A computational model of four regions of the cerebellum based on feedback-error learning

Mitsuo Kawato [1,2] **and Hiroaki Gomi** [1]

[1]ATR Human Information Processing Research Laboratories, Hikaridai 2-2, Seika-cho, Soraku-gun, Kyoto 619-02, Japan
[2]Research Institute for Electronic Science, Hokkaido University, 6-tyome nishi, 12-jo kita, Kita-ku, Sapporo, Hokkaido 060, Japan

Abstract. We propose a computationally coherent model of cerebellar motor learning based on the feed-back-error-learning scheme. We assume that climbing fiber responses represent motor-command errors generated by some of the premotor networks such as the feedback controllers at the spinal-, brain stem- and cerebral levels. Thus, in our model, climbing fiber responses are considered to convey motor errors in the motor-command coordinates rather than in the sensory coordinates. Based on the long-term depression in Purkinje cells each corticonuclear microcomplex in different regions of the cerebellum learns to execute predictive and coordinative control of different types of movements. Ultimately, it acquires an inverse model of a specific controlled object and complements crude control by the premotor networks. This general model is developed in detail as a specific neural circuit model for the lateral hemisphere. A new experiment is suggested to elucidate the coordinate frame in which climbing fiber responses are represented.

1 Introduction

Based on detailed knowledge of the neural circuits in the cerebellum, Marr (1969) and Albus (1971) proposed cerebellar perceptron models. Purkinje cells, inhibitory output neurons in the cerebellar cortex, received two different types of main synaptic inputs: those from parallel fibers and those from climbing fibers. In the perceptron models, the efficacy of a parallel-fiber-Purkinje-cell synapse was assumed to change when there is a conjunction of parallel-fiber and climbing-fiber input.

The presence of the putative heterosynaptic plasticity of Purkinje cells was demonstrated as long-term depression (LTD; see Ito 1989 for review). In whole-animal preparations of rabbits, Ito, Sakurai, and Ton-

Correspondence to: M. Kawato

groach (1982) found that the efficacy of the parallel-fiber-Purkinje-cell synapse decreases when both the parallel fibers and the climbing fibers are simultaneously stimulated. Sakurai (1987) then confirmed the LTD in a slice preparation of guinea pig cerebellum.

The Marr-Albus model regards the cerebellum as a pattern classifier and does not account for the dynamic processing associated with motor control. Fujita (1982a) expanded the Marr-Albus model by incorporating a dynamic viewpoint and proposed an adaptive-filter model of the cerebellar cortex. Adaptive modification of the vestibul-ocular reflex was successfully simulated based on a detailed neural-network model and LTD (Fujita 1982b).

The cerebellum is divided into separate sagittal regions with distinctive anatomical connections: the flocculonodular lobe, the vermis, the intermediate zone of the hemispheres, and the lateral zone of the hemispheres. These divisions form three functionally distinct parts of the cerebellum: the vestibulocerebellum, the spinocerebellum, and the cerebrocerebellum. Each region is further subdivided into longitudinal microzones 200 μm wide and more than 50 mm long (Andersson and Oscarsson 1978; Oscarsson 1980). Several research groups provided data which suggest that different regions of the cerebellum play important roles in the learning of different motor behaviors, such as arm movement (Gilbert and Thach 1977; Gellman et al. 1985; Wang et al. 1987), locomotion (Udo et al. 1980; Matsukawa and Udo 1985), posture control (Nashner 1981), and classical conditioning of eye-blink responses (Thompson 1987).

Although the inputs, outputs and functional roles of various regions of the cerebellum are vastly different, the neural circuit in the cerebellar cortex is rather uniform. Given this histological uniformity of the cerebellar cortex and its different functional modules, it seems reasonable to seek a computational framework which can explain motor learning of corticonuclear microcomplexes in different cerebellar regions. Ito (1990) proposed a comprehensive functional model in which a cerebellar microcomplex composed of a cortical

microzone and a small cell group in a cerebellar or vestibular nucleus (Andersson and Oscarsson 1978; Oscarsson 1980) acts as an adaptive controller based on the LTD-type synaptic plasticity in Purkinje cells, which is caused by control-error signals from climbing fibers. In this model, microcomplexes are inserted in reflex arcs, in command systems for voluntary motor control, and probably even in the cortical systems performing certain mental activities, providing them with adaptive-learning capabilities.

The feedback-error-learning scheme, a computational theory of supervised motor-learning (Kawato et al. 1987; Kawato 1990a, b, 1992), and its application to robotics and control problems (Miyamoto et al. 1988; Katayama and Kawato 1991) elucidated several computational constraints on the characteristics of control-error signals for cerebellar motor learning. Based on these computational studies and previous physiological models, we develop a computationally coherent model of different regions in the cerebellum.

2 Feedback-error learning: a biologically plausible supervised motor learning scheme

Although Fujita's adaptive filter model (1982a) was epoch-making, how to extend the model from the vestibulocerebellum to other regions of the cerebellum remained to be explored. Adaptive modification of the horizontal vestibulo-ocular reflex involves a system with only a single degree of freedom and roughly linear dynamics. On the other hand, for controlling multi-joint limbs and the torso, we have to deal with multiple variables and predictive control of complex objects with highly nonlinear dynamics.

Our proposition here is that the cerebellum, by learning, acquires an internal model of the inverse of the controlled object. An inverse model is a model system whose input and output correspond to the output and input, respectively, of the controlled object. It makes an ideal feedforward controller (Atkeson 1989), and can also be used for coordinate transformation and trajectory planning (Kawato 1992). We will discuss different computational approaches to acquiring the inverse model, and discuss which approach is most probably adopted by the cerebellum.

How can an internal inverse model be acquired? If a computational "teacher" can provide the correct motor commands, motor learning can be done in the framework of the Widrow-Hoff rule (1960), consistent with biologically demonstrable heterosynaptic plasticity processes (Barto 1990). In the context of motor learning, however, it is unrealistic to assume the existence of a teacher that has access to the correct motor commands before the movement pattern itself is learned. It is more realistic to assume that a teacher has access only to the movement trajectory desired for the controlled object. Just as parents teach correct pronunciation of words to children by providing speech samples in acoustic space, and cannot directly communicate the neuronal firing patterns that activate articulator muscles, a biologically plausible teacher for a neural network would have direct access, not to the correct pattern of articulatory commands, but rather to the desired "higher level" trajectory and the resultant discrepancy between the trajectory desired and the currently produced. In order to train the inverse model, such trajectory errors must first be converted to motor-command coordinates.

Three learning schemes have been proposed to address these issues. In the direct inverse modeling approach (Fig. 1A), the inverse model receives as input the realized trajectory, and outputs an estimated motor command. The difference between the estimated motor command and the actual motor command is used as an error signal for learning the inverse model. Although this learning scheme is simple, it has several drawbacks. For one, the inverse model cannot be used for control during training. Furthermore, there is no mathematical guarantee that desired trajectories will be rigorously achieved after training using this learning scheme (Jordan and Rosenbaum 1989). Another major problem with this approach is that it cannot properly control a redundant object. If the controlled object has kinematic redundancy (i.e. the number of degrees of freedom of the mechanical linkage exceeds that of the task space) and/or dynamic redundancy (i.e. the number of actuators exceeds the number of degrees of freedom of the mechanical linkage) as primate limbs do, many sets of motor commands will correspond to the same movement. In this case, a unique, invertible relationship between the desired goal and the motor command does not exist, and this learning scheme generally generates faulty commands, as pointed out by Jordan (1990).

In the forward-inverse modeling approach (Fig. 1B; Jordan 1990), the forward model of the controlled object is first learned by monitoring both the input and the output of the controlled object. The desired movement trajectory is then fed to the inverse model to calculate a feedforward motor command. The resulting error in the trajectory space is back propagated (Rumelhart et al. 1986) through the forward model to calculate the error in the motor command space, which is then used as an error signal for training the inverse model. This approach resolves several shortcomings inherent in the direct inverse method, in that learning and motor control can take place simultaneously, the goal-directed properties of learning are guaranteed (Jordan and Rosenbaum, 1989), and it can be applied to redundant controlled objects. Backpropagation itself, however, is difficult to implement neuronally.

In the feedback-error-learning approach (Fig. 1C), the summation $\tau(t)$ of the feedback motor command $\tau_c(t)$ and the feedforward command $\tau_n(t)$ generated by the inverse model is fed to the controlled object, and the feedback controller transforms the trajectory error into the motor-command error (Kawato et al. 1987). The inverse model is trained during motor control using the feedback motor command as the error signal. Here, the feedback controller functions as a linear approximation of the inverse model of the controlled object. The feedforward controller does not mimic

A direct inverse modeling
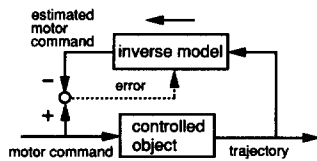
B forward and inverse modeling
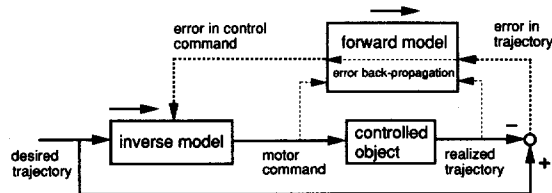
C feedback error learning

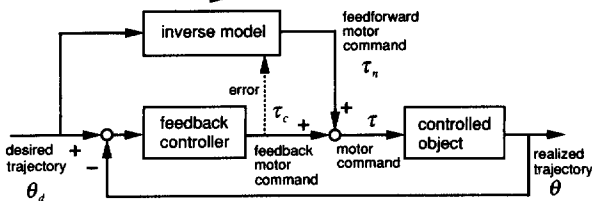$$\Phi(d^2\theta_d/dt^2, d\theta_d/dt, \theta_d, w)$$

Fig. 1A–C. Three computational schemes for acquiring an inverse model through learning. Direction of information flow is indicated by solid lines. Broken lines show information used for training. **A** Direct inverse modeling approach. **B** Forward and inverse modeling approach. **C** Feedback-error-learning approach

the feedback controller, but acquires a fully nonlinear inverse model by trying to eliminate the feedback motor commands.

The inverse model receives the desired trajectory θ_d and monitors the feedback torque $\tau_c(t)$ for the error signal. τ_n is calculated from the desired trajectory θ_d and the synaptic weights w by

$$\tau_n = \Phi(d^2\theta_d/dt^2, d\theta_d/dt, \theta_d, w). \tag{2.1}$$

The shape of the function Φ depends on what kind of neural network actually constitutes the feedforward controller. Here, θ and θ_d are n-dimensional vectors, τ, τ_c and τ_n are m-dimensional vectors, w is an l-dimensional vector, and Φ is an m-dimensional vector function.

The synaptic modification rule of the feedback-error-learning scheme is represented in a general manner as,

$$dw/dt = (\partial\tau_n/\partial w)^T\tau_c. \tag{2.2}$$

As a result of this synaptic modification rule, the feedback motor command tends towards zero as learning proceeds. If one compares this learning rule with various supervised learning schemes such as the Widrow-Hoff rule (1960), it is evident that the feedback motor

command plays the role of the error signal. This learning scheme is called *feedback-error learning* to emphasize the importance of using the feedback motor command as the error signal for the heterosynaptic plasticity.

The mathematical foundations of feedback-error learning were recently investigated (Kawato 1990b). It can be shown that feedback-error learning is a Newton-like method in a functional space.

3 Coherent computational model of cerebellar motor learning

3.1 General anatomical model

Feedback-error learning has the feedback controller convert the trajectory error into a motor-command error. In order for the feedback-error-learning scheme to be considered a computational framework for learning in the cerebellum, some parts of the central nervous system must play the role of feedback controller and, furthermore, climbing-fiber responses must represent the motor-command error instead of the movement-trajectory error. How might this be realized in the central nervous system? In this section, we present the conceptual anatomical and physiological base of the present theory in a general fashion.

Figure 2 is a schematic diagram showing how we envision cerebellar motor-learning to be incorporated into sensory-motor control. Most of this schema is not unique to the present model. Actually, Fig. 1 in Houk and Barto (1991) was one basis of the present figure. We modified the arrangement of the premotor network and the inferior olive.

We assume that climbing-fiber responses represent motor-command errors generated by some of the premotor networks, networks upstream of the motor neurons that include feedback controllers at the spinal, brainstem and cerebral levels. Thus, in our model, climbing-fiber responses convey motor errors in motor-command coordinates rather than in sensory coordinates. Some, but not all, of the premotor networks are inhibited by the cerebellar cortex. Premotor networks can control movement without regulation by the cerebellum. In this case, however, movements either are stereotyped, clumsy, or slow, or require laborious control by the cerebrum.

Parallel fibers leading to Purkinje cells carry vast amounts of information necessary for coordinative and predictive control from both sensory receptors and the cerebrum. The other major synaptic input to Purkinje cells, climbing-fiber input, is assumed to carry the motor error represented in motor-command coordinates, not the sensory performance error; this is the most important and novel proposal in our theory. Based on LTD in Purkinje cells, each microzone in the cortex, in conjunction with the small portion of the deep cerebellar nucleus connected to it, learns to execute predictive and coordinative control of different types of movements. This is achieved by a closed loop and 1-to-1 anatomical correspondence between each premotor net-
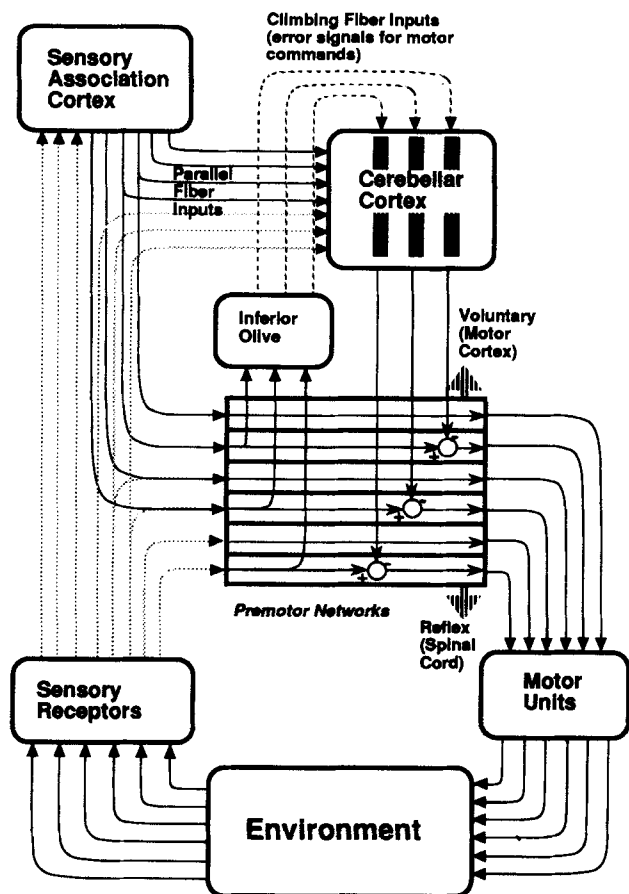
Fig. 2. Anatomical organization and information flow in sensorimotor control and cerebellar motor learning. Motor learning is postulated to occur in the cerebellar cortex based on LTD of parallel-fiber-Purkinje-cell synapses. Shaded rectangles in the cerebellar cortex indicate microzones. Note that each microzone is connected to a specific premotor network by both its input from the inferior olive and its output

work, a small region in the inferior olive, and a microzone in the cerebellar cortex. If one premotor network is regulated by one microzone in the cerebellar cortex, then the latter must receive climbing-fiber inputs from the specific part of the inferior olive that requires inputs from the earlier part of the same premotor network (see Fig. 2 for detailed linkage). Because the earlier parts of the premotor networks are the origins of afferents to the inferior olive, error signals must be represented in the motor-command coordinates. A one-to-one correspondence between the microzone in the cerebellar cortex and the premotor network assures that the microzone received exactly the right error signal, and thus can improve the relevant movement of that specific part of the body which is controlled by the premotor network. Our model is an extension of Oscarrson's microzone notion: correspondence between the inferior olive, the cerebellar cortex, and the cerebellar deep nucleus (Anderson and Oscarsson 1978; Oscarsson 1980; for the related concept of microcomplex see Ito 1984). Six different premotor networks are drawn in

Fig. 2. Some premotor networks receive direct sensory information from sensory receptors, but others do not. Some receive information from sensory-association cortices, and some premotor networks are connected with specific microzones in the cerebellum. The premotor networks shown at the bottom of the large rectangle represent those located in the spinal cord that mediate simple reflexes. The ones at the top represent motor cortical circuits which do not receive direct sensory information from the periphery, only highly processed information from sensory-association cortices, and which send motor commands to motor units via the pyramidal tract.

With this anatomical organization, the cerebellar microzone is trained with feedback error representing the motor-error command generated by the corresponding premotor network. Each microzone ultimately acquires an inverse model of a specific controlled object, and complements the relatively crude feedback control provided by the premotor networks. Thus, the activity of the corresponding earlier part of the premotor network decreases as cerebellar learning proceeds. However, the latter half of the premotor circuit is quite active. Moreover, it must be noted that other premotor networks which are not connected to the cerebellum (see Fig. 2 for such independent premotor networks) may be active even after learning.

Despite the crude nature of the signals from the premotor feedback network, however, the premotor commands are the only source of motor coordinate information for training the cerebellum. The reasons why the relatively crude premotor command can serve as training information for the correct cerebellar command are threefold. First, the premotor command is not the teaching signal but the error signal. Second, although the premotor command is faulty, it at least roughly indicates the directions and magnitudes of cerebellar command modifications. Third, in the learned state, when the cerebellum is computing almost perfect motor commands, there is almost no early activity in the premotor network, and the synaptic weights in the cerebellum need not change further.

3.2. Conceptual models of different regions

Here, we conceptually explain how this general model can be accommodated to specific regions of the cerebellum, and give some examples of premotor networks, climbing-fiber inputs, and the corresponding parts of the cerebellum.

The cerebellum flocculus is known to play an essential role in adaptive modification of the vestibulo-ocular reflexes and the optokinetic eye-movement responses. Its relevant premotor network is the neural circuit starting from the retina, going to the pretectal area, then to the nucleus reticularis tegmenti pontis and the inferior olive, and converging onto the vestibular nucleus. This is a premotor network because the vestibular nuclei project either monosynaptically or disynaptically to motor neurons in abducens and oculomotor nuclei. The vestibular nucleus is inhibited by the Purkinje cells.

The motor command for the optokinetic eye-movement response is the error signal computed from the retinal-slip signal detected by the retina. A copy of one part of this motor command, which is sent from the inferior olive to the vestibular nuclei, is also sent to the Purkinje cells as climbing-fiber inputs. This error signal to the flocculus is consequently defined in the motor-command (muscle) coordinate. Gomi and Kawato (1992) give a more detailed computational account, a block diagram, and a neural circuit, and describe computer simulation experiments regarding this example. The lower premotor network in Fig. 2. corresponds to this example.

The cerebrocerebellum plays an essential role in motor learning of voluntary movements. We propose an afferent limb of the transcortical loop, the negative feedback loop via the cerebral cortex, as the premotor network for the cerebrocerebellum: the neural circuit starting from somatosensory receptors to pyramidal-tract neurons in the motor cortex. This is a premotor network because the pyramidal-tract neurons send descending motor commands to motor neurons in the spinal cord. A part of the premotor network is regulated by the cerebellar cortex because the cerebrocerebellum outputs to the motor cortex via the dentate nucleus, the ventrolateral part of the thalamus. We suggest that the motor command calculated by the premotor network based on transcortical feedback information and provided to the pyramidal-tract neurons is also sent to the inferior olivary nucleus and then transmitted to the lateral hemisphere of the cerebellum as the climbing-fiber input. Because the premotor network generates a motor command when there is a discrepancy between a desired movement pattern and the actual movement measured by somatosensory receptors, the climbing-fiber input is considered to be the error signal defined in the motor-command coordinates. In Sect. 5, we give a block diagram, a neural circuit, an example of an experiment to test this theory, and references to robot control experiments based on this computational model. The upper premotor network in Fig. 2 corresponds to this example.

The vermis and the intermediate zone of the cerebellum are considered to play important roles in motor learning of posture control, locomotion, and so on. Related premotor networks are motor-control networks in the spinal cord, the brainstem, and the cerebral cortex which calculate motor commands based on the difference between feedback information from sensory receptors and the desired movement pattern descending from the higher motor center. Well-documented examples of premotor networks are the spinal motor centers which give rise to the spino-olivo-cerebellar paths. The inputs fed to motor neurons are calculated by this center based on feedback information provided by the cutaneous and proprioceptive receptors. The interneurons of the spino-olivo-cerebellar paths behave, under a variety of tests, as those mediating the segmental flection reflex (Oscarsson, 1980). The spino-olivary paths thus presumably carry information about the activity in segmental mechanisms activated by descending paths

and segmental afferents, and represent lower motor centers. Afferents connected to the spinal motor center, such as flexor reflex afferents, probably encode motor error, because their activity indicates that some undesirable event happens. If the actual movement is exactly that desired, the spinal motor center does not need to add modifying commands to the descending motor command from the higher motor centers. Furthermore, this motor error is represented in such a way that it can be readily used by motor neurons to send final commands to muscles. The climbing-fiber inputs conveyed by the spino-olivo-cerebellar paths can thus be thought of as motor errors represented in the motor-command coordinates. Gomi and Kawato (1992) give its mathematical foundations, block diagrams, neural circuits, and references to related computer simulations of posture control (adaptive feedback control of an inverted pendulum). The middle premotor network in Fig. 2 corresponds to this example.

This theory predicts, first, that the climbing-fiber responses are represented in muscle rather than sensory coordinates, and second that sensory error is temporally differentiated according to the approximated inverse dynamics of the controlled object, which is provided by the premotor network. We will describe a critical experimental test designed to examine these theoretical predictions in the following sections.

4 Long-term depression as a basis of feedback-error learning

The LTD in Purkinje cells may be the synaptic plasticity mechanism in feedback-error learning. The two basic equations (2.1) and (2.2) are rewritten for this case. For simplicity, in the following equation, the output of a Purkinje cell y is assumed to be a linear weighted summation of its parallel-fiber inputs:

$$y = \sum_n w_i x_i , \qquad (4.1)$$

where w_i is the synaptic weight of the i-th parallel-fiber-Purkinje-cell synapse. The nonlinear transformation necessary for nonlinear controlled objects is provided by the circuits before and within the cortex or by nonlinear synaptic interaction in the dendrites of Purkinje cells. The feedforward motor command fed to deep cerebellar nuclei is the negative of y because the Purkinje cell is an inhibitory neuron. The following synaptic modification equation, based on the LTD, is

$$dw_i/dt = -x_i(F - F_{spont}) , \qquad (4.2)$$

where F is the firing frequency of the climbing fiber input and F_{spont} is its spontaneous level. This is equivalent to Fujita's equations (2.20) and (2.21) (Fujita 1982a). The synaptic weight decreases in proportion to the product of the parallel-fiber input and the feedback motor command, that is, the increment of the climbing fiber input. When F is lower than F_{spont}, w_i increases. This corresponds to the long term potentiation which occurs when only parallel fibers are stimulated and the climbing fibers are silent (Sakurai 1987).

5 Circuit model of the lateral cerebellum and critical experimental test

5.1. Neural circuit model

The cerebrocerebellum is the lateral zone of the cerebellum. Its inputs originate in the pontine nuclei which relay information from the cerebral cortex, and its output is conveyed by the dentate nucleus to the thalamus and then to the motor cortex.

We originally proposed the feedback-error-learning scheme as a model of voluntary motor learning in the lateral cerebellum (Kawato et al. 1987). In our model (Fig. 3), the feedback controller and the summation of the feedforward and feedback command reside in the motor cortex of the cerebrum. The feedback loop is a transcortical loop. The desired trajectory is sent to the cerebellum and the motor cortex from the association cortex. The output of the cerebellum is sent back to the motor cortex via the thalamus. It should be noted that Fig. 3 shows a model of one corticonuclear microcomplex (Ito 1984) in the lateral part of the cerebellum.

An industrial robotic manipulator with 3 degrees of freedom and nonlinear dynamics based on this neural network model succeeded in learning trajectory control (Miyamoto et al. 1988). In subsequent studies, we found that an accurate inverse-dynamics model of the manipulator can be acquired without prior knowledge of the mechanical structure (Kawato 1990a). Furthermore, Katayama and Kawato (1991) expanded the previous model to deal with the inverse statics problem (equilibrium for the spring-like properties of muscles) separately from the inverse dynamics problem. They succeeded in having an arm with 16 muscle-like actuators and 5 degrees of freedom learn trajectories. The artificial arm had highly nonlinear dynamics and suffered from long feedback delay (about 300 ms) and redundancy at the dynamics level because each joint was controlled by agonist and antagonist muscle-like actuators, like the musculoskeletal system. We experimentally demonstrated that the proposed neural-network model can account for computationally efficient trajectory-control learning by the musculoskeletal system.

A schematic diagram of the neural circuit around the lateral cerebellum based on the review by Allen and Tsukahara (1974) is shown in Fig. 4. The association cortex neurons send the desired trajectory θ_d to the lateral cerebellum via the pontine nuclei as well as the
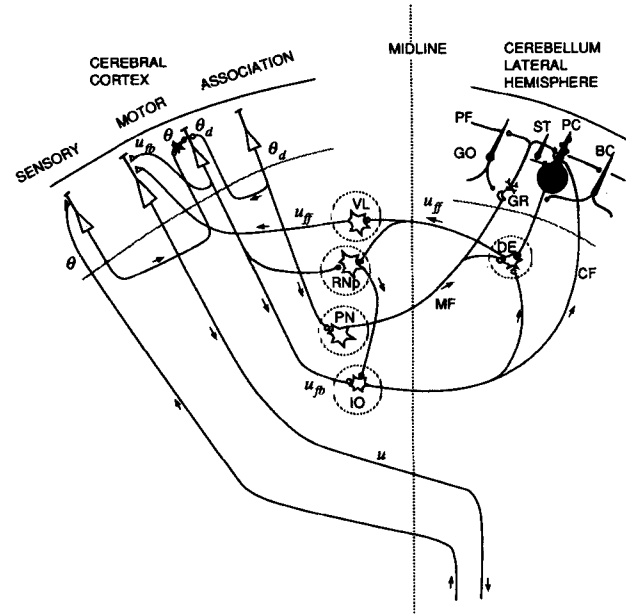

Fig. 4. Schematic diagram of a neural circuit for voluntary-movement learning control by cerebro-cerebellar communication loop. CF: Climbing fiber, BC: Basket cell, GO: Golgi cell, GR: Granule cell, MF: Mossy fiber, PC: Purkinje cell, PF: Parallel fiber, ST: Stellate cell, DE: Dentate nucleus, IO: Inferior olivary nucleus, PN: Pontine nuclei, RNp: Parvocellular red nucleus, VL: Ventrolateral nucleus of the thalamus

motor cortex. The motor cortex neurons are informed of the realized trajectory θ via the transcortical loop. By calculating the difference between the desired and actual trajectories $\theta_d - \theta$, neural circuits in the motor cortex calculate the negative feedback motor command u_{fb}. This command is sent to the output neurons in the motor cortex. A copy is simultaneously sent to the inferior olivary nucleus as the error signal and expressed as complex spikes in Purkinje cells (see, for example, Gilbert and Thach 1977). The output of the corticonuclear complex is the feedforward motor command u_{ff}, which is sent to the thalamus from the dentate nucleus, and then to the motor cortex. The feedforward and feedback motor commands are summed at the output neurons in the motor cortex to form u, which descends the corticospinal tract. Theory predicts that the signal sent from the cerebellum to the motor cortex increases as the motor learning proceeds, which agrees with experimental data (Sasaki and Gemba 1982).

In this figure, the most critical assumption is that the pyramidal neurons which calculate the feedback motor command u_{fb} output to both the pyramidal-tract neurons and the inferior olive. This comes largely from the computational requirements of feedback-error learning, and we do not have any compelling physiological or anatomical evidence. It might thus be interesting to label axons retrogradely from the sensory-motor cortex to the inferior olive and examine the anterogradely labeled axon collaterals in the motor cortex. A simple expectation is that synaptic terminals of axon
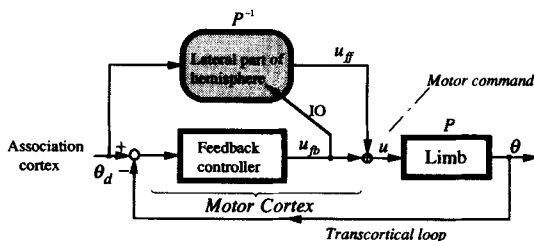

Fig. 3. Block diagram for voluntary-movement learning control by a corticonuclear microcomplex in a cerebro-cerebellar communication loop

collaterals would be seen on pyramidal-tract neurons if dyes were injected into a very limited region of the inferior olive projecting into the lateral hemisphere of the cerebellum. If, however, interneurons are interposed on the pathway either to the inferior olive or the pyramidal-tract neurons, this expectation obviously does not hold.

5.2 Critical experimental test

The most critical point in our model is whether the climbing-fiber responses encode the motor-command error or the movement-trajectory error. To test this, we propose the following experiment, illustrated in Fig. 5.

The climbing-fiber responses of an alert monkey are recorded. The monkey's hand position is measured by, for example, a manipulandum, and a hand cursor is presented on a CRT display. The monkey can not see his hand directly. The start position and the first and second targets are displayed on the CRT. The reasons for using the target change paradigm are two-fold. First, it was found that complex spike activity is high when the target is changed (Wang et al. 1987). Second, by placing the second target to the left or right of the first target, we can manipulate the sign of the trajectory error and hence the sign of the motor-command error.

Two types of coordinate transformations are introduced between the hand position measured and the hand cursor presented in order to associate or dissociate the trajectory error and the motor-command error. In the normal condition, movement orientation is the same for the hand and the cursor. In this case, the direction signs of the trajectory and motor-command errors are the same. But in the mirror-image condition, the left-right axis is reversed. The monkey needs to move his hand right in order to move the hand cursor left. Here the trajectory and command errors have opposite direction signs. In both cases the monkey moves his hand along similar trajectories. Table 1 shows the firing patterns of the climbing fibers under various conditions: representing the movement-trajectory error and the motor-command error, normal or mirror-image coordinate transformations, and the second target presented to the right and left of the first
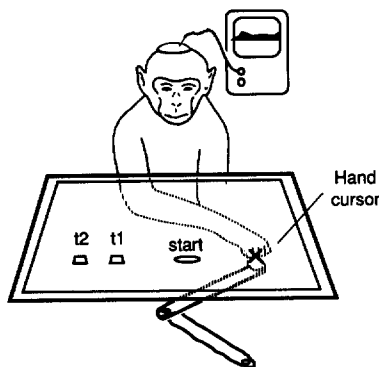
Table 1. Firing patterns of the climbing fibers under different conditions in the proposed experiment

	command error		trajectory error	
	$t1 < t2$	$t1 > t2$	$t1 < t2$	$t1 > t2$
normal	A	B	A	B
mirror	B	A	A	B

($t1 < t2$ and $t1 > t2$). A and B show two different firing patterns for the climbing fibers.

If the climbing-fiber response encodes the movement-trajectory error, the complex-spike patterns for the two kinds of target change should be the same for the normal and the mirror-image coordinate transformation. If, on the other hand, the command error is represented, the firing patterns should be reversed for the normal and the mirror-image conditions.

The basic assumptions behind this proposed experiment for testing our model are as follows. We assume that the sensory motor learning required for movement under the mirror-image condition takes place first in the cerebral cortex, and then in the cerebellum. The coordinate transformation required for computing motor commands from the target and the hand cursor positions on the CRT is learned first in the cerebral cortex, probably in the parietal association area, premotor area, and motor area. Even after this initial cognitive learning is completed, however, movement is under conscious control, and is clumsy. The feedback motor command generated in the cerebral cortex is next sent to the cerebellum as climbing-fiber input. Procedural motor learning then occurs, and smooth, fast, unconscious movements become possible even under the mirror-image condition.

If the cerebellum is not involved in this kind of sensory motor learning under such artificial coordinate transformations, the proposed experiment does not make sense. For example, if the cerebral cortex completely solves the transformation from the CRT coordinates to the intrinsic body coordinates and sends the latter information to the cerebellum, then the cerebellum deals only with the inverse-dynamics control problem. In this case, relearning in the cerebellum is not necessary, and hence the proposed experiment does not tell us anything.

However, if the above assumptions hold, we predict that before the monkey learns the mirror-image condition, trajectory error will be observed, because the coordinate-transformation mechanism dealing with the mirror-image condition still does not exist. But once the monkey does learn the mirror-image condition, while his movement becomes more skillful, the command error pattern will be observed. Some part of the cerebral cortex, most likely the parietal lobe, transforms the error detected in the visual coordinates into muscle coordinates. The motor command error is then sent to both the cerebellum and the motor cortex.

Fig. 5. Proposed target-change experiment under normal and mirror-image coordinate transformations which reveals the reference coordinates in which climbing-fiber responses are represented

6 Discussion

The computational theory developed here is conceptually based on Ito's pioneering work (1970), and there is thus a similarity between our Fig. 3 and his Fig. 7B. Both figures are diagrams of the neocerebellum. One obvious difference between the two models is what is acquired in the cerebellum. In our model, the inverse-dynamics model of the controlled object is acquired, whereas in Ito's, forward models of the spinal motor center, musculoskeletal system, and sensory-association cortex are acquired. Thus, in Ito's model, internal feedback control is executed by the cerebellum. Although the input-output directions of internal models acquired in the cerebellum are opposite, the models are still similar because internal feedback control using forward models can be naturally developed into feedforward control using inverse-dynamics models.

In our theory, climbing-fiber responses must possess magnitude and direction information. This point is actually controversial, since the range of climbing-fiber firing frequencies is unusually low (the maximum is 4 pulses/s and the spontaneous level is about 1 pulse/s) and hence it has been difficult to see how climbing-fiber activity could convey directional or amplitude information. Their apparent all-or-nothing firing characteristics may rather be useful for somatic event detection (Gellman et al. 1985), providing information to the Purkinje cells about undesirable movements (penalty signals). Houk, Barto and their colleagues (1990, 1991) proposed a quite comprehensive and attractive related model of the cerebellum with an anatomical and physiological basis. Their scheme is computationally based on reward-penalty learning (Barto et al. 1981). In this model, the LTD of the Purkinje cells is assumed to provide the computational mechanism for the associative search. The climbing-fiber responses are therefore assumed to provide a "one-sided penalty signal," such as a somatic event detector. In this view, the binary all-or-nothing nature of the climbing-fiber responses is emphasized, and it is assumed that directional information is not involved.

Because LTD has a time constant of about 1 hour, however, even a low firing frequency can be integrated to give analog information (14,400 pulses/h to 3,600 pulses/h). If the firing frequency is lower than the spontaneous level, it can give direction (negative) information. In the feedback-error-learning framework, the climbing fibers must be able to convey amplitude as well as directional information about the error. This prerequisite is fulfilled in the vestibulo-cerebellum (Simpson and Alley 1974). The firing frequencies of the visual climbing fiber change with the velocity of the retinal slip. Furthermore, they were lower than the spontaneous level for visual stimuli whose direction was opposite to the optimum direction. The problem is still open for other regions, however. In the previous section, we proposed that climbing-fiber responses be measured in monkeys during a target-change experiment in order to clarify this point. By changing the direction and magnitude of the difference between the second

target and the hand cursor presented on a CRT screen, the direction and magnitude dependence of climbing-fiber responses could be examined. Furthermore, such an experiment could be used to answer the basic question of whether movement errors are represented in sensory or motor coordinates, by dissociating the trajectory error displayed on the CRT screen (the visually perceived distance between the target points and the hand cursor) from the motor-command error (the distance between the ideal and actual motor commands). Before we know the experimental results, we are very much interested in integrating various aspects of our theory with Houk and Barto's.

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