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Is the Cerebellum a Smith Predictor?

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ABSTRACT. The motor system may use intemal predictive models of the motor apparatus to achieve better control than would be possible by negative feedback. Several theories have proposed that the cerebellum may form these predictive representations, In this article, we review these theories and try to unify them by reference to an engineering control model known as a *Smith Predictor*. We suggest that the cerebellum forms two types of internal model. One model is a *forward* predictive model of the motor apparatus (e.g. , limb and muscle), providing a rapid prediction of the sensory consequences of each movement. The second model is of the time delays in the control loop (due to receptor and effector delays, axona] conductances, and cognitive processing delays). This model delays a copy of the rapid prediction so that it can be compared in temporal register with actual sensory feedback from the movement. The result of this comparison is used both to correct for errors in perf.ormance and as a training signal to learn the first model We discuss evidence that the cerebellum could form both of these models and suggest that the cerebellum may hold at least two separate Smith Predictors. One, in the lateral cerebellum, would predict the movement outcome in visual, egocentric, or peripersonaJ coordinates. Another, in the intermediate cerebellum, would predict the consequences in motor coordinates. Generalization of the Smith Predictor theory is discussed in]ight of cerebellar involvement in nonmotor control systems, including autonomic functions and cognition

Key words: cerebellum, internal models, tracking

The need for a unifying theory for the role of the cerebellum in motor control has been recognized for many years. Its absence is particularly frustrating because of our detailed knowledge of cerebellar anatomy and electrophysiology, and the extreme regularity of cerebellar cortical circuitry (see, for example, Ito, 1984) . Mitchell Glickstein has likened our understanding of the known facts about the cerebellum to the difficulties experienced before Kepler in understanding the apparently bizarre orbits of the planets. Encouraged by the apparent simplicity of its structure, many different models have been suggested for the cerebellum. Most are based on physiological and clinical evidence, some on its suggestive anatomy, a few on both. Perhaps unsurprisingly, no one model seems sufficient to meet with all the diverse information that we have on the cerebellum, nor with what is increasingly recognized as its involvement in a wide range of *nonmotor* physiological systems.

In this article we suggest that the cerebellum acts as a *Smith Predictor:* This is a form of controller, first devised for engineering systems that suffer long and unavoidable feedback delays, which is based on internal representations of the object that is to be controlled. We have presented the basic hypothesis in earlier abstracts (Miall, 1989; Miall, Stein, & Weir, 1989). We based our suggestions mainly on data from the control of the primate arm in visually guided tracking tasks (Miall, Weir, & Stein, 1985, 1986, 1987), but in the discussion we attempt to broaden the scope of the theory to cover other areas of cerebellar concern. We propose that different regions of the cerebellum hold separate Smith Predictors, comprised of adaptive neural networks, each trained to accurately represent the behavior of their own controlled object. Thus the same basic computational process could apply to all regions of the cerebellar cortex, as is suggested by its striking uniformity of structure. We start, however, with a very brief review of some earlier theories.

Theories of the Cerebellum

The motor contribution of the cerebellum was realized by Flourens (1968/1824) , who suggested that its role is to coordinate movement. Quite what was meant by the term coordination is not clear, but the phrase nicely summarizes even present-day knowledge. The cerebellum is not necessary for movement, but without it movements of the limbs tend to be jerky, tremulous, weak, and inaccurate. Complex

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multijoint movements disintegrate into a series of separate responses, the normal fluent flow of speech breaks down to "scanning speech;' and there are difficulties in forming normal muscle synergies (dyssynergia). There are also problems in timing, with delayed movement onset, and difficulties with matching target speeds. These varied symptoms are usually classified as a triad of hypotonia, hypermetria, and intention tremor. Although there is some disagreement about the extent of these symptoms in different tasks, they are generally most pronounced in movements requiring sensory guidance or complex, multijoint control. There are also disturbances of the oculomotor system, with inaccurate saccades, breakdown of smooth pursuit, and nystagmus-the continual drift and realignment of gaze.

Holmes (1917, 1939), in a detailed study of visually guided movements, ascribed to the cerebellum the role of a comparator. A comparator compares desired and actual levels of a reference parameter, the difference forming an error signal that could be used for negative feedback control. Holmes felt that the intention tremor, hypermetria, and positional corrections were suggestive of the performance of a servo with an inaccurately adjusted comparator. His proposal was that the cerebellum detects errors in motor performance and issues corrective motor commands (see also Eccles, Ito, & Szentogothai, 1967; Oscarsson, 1979). This model now seems limited in scope, however, as it does not account for the deficits in timing, recent evidence of the adaptive nature of the cerebellum, nor its complexity of architecture.

The next group of models are known variously as metasystems, parameter adjustors, or gain controllers. The ideas behind these models (McKay & Murphy, 1979; Prochazka, 1989) are that the cerebellum holds control parameters of reflex arcs and of voluntary control pathways-parameters such as the gain of a reflex, or the amplitude/velocity relationship of a movement (Brooks, Kozlovskaya, Atkin, Horvath, & Uno, 1973). The behaviors can then be executed without the need for continuous feedback control. For example, it is well established that the cerebellum is involved in the vestibuloocular reflex (VOR). This reflex causes eye movements that normally compensate for head movement, keeping gaze position stable. To correctly set the gain of this reflex, a link is necessary between the retina (signaling the success or failure of the compensatory eye movement) and the vestibular pathway driving the reflex. The cerebellum acts to provide that link (see, e.g., Ito, 1982), and is vital for adjusting the gain when, for example, a subject is wearing magnifying spectacles. The cerebellum may well provide a similar regulating function in many other reflexes (Prochazka, 1989) . Its main function under this hypothesis is to set appropriate control parameters for the feedforward control of movements for which negative feedback control would be difficult, either because the feedback loop is not complete (as in the VOR) or is too slow. Pellionisz formulated this idea somewhat differently, but with much the same flavor, when he stressed the tensorial properties of the cerebellar cortical matrix (Pellionisz & Llinas, 1979, 1980). The correct values for control parameters of movements or reflex arcs cannot always be known in advance and therefore need to be adjusted on the basis of previous experience. Hence, a common feature of this class of models is that they require the cerebellum to adapt or learn new parameter values. This then leads on to the latest class of models, of the cerebellum as a learning machine. A distinction that can be made between reflex gain control and learning is that learning can involve forming relationships between previously unconnected events (as in classical conditioning) whereas gain control requires setting the strength of an existing control pathway.

Areas in which the role of the cerebellum in learning has been extensively studied are in the classical conditioning of reflexes and in learning motor skills. The cerebellum has recently been shown to have a crucial role in associative learning (classical conditioning). For example, the cerebellum is necessary for learning to associate a conditional stimulus, such as an auditory tone, with a very simple, stereotyped motor response (an eye-blink; McCormick, Lavond, Kettner, Rising, & Thompson, 1981). It is also involved in learning more complex motor skills, including new relationships between movement of a lever and visual feedback of its position (Gilbert & Thach, 1977; Keating & Thach, 1990; Miall, Kerr, Stein, & Phillips, 1991; Ojakangas & Ebner, 1990). Thus, if the cerebellum is damaged, the subjects are slow to adapt to a change in task requirements-they fail to adjust the amplitude of lever movement, overshooting or undershooting the target if the gain is increased or decreased. It is often suggested that cerebellar lesions would impair other motor learning tasks-learning to ride a bicycle or to perform a new sport-although there seems little documented evidence for this.

A number of influential articles took up the question of how the cerebellum could learn. Brindley (1967) first suggested that the synapses between parallel fibers and Purkinje cells, if modifiable, could form a memory. Marr (1969) and then Albus (1971) presented detailed models that could indeed form associative memories. The basic idea was that the parallel fiber/Purkinje cell synapses would be modified by input from the climbing fibers, so that the Purkinje cells in the cerebellar cortex would learn to respond to particular input patterns. Kanerva (1988) followed these with a model of the cerebellum in learning distributed patterns. Gilbert (1975) extended the Marr-Albus models to include control of temporal movements rather than learning arbitrary input-{)utput patterns (see also Blomfield & Marr, 1970) . However, these theories do not immediately link with the clinical symptoms of cerebellar damage: They do not easily explain intention tremor, hypermetria, delayed movement initiation, or the oculomotor problems mentioned earlier. Furthermore, the Marr-Albus models suggested that activity in each climbing fiber represented "elemental movements" by which the cortex instructed the cerebellum to learn the "context states" in which the elements occurred, so that these components of movement could be replayed later in sequence without cortical instruction. Recent evidence suggests instead that climbing fibers signal errors in performance, or unexpected sensory events (see, below, "The Role of the Inferior Olive in Learning"). Fujita (1982) then modified the basic Marr-Albus models to incorporate dynamic responses, proposing that the cerebellum is an adaptive filter that could learn to provide phase-lead compensation for the time lags inherent in the motor system.

Other models to mention in passing include a model of the cerebellum as a timing device. Braitenberg (1961) suggested that thc parallel fibers could form a delay line suitable to control a series of elemental components comprising a complete movement. This model accounts well for the very noticeable cytoarchitecture of the parallel fibers and could account for the clinical data of timing deficits, but, in fact, the parallel fibers are too short to provide a time delay of the required magnitude (Braitenberg, 1983). A variation of this scheme allowed the cerebellum to torm short-term predictions of incoming data by forming a predictive Taylor series expansion (Pellionisz & Llinas, 1979, 1982), and could relate to recent data indicating impairment in time and velocity perception (Ivry, Diener, & Keele, 1988; Ivry & Keele, 1989; Keele & Ivry, 1991).

The final group of theories to mention are those most closely related to the one we present here, and postulate that the cerebellum forms an *internal model* of the motor system. By this we mean a neural representation of the behavior of the controlled object *(plant)* such that the output from this model reflects in some fashion the behavior of the plant. To understand this concept, consider the conflict of priorities suffered by the motor system because of the delays in receiving and processing visual or proprioceptive feedback (Figure 1). On one hand, actions often need to be performed as quickly as possible. Thus, for speed, the control process should be feedforward and independent of sensory feedback. This could be achieved through an *inverse dynamic model* (Atkeson, 1989) of the controlled object (the limb). An inverse model transforms the desired goal of a movement into a set of control actions (a motor command) that achieve the goal (Figure 2A). In other words, it inverts the direct-or *jorward-dynamic* relationship between a motor command and the movement of the limb. The brain could define the goal of the movement, and this signal could be transformed by the inverse model into the correct motor command. On the other hand, the uncertainties of executing actions with biological effectors means that the motor control process can never be completely divorced from error corrections. Thus, for accuracy, the control process should incorporate feedback. Negative feedback control is slow, however. **In** any biological system, the feedback signals from the environment will lag behind the issue of each motor command because of inevitable delays in the control pathways. First, there are the afferent delays from receptors to the central nervous system (CNS). If the feedback is visual, as is the case for many human voluntary movements, then the afferent delay can be significant: 50 ms from retina to visual cortex, longer still to reach the associative and motor cortices. Then there are delays incurred in processing the motor command, and finally, there are efferent delays in issuing the command to the muscle (axonal delays) and in the response of the limb (muscle latencies and delays between acceleration and significant change of position). Thus the total feedback-Ioop delays could be as high as 130 ms for oculomotor control (Michael & Melvill Jones, 1966; Robinson, Gordon, & Gordon, 1986), 110-1s0 ms for proprioceptive control (Flanders & Cordo, 1989; Flanders, Cordo, & Anson, 1986), and perhaps 200-250 ms for visuomotor control (Georgopoulos, Kalaska, & Massey, 1981) The motor control system would therefore benefit from a forward model of the plant (Figure 2B). A forward model is a direct mimic of the controlled object, which, when given a motor command as input, outputs the expected movement of the limb. Because the model can respond well before the central nervous system (CNS) receives feedback about the actual movement, it allows rapid estimation of the results of a planned movement. The controller (the cerebral cortex) could therefore issue motor commands through the internal model and update these commands on the basis of predictive feedback from the model, thus avoiding the long delays in the actual feedback loop. Forward models also allow the brain to explore the consequences of proposed actions, testing them out on the model before executing them in the real world, and thus the models can form an integral part of the motor planning process.

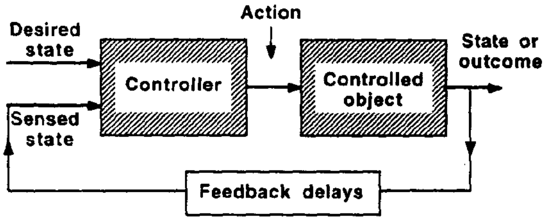

FIGURE 1. A simple control loop. To accurately control an effector, the motor system requires sensory feedback of its actions Because the feedback is delayed, however. actions are then based on out-of-date sensory inputs.

Experimental evidence for such internal models is drawn mainly from the speed of human movements, which, with durations of only 200-300 ms, are too fast to be controlled by visual feedback. For example, when humans track visual targets, they can issue rapid positional corrections at up to 3 or 4 Hz, which is too rapid to allow visual feedback of the earlier movements. When forced to use visual feedback that has been delayed by up to 300 ms, the rate of their corrections is clearly related to the total loop delay, with a basic correction rate of about 1.5-2 Hz (Miall et al., 1985). We also know the normal movements are not purely feedforward controlled, because disturbing the feedback signals during a movement leads to corrections before the movement is complete: To know that modification of an ongoing

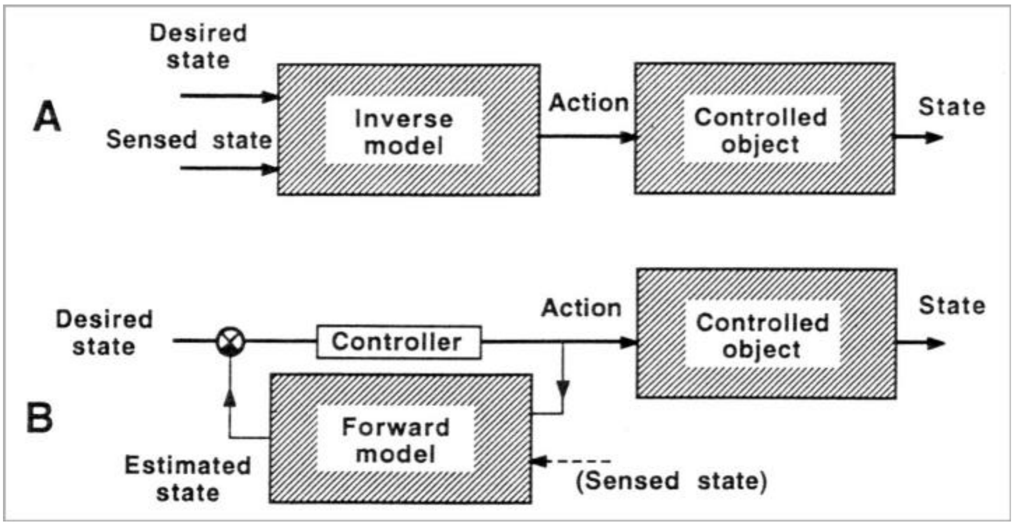

FIGURE 2. Two control strategies involving internal models. A. Inverse modeling. Here the model transforms a goal, or desired state, into a motor command, or action. The action shifts the controlled object into a new state, which will be close to the desired state if the inverse model is accurate. B. Forward modeling within a negative-feedback loop. The outcomes of the controller's actions are predicted by a forward model of the controlled object lying on a fast, internal control loop Here, the desired state is compared with the output of the forward model, and the error translated by a controller into actions. The comparator is indicated by the circle with one filled quadrant In a more general form, the controller itself could perform the comparison. We have also indicated that the forward model could receive sensory inputs: these could be used to update the forward model

movement is needed implies knowledge of its expected outcome.

The cerebellum could therefore act as an inverse model on the feedforward pathway (Ito, 1990, 1991; Kawato, Furukawa, & Suzuki, 1987; Neilson, Neilson, & O'Dwyer, 1988), or as a forward model on a feedback pathway (Ito, 1970; Kawato et al., 1987; Keeler, 1990; Miall, 1989; Miall et al. , 1989) . Like the earlier learning theories, these theories require that the cerebellum be adaptive, so that a neural model can be learned that represents the controlled object and can be adapted to reflect changes in the performance of the modeled system. They also provide a clear role for the cerebellum in the coordination of movement. Motor performance based on the use of such internal models would be degraded if the model was unavailable or inaccurate. These theories could therefore account for dysmetria, tremor, and dyssynergia, and perhaps also for increased reactions times .

However, many theories of internal models (whether in the cerebellum or not) fail to fully account for the mismatch in time delays between the neural model of the controlled object and actual feedback from that object. For example, an inverse model transforms motor goals into motor commands and so can allow rapid actions. A forward model provides a rapid prediction of the outcome of the current movement; when incorporated in a fast. internal feedback control loop, the output of the internal loop is also a motor command that will drive the plant to the desired position. In other words, this arrangement achieves the same result as an inverse model (compare Figures 2A and 2B) In either case, however, the CNS cannot know the real outcome of the action until actual feedback is received. If the plant behaves unreliably or the models are inaccurate, then errors result that need to be incorporated into subsequent actions. Thus, to be effective, an internal neural model of the controlled object should not only allow much of the actual feedback delay to be avoided, but it should also allow errors signaled at a later moment in time to be incorporated into the control. The difficulty then becomes one of detecting mismatches between a rapid prediction of the outcome of a movement and the real feedback that arrives later in time. What is required is an estimate of the delay before actual feedback will be received. Then the controller can distinguish between the expected reafferent feedback from its own performance and the sensations caused by errors in performance or from unexpected changes in the external environment.

The Smith Predictor

In the late 1950s, O. I. M. Smith proposed a controller that became known as a *Smith Predictor:* He first suggested this control scheme for factory processes with long transport delays, for example catalytic crackers and steel mills (Smith, 1959), but the idea can be generalized to all control processes that have long loop delays. Figure 3A shows a block diagram of the scheme, in which a plant (the limb, for example) lies in a negative-feedback loop with both feedforward (Delayl) and feedback (Delay2) delays. The Smith Predictor is very simple. The controller operates on two separate models of the plant, both lying on internal feedback loops. One loop (labeled *i* in Figure 3A) includes the dynamic components of the plant (Plant Model1) but excludes all transport delays; the other includes these delays (Delay Model = Delay1 + Delay2). Because the transport delays are excluded from the first model, the model can be situated in a high-gain, low-delay, negative-feedback loop (Loop I). If this model is accurate, and the plant performance reliable, this loop can provide near-optimal control of the plant. The second model (on Loop 2) is used to compare the actual performance of the plant with the expected performance. Because the second model includes an accurate representation of all plant transport delays, it will delay the output from the controller to match the delayed feedback from the periphery, and these two temporally matched signals normally cancel out. This is most easily seen in Figure 3B, which is a functionally identical reconfiguration of the system. Any error between these two signals (Loop 2 versus Loop 3) can simply be added back into the input channel. For example, if the plant behaves unreliably, then the second control loop comparator can detect and correct the errors without destabilizing the high-gain control process. It would add these errors to the input of Loop I, but that loop is stable, as it has negligible feedback delays.

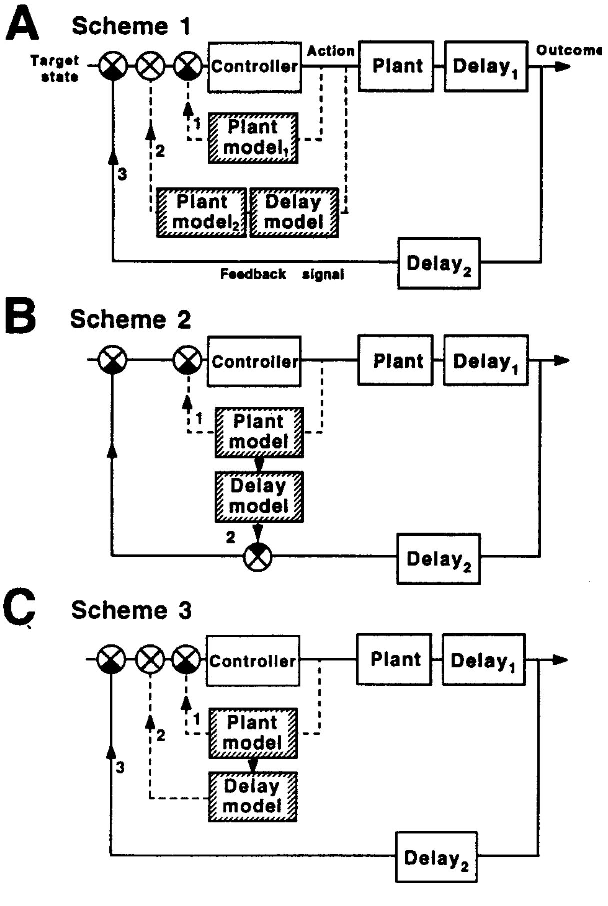

FIGURE 3. Three alternative Smith Predictor architectures In Scheme I, a negative-feedback loop containing a controller, the plant, and two feedforward and feedback transport delays (Delay, and Delay,) is shown by the solid line. 1wo internal, predictive loops are indicated by broken lines Reference is made in the text to these three numbered loops. Comparators are indicated by circles with one filled quadrant; the empty circle is a positive-feedback connection Schemes 2 and 3 show functionally equivalent circuits with rearranged internalloop5.

The power of the proposal is that as long as the predictive plant and delay models are accurate, the transport delays are effectively moved outside the feedback control loop, as the actual and predicted feedback cancel each other out. The time Delay[remains on the feedforward path, of course, but does not destabilize the control.

Smith pointed out that the models can be partially combined (F'igure 3 B) , so that one model represents the plant without delays, the other forms a pure time delay. The models can also be rearranged to allow a positive-feedback loop, by shifting the comparator from the external feedback path onto the feed forward path (Figure 3C) .

It is important to realize that the models contained within the Smith Predictor predict the expected response of the plant to a command. In physiological terms, they predict the sensory consequences of movement. Thus the inner loop (Loop I) provides a rapid prediction of the outcome of each motor command sent to the arm, whereas the outer loop (Loop 2) provides a prediction of the feedback synchronous with the actual feedback.

An Illustration of Smith Prediction

A Computer Simulation

To demonstrate the advantages of the control scheme, we present a very simple simulation of the control loop for arm movements (Figure 4A). In a visually guided tracking task, the subject's responses can be approximated by a first-order low-pass filter with a corner frequency of 0.9 Hz and a delay of about 150 ms (Miall et al. , 1986). In practice, the system must be organized as a negative-feedback loop with a gain term and an integrator; and it seems to be an intermittent or sampled controller (Craik, 1947; Miall, Weir, & Stein, 1993; Wolpert, Miall, Winter, & Stein, 1992). In the present simulations, however, we have ignored the intermittent nature of the tracking. The gain term was then set as high as is compatible with stable performance. We present simulations of the model tracking a step change in the input (upper panel of Figure 4B), and a 0.3-Hz sine wave (lower panel). For comparison, the record in Figure 5A is of the movement of a joystick held by a rhesus monkey trained to track a sinusoidal target. Similar records are found from humans, as long as the target function is unpredictable (if the target is a predictable sinusoid, the human subject can reproduce it without significant error and with zero lag; Weir, Miall, & Stein, 1989).

The Effect of increasing Feedback Delay

To demonstrate how the delays are effectively isolated from the control loop, we tested the simulation in Figure

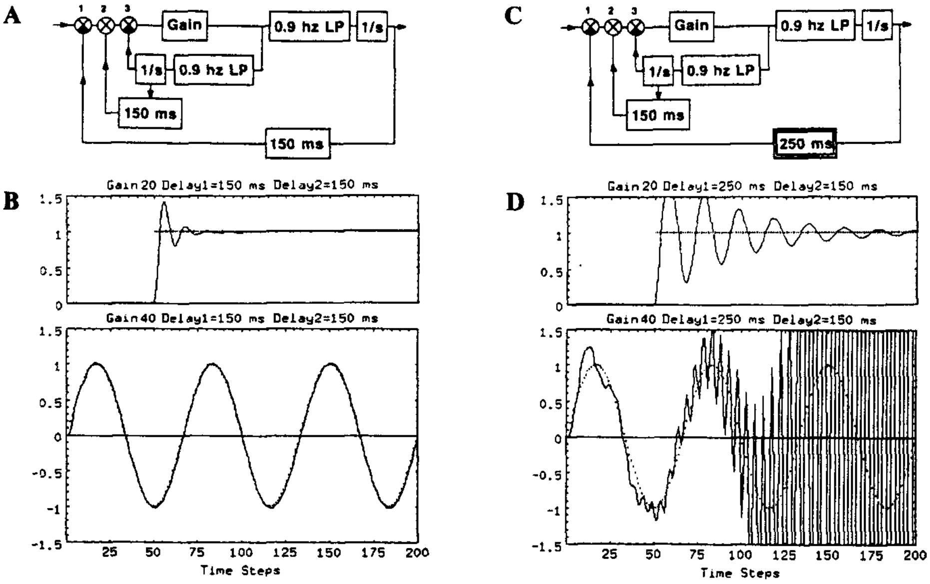

FIGURE 4. A. A simple Smith Predictor simulation of visually guided tracking The feedback loop contains a gain term, the controlled object (modeled as a 0 9-Hz low-pass filter), an integrator, and a 150-ms time feedback delay The simulation was run with a 0.05-s time step. B. Responses of the simulation to unit step (upper panel, from 0 to I on the 50th time step) or to a sinusoid (lower panel, 03 Hz, amplitude 1.0) The dotted line represents the target position; the solid line the model's response C. The simulation with a 100-m5 mismatch between the feedback loop delay and internal Smith Predictor delay D. Responses of the simulation with a delay mismatch-errors in the outer loop are amplified by the high gain, leading to instability

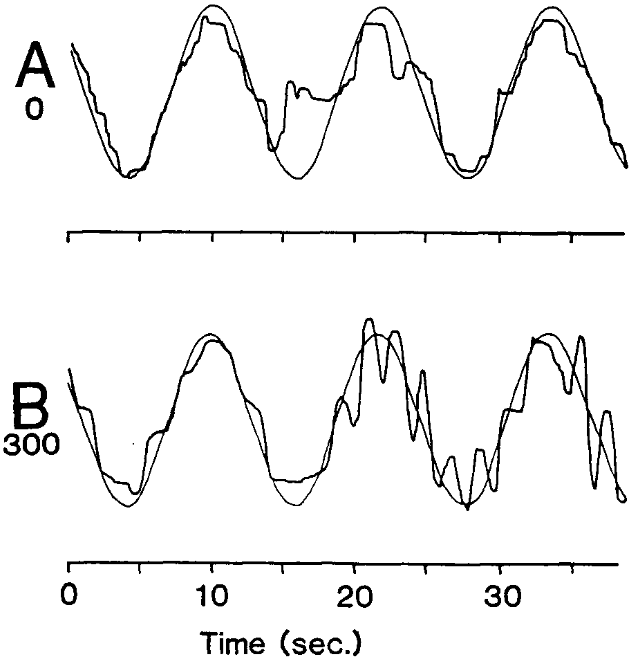

FIGURE 5. Tracking responses of primates. Each graph shows the position of a joystick (thick line) held by a monkey trained to follow a target (thin line) displayed on a computer screen. A. Normal responses. B. Responses when the cursor providing visual feedback was delayed by 300 ms. On the left is a period of slow, intermittent tracking; on the right, the monkey has slipped into instability. (Modified from Miall et al, 1986.)

4C with an additional loop delay of 100 ms. Because the internal model of the delay was then inaccurate, errors accumulated as the output of Loop 2 failed to match that of Loop 3, and the model became unstable (Figure 4D). For comparison, Figure 5B shows the monkey tracking with an experimentally increased feedback delay (Miall et al. , 1985). The simulation's stability could be regained by reducing its open-loop gain (Figure 6A; compare with Figure 58, left), but at the cost of sluggish responses and significant lag (Figure 6B). If the internal model of the delay was now adjusted to accurately reflect the increased external delay (Figure 6C), however, then the system would be again stable (Figure 6D). Hence. it operated at the same high gain as shown in Figure 4A and B, despite a 66% increase in the loop delay from 150 to 250 ms.

The Effect ofan Inaccurate Dynamic Model

To indicate the type of errors expected from a Smith Predictor with an inaccurate model of the plant dynamics, we ran the same simple simulation with a corresponding 66% change in the dynamic model, changing the low-pass filter frequency from 0.9 to 0.54 Hz (Figure 7 A). The model again showed performance typical of a poorly adjusted servo, with overshooting leading gradually toward instability (Figure 7B).

Reducing Dynamic Phase Lags

Although the Smith Predictor effectively removes pure feedback delays from the control loop, there also are delays introduced by the plant dynamics. A low-pass filter has a phase lag (a delay) that cannot be simply isolated and modeled within the second control loop of the Predictor. If some inaccuracy is allowed in forming the internal dynamic model of the Predictor, however, then it is possible to reduce the phase lag introduced by the dynamic components of the plant. For example, a plant comprised of a 0.9-Hz low-pass filter in series with a 150-ms time delay has, for input frequencies of under 2 Hz, approximately the same phase characteristics as a 1.35-Hz filter and a 200-ms time delay. Because the Smith Predictor can compensate for pure time delays in the feedback control loop, the latter system would have better response characteristics: It reduces to a filter with a higher cut-off frequency (1.35 Hz instead of 0.9 Hz) and thus a smaller intrinsic phase lag. This would improve the control characteristic of the inner feedback loop, without seriously impairing the complete controller. The predictions of such a model would not be completely accurate, however, so some corrections based on the actual outcome of the movements would be needed. Such approximations would seem quite likely in physiological systems. Voluntary movements are known to require intermittent feedback for accuracy, suggesting that the CNS does not form accurate predictions of the movement outcome. For example, although capable of operating on predicted feedback at 3 or 4 Hz in visually guided tracking, subjects seem to require periodic updating of their actual performance; and they are unable to execute accurately a long sequence of prediction-based movements. The approximations could be either in the dynamic model, as above, or in the time delay estimations. Schleck and Hanesian (1978) have shown that the Smith Predictor can tolerate some errors in its models of the real controlled object and that the dynamic model accuracy is less critical than that of the delay model. They suggested that up to 60% error in the specification of the time constant of a low-pass filter dynamic plant can be tolerated, and 30% error in the specification of the time delays, before the Smith Predictor's performance becomes less accurate than that of an optimally tuned linear proportional-integral-differential controller.

A Physiological Model

The previous section has indicated briefly how a Smith Predictor could assist in motor control. In this section, we try to describe how the Smith Predictor model may be realized within the cerebellum, how the internal models could be learned through experience, and how our hypothesis compares with other forms of internal control model.

Fitting the Model Jnto Cerebellar Physiology

The Smith Predictor hypothesis has a number of constraints. One is that there should be separate dynamic and time delay neural models. The models should receive as inputs an efferent copy of the motor command being sent to the controlled object (the limb), and also proprioceptive information about the current state of the body. The latter is needed for an accurate internal representation of the limb, as the arm's mechanical properties depend on its position. Hence, the internal model must be updated by the proprioceptors. The internal models should lie on feedback loops, so that their output feeds back onto the input as indicated in Figure 3. Finally. there must be a mechanism to allow

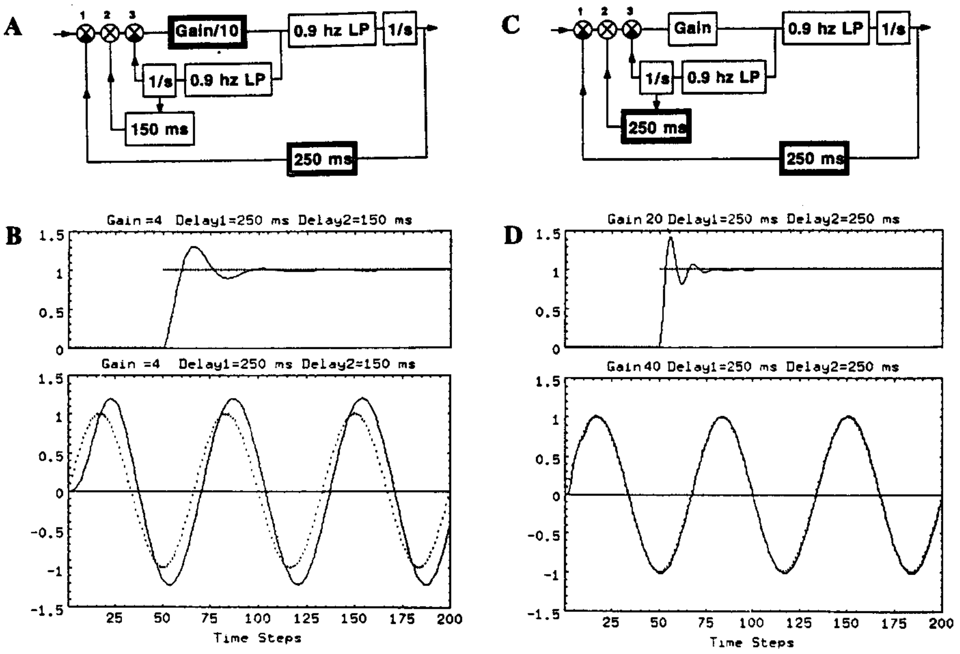

FIGURE 6. Modifications of the simulation to return to stability A. The gain was reduced by a factor of 10; responses were then stable but slow (8). C. The Smith Predictor loop delay modcl is adjustcd to accuratcly rcflcct thc longer loop delay; stablc control can then be achieved even with the original high gain (D)

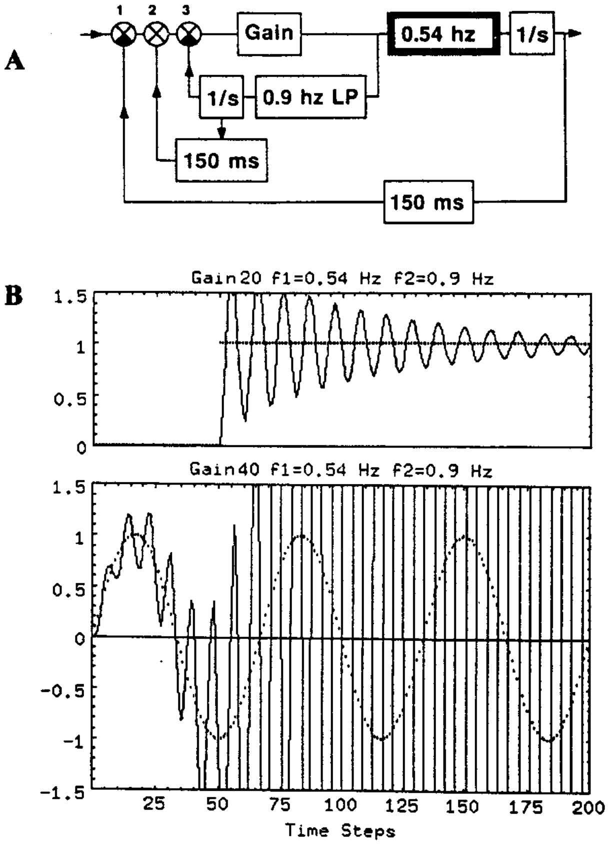

FIGURE 7. Responses of a Smith Predictor to dynamic model mismatch. The simulation shown in Figure 2A was tested after reducing the cut-off frequency of the low-pass filter from 0.9 Hz to 0.54 Hz (A), resulting in instability (8).

the model to be adapted to predict accurately the behavior of the controlled object, that is. a neural learning mechanism. For visual guidance of movement, the cerebellum is an obvious candidate. The lateral cerebellum forms a link between visual association areas, especially the posterior parietal cortex, and the motor and premotor cortices. The posterior parietal cortex is believed to be concerned with the localization of targets of interest in visual/egocentric coordinates (Andersen & Gnadt, 1989; Stein. 1989). There are strong connections from the posterior parietal cortex , via the pontine nuclei, to the lateral hemispheres of the cerebellum (Mower, Gibson, Robinson, Stein, & Glickstein, 1980) . The lateral cerebellum projects via the dentate nucleus to the ventrolateral thalamic nucleus, and then to the premotor and motor cortices (Alien & Tsukahara, 1974). This cerebrocerebellar pathway may well be the major route by which visual information reaches the cortical motor areas for the guidance of the limbs (Stein, 1986). *If* this route was to contain a Smith Predictor, it would serve to transform a movement command (an instruction to reach a desired goal) specified by the posterior parietal cortex in visual, egocentric coordinates (Stein, 1989) into a motor control signal, and transfer it to the motor cortex. The inner control loop of the Smith Predictor (Loop I) might be formed by interaction between the cerebellar cortex and the deep cerebellar nuclei, as there are reciprocal connections between the two (Chan-Palay, 1977; Tolbert, Bantli, & Bloedel, 1976, 1978). Thus, for limb control, the input to the lateral cerebellum would be the current error in hand position or the desired movement of the hand. The cerebellar cortex would contain the forward model of the limb, and the inhibitory projection of Purkinje cells onto the dentate nucleus would provide the negative output of the model. The outer control loop of the Smith Predictor (Loop 2) requires an output that is delayed to match the returning visual feedback, perhaps 150-250 ms later. This loop could contain either a combined dynamic and delay model in parallel to the first (Scheme I, Figure 3) , or a pure time delay model following the dynamic model (Schemes 2 and 3, Figure I). Scheme I would mean that the cerebellum holds two similar models of the plant, which operate in parallel. This scheme may be difficult to implement, however. It requires that the two internal dynamic components (Plant Model1 and Model2) be identical; if they are not, the models in the outer loop (Plant Model1 and Delay Model) cannot correct for the performance errors caused by the inner control loop. Thus, even when the dynamic Plant Modell and Plant Model2 are inaccurate representations of the actual plant, they must be identical to each other, which places a hard constraint on their learning mechanism. Schemes 2 and 3 require serial models in which the dynamic and delay components are clearly separate. Thus, one can be adapted in isolation from the other, and the learning task simplified. Their interaction could be realized by reentrant loops from the cerebellar nuclei back to the cerebellar cortex, either directly or via precerebellar mossy fiber sources (NRTP, LRN, etc.).

Because the internal models must predict the expected outcome of movement in a form suitable to compare with the actual outcome, these internal models would operate in visual or egocentric coordinates. Scheme 2 requires that the output from the second internal loop be directly compared with the actual sensory feedback, so that the output of the cerebellar model should inhibit direct sensory inflow. In the visual tracking model, this would require modulation of visual signals. Scheme 3. by rearrangement of the Smith Predictor loops, has the advantage that direct sensory feedback pathways are undisturbed. Instead it requires a positive-feedback pathway (Loop 2), for which there are a number of candidate circuits: via the red nucleus, ventrolateral thalamus, or premotor and motor cortices. This model is then related to a model of oculomotor smooth pursuit suggested by Robinson et al. (1986), who included time delays in a positive-feedback loop to cancel reafferent feedback signals. It is very close to a model by Schlag, Schlag-Rey, and Dassonville (1989) for control of saccades.

Multiple Smith Predictors

The model discussed so far would be expected to operate in a circuit between association cortex and motor cortex, via the lateral hemispheres. However, there are also strong interconnections between the intermediate cerebellar cortex, the red nucleus, and the motor cortex (Allen & Tsukahara, 1974). There could then be a second Smith Predictor model situated in the intermediate cerebellar cortex, operating on the outflow from the motor cortex. In other words, the loop would be formed by the corticobulbar fibers and collateral branches of corticospinal fibers reaching the intermediate cerebellum, via the pontine nuclei, and then either projecting back to the motor cortex or to the red nucleus and reticular formation, en route to spinal circuits. This would therefore be a model that was predicting the consequences of descending motor commands in *motor* coordinates, and would thus predict the kinematic consequences of limb movement. Figure 8 shows how these two control loops could be hierarchically nested. A third model could even be formed in a spinocerebellar circuit, predicting the outcome of the spinal drive to motor neurons and perhaps predicting proprioceptive events at the level of single muscles. The path here would be from long propriospinal neurons in the ventral spinocerebellar tract to the medial zones of the cerebellum, and back via the reticulospinal fibers .

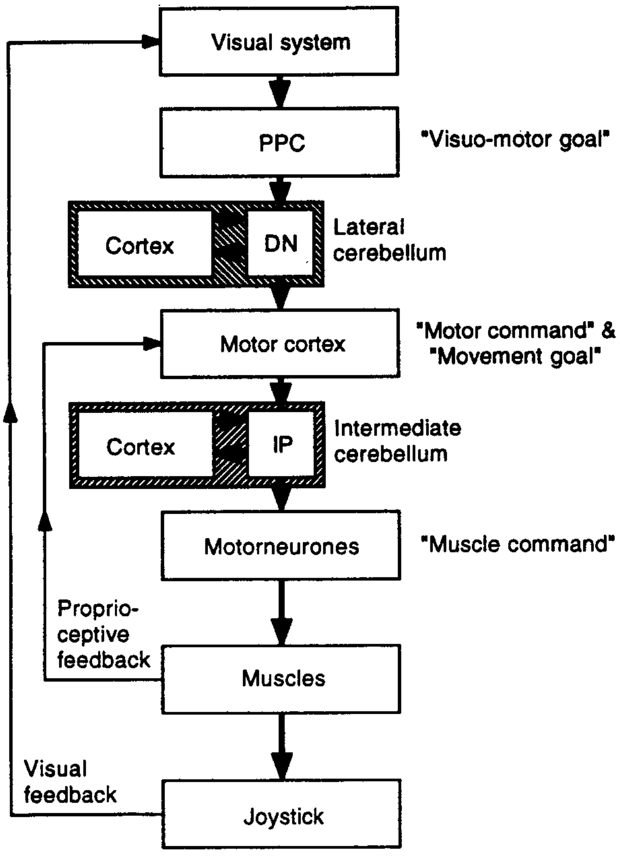

FIGURE 8. A schematic model of visually guided tracking.

Visual inputs (target and cursor positions) are fed to the posterior parietal cortex (P PC). which calculates a movement goal in visual, egocentric coordinates. The Smith Predictor model in the lateral hemispheres of the cerebellum converts this signal into a motor command, fed forward to the motor cortex This then issues a movement goal. specified in motor coordinates, that is converted by the intermediate cerebellum into a muscle command to the spinal cord. Feedback returns from the proprioceptors in motor coordinates and from the joystick-controlled cursor in visual coordinates

Of course transport delays in these short control loops are progressively smaller as one approaches the motor neurons. and so the demand for advanced predictions may become somewhat less critical. However, other predictive models could be held within the cerebellum, for any situation where the normal control loop would entail long loop delays (see "Generalization of the Predictor Concept").

Other Forms of Control Based on Internal Models

How does this control scheme relate to other proposed schemes'? The main alternative idea is that of inverse dynamic, feedforward modeling. Inverse dynamic models reverse the dynamic responses of the controlled object (Atkeson, 1989). Dynamic equations govern the *forward* transition from muscle torques to limb motion, and therefore describe the behavior of the controlled object to a motor command. An inverse dynamic equation transforms a desired limb motion signal back into the corresponding muscle torques. In other words, it acts to translate a motor goal specified in egocentric or peripersonal coordinates into an optimized control signal to achieve the required goal. Kawato et al., (1987; Kawato & Gomi, 1992) and Ito (1990, 1991) have proposed that the lateral hemisphere of the cerebellum holds an inverse dynamic representation of the limb and thus forms a feedforward pathway from the visual association areas to motor areas. In addition, they proposed that the intermediate cerebellum forms a feedback loop similar to the loop we proposed here.

The inner loop of a Smith Predictor (Loop I) effectively achieves in practice the same result as an inverse dynamic model. The output from a negative-feedback loop with negligible delay and with a high open-loop gain will drive its plant in the direction that minimizes the comparator error. Thus, it acts to convert the input reference or goal signal into a motor command suitable to achieve that goal. A fast internal loop through a forward neuronal model is therefore functionally equivalent to an inverse-dynamic model; it is the linear equivalent to the nonlinear inverse dynamic model (Deno, Keller, & Crandall, 1989; Kawato & Gomi, 1992). Thus, using negative feedback loops, the same basic computational process could operate in both lateral and intermediate cerebellar circuits, alleviating the need to propose different model architectures for each cerebellar region.

Another problem with the inverse filter idea is that it is not clear how an inverse dynamic model could be generated by the cerebellum. Training schemes have been proposed that could implement the inverse model in artificial neural networks, but these are computationally complex (Barto, 1990; Jordan & Rumelhart, 1992). The primate limb is a highly redundant manipulator, able to position the fingertip in space with anyone of many combinations of joint angles. Thus, there is no unique inverse kinematic relationship between finger position and joint angles, and so no unique path for the elbow when the finger is moving to the target. Furthermore, no unique invertable relationship between desired goal and motor command can exist for the primate limb, and so no unique inverse dynamic model can be developed to specify the desired trajectory along any selected path. It is therefore not trivial to decide which of many inverse models should be learned. Jordan (1988) has proposed that one can first form a forward model and then back-propagate errors through this model to derive a suitable error signal to train a neural network to form an inverse dynamic model. This would not seem a likely training scheme for the cerebellum, as back-propagation itself is difficult to implement neuronally (Mitchison, 1989). However, Kawato and colleagues have developed a technique to form the inverse model that does not require this forward model (Kawato et al. , 1987; Kawato & Gomi, 1992). Their technique, called *feedback-error-learning,* uses the motor commands from an auxiliary feedback controller as an error signal; by reducing this error signal to zero, the network necessarily becomes an inverse feedforward model and functionally replaces the feedback controller. Their technique requires that the basic feedback control pathway be very low gain when used with significant feedback delays, however. In contrast. a Smith Predictor model sits within a high-gain feedback loop; so it may be possible to distinguish between the two schemes by studying their responses when the internal model is inaccurate. We also believe that the forward model of the Smith Predictor may be more easily learned than an inverse filter because its task is to mimic actual limb behavior on the basis of known motor commands, in other words, to form a unique model. In addition, the time delay component of the Smith Predictor mimics the actual feedback delays.

Learning the Smith Predictor Models

A second important constraint on the Smith Predictor hypothesis is that sufficient information should be available to allow the cerebellum to not only generate but also modify each neural model. It is most unlikely that the central nervous system could develop *in utero* with a precise neural representation of all the effectors of the body. Clearly, in addition, the representation would need to be plastic to adapt to changes in the motor system performance. The dynamic responses of a limb change greatly during growth, whereas delays can change either because of increased axonallengths, or following changes in the sensory responses (Deno et al. , 1989; Wolpert et al. , 1992). Thus, to lay down useful internal representation of the motor system the controller is required to actively explore the environment to assess the outcome of its actions (Barto, 1989). The responses received back from the environment tell the controller not only about its effects on the external world but also about the controlled object, that is, the arm. Thus, generation and modification of the internal models needed for a Smith Predictor controller is a learning problem in which two processes have to be learned: early estimation of the outcome of actions and estimation of the delay before actual feedback will be received. These must be learned by using delayed signals from the periphery.

The dynamic behavior of the controlled object can be learned by a predictive process. The neuronal network would receive an efferent copy of the current motor command as well as the current state of the effectors from proprioceptive, cutaneous, or visual inputs. The network's output would be passed through the delay model for comparison with the actual feedback from the movement. Hence, the output of the dynamic model will be correct only if it anticipates actual feedback by an amount equal to the time delay (Barto, 1990).

The size of the feedback time delay could be estimated by measuring the delay between issuing a motor command and assessing its result. This would be most easy to do if the motor command were discrete (Craik, 1947; Miall et al. . 1986, 1993), for the reafferent signal would then change abruptly. It is thought that some test-pilots "jiggle the controls" to get this same sense of feedback delay. The parallel fibers within the cerebellar cortex could act as a "tapped delay line" (Braitenberg, 1961), thus allowing the encoding of a time interval; Desmond and Moore (1988) proposed that chains of pontine nuclear cells do the same thing. Neither scheme is suitable for long time delays, however. Instead, a predictive neural network can be trained to predict backward in time as easily as forward; and back-prediction of a signal is equivalent to delaying it. Thus, just as we suggest that the lateral and intermediate cerebellar regions have the same functional role as Smith Predictors, we suggest that both models within the Smith Predictor consist of predictive neural networks. The first model makes a torward prediction of the outcome of the controller's actions. The second model makes a backward prediction, based on the output of the first model, and resulting in a delayed copy of the controller's actions.

The Role of the Inferior Olive in Learning

Several authors have suggested that the climbing fiber input from the inferior olive (IO) may provide a training input to the cerebellar cortex (see Ito, 1984; or Strata, 1989). The climbing fibers should therefore signal the need for adaptation. in other words, signal back the fact of a mismatch in predicted and actual feedback. A mismatch could mean that the prediction was inaccurate or the effector's behavior had changed, but in either case the models would require adaptation. Gilbert and Thach (1977) showed that the average rate of climbing fiber activity increased as monkeys adapted their movements to a novel load; it is also known that the climbing fibers signal retinal slip, "Which is the appropriate error signal to modify the VOR reflex (Graf, Simpson, & Leonard, 1988). Armstrong, Edgley, and Lidierth (1988) and Gellman, Gibson, and Houk (1985) have shown that the most potent stimulus for climbing fibers is an unexpected sensory event and that similar "reafferent" sensory stimuli resulting from the animal's own actions do not excite the climbing fibers. There is now strong evidence that coincidence of climbing fiber and parallel fiber inputs to Purkinje cells results in long-term depression of the parallel fiber:Purkinje cell synapse (Crepel & Jaillard, 1991 ; Ito, 1989). This may allow the cerebellar cortex to learn or modify a neural representation of the limb dynamics. These data therefore suggest that the inferior olive signals differences between the prediction of sensory reafference and the actual reafference. In other words, we suggest that the delayed prediction from the cerebellum is fed to the IO for comparison with sensory feedback signals. There are indeed inhibitory pathways direct from the cerebellar nuclei to the IO, and also indirectly via the red nucleus (Weiss, Houk, & Gibson, 1990). Thus the inferior olivary signals should modify the dynamic model, to ensure that the inner loop of the Smith Predictor accurately mimics actual performance. The climbing fiber inputs probably cannot signal the quantitative size of the mismatch, however. Instead, they may signal the event of a mismatch, and perhaps also the direction of the error (Houk, 1990). Barto (1990) reviewed techniques to train neural networks with this sort of reinforcement signal. Thus the major role that we would attribute to the IO is making the comparison between expected and actual sensory signals. This is vital to provide a teaching signal for the cerebellum.

The Role (~f Adrenergic Inputs to the Cerebellum

The fact that the Smith Predictor contains two separate models requires training signals for both. We propose that the IO provides one, allowing the dynamic model to be learned. The second training signal could be provided by the diffuse noradrenergic and serotonergic inputs from the locus coerulus and raphe nucleus. These could provide a "performance measure" reporting to the cerebellum on the overall success of the behavior (Gilbert, 1975). We imagine that this measure could be something like a running average of positional errors in a tracking task, or the retinal slip accumulated over a few minutes in a VOR task. In support of this view, Van Neerven, Pompeiano, Collewijn, and Van der Steen (1990) have shown that beta-noradrenaline can interfere with VOR adaptation in the rabbit, whereas D'Ascanio, Manzoni, and Pompeiano (1991) have shown than noradrenaline blockers reduce the gain of vestibulospinal reflexes. Thus the time delay model within Loop 2 of the Smith Predictor might be trained with reinforcement learning on the basis of nonspecific performance criteria (Barto, 1990), whereas the more specific signals provided by climbing fibers train the dynamic model within Loop I. An alternative is that both models would be modified by climbing fiber input, but with very different learning rates. We have shown that humans (Miall, Kerr, Wolpert. & Forsyth, 1990) and monkeys (unpublished data) are very much faster to adapt to changes in the gain or load of a tracking manipulandum than they are to a change in its feedback delay. This would suggest that the dynamic model is rapidly modified within the cerebellum, whereas the temporal delay model is much slower to adapt. Deno et al. (1989) have shown that oculomotor adaptation to feedback delays does occur over several days; and long experience with delayed feedback in tracking paradigms certainly improves performance (unpublished data). Thus adaptation to time delays does take place in primates, as would be expected from an adaptive Smith Predictor, but is slow. Hence, we propose that the inner loop of the Smith Predictor would adapt rapidly to changed dynamics, driven by IO input, whereas the outer loop would adapt more slowly to changed feedback delays, driven either by the same IO signal or by the noradrenergic or serotonergic inputs. The difference in learning rates may be functionally unimportant; as in everyday experience it is the dynamic behavior of the motor system that changes rapidly, for example, when carrying heavy objects, rather than the feedback delays.

Generalization of the Smith Predictor Concept

It is clear that the cerebellum is involved in a wide range of physiological processes, some of which seem to have rather little direct relationship to motor control. Straightforward extrapolation of the Smith Predictor control strategy to other areas may explain some of these. For example, the cerebellum has a number of autonomic functions, including cardiovascular control, gut motility, and others (for a review, see Haines & Dietrichs, 1989). The reason for its role in these processes may be closely related to its roll in motor control: Most autonomic control systems have significant loop delays and so are potentially difficult to control with negative feedback. Prediction of the responses of the humoral system or the cardiovascular system to a change in hormone or neurotransmitter release would be advantageous.

Evidence is accumulating for a cerebellar role in associative learning of word pairs, colors, and other non-movement-related tasks (Barker et al., 1991; Bracke-Tolkmitt et al. . 1989; Decety. Sjoeholm, Ryding, Stenberg, & Ingvar. 1990). In associative learning, the task is to choose an action on the basis of one of two previously presented stimuli. In classical conditioning, a reflex act such as an eye-blink becomes associated with a conditional stimulus such as an audible tone; the cerebellar involvement in classical conditioning of the nictitating membrane response was mentioned earlier. In both of these cases, the output behavior is such a simple motor act that it seems unlikely that the cerebellum would be concerned with the movement's metrics. Thus, the cerebellum is probably only peripherally involved in the movement itself (an eye-blink, a simple key-stroke, or vocalization of a simple word) but seems to be involved in the learning process.

We suggest that these and other cases of cerebellar function may be linked together if one extracts the essential predictive features of the Smith Predictor away from its role within negative-feedback motor control. If the cerebellum is assumed to predict the sensory consequences of actions, then it becomes potentially invaluable in all activities. Thus the twin models within the Smith Predictor suggest that the dynamic prediction and temporal predictions (delays) could be separated, and either function applied to other processes. For example, the most likely role of the cerebellum in the nictitating membrane response is in timing the conditioned response with respect to the unconditioned stimulus (Desmond & Moore, 1988). The unconditioned stimulus (for example, an air-puff) normally evokes a blink, and so, during conditioning, the conditional stimulus (an auditory tone) must become associated with a motor command timed to shut the eyelid at the moment of the air-puff. The cerebellum, by predicting the time of the unconditioned stimulus after the conditional stimulus, is predicting a later sensory event, which is clearly related to the sensory predictions made by the Smith Predictor temporal model. Ivry and Keele (1989) have shown that the cerebellum has *a* role in tasks involving estimation of time intervals and in production of simple rhythmical sequences; and again - these could easily be related to the timing model within a Smith Predictor. Timing forthcoming events can therefore be considered as the same process as prediction. As Keeler (1990) also pointed out, assigning the cerebellum a predictive role may explain why it is so prominent in electric tish-animals with a limited motor repertoire but with a great need to differentiate the effects on their electrical-discharge echoes of their own movements from those changes due to reflection by unexpected objects in the environment. Again, the task requires accurate temporal registration of the prediction and the returning signals.

In contrast to an inverse model, a forward model allows the CNS to evaluate actions before making a movement. Decety et al. (1990) have recently shown that cerebellar local blood flow rates are enhanced if a subject only thinks about making a movement sequence, which implies that the subjects are indeed using a forward model to assist in movement planning. The Smith Predictor model situated in the lateral hemispheres of the cerebellum would be involved, converting the intention to move into a potential movement command, whereas execution of the command could be gated out by the motor and premotor cortices.

In the vestibuloocular reflex, the control task can be stated as one of predicting from head movement the correct compensatory eye movements. There is no direct feedback from the visual system to the vestibular nuclei and no time to use visual feedback to maintain a steady gaze position. In fact, the VOR is a complex task, as the amount of eye movement required to stabilize an image depends on the target's distance from the eye: The eyes are not exactly at the center of rotation of the head. so that a fixation point close to the head appears shifted by a different angle than one at infinity. In translational rather than rotational VOR, this effect can be pronounced. Thus these compensatory reflexes may require complex inverse models to accurately compensate for head movements (Keeler, 1990). In this case, the Smith Predictor in the cerebellum would probably function on a feedforward pathway, using the inner negative-feedback Loop 1 to form the inverse model. Because the VOR has no feedback pathway, the outer loop of the Smith Predictor delaying the fast prediction is not required.

Finally, it is tempting to suggest that the cerebellum may be involved in much more complex predictions, linking it to more cognitive processes (lto, 1990). There is a link between autism and cerebellar degeneration (Holroyd, Reiss, & Bryan, 1991) . and autism seems to be characterized by an inability to understand the mental reasoning of others. Perhaps the autistic child cannot model or predict the behavior of other people. It will be very interesting to see how extensive are the predictions made by the cerebellum.

Summary

We suggest that the role of the cerebellum is to form linked pairs of neural models for motor control. We liken these models to the engineering control strategy known as a Smith Predictor. The key feature of this scheme is that the models provide, first, a rapid prediction of the outcome of a motor command and, second. a delayed copy of that prediction, which will match in time the actual feedback arising from the movement. By combining both these functions, fast and stable control can be achieved even in the face of long loop delays. The advantages of such a system for physiological motor control are that the models ought to be easier to generate than inverse dynamic models and that they are incorporated into a feedback loop, so that any errors or inaccuracies are automatically compensated throughout development of the models. The scheme also maintains a common computational role for all areas of the cerebellum, as its anatomy suggests.

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