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Abstract

We propose computationally coherent models of the four regions of the cerebellum based on the feedback-error-learning scheme. We assume that climbing fiber responses represent the efference copy of motor commands generated by premotor networks such as feedback controllers at the spinal-, brain stem- and cerebral levels. 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. Thus, premotor network activity decreases as the learning proceeds. As a representative example, computer simulation of simultaneous adaptation of the vestibulo-ocular reflex and the optokinetic eye movement response was successfully performed while the Purkinje cells receive eye-velocity signal by recurrent neural connections as well as the vestibular input and the retinal slip as parallel fiber inputs.

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, receive two different types of main synaptic inputs: parallel fibers and climbing fibers. In the perceptron models, the efficacy of a parallel fiber-Purkinje-cell synapse was assumed to change when the conjunction of the parallel-fiber input and the climbing-fiber input occurs. Furthermore, Ito (1970) proposed that the flocculus of the cerebellum is the site of synaptic plasticity for adaptive modification of the vestibulo-ocular reflex. The vestibulo-ocular reflex is the reflex to move the eye in the direction opposite head rotation in order to stabilize the retinal image.

The presence of the putative heterosynaptic plasticity of Purkinje cells was demonstrated as long-term depression (see Ito, 1989 for review). In whole animal preparation of rabbits, Ito, Sakurai and Tongroach (1982) found that the efficacy of the parallel-fiber-Purkinje-cell synapses decreases when both parallel fibers and climbing fibers are simultaneously stimulated. Recently, Sakurai (1987) confirmed the long-term depression in slice preparation of guinea pig cerebellum.

The Marr-Albus model regards the cerebellum as a pattern classifier and does not account for the dynamical processing associated with motor control. Fujita (1982a) expanded the Marr-Albus model by incorporating a dynamical viewpoint and proposed an adaptive filter model of the cerebellar cortex. Adaptive modification of the vestibulo-ocular reflex was successfully simulated based on a detailed neural network model and the long-term depression (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 (Ito, 1984). These divisions form three functionally distinct parts of the cerebellum: the vestibulocerebellum, the spinocerebellum, and the cerebrocerebellum. The cerebrocerebellum is the lateral zone of the cerebellum. Its inputs originate in 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. The spinocerebellum includes the vermis at the midline and the intermediate zone 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 zone is related to distal motor control; the vestibulocerebellum occupies the flocculonodular lobe. Furthermore each region is subdivided into corticonuclear microcomplexes (Ito, 1984). Several research groups provided data which suggest that different regions of the cerebellum play important roles in learning of different motor behavior, such as arm movement (Gilbert & Thach, 1977; Gellman, Gibson & Houk, 1985; Wang, Kim & Ebner, 1987), locomotion (Udo et al., 1980; Matsukawa & Udo, 1985), posture control (Nashner, 1981; Amat, 1983), and conditioning (Thompson, 1987).

Although inputs and outputs, and functional roles of different 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 different functional modules, it seems reasonable to seek a computational framework in which motor learning of corticonuclear microcomplexes in different cerebellar regions is coherently understood. Ito (1970) asked: "What is the role of the cerebellum should thus be asked in the following two ways; i) common throughout the cerebellum, how does a given portion of the cerebellum process the incoming and outgoing information?; ii) specific to each part of the cerebellum, how is a given portion involved in regulation of a particular motor activity?". 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 acts as an adaptive controller based on the synaptic plasticity of the long-term depression type in Purkinje cells, which is effected by control error signals of climbing fibers. In this model, microcomplexes are inserted in reflex arcs, command systems of voluntary motor control, and probably even cortical systems performing certain mental activities, providing adaptive-learning capabilities to these systems. Based on this physiological model, we develop a computationally coherent model of different regions of the cerebellum. Especially, we try to characterize structural features of the cerebellar learning based on the feedback-error-learning model (Kawato, Furukawa, Suzuki, 1987).

2. Feedback-error-learning as a computational principle of cerebellar learning

2.1 Feedback-error-learning: biologically plausible supervised motor learning scheme

Although Fujita's adaptive filter model (1982a) was epoch making in dynamical modelling of the cerebellar learning, it was still to be explored how to extend the modeling from the vestibulocerebellum to other regions of the cerebellum. In adaptive modification of the horizontal vestibulo-ocular reflex, one needs to deal with a single-degree-of-freedom system with roughly linear dynamics. On the other hand, for controlling multijoint limbs and the torso, we have to deal with multi-variable and predictive control of complex controlled objects with highly nonlinear dynamics. Feedforward control is essential to achieve fast and smooth movements for large-scale, complicated and nonlinear objects because feedback loops at spinal-, brain stem- and cerebral levels have long delays and small gains.

Our proposition here is that the cerebellum, by learning, acquires an internal model of the inverse of the controlled object. An inverse model is the model system whose input and output correspond respectively to the output and input of the controlled object. An inverse dynamics model can be used as an ideal feedforward controller (Atkeson, 1989). Furthermore, the inverse system model can be used as an essential computational element for coordinate transformation and trajectory planning (Kawato, 1991). In the following, we discuss different computational approaches to acquire the inverse model, and discuss which approach is the one most probably adopted by the cerebellum.

One of the features of the central nervous system in its control of movement is the capability of motor learning. For higher mammals, especially humans, supervised learning is probably the most important class of motor learning. In nearly every case, the teacher cannot directly demonstrate the correct motor command to the student, but can only show the desired movement trajectory. How might such learning proceed? Perhaps the answer entails a neural network that receives a desired motor pattern and outputs a motor command to realize a desired movement. If a teacher were to able to give the difference between an ideal motor command and an actual motor command, then various supervised learning rules could be used to train the motor-control network. However, this last step is not possible in practice, so the problem of converting errors from task-oriented coordinates to the motor-command space is an essential and difficult one. It has been addressed by Jordan (1990), under the rubric "supervised learning with a distal teacher." Barto (1990) has reviewed the topic and compared several different approaches.

Two approaches have been proposed and used to resolve this problem. The direct inverse modeling approach is the simplest one. In this scheme, the inverse model is oriented in the input-output direction opposite that of the controlled object. The inverse model receives the trajectory as an input and outputs an estimated motor command. The difference between the estimated motor command and the actual motor command is used as the error signal for learning. For several reasons, it can not be considered a plausible model of learning in the brain (Kawato, 1990a). In the forward-inverse modeling approach (Jordan, 1990), the forward model of the controlled object is first learned by monitoring both the input and the output of the controlled object. Then, the desired movement trajectory is fed to the inverse model to calculate a feedforward motor command. The resulting error in the trajectory space is back propagated through the forward model to calculate the error in the

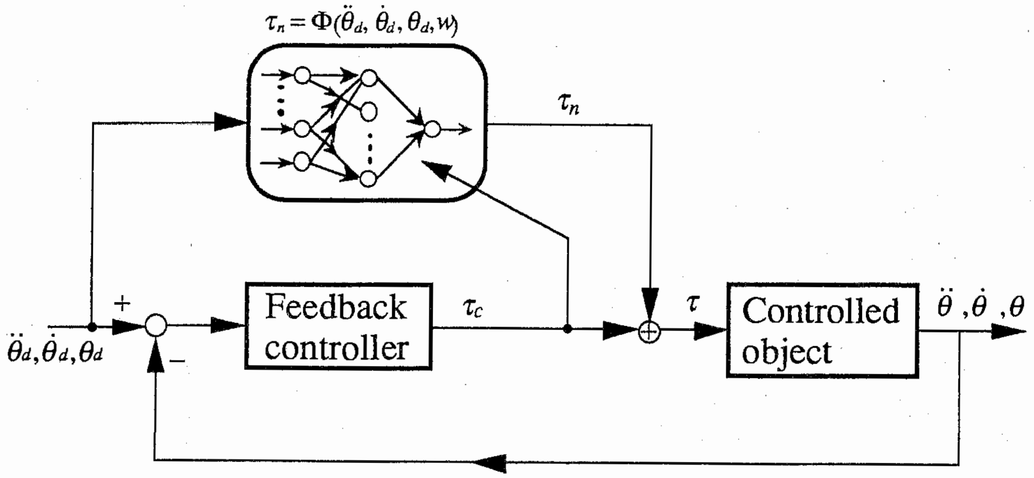


Figure 2..1: Control structure of open-loop feedback-error-learning.

motor command space, which is then used as the error signal for training the inverse model. Although this approach is very attractive, it can not be considered a model of the cerebellum because backpropagation is necessary.

Exploring such approaches further, we have proposed a *feedback-error-learning* neural network as a model of the lateral cerebellum and the parvocellular part of the red nucleus (Tsukahara & Kawato, 1982; Kawato et al., 1987). Figure 2..1 shows a block diagram of this scheme. Here the total torque $\tau(t)$ fed to the controlled object is the sum of the feedback torque $\tau_c(t)$ and the feedforward torque $\tau_n(t)$ calculated by the feedforward controller. In the pure feedforward control case shown, an ideal feedforward controller is given by an inverse model of the controlled object. 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:

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

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 a l-dimensional vector. Φ is a m-dimensional vector function.

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

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

As a result of this synaptic modification rule, the feedback motor command tends to be 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 of the heterosynaptic plasticity.

Mathematical foundations of the feedback-error-learning were recently investigated (Kawato, 1990b). It can be shown that the feedback-error-learning scheme is a Newton-like method in a functional space. In this interpretation, the feedback controller provides a linear approximation of the inverse model of the controlled object. Thus, conceptually, the feedback-error-learning is defined as the method to acquire the exact nonlinear inverse model of the controlled object based on the error signal provided by an approximated linear inverse model. The necessity of the approximated inverse model in calculating the error signal is best understood in situations where coordinate transformation is required between the sensory space and the motor space. For example, if we are asked to follow a straight line drawn on a paper, the visual system measures the error between the line and the realized trajectory in the retinal coordinates. However, because the arm-muscle coordinates are completely different from the retinal coordinates, the sensory error should be transformed into the muscle coordinates before it can be used for motor learning. Any computational mechanism which executes this task can be regarded as an approximated inverse model of the controlled object. In this case, the controlled object receives muscle activations and outputs the trajectory in the visual coordinates.

2.2 Long-term depression as basis of feedback-error-learning

Feedback-error-learning has the feedback controller convert trajectory error into motor-command error. Thus, in order for the feedback-error-learning scheme to be considered a computational framework of learning in the cerebellum, climbing fiber responses must represent the motor-command error instead of the movement-trajectory error. The most fundamental and important assumption of our model is that the climbing fiber responses represent the efference copy of motor commands generated by the premotor networks. Premotor networks are defined as fundamental motor control networks that are upstream of the motor neurons but downstream of the cerebellum. Feedback loops at the spinal-, brain stem- and cerebral cortical level are examples of the premotor networks. According to Houk and Barto (1991), the premotor networks range in complexity from simple spinal reflexes to motor cortical circuits controlling voluntary movement. Mathematically speaking, we believe that each premotor network which controls a specific movement of a specific controlled object can be assumed to provide a rough approximation of the inverse system of the controlled object. Correspondingly, each cerebellar microcomplex connected to the premotor network and the controlled object is trained to acquire a better inverse model of the controlled object while monitoring the activity of the premotor network as climbing fiber inputs.

The above assumption leads to the following predictions about the spatial and temporal coordinate frames in which climbing fiber responses are represented. First, the coordinates in which the climbing fiber responses are represented must be muscle coordinates rather than sensory coordinates. Second, sensory error should be temporally differentiated according to the approximated inverse dynamics of the controlled object, which is provided by the premotor network.

If these conditions are satisfied, the feedback-error-learning can be realized by using the long-term depression in Purkinje cells as the synaptic plasticity mechanism. 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.

$$y = \sum_{n} w_i x_i \tag{2.3}$$

Here, 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 circuit within and before the cortex or by nonlinear synaptic interaction in 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 is based on the long-term depression.

$$dw_i/dt = -x_i(F - F_{spont}) \tag{2.4}$$

Here, F is the firing frequency of the climbing fiber input and F_{spont} is its spontaneous level. 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 fiber is stimulated and the climbing fiber is silent (Sakurai, 1987).

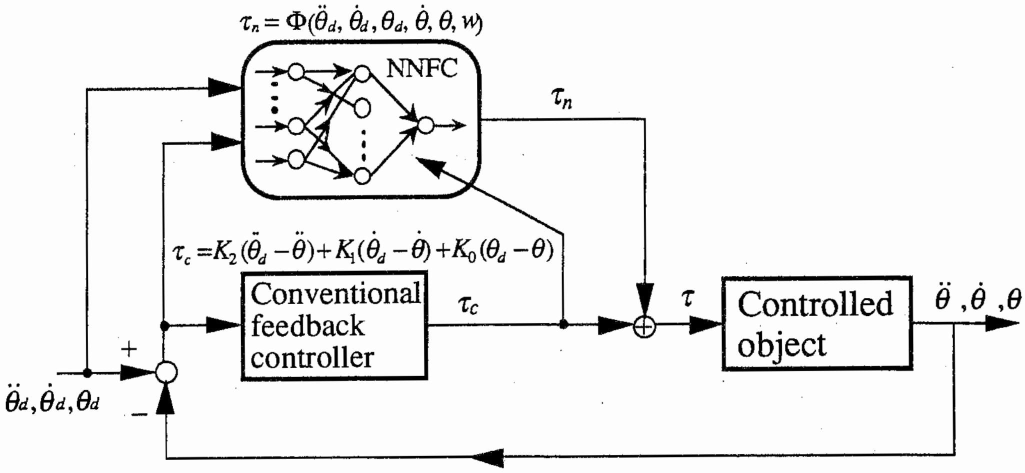


Figure 2..2: Control structure of closed-loop feedback-error-learning.

2.3 Adaptive closed-loop control by feedback-error-learning

The spinocerebellum receives direct feedback information from the periphery, unlike the lateral cerebellum. It is also widely accepted that the cerebellum is involved in movements which require feedback control rather than feedforward control, such as posture control, the optokinetic eye movement response and the smooth pursuit. Even some experimental paradigms designed to investigate voluntary movement, for example wrist tracking movement (ramp and slow ramp in Mano, Kanazawa, Yamamoto, 1986), can be executed only by feedback control. Thus, in order to coherently deal 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 as feedforward control.

We proposed a closed-loop control system shown in Fig. 2..2 based on the feedback-error-learning scheme (Gomi & Kawato, 1990).

The state of the controlled object θ obeys the following nonlinear differential equation.

$$d^2\theta/dt^2 = f(d\theta/dt, \theta, \tau). \qquad (2.5)$$

Here, f is a 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 feedback controller (NNFC in Fig. 2..2). τ_n is given as follows.

$$\tau_n = \Phi(d^2\theta_d/dt^2, d\theta_d/dt, \theta_d, d\theta/dt, \theta, w). \tag{2.6}$$

Please note that the NNFC receives the feedback information abut 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.

$$\tau_c = K_2 d^2(\theta_d - \theta)/dt + K_1 d(\theta_d - \theta)/dt + K_0(\theta_d - \theta). \tag{2.7}$$

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 Eq. 2.2.

$$dw/dt = (\partial\tau_n/\partial w)^T \tau_c. \tag{2.8}$$

As learning proceeds, the motor command generated by the conventional feedback controller decreases. It can be mathematically shown that based on this learning equation NNFC 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.

$$K_2 d^2(\theta_d - \theta)/dt + K_1 d(\theta_d - \theta)/dt + K_0(\theta_d - \theta) = 0 \tag{2.9}$$

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 defines an inverse reference model for the model-reference-adaptive control as shown in Eq. 2.9. For example, suppose that we prepare a PDA feedback controller in the Cartesian space. 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.

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

First, we briefly summarize experimental support for the flocculus hypothesis of adaptive modification of the vestibulo-ocular reflex (VOR). Three different approaches support the flocculus hypothesis (see Ito & Nagao, 1991 for review). First, the VOR adaptation is abolished when the flocculus in cats, rabbits, and monkeys, or only the visual climbing fiber pathway in rabbits, is destroyed. Second, recordings from floccular H-zone Purkinje cells in rabbit and monkey revealed that Purkinje cell responses to mossy fiber inputs change in the direction which causes adaptive modification of the VOR. Gerrits & Voogt (1989) reported that the ventral paraflocculus of the monkey, which, until quite recently was thought to be part of the flocculus (see for example Stone & Lisberger, 1990), is anatomically distinct from the flocculus. Recently, Nagao (1991) found that neuronal responses in the monkey ventral paraflocculus are quite different from those of the flocculus. Thus, it seems that the ventral paraflocculus is not involved in the VOR. Third, the VOR neural circuit and computer simulation by Fujita (1982a, b) also support the flocculus hypothesis.

A circuit diagram of the adaptive modification of the horizontal VOR and the optokinetic eye movement response (OKR) is shown in Fig. 3..1. The visual-climbing-fiber system provides the error signal in learning, that is, the retinal slip (Maekawa & Simpson, 1973).

Figure 3..2 is a block diagram of the neural circuit. This is a model of only the microzone of the flocculus (H-zone) which is related to the horizontal VOR and OKR, and should not be taken as the model of the whole vestibulocerebellum. Here, θ_h, θ_e and θ_{ext} denote the head rotational angle, the eye rotational angle and the rotational angle of the external world, respectively. u is the motor command sent to muscles. Superscripts w, r, c and m indicate that each variable is represented in the world coordinates, the retinal coordinates, the canal coordinates, and the muscle coordinates. s indicates the Laplace operator that is temporal differentiation, and $1/s$ is temporal integration. T_{wc} and T_{wr} represent coordinate transformations from the world frame to the canal frame, and from the world frame to the retinal frame, respectively. The vestibular organ sends the head rotational velocity in the canal coordinates $d\theta_h^c/dt$ to the vestibular nucleus and the flocculus. The forward dynamics of the eyeball is represented by the operator P. Because some portion of VOR is

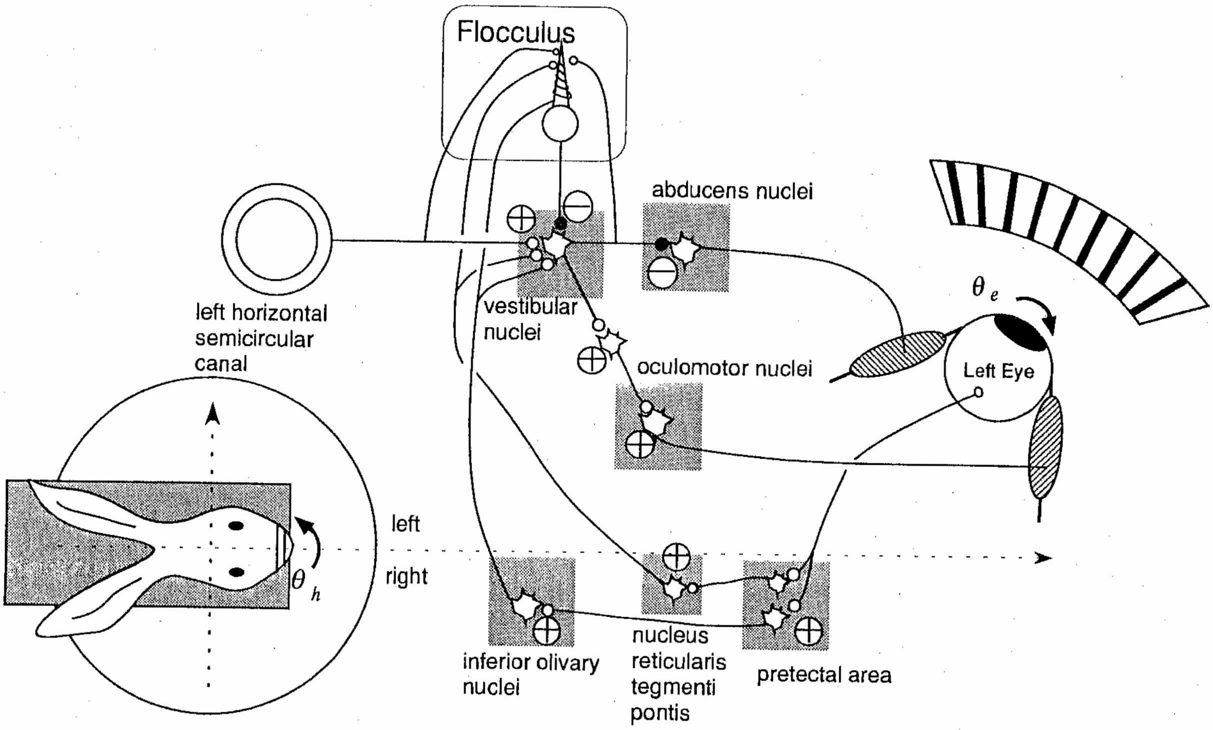


Figure 3..1: Schematic diagram of neural circuit for horizontal vestibulo-ocular reflex and optokinetic response.

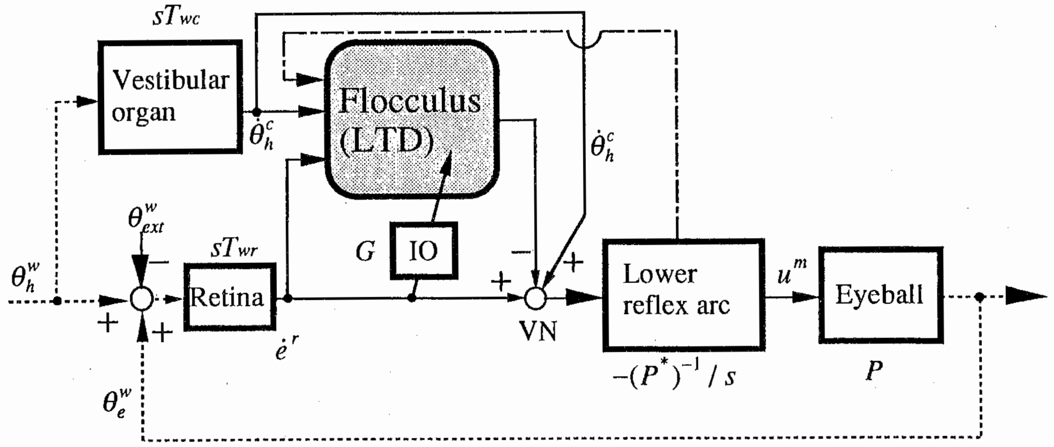


Figure 3..2: Block diagram of adaptive modification of vestibulo-ocular reflex and optokinetic response by the flocculus H-zone. VN is the vestibular nucleus and IO is the inferior olive nucleus.

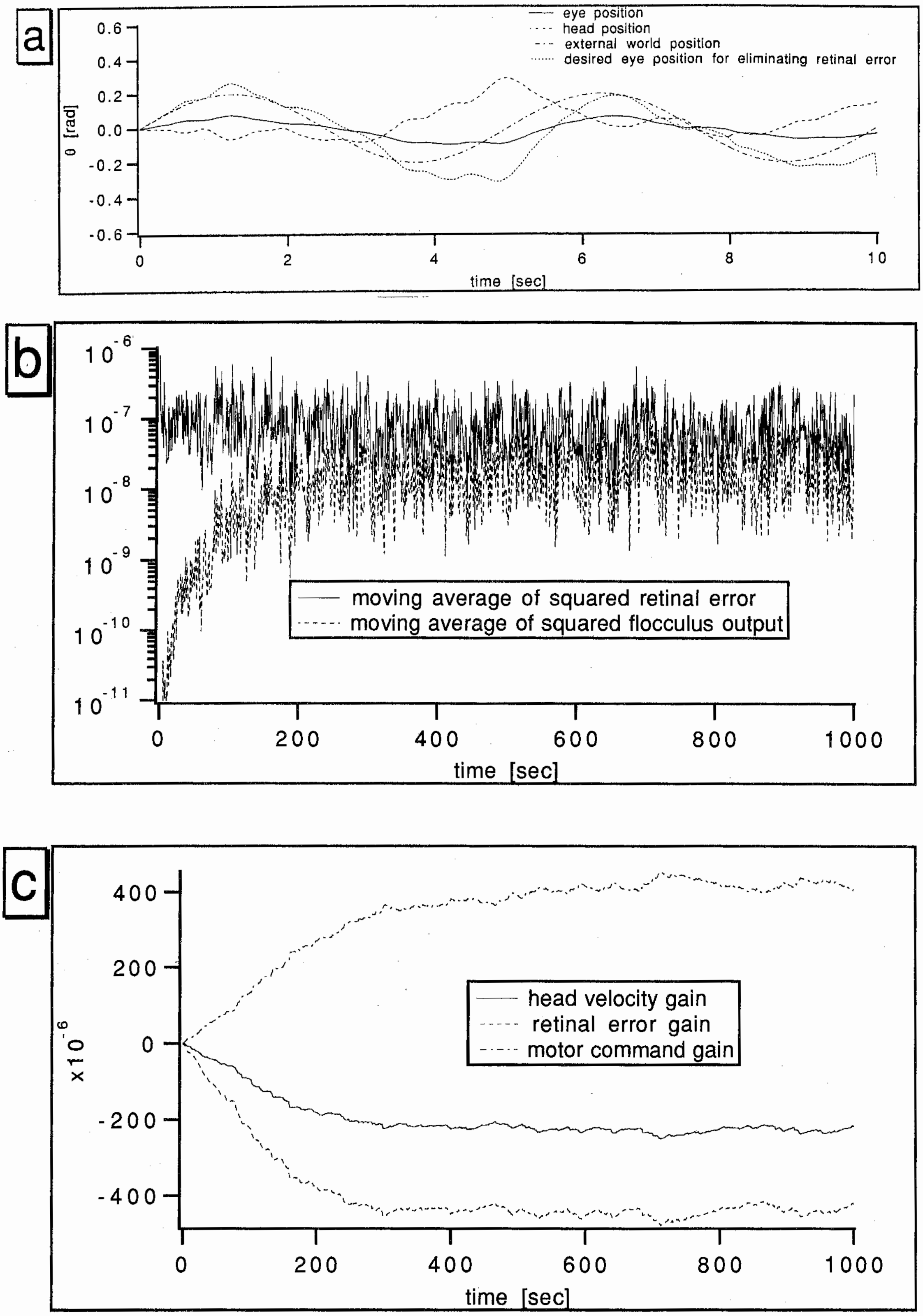
left even when the flocculus is destroyed, the lower reflex arc should provide the minus of the approximated inverse of the controlled object convoluted with integration $-(P^*)^{-1}/s$. This is because the transfer function of the main reflex arc should be roughly -1: $s \cdot -(P^*)^{-1}/s \cdot P \sim -1$.

Simpson and Alley (1974) showed that the visual system, which provides climbing fiber input, senses the retinal slip velocity de^r/dt. If the external world is stationary, the climbing fiber system calculates the summation of the head and eyeball velocities from retinal slip: $d(\theta_h + \theta_e)/dt$. Because the negative of the head velocity $-d\theta_h/dt$ is the desired eyeball velocity for perfect VOR, the summation of the two velocities equals the differential negative feedback term: $de/dt = d(\theta_h + \theta_e)/dt = -d(\theta_{ed} - \theta_e)/dt$. The minus sign in the third equation is canceled if one considers the three sign inversions, that is, long-term depression, inhibitory action of the Purkinje cells, and the minus sign of the lower reflex arc. If one compares Fig. 3..2 with the block diagram of the feedback-error-learning in Figs. 2..1 and 2..2, it should be clear that the visual-climbing-fiber system computes the error signal as a derivative type feedback controller. 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 well corresponds to the approximated inverse dynamics of this combined system. Consequently, the adaptive function of the flocculus can be understood based on the feedback-error-learning scheme.

We assume that the output of the VOR system and the OKR system is summed linearly at the vestibular nucleus (Robinson, 1977). Furthermore, the flocculus is responsible for simultaneous adaptation of the VOR and OKR (Nagao, 1988,1989). Accordingly, the flocculus receives three kinds of synaptic inputs via parallel fibers: the head velocity signal measured by the vestibular organ $d\theta_h^c/dt$, the retinal slip signal measured by motion detectors in the retina and sent from the nucleus reticularis tegmenti pontis $d(\theta_h^r + \theta_e^r - \theta_{ext}^r)/dt$, and the eye velocity signal or the efference copy of the motor command $d\theta_e^w/dt$. The VOR system in Fig. 3..2 corresponds to the open-loop feedback-error-learning shown in Fig. 2..1, whereas the OKR system corresponds to the closed-loop feedback-error-learning shown in Fig. 2..2. For both systems, the direct arc from the retina to the vestibular nucleus plays the role of the conventional feedback controller.

We simulated simultaneous adaptation of the VOR and OKR based on the block diagram Fig. 3..2. Feedback delay of 10 ms was assumed for the motor command feedback to the flocculus. For the calculation of the retinal slip, 20 ms feedback delay was assumed. The dynamics of the eyeball is modeled by taking into account the mass, viscosity and the stiffness. Numerical integration was done with 0.2 ms time increment which is shorter than the natural frequency of the eyeball. Initially, synaptic efficacies of the three inputs to the flocculus, that is the vestibular input, the retinal error input and the motor command feedback, are assumed all zero. Thus, VOR and OKR are executed only by the fixed feedback loop at the beginning of 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 position, velocity and acceleration of the retinal slip. But the velocity term was chosen dominant according to the experiment data (Simpson and Alley, 1974, Nagao, 1988).

We show simulation results in Fig. 3..3. **a** shows the eye position, the head position, the external world position and the desired eye position during the first 10 s of the total 1000 s training. The external world was rotated sinusoidally with 0.2 Hz and 0.4 radian peak to peak. The head was rotated by a stochastic process which has similar time course and amplitude. The eye should move according to the difference of the head angle and the visual world if VOR and OKR work perfectly. Before learning, they were quite different. **b** shows the time course of the moving average of the squared retinal error and the moving average of squared flocculus output. The flocculus output increased rapidly while the retinal error decreased only modestly. **c** shows changes of the synaptic efficacies of three different inputs to the flocculus:


a
eye position
head position
external world position
desired eye position for eliminating retinal error
θ [rad]
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
0
2
4
6
8
10
time [sec]
b
10^{-6}
10^{-7}
10^{-8}
10^{-9}
10^{-10}
10^{-11}
moving average of squared retinal error
moving average of squared flocculus output
0
200
400
600
800
1000
time [sec]
c
400
200
0
-200
-400
$x10^{-6}$
head velocity gain
retinal error gain
motor command gain
0
200
400
600
800
1000
time [sec]

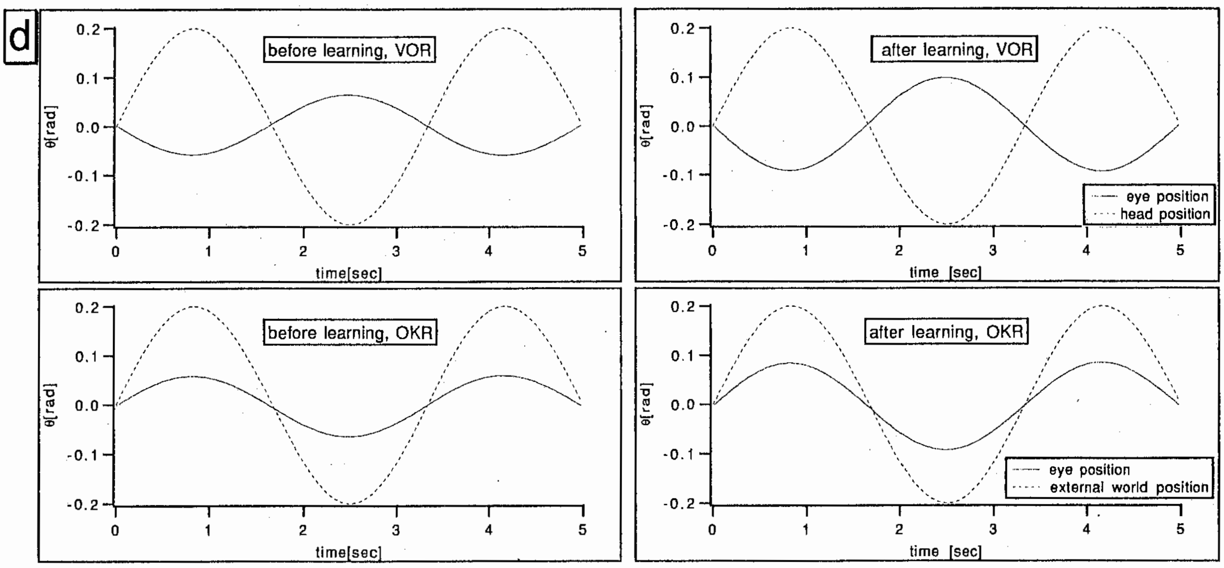


Figure 3..3: Simulation results for adaptive modification of vestibulo-ocular reflex and optokinetic response. **a** eye position, head position, external world position and the desired eye position at the beginning of the training. **b** moving average of the squared retinal error and moving average of squared flocculus output. **c** synaptic efficacies of three different inputs to the flocculus. **d** system performance before (left) and after (right) the training for VOR (upper) and OKR (below).

the vestibular input which codes the head velocity, the visual input which codes the retinal slip, and the motor command feedback. 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 and monkeys (Nagao, 1991), the synaptic contribution of gaze velocity is quite small. Although the gain of the motor command feedback is considerably high in **c**, this should be small in the real system. Because we did not include the neural integrator in the lower reflex arc, the flocculus tried to construct its substitute unnaturally. **d** compares system performance before (left) and after (right) the training for VOR (upper) and OKR (below). 0.3 Hz and 0.4 radian peak to peak oscillation was used both for VOR and OKR. The VOR gain increased from 0.30 to 0.45 while the OKR gain increased from 0.28 to 0.43.

This is a new simulation which first examines simultaneous adaptation of VOR and OKR (Nagao, 1988,1989). The inclusion of the recurrent connection in the learning is also important. This is considered a part of the neural integrator. It is very interesting that a biologically plausible learning scheme such as the feedback-error-learning works quite well even when the recurrent connection is included. This is in sharp contrast to using the recurrent backpropagation (Anastasio, 1991) or random search method (Arnold & Robinson, 1991) which are biologically implausible.

The question about the coordinate frame, in which the climbing fiber responses are represented, arises when vertical and rotatory VOR as well as horizontal VOR are studied. Simpson, Graf and Leonard (1989) examined the rotational axis of the visual world to which visual climbing fibers optimally responded in rabbits. They found that these three axes match well the three axes about which the three pairs of extraocular muscles rotate the eyeball. Thus, the coordinate system in which the error signal is represented is the muscle coordinate system in the three-dimensional VOR, which is in good agreement with our model prediction. However, for lateral-eyed animals such as rabbits, coordinate frames of the semicircular canal and extraocular muscles are not overly different. Thus, similar experiments using frontal-eyed animals should allow us to clarify this coordinate problem.

4. Lateral Cerebellum

We originally proposed the feedback-error-learning scheme as a model of the lateral cerebellum for voluntary motor learning (Kawato et al., 1987). In our model (Fig. 4..1) the feedback controller and the summation of the feedforward and feedback command reside in the motor cortex of the cerebrum. The feedback loop is the transcortical loop. The desired trajectory is sent to the cerebellum and the motor

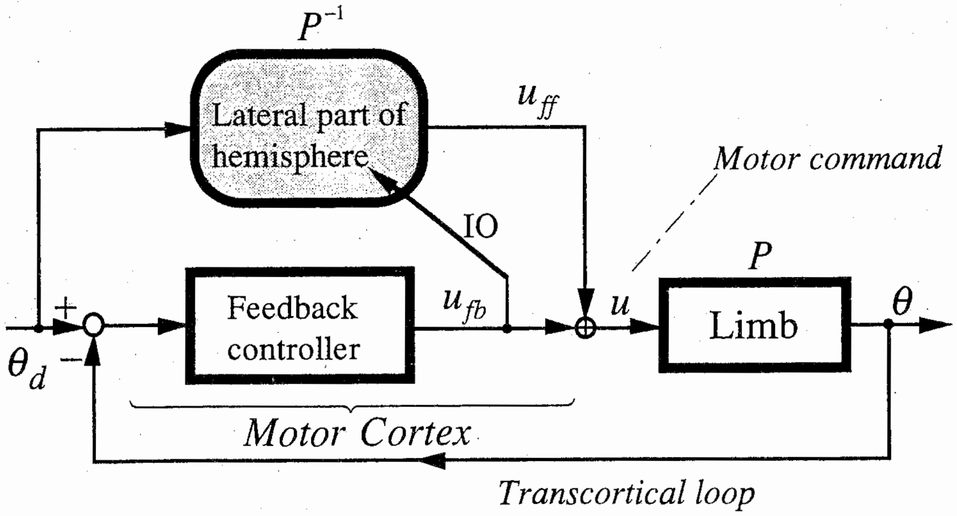


Figure 4..1: Block diagram for learning control of voluntary movement by a corticonuclear microcomplex in cerebro-cerebellar communication loop.

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. 4..1 shows a model of one corticonuclear microcomplex (Ito, 1984) in the lateral part of the cerebellum, and should not be taken as a model of the whole lateral cerebellum.

Based on this neural network model, we succeeded in trajectory control learning of an industrial robotic manipulator with 6 degrees of freedom and nonlinear dynamics (Miyamoto et al., 1988). In subsequent studies, we found that an accurate inverse dynamics model of the manipulator can be acquired without prior knowledge about the mechanical structure (Kawato, 1990a). Furthermore, Katayama and Kawato (1991) expanded the previous model to deal with the inverse statics problem (equilibrium for muscle spring like property) separately from the inverse dynamics problem. They succeeded in trajectory learning of an arm with 16 muscle-like actuators and 5 degrees of freedom. The artificial muscle arm has strongly nonlinear dynamics and suffers from redundancy at the dynamics level because each joint is controlled by agonist and antagonist muscle-like actuators like the musculoskeletal system. Consequently, we experimentally demonstrated that the proposed neural network model is computationally efficient in trajectory control learning of the musculoskeletal system.

A schematic diagram of the neural circuit model around the lateral cerebellum is shown in Fig. 4..2 based on Allen and Tsukahara (1974). The association cortex neurons send the desired trajectory θ_d to the lateral cerebellum via the pontine nuclei as well as to the motor cortex. Via the transcortical loop, the motor cortex neurons are informed of the realized trajectory θ. By calculating the difference between the desired and the realized trajectory $\theta_d - \theta$, 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. Simultaneously, its efference copy is sent to the inferior olive nucleus and expressed as complex spikes in Purkinje cells as the error signal (see for example Gilbert & Thach, 1977 for support). 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 the feedback motor commands are summed at the output neurons in the motor cortex to form u which descends the corticospinal tract. It is predicted that the signal sent from the cerebellum to the motor cortex increases as the motor learning proceeds, which is in agreement with the experimental data (Sasaki, Gemba & Mizuno, 1982, Sasaki & Gemba, 1982).

The most critical point here is whether the climbing fiber response encodes the motor-command error or the movement-trajectory error. To test this, we propose the following experiment which is shown in Fig. 4..3.

The climbing fiber responses of an alert monkey are recorded. The monkey 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, the first target and the second target are displayed on the CRT. The reasons for using the target change paradigm are two-fold. First, Ebner's group found that complex spike activity is high when the target is changed (Wang, Kim, Ebner, 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, orientation of movement is the same between the hand and the cursor. In this case, direction signs of the trajectory error and the motor command error are the same. But in the mirror-image condition, the left-right axis is inverted. Accordingly, the monkey needs to move his hand right in order to move the hand cursor left. In this case, direction signs of trajectory and command errors are opposite. In both conditions, the monkey moves his hand along similar trajectories. The following table shows firing patterns of the climbing fibers under various conditions, that is, whether they

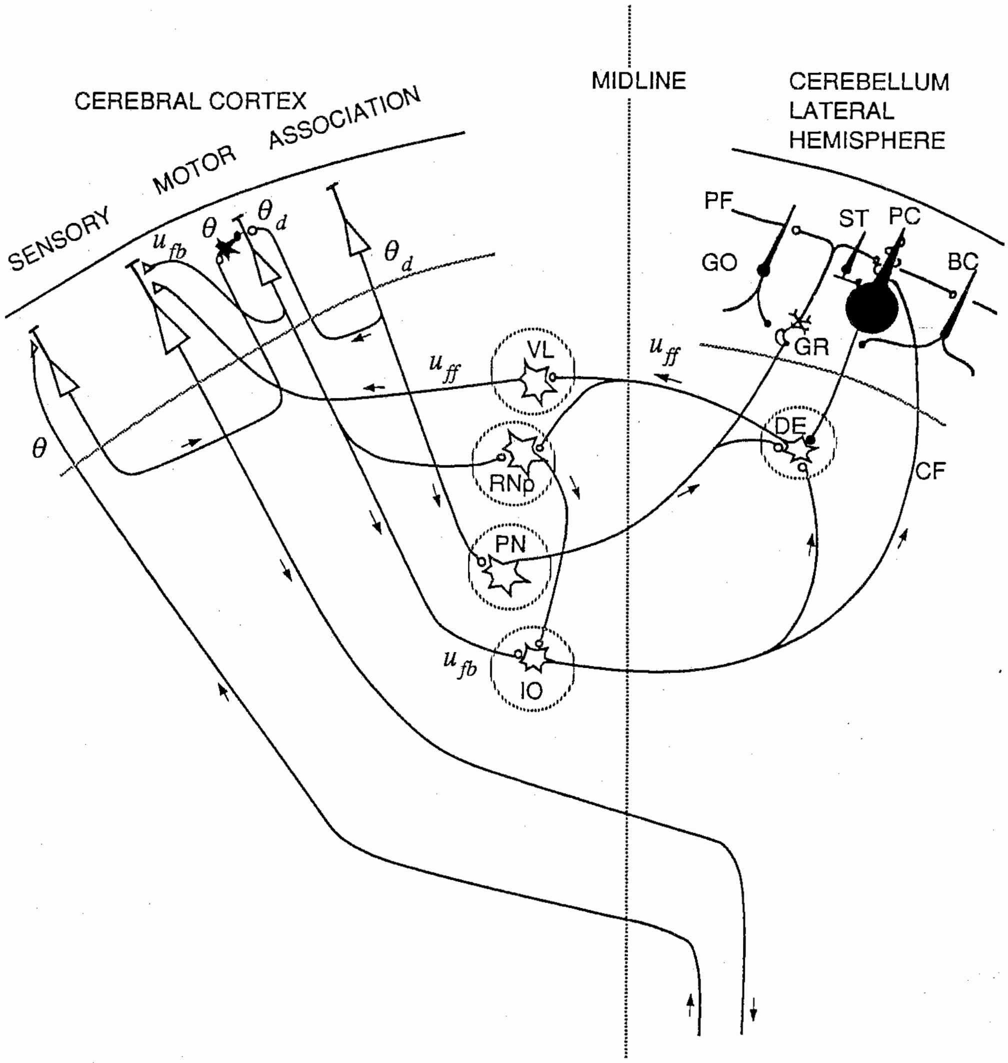


Figure 4..2: Schematic diagram of neural circuit for learning control of voluntary movement by cerebro-cerebellar communication loop. CF: Climbing fiber, BC: Basket cell, GO: Golgi cell, GR: Granule cell, MF: Mossy fiber, PC: Purkinje cell, PF: Parallel fiber, ST: Stellate cell, DE: Dentate nucleus, IO: Inferior olivary nucleus, PN: Pontine nuclei, RNp: Parvocellular red nucleus, VL: Ventrolateral nucleus of the thalamus.

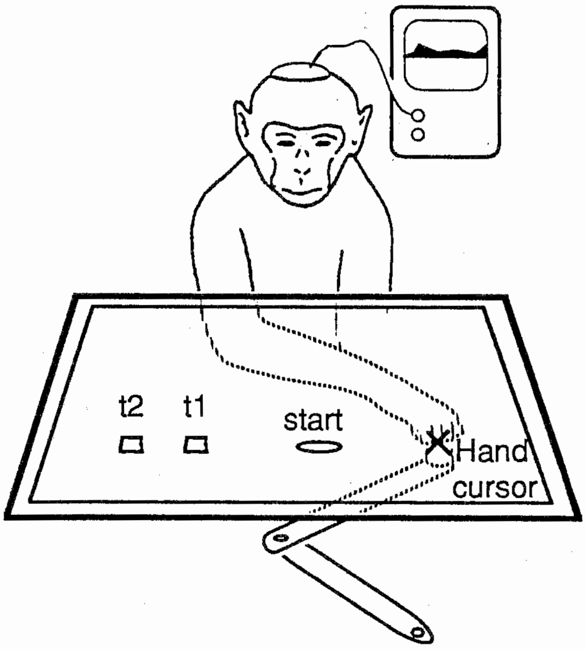


Figure 4..3: Proposed target-change experiment under normal and mirror-image coordinate transformation which reveals reference coordinates in which climbing fiber responses are represented.

represent the movement trajectory error or the motor command error, whether the coordinate transformation is normal or mirror-image, and whether the second target presented is to the right or left of the first target; t1< t2 or t1 >t2. A and B show two different firing patterns of the climbing fibers.

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

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

Our prediction is as follows. Before the monkey learns the mirror-image condition, the case for 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 he is improving the skillfulness of his movement, the case for command error pattern must be observed. Some part of the cerebral cortex, most likely the parietal lobe, transforms the error detected in the visual coordinates into muscle coordinates. Then, the motor command error is sent both to the cerebellum and the motor cortex. Burnod and Dufossé (1990) proposed an interesting model which might be related to this imaginary experiment.

5. Spinocerebellum

In this section, we propose models of the vermis and the intermediate part of the hemisphere based on the feedback-error-learning scheme for the closed-loop control system shown in Fig. 2..2. In these models, the cerebellum provides an adaptive feedback controller. With learning capability realized by the long-term depression, the cerebellum learns to execute coordinative and predictive control of nonlinear controlled objects. This adaptive feedback controller is overlaid on the more fundamental feedback system in the spinal cord, the brain stem, and via the cerebral cortex. The two feedback controllers cooperate in the execution of movements. The efference copy of motor commands generated by the lower feedback controller is sent to the cerebellum by the climbing fiber system. The long-term depression tries to decrease the activity of the climbing fiber system. Thus, as the 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. Thus, feedback control is essential.

5.1 Vermis

Figure 5..1 shows a block diagram of adaptive posture control conducted by a corticonuclear microcomplex in the vermis of the cerebellum. Among several functional roles of the vermis in motor control, adaptive control of posture is chosen as a representative example in Fig. 5..1. Human control performance of posture is degraded when proprioceptive feedback information is injured. However, loss of certain information is compensated by using other sources of information (e.g. Romberg's sign). Nashner (1981) showed that adaptive modification of reflexes in posture control is severely impaired in patients with cerebellar disease. Thus, the cerebellum is assumed to be the site of adaptive control of posture. The vermis receives information about the position, velocity and acceleration of the head and the torso from proprioceptors, visual sensors and the vestibular organ. Its output is directed mainly to the medial brain stem system and the axial regions of motor cortex.

By computer simulation, Gomi and Kawato (1990) ascertained that the proposed scheme works well for controlling an inverted pendulum system, which is considered the simplest model of the trunk and legs. We found that an error in posture induced by physical perturbation (disturbance in Fig. 5..1) decreased as the learning process proceeded. Ultimately, the behavior of the total system obeys the ideal response which is determined by the reference model embedded in the fundamental feedback controller.

A schematic diagram of the neural circuits around the vermis is shown in Fig. 5..2. Information about the state of the controlled object is sent to the Purkinje cells by the spinocerebellar tracts from the periphery. The inferior olive sends the efference copy of the activity of the premotor network while receiving information from the periphery (spino-olivo-cerebellar paths) and the cerebral cortex. The output from the microcomplex is sent to the spinal cord and the cerebral cortex from the fastigial nucleus. We propose that the loop SCT-parallel fiber-Purkinje cell-fastigial nucleus-CRST/CVST forms an adaptive feedback controller.

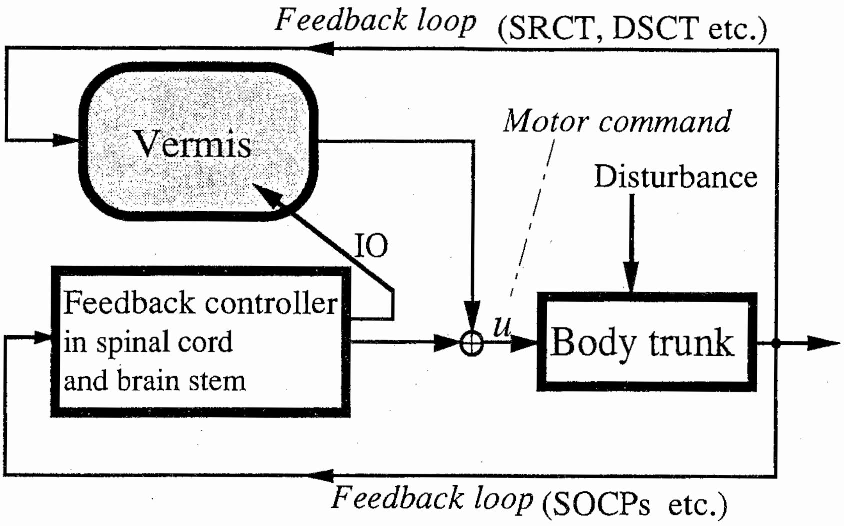


Figure 5..1: Block diagram of adaptive posture control by a corticonuclear complex in the vermis of the cerebellum. SRCT: spino-reticulo-cerebellar tract, DSCT: dorsal spinocerebellar tract, SOCPs: spino-olivo-cerebellar paths.

5.2 Intermediate part of the hemisphere

The model for the intermediate part of the hemisphere is more complicated than that of the vermis, but we propose a similar closed-loop model shown in Fig. 5..3.

Among many functional roles of the intermediate part in motor control, adaptive control of locomotion is chosen in Fig. 5..3 as an interesting example. Neural oscillators generate a desired rhythmic movement pattern. Because the desired movement pattern is time varied, feedforward control is necessary to execute smooth movement. On the other hand, the controlled object is unstable, thus feedback control is also essential. Consequently, adaptive control of locomotion requires both feedforward- and feedback control. The intermediate part receives the parallel fiber inputs both from the periphery and the brain stem and satisfies input required to execute simultaneous feedback and feedforward control. Udo and colleagues (1980) showed that cooling of the cerebellar intermediate cortex interferes with interlimb coordination in locomotion. Matsukawa and Udo (1985) found that complex spikes were frequently evoked by mechanical perturbations to the paw during locomotion of decerebrate cats.

Theoretically, the most interesting and challenging problem is to set an appropri-

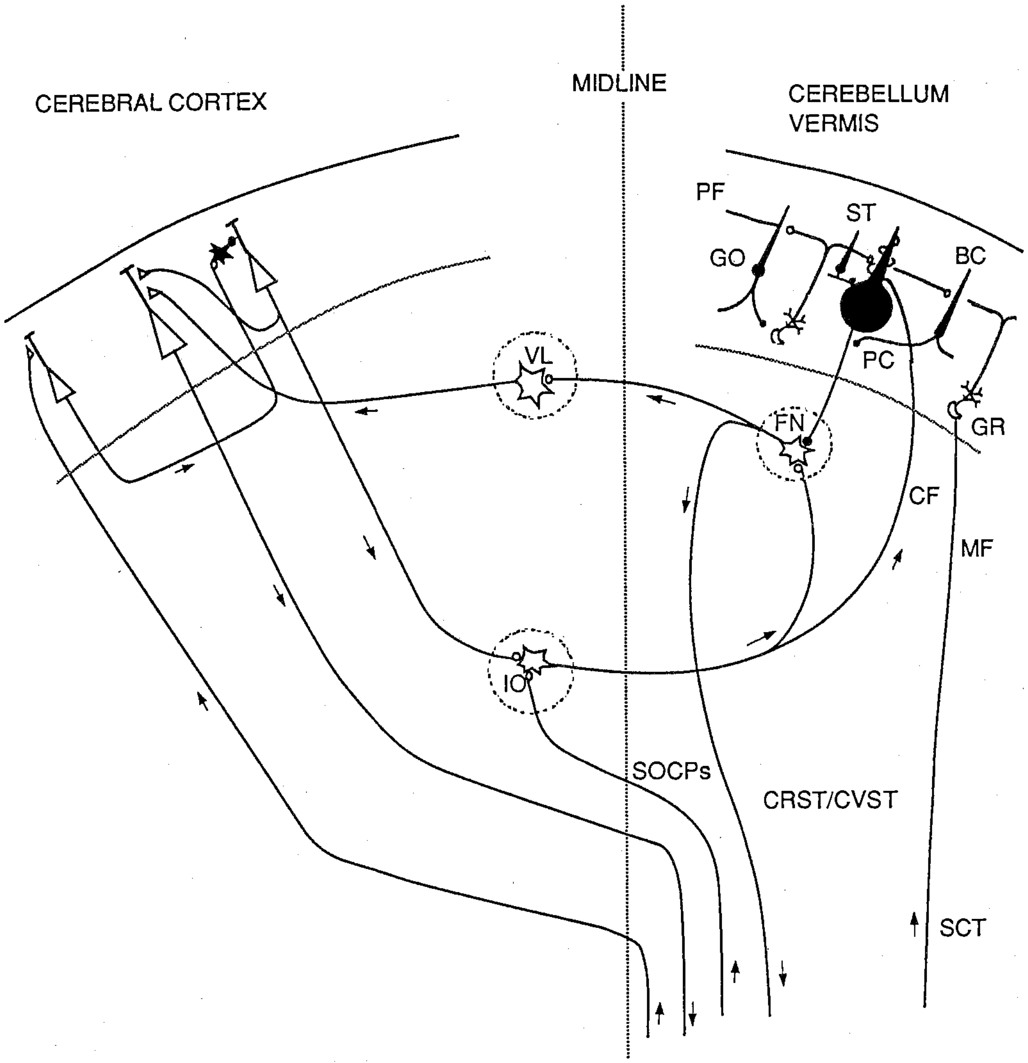


Figure 5..2: Schematic diagram of the neural circuits around the vermis of the cerebellum. SCT: Spinocerebellar tracts, CRST: Cerebelloreticulospinal tract, CVST: Cerebellovestibulospinal tract, SOCPs: Spino-olivo-cerebellar paths. FN: Fastigial nucleus.

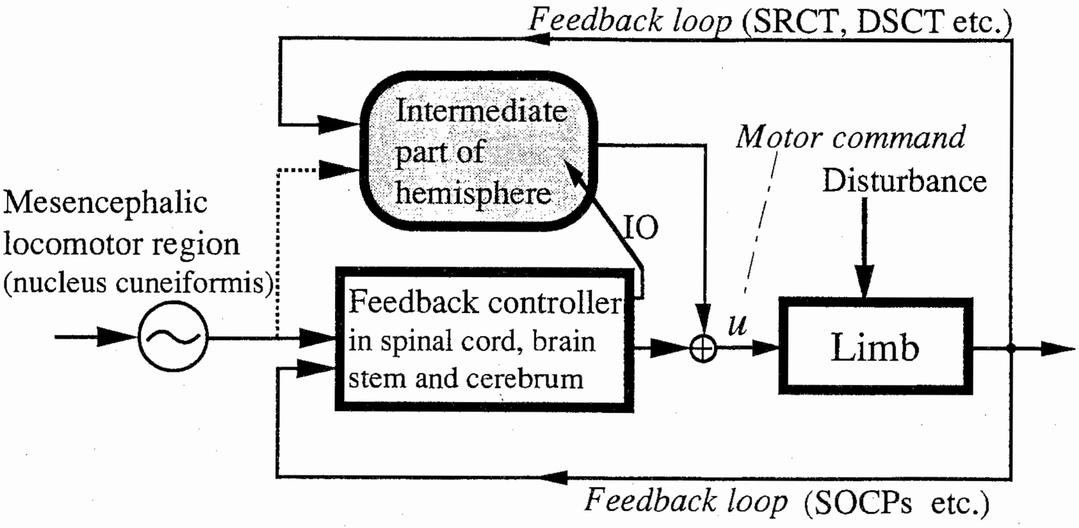


Figure 5..3: Block diagram of adaptive control of locomotion by a corticonuclear microcomplex in the intermediate part of the hemisphere of the cerebellum.

ate inverse reference model in the feedback controller at the spinal- and brain stem level. We have little experience in designing an inverse reference model for a multi-degrees-of-freedom system in a very dynamic situation like locomotion. However, we expect that some of the known interlimb reflexes should provide part of the reference model.

A schematic diagram of the neural circuit around the intermediate part is shown in Fig. 5..4. The spinocerebellar tracts convey feedback information from the periphery while the pontine nuclei carry feedforward information from the cerebral cortex to parallel fiber inputs. The inferior olive conveys the premotor activity as climbing fiber inputs. The output from the microcomplex is sent to the red nucleus as well as the motor cortex from the interpositus nucleus. We propose that a microzone in the intermediate part executes simultaneous feedback and feedforward adaptive control.

6. Discussion

We showed that functional roles of different regions of the cerebellum can be coherently understood based on the feedback-error-learning scheme. The most important assumption here is that climbing fiber responses represent efference copy of motor

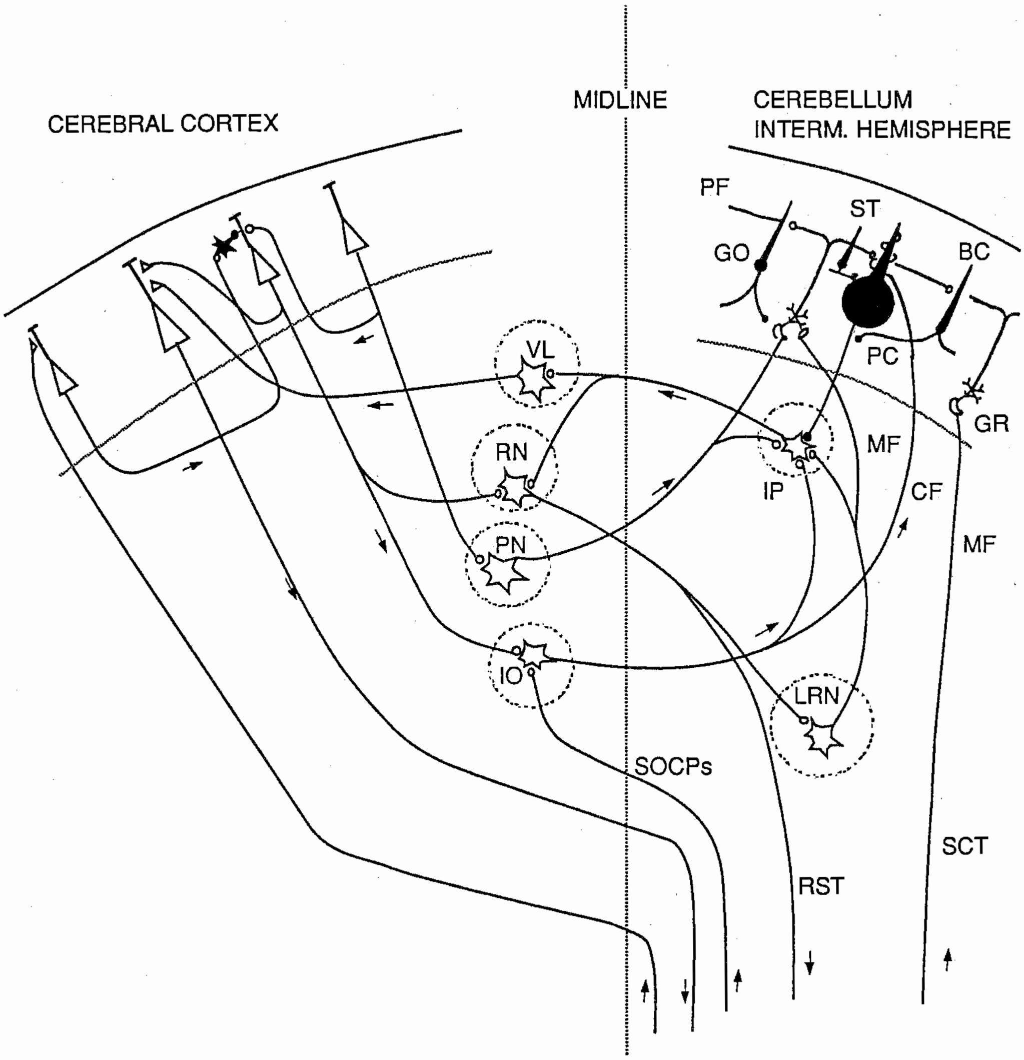


Figure 5..4: Schematic diagram of neural circuit around the intermediate part of the hemisphere of the cerebellum. RST: Rubrospinal tract, IP: Interpositus nucleus, PN: Pontine nuclei, RN: Red nucleus.

commands generated by premotor networks. Thus, climbing fiber responses must possess magnitude information and direction (sign) information. This was well established for the visual climbing fiber responses of the vestibulocerebellum. Firing frequencies of the visual climbing fiber change with the velocity of the retinal slip (Simpson & Alley, 1974). Furthermore, they were lower than the spontaneous level for the visual stimuli whose direction was opposite that of the optimum direction. However, we still do not have definite experimental data about information represented by the climbing fiber responses in other regions of the cerebellum.

Houk, Barto and colleagues (1990, 1991) proposed a quite comprehensive and attractive model of the cerebellum based on anatomical and physiological knowledge. Computationally, their scheme is based on reward-penalty learning (Barto, Sutton, Brouwer, 1981). In this model, the long-term depression of the Purkinje cells is assumed to provide the computational mechanism for the associative search. Therefore, the climbing fiber responses are assumed to give a “one-sided penalty signal," such as a somatic event detector. In this view, the all-or-nothing (binary) nature of the climbing fiber responses is emphasized, and it is assumed that directional information is not involved. These assumptions are in sharp contrast to ours. We have confidence that ours are correct for the vestibulo-cerebellum, but the real question is which is more appropriate for other regions of the cerebellum (vermis, intermediate part of the hemisphere, lateral part of the hemisphere).

The range of firing frequencies of the climbing fiber is unusually low (the maximum is 4 pulses/sec and the spontaneous level is about 1 pulse/sec). This is usually used to support the 0 and 1 nature of the information conveyed. However, this is not true. Because the long-term depression has a time constant of about 1 hour, even a low firing frequency can be integrated to give analog information (14,400 pulses/hr to 3,600 pulses/hr). If the firing frequency is lower than the spontaneous level, it gives direction (negative) information.

The non-sensory nature of the climbing fiber responses was reported (Gellman, Gibson, Houk, 1985). Some climbing fibers are activated by paw touch induced by forced movements. However, the identical stimulus does not induce firing of the climbing fibers when paw touch is induced by active movements. This is well explained by our model based on feedback-error-learning. If some sensory events are expected based on desired movement patterns, no extra activity is generated by the premotor networks. Thus, 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, following which, the climbing fibers are activated.

We need to wait for new experimental data such as that proposed in Fig. 4..3 before we form firm conclusions regarding information represented by the climbing fibers. Meanwhile, we are very much interested in integrating our theory and Houk and Barto's in various respects.

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