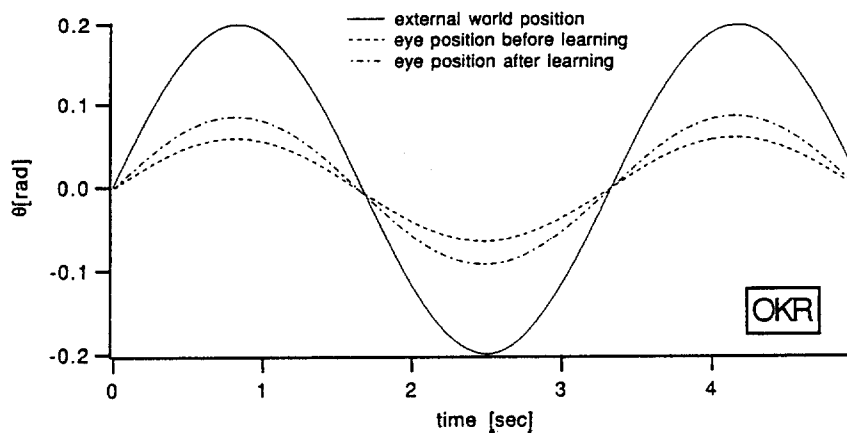
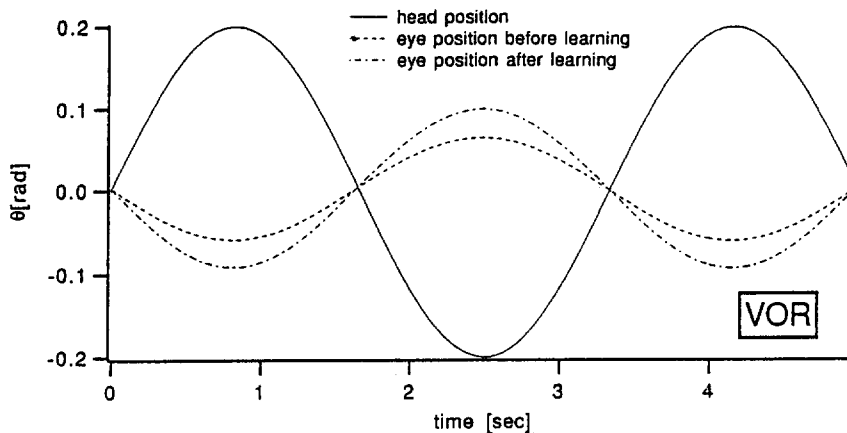


(b)

Fig. 4. (a), (b)



(c)



(d)

Fig. 4a–d. Simulation results for adaptive modification of the vestibulo-ocular reflex and optokinetic response. **a** Eye position (solid line), head position (broken line), external world position (dot-dash line) and the desired eye position (dotted line) at the beginning of the training. **b** Moving average of the squared retinal error (solid line) and moving average of the squared flocculus output (broken line). **c** Synaptic efficacies of three different inputs to the flocculus. The solid line, the broken line and the dot-dash line show the head-velocity gain, the retinal-error gain, and the motor-command gain, respectively. **d** System performance before (broken line) and after (dot-dash line) the training for VOR (above) and OKR (below)

0.2 Hz and 0.4 radians peak-to-peak. The head was rotated by a stochastic process with a similar time course and amplitude. The eye should move according to the difference between the head angle and the visual world if the VOR and OKR work perfectly to stabilize the retinal image. Before learning, the eye movement was quite different from the desired movements. Graph **b** shows the time course of the moving average of the squared retinal error and the moving average of the squared flocculus output. The flocculus output increased rapidly while the retinal error decreased only

modestly. Graph **c** shows changes in the synaptic efficacies of the three different inputs to the flocculus: the vestibular input, which codes the head velocity; the visual input, which codes the retinal slip; and the copy of the motor command. These three approached a stable equilibrium where the long-term depression and passive weight decay just balance. It was experimentally shown that in the flocculus of rabbits (Nagao 1991), the synaptic contribution of eye velocity is rather small. Although the gain of the motor-command copy (eye velocity) might be a little high in Graph **c**, it should be

smaller in the actual system. Because we did not include the neural integrator in the lower reflex arc, the flocculus tried to construct its substitute unnaturally. Graph **d** compares system performance before (broken line) and after (dot-dash line) the training for the VOR (above) and the OKR (below). Peak-to-peak oscillations of 0.3 Hz and 0.4 radians were used for both the VOR and OKR. The VOR gain increased from 0.29 to 0.45 while the OKR gain increased from 0.29 to 0.43.

This is a new simulation which examines for the first time simultaneous adaptation of the VOR and OKR (Nagao 1988). The inclusion of the "recurrent connection" in the learning is also important. In Fig. 2, the recurrent connection is schematically diagramed as the axon collateral of the vestibular nucleus neuron linked to the abducens nuclei. This collateral forms parallel-fiber synapses with Purkinje neurons. Because the Purkinje neurons and vestibular nuclei form a closed-loop connection, we call this collateral the recurrent connection. Note that Fig. 2 is a schematic diagram, and that parallel-fiber inputs to the flocculus might quite plausibly originate from different neural populations from those in the vestibular nuclei that send axons to the abducens and oculomotor nuclei. This recurrent connection is believed to convey mainly the eye velocity, and to some extent eye acceleration and position. This is considered a part of the neural integrator. It is very interesting that a biologically plausible learning scheme such as feedback-error learning works quite well even when a recurrent connection is included. This contrasts sharply to recurrent back-propagation (Anastasio 1991) or the random search method (Arnold and Robinson 1991), which are difficult to neuronally implement.

The question of which coordinate frame the climbing fiber responses are represented in arises when the vertical and rotatory as well as horizontal VOR are studied. Nagao et al. (1985) mapped the H-zone, two V-zones, and the R-zone from which local electrical stimulation induced horizontal, vertical, and rotatory eye movements, respectively. Neurons inhibited by the H-zone, V-zones, and R-zone seem to relay signals to the horizontal recti, the vertical recti, and the obliques, respectively. Simpson et al. (1989) examined the rotational axis of the visual world to which visual climbing fibers optimally responded in rabbits. They found that these three axes well match the three axes about which the three pairs of extraocular muscles rotate the eyeball. The coordinate system in which the error signal is represented thus seems to be the muscle-coordinate system for the three-dimensional VOR. Our computational model further predicts that the optimal rotational axis for the visual climbing fibers for the H-zone, V-zones and R-zone are respectively the axes of the horizontal recti, the vertical recti, and the obliques.

Because the visual climbing fibers convey the retinal slip, they may be expected to be expressed in sensory retinal coordinates and it may sound quite odd when we assert that they are expressed in muscle coordinates instead. Where optimal movement directions or rotational axes are concerned, however, the topographic

retinal map of the visual field has nothing to do with the relevant coordinate frame. There are consequently no obvious "retinal coordinates" used for signals in the visual climbing fibers. Then two relevant coordinate frames here are the sensory coordinates defined by the semicircular canals and the motor coordinates defined by the extraocular muscles. Ezure and Graf (1984) found that these two coordinate frames slightly but consistently differ from each other. For lateral-eyed animals such as rabbits, however, these two coordinate frames are not all that different. Thus, experiments similar to those done by Simpson et al. (1989) using frontal-eyed animals may clarify this coordinate problem.

4 Neural circuit models of spinocerebellum

The spinocerebellum includes the vermis and the intermediate zones of the hemispheres. These two regions are the areas of the cerebellum which receive sensory information from the periphery. The vermis is related to axial motor control; the intermediate zones to distal motor control.

In this section, we propose models of the vermis and the intermediate zones based on the feedback-error-learning scheme for the closed-loop control system shown in Fig. 1. In these models, the cerebellum provides an adaptive feedback controller. With learning capability realized by the LTD, the cerebellum learns how to execute coordinative and predictive control of complicated controlled objects such as limbs and the body trunk. This adaptive feedback controller is overlaid onto the more fundamental feedback systems in the spinal cord, the brain stem, and the cerebral cortex. The two feedback controllers cooperate to execute movements. A copy of the motor command generated by the lower feedback controller is sent to the cerebellum by the climbing-fiber system. The LTD tries to decrease the activity of the climbing-fiber system. Thus, as learning proceeds, the lower feedback controller becomes less active, and the movement is mainly controlled by a sophisticated controller in the cerebellum.

There are two compelling reasons to regard the spinocerebellum as the adaptive feedback controller. First, unlike the lateral cerebellum, it receives information directly from the periphery. Second, the controlled object in posture control and locomotion is a physically unstable system, similar to an inverted pendulum, and feedback control is computationally essential.

4.1 Model of the vermis

Human posture control performance is degraded when proprioceptive feedback information is degraded, but the loss of certain information is compensated for by using other sources of information (e.g. Romberg's sign). Nashner (1981) showed that adaptive modification of posture control reflexes is severely impaired in patients with cerebellar disease. The cerebellum is therefore assumed to be the site of adaptive posture control. The vermis receives information about the position,

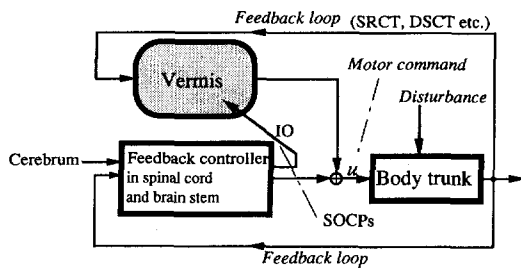


Fig. 5. Block diagram of adaptive posture control by a corticonuclear complex in the vermis of the cerebellum. SRCT: spino-reticulo-cerebellar tract, DSCT: dorsal spinocerebellar tract, SOCPs: spino-olivo-cerebellar paths

velocity, and acceleration of the head and torso from proprioceptors, visual sensors, and the vestibular organ. Its output is directed mainly to the medial brainstem system and the axial regions of the motor cortex.

Figure 5 shows a block diagram of adaptive posture control conducted by a corticonuclear microcomplex in the vermis of the cerebellum. Among the several functional roles of the vermis in motor control, adaptive posture control is chosen as a representative example in Fig. 5. Even if the vermis is not involved in posture control, the body trunk can be controlled by premotor networks in the spinal cord and the brain stem. In particular, the premotor networks can be regarded as feedback controllers because they monitor the state of the controlled object by sensory feedback, and send motor commands back to it. This fundamental feedback loop in Fig. 5 corresponds to the conventional feedback controller in Fig. 1 which provides the error signal in motor-command coordinates. We propose that parallel to this basic feedback loop, another feedback loop is formed by a cerebellar afferent system such as that consisting of the spino-reticulo-cerebellar tract (SRCT), dorsal spinocerebellar tract (DSCT), the vermis, and cerebellar efferent pathways from the vermis to the spinal cord such as the cerebelloreticulospinal tract (CRST) or the cerebellovestibulospinal tract (CVST). The reason the SRCT and DSCT are said to form an afferent limb of the feedback loop is that they carry information from the spinal cord and periphery to the cerebellum regardless of whether it is related to the activities of spinal interneurons or whether the information is a faithful representation of sensory receptor activity.

Whereas the feedback controller in the basic loop guarantees fundamental, robust but rather clumsy control, the feedback loop via the vermis provides more advanced predictive and coordinative control. However, this complicated controller must be acquired by motor learning based on synaptic plasticity of the parallel-fiber/Purkinje-cell synapses.

We assume that motor error signals represented in the motor-command coordinates at earlier parts of the premotor networks are sent to the vermis via the inferior olive by pathways such as the spino-olivo-cerebellar paths (SOCPs). This view is largely based on studies by Oscarsson and his colleagues (Oscarsson 1980). Because

this assumption is crucial to our computational theory, here we introduce some experimental support. Although parallel-fiber pathways from the spinal cord carry information either directly from receptors (the DSCT and the CCT: proprioceptive component of cuneocerebellar tract) or from both spinal motor centers and receptors (the VSCT: ventral spinocerebellar tract, the RSCT: rostral spinocerebellar tract), climbing-fiber pathways serve as feedback channels that monitor activity in lower motor centers, and in some cases, also in higher motor centers. The first well-documented example is the spino-olivo-cerebellar paths ascending through the ventral funiculus (VF-SOCPs). The VF-SOCPs are activated by the flexor reflex afferents (FRA) from wide receptive fields. The interneurons of the VF-SOCPs, terminating in the α -zone of the cerebellar anterior lobe, behave, under a variety of tests, as those mediating the segmental flexion reflex (Oscarsson 1980). These SOCPs are assumed to carry information about the activity in the flexion reflex arcs. Most SOCPs presumably carry this information in segmental mechanisms activated by descending paths and segmental afferents, and presumably represent lower motor centers (Oscarsson 1980). Another well-documented example is SOCPs ascending through the dorsolateral funiculus (DLF-SOCPs). The d_1 zone is assumed to control a motor center in the lumbar enlargement which facilitates dynamic gamma motor neurons and inhibits the effects of the flexor reflex afferents on alpha motor neurons and primary afferents (Oscarsson 1980). Activity in the motor center is monitored by the DLF-SOCP which is formed by ascending axon collaterals from the neurons in this center (Jeneskog and Johansson 1977). In this case in particular the same portion of the inferior olive which projects to the d_1 zone monitors the activity of the higher motor center (the rostral part of the red nucleus) as well as the lower motor center in the spinal cord.

Based on this physiological and anatomical interpretation, the block diagram in Fig. 5 can be mapped onto the adaptive feedback control scheme based on feedback-error learning shown in Fig. 1.

By computer simulation, Gomi and Kawato (1990) ascertained that the proposed scheme works well for controlling an inverted pendulum system, the simplest model of the trunk and legs. We found that the error in posture induced by a physical perturbation ("disturbance" in Fig. 5) decreased as the learning process proceeded. The behavior of the total system ultimately achieves the ideal response determined by the reference model embedded in the fundamental feedback controller. A schematic diagram of the neural circuits around the vermis is not shown here because it is similar to that of the intermediate zones which will be shown in the next section.

4.2 Circuit model of intermediate part of the hemisphere

Udo and his colleagues (1980) showed that cooling the cerebellar intermediate cortex interferes with interlimb coordination in locomotion. Matsukawa and Udo (1985) found that complex spikes were frequently

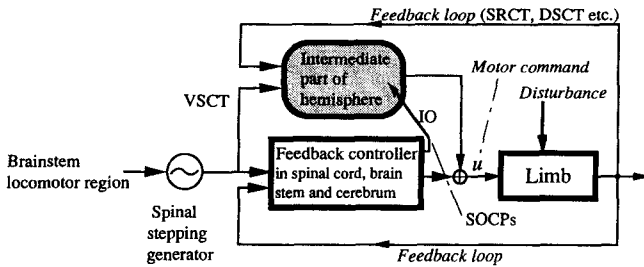


Fig. 6. Block diagram of adaptive control of locomotion by a corticoculcular microcomplex in the intermediate zone of the hemisphere of the cerebellum

evoked by mechanical perturbations of the paw during locomotion of decerebrate cats. Among the many functional roles of the intermediate zones in motor control, adaptive control of locomotion is shown in Fig. 6 as an interesting example. Neural oscillators generate the desired rhythmic movement pattern. Because the desired movement pattern varies with time, feedforward control is necessary for smooth movement. On the other hand, the controlled object is unstable and so feedback control is also essential. Adaptive control of locomotion consequently requires both feedforward and feedback control. The intermediate zones receive the parallel fiber inputs from both the periphery and the brainstem and satisfy the input conditions required to execute simultaneous feedback and feedforward control.

The model for the intermediate zones of the hemispheres is more complicated than that of the vermis, but we propose a similar closed-loop model, shown in Fig. 6. The difference between Figs. 5 and 6 is that in Fig. 6 both the cerebellum and the premotor network for locomotion receive information about the desired rhythmic movement pattern from spinal stepping generators, shown as an oscillator. At the very least, we know that a part of this information is carried by the VSCT, because its rhythmic burst activities during locomotion do not disappear even after the dorsal root is cut. The DSCT, on the other hand, must carry information from sensory receptors, because its burst activities disappear after the dorsal root is cut.

Fundamental coordination between different limbs is achieved by feedback controllers in the spinal cord, the brainstem, and the cerebrum. The intermediate zones are supposed to provide better limb coordination under circumstances such as staircases, slippery floors, obstacle avoidance, or outside disturbances. The feedback controllers receive both desired trajectory information from the stepping generators and somatosensory information from the periphery, and then calculate motor commands by comparing these two kinds of information. Accordingly, the motor error signals, which are calculated by these premotor networks and are sent to the cerebellum through pathways such as SOCPs, depend both on afferent sensory information and efferent motor-command information.

The non-sensory nature of the climbing-fiber responses has been reported (Gellman et al. 1985). Some climbing fibers are activated by paw contact caused by

forced movements. However, identical stimuli do not induce firing of the climbing fibers when paw contact is caused by active movements. Our theory explains this as follows: If some sensory events are expected based on desired movement patterns, no extra activity is generated by the premotor networks, because the higher motor center (e.g. the motor cortex) sends the desired movement pattern to the lower center (the premotor network). If the sensory events match this desired movement pattern, the premotor network does not need to generate motor commands, and the climbing fibers are not activated. On the other hand when sensory events are unexpectedly detected, the premotor networks generate motor activity to deal with them because there is a discrepancy between the instructions given by the higher center and the motor act detected by the sensory system. Following generation of the motor command, a copy of it is sent to the cerebellum, activating the climbing fibers. Our view that the climbing fibers convey control-error information, the difference between the instructions and the motor act, is common to most cerebellar motor-learning models; however, ours is unique in that this error information is represented in the motor-command coordinates.

The most interesting and challenging theoretical problem is setting an appropriate inverse reference model in the feedback controller at the spinal and brainstem levels. We have little experience in designing an inverse reference model for a system with multiple degrees of freedom in very dynamic situations like locomotion. We expect, however, that some of the known interlimb reflexes should provide part of the reference model.

A schematic diagram of the neural circuits around the intermediate zones is shown in Fig. 7. Information about the state of the controlled object θ is sent from the periphery to the Purkinje cells by the spinocerebellar tracts (SCTs) such as the DSCT, CCT, VSCT and RSCT. Similar information θ is also sent to the cerebral cortex by the afferent limb of the transcortical loop. The association cortex neurons send the desired trajectory θ_d to the intermediate cerebellum via the pontine nuclei as well as to the motor cortex. The inferior olive sends a copy of the activity of the premotor networks u_{fb}^{SP} while receiving information from the periphery u_{fb}^{CX} by SOCPs, and also from the cerebral cortex u_{fb}^{CX} . Here, the feedback motor command u_{fb} transmitted by the climbing-fiber system is composed of that generated by the spinal motor center u_{fb}^{SP} and that generated by the cerebral motor center u_{fb}^{CX} . The output from the microcomplex u_{CBL} is sent to the red nucleus and then descends via the rubro-spinal tract and the cerebral cortex from the interpositus nucleus. u_{CBL} is trained to become a good predictive and coordinative feedback as well as feedforward motor command by using u_{fb} as the error signal and θ as the input signal. The pyramidal-tract neurons in the motor cortex send the descending motor command u_{CST} , which is summation of the feedback motor command u_{fb}^{CX} generated by the transcortical loop and the motor command u_{CBL} generated by the cerebellum. We propose that the SCT/parallel-fiber/

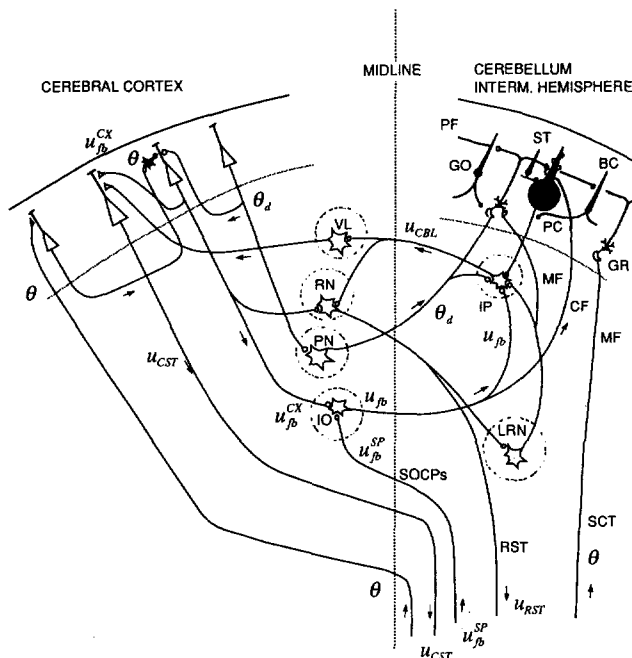


Fig. 7. Schematic diagram of a neural circuit around the intermediate zone of one hemisphere of the cerebellum. RST: Rubrospinal tract, IP: Interpositus nucleus, PN: Pontine nuclei, RN: Red nucleus, LRN: Lateral reticular nucleus

Purkinje cell/interpositus-nucleus/red-nucleus/rubrospinal-tract and SCT/parallel-fiber/Purkinje-cell/interpositus-nucleus/thalamus/cerebral-cortex/pyramidal-tract loops form an adaptive feedback and feedforward controller.

5 Discussion

In this paper we showed that different functions of the vestibulocerebellum and spinocerebellum can be understood using an adaptive feedback control scheme derived from feedback-error learning wherein an inverse model of each part of the motor apparatus is acquired in an adaptive feedback controller based on LTD using the motor command generated by the premotor network as the error signal. We admit that our theory is quite speculative for the spinocerebellum and is based mainly on computational and anatomical constraints rather than physiological data. For the vestibulocerebellum model, however, we have quite solid physiological support.

There has been a long-standing controversy regarding the site of adaptive change of the VOR in primates. Lisberger and Miles proposed that the modification sites are the vestibular-input synapses of flocculus target neurons (FTN) in the medial vestibular nucleus receiving monosynaptic inhibition from the flocculus (the FTN hypothesis) (Lisberger 1988). On the other hand, Watanabe (1985) concluded that the adaptive modification site in monkeys is the flocculus just as in rabbits. Recent anatomical and physiological experiments may help resolve this controversy. Gerrits and Voogd (1989) demonstrated that the rostral half of the traditionally

defined monkey flocculus, from which the first group of authors mainly recorded (Stone and Lisberger 1990), was homologous to the ventral paraflocculus, but not to the flocculus. Nagao (1992) then found that the activities of the Purkinje cells in the ventral paraflocculus and the flocculus per se are different during the VOR, smooth-pursuit eye movement, and VOR suppression. The ventral paraflocculus results agree with the findings of Miles and Lisberger, while the flocculus results agree with Watanabe's. These new findings seem to favor the flocculus hypothesis for primates.

Results from recent computational studies may also be used to address the issue of the adaptation site in primates. In the context of all three schemes of supervised motor learning (direct inverse modeling, forward inverse modeling, and feedback-error learning; see Kawato 1990; Kawato and Gomi 1992 for review), it is clear that both the vestibular inputs and the retinal slip signals must be available at the modification site. On the one hand, the flocculus Purkinje cells satisfy these computational constraints because complex spikes encode the retinal-slip velocity (the error signal) (Watanabe 1985). On the other hand, Lisberger (1988) suggested that the flocculus provides error-signal information to FTN neurons. However, as their own data and others show (Stone and Lisberger 1990; Nagao 1992), flocculus Purkinje cell activities reflect vestibular input and eye movement as well as retinal slip. Thus, it seems that if the FTN hypothesis is true, all three of the supervised learning schemes must be modified in order to accommodate the situations in which the error signal is carried by flocculus output.

Computational models have not completely solved the puzzle of cerebellar motor learning. These models have, however, introduced the notions of heterosynaptic plasticity for motor learning, acquisition of internal neural models of the motor apparatus, and necessary transformation of the error signals from the trajectory space to the motor-command space. With these concepts, neurophysiologists have a framework to further explore the hardware responsible for the cerebellar motor learning.

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