A cerebellar model for predictive motor control tested in a brain-based device

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Contributed by Gerald M. Edelman, December 29, 2005

The cerebellum is known to be critical for accurate adaptive control and motor learning. We propose here a mechanism by which the cerebellum may replace reflex control with predictive control. This mechanism is embedded in a learning rule (the delayed eligibility trace rule) in which synapses onto a Purkinje cell or onto a cell in the deep cerebellar nuclei become eligible for plasticity only after a fixed delay from the onset of suprathreshold presynaptic activity. To investigate the proposal that the cerebellum is a general-purpose predictive controller guided by a delayed eligibility trace rule, a computer model based on the anatomy and dynamics of the cerebellum was constructed. It contained components simulating cerebellar cortex and deep cerebellar nuclei, and it received input from a middle temporal visual area and the inferior olive. The model was incorporated in a real-world brain-based device (BBD) built on a Segway robotic platform that learned to traverse curved paths. The BBD learned which visual motion cues predicted impending collisions and used this experience to avoid path boundaries. During learning, the BBD adapted its velocity and turning rate to successfully traverse various curved paths. By examining neuronal activity and synaptic changes during this behavior, we found that the cerebellar circuit selectively responded to motion cues in specific receptive fields of simulated middle temporal visual areas. The system described here prompts several hypotheses about the relationship between perception and motor control and may be useful in the development of general-purpose motor learning systems for machines.

Recent theory of the cerebellum (1), consistent with much of the neurophysiological, behavioral, and imaging data regarding motor control, proposes that the cerebellum learns to replace reflexes with a predictive controller. This predictive controller produces a correct motor control signal earlier than less adaptive reflex responses. Numerous adaptive cerebellar functions are subject to this type of control, including eye-blink conditioning, the vestibular–ocular reflex, smooth pursuit eye movement, spinal nociceptive withdrawal reflex, grip force adjustments, arm movements, and saccadic eye movements. At present, however, the mechanisms responsible for this predictive capability are still debated. Proposals for such mechanisms include delay lines, spectral timing, oscillators, or dynamic recurrent activity in granule cells (for a review, see ref. 2).

It has been suggested that reflexive motor commands are used as error signals for the predictive controller and that they are delivered to the cerebellum by way of climbing fibers from the inferior olive (IO) (1, 3). Synaptic eligibility traces in the cerebellum have recently been proposed as a specific mechanism for such motor learning (4). Based on motor timing studies, Medina et al. (4) proposed an eligibility trace that is triggered by motion onset and that peaks at 150–200 ms with durations of 1–2 s. We suggest a slightly different mechanism. In our model, we incorporate a learning rule in which the synapses onto a Purkinje cell (PC) or onto a cell in the deep cerebellar nuclei (DCN) became eligible for plasticity only after a fixed delay from the onset of suprathreshold presynaptic activity. Synaptic strength changes would occur at eligible synapses only when the climbing fibers from the IO signaled a motor error. This delayed eligibility trace learning rule was formulated to shape cerebellar responses to anticipate and avoid an impending motor error.

To provide a stringent test of this rule, we embodied a cerebellar model incorporating the rule in a brain-based device (BBD) (5–8), which had to smoothly traverse a curved course outlined by a series of traffic cones. As in other neurorobotic systems (9–13), the behavior of such a BBD is guided by a simulated nervous system, incorporating features of vertebrate neuroanatomy and neurophysiology, which determine the device’s interaction with the environment. These means allowed us to simultaneously record the state of all components of the selected nervous system during the performance of a behavioral task in the real world. The BBD’s task was to associate predictive visual motion cues with the correct movements to avoid collisions with the cone boundaries.

The computer simulation incorporated into the BBD included visual input from the middle temporal visual area (MT) (14), a cerebellar cortex, DCN, and climbing fiber input from the IO (Fig. 1). To distinguish modeled areas from corresponding regions in the mammalian nervous system, the names of simulated areas are indicated in italics (e.g., MT). The simulated MT, which contained retinotopically mapped neuronal units, was constructed to use the idea that image blur can provide motion information (15, 16). Simulated MT neuronal units responded to a combination of direction-selective cells (17) and orientation-selective cells from a simulated primary visual area (V1) (15). The BBD received an error signal through climbing fibers triggered by IR proximity detectors when the device was within 1 foot of the cones in the path boundary. The error signal, which initiated braking and movement away from boundary, also caused changes in synaptic efficacy between MT and cerebellar neuronal units. After learning by the BBD, MT input that predicted potential errors resulted in movement away from path borders well before the occurrence of an error signal.

The results of this study suggest that a delayed eligibility trace rule may account for the predictive ability of the cerebellum in motor control tasks under real-world conditions. Our findings provide additional support for the theory that the cerebellum can learn to replace an arbitrary reflexive neural control system with a more adaptive, predictive controller or “preflex” (1). Moreover, the embodied approach adopted here allows detailed analysis of the types of motion signals a cerebellar circuit may select in motor control tasks.

Results
Motor learning was assessed on various “S”-curved courses marked by a set of orange traffic cones (Fig. 2). The platform for

Conflict of interest statement: No conflicts declared.
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Abbreviations: BBD, brain-based device; DCN, deep cerebellar nuclei; IO, inferior olive; MT, middle temporal visual area; PC, Purkinje cell; PN, precurricular nucleus; RMP, robotic mobility platform; Velo, velocity.

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this task was a Segway (Bedford, NH) robotic mobility platform (RMP) modified to have a camera, a laser range finder, and IR proximity detectors as inputs. The BBD’s simulated nervous system contained 28 neural areas, 27,688 neuronal units, and \( \approx 1.6 \) million synaptic connections (see Materials and Methods). Computation was carried out by an embedded Beowulf computer cluster on the device. It took \( \approx 40 \) ms of real time to update all of the neuronal units and plastic connections in the model each simulation cycle.

The BBD’s performance was tested on three different courses (Fig. 2B): a sharp set of turns (“sharp”), a moderate set of turns (“middle”), and a gentle set of turns (“gradual”). The device traversed each course until it reached the end; it then turned around and traversed the course in the opposite direction. Each traversal is referred to here as a lap. Training consisted of 20 laps and was followed by 4 laps of testing, during which the IR-driven reflex was inactivated and only visual cues were available to the device.

The IO is thought to transmit motor error information to the cerebellum (1, 18–20). In the present visuomotor task, motor error was signaled by IR proximity detectors when the device was within 1 foot of an obstacle. IR detector responses were converted into IO activations for turn errors (IO-Turn in Fig. 1 and Supporting Materials and Methods) and velocity (also referred to as “Velo”) errors (IO-Velo in Fig. 1 and Supporting Materials and Methods), which caused the device to reflexively turn away from obstacles and to slow down in the presence of obstacles. After learning, visual motion cues alone were sufficient to drive smooth movement down the center of the curved course (MT\( \rightarrow \)PN\( \rightarrow \)DCN\( \rightarrow \)Motor and MT\( \rightarrow \)PN\( \rightarrow \)PC\( \rightarrow \)DCN\( \rightarrow \)Motor in Fig. 1).

Learning was measured by the magnitude of a motor error, reflecting the average per lap IR responses to obstacles, where IR values range from 0 (no object within IR range) to 1 (an object within 1 inch of the IR detector). Training and testing in the task were repeated with five different “subjects.” Each subject consisted of the same physical device, but each possessed a unique simulated nervous system. This variability among subjects was a consequence of random initialization in the probability distributions of connections between individual neuronal units and the initial connection strengths between those units (Table 1, which is published as supporting information on the PNAS web site). The overall pattern of connectivity among neural areas remained similar, however, among different subjects. Each simulation cycle, the motor error, the device turn rate and speed, and the state of all neuronal units were recorded for analysis.

**Tests of the Delayed Eligibility Trace Learning Rule.** The effect of the trace delay (see Materials and Methods) on the ability to navigate a path outlined by the orange cones was tested by varying the delay interval. Delay intervals of 0, 2, 4, and 8 s were tested on the middle course (Fig. 2B) at a constant speed (60% of maximum speed or 0.75 m/s). During these experiments, the neural pathways controlling speed were absent. As a control, there was a “no learning” group in which the DCN\( \rightarrow \)Motor connections were lesioned, and behavior was driven by only the IR reflex.

The delayed eligibility trace learning rule was most effective at delays of 2 and 4 s in this task (Fig. 3A). After approximately five laps, the subjects with rules having 2- and 4-s delays transitioned from awkward movements and cone collisions to smooth movement down the center of the path. After training, connections from the IO were lesioned, and the system was tested with only visual cues (Fig. 3B). The motor error was significantly lower in subjects with moderate delays (2 or 4 s) than in control subjects with no learning. The motor error of subjects trained with no delays or long delays (8 s) were not significantly different from subjects with no learning (\( P > 0.5 \), Wilcoxon rank-sum test). In all subsequent experiments, the delay was held constant at 4 s.
Successful performance across the three courses with varying turns required a combination of braking and turning of the proper magnitude at the proper time. The 4-s delay incorporated into the delayed eligibility trace learning rule was sufficient for successful navigation on all three courses (Fig. 4). Subjects learned to slow down before and during turns, and they learned to turn in the proper direction at the proper time. Subjects on the sharp course, which contained nearly 90° turns, had slightly worse performances than on the other courses. Nevertheless, in the testing phase, subjects with cerebellar learning performed significantly better on all three courses than did subjects without learning (Fig. 4 B–D).

Subjects adapted their behaviors to the particulars of each course (Fig. 7, which is published as supporting information on the PNAS web site). For example, subjects were faster on the gradual course than on the sharp course. Success on the sharp course required slower speed and more frequent turning to the left or the right. Subjects on the gradual course typically proceeded at maximum velocity on the straightaways and simultaneously slowed and turned slightly on the curves. Learning on one course generalized to other courses. For example subjects trained on the sharp course were retrained on the gradual course (Fig. 8A, which is published as supporting information on the PNAS web site), and subjects trained on the gradual course were retrained on the sharp course (Fig. 8B). In both cases, initially trained subjects showed significantly better performance on the early training laps (e.g., laps 1–6) than naïve subjects (P < 0.005, one-tailed t test). Adapting from the gradual to the sharp course, however, required additional training to reach peak performance.

Neuronal Responses and Synaptic Plasticity During Behavior. An advantage of the synthetic neural modeling approach employing BBDs is that it allows simultaneous recording of the state and interactions of all components of the simulated nervous system at all levels during performance of a behavioral task in the real world. To understand what cues were triggering the BBD’s motor commands, we analyzed responses from the neuronal units as well as synaptic weight changes throughout the BBD’s training and testing. It was of particular interest to trace activity from the motor output units back to the simulated cortical areas for visual motion.

To be successful, the network had to initiate the appropriate motor responses based on motion cues. We previously developed a method, called a backtrace procedure (7), that identifies functional pathways by choosing a particular reference neuronal unit at a specific time and recursively examining the previous activities of all neuronal units that caused the observed activity in that reference unit.

We traced back for four 40-ms time steps, from the reference neuronal units in the motor areas (Motor-Turn and Motor-Velo) to the motion-selective neuronal units in MT. These backtraces were carried out after learning had taken place, laps 11–20, and on laps where there were low motor errors. Starting with a motor reference unit in Motor-Turn or Motor-Velo, the backtrace proceeded by first identifying a list of other neuronal units that were physically connected to the reference unit and that were active during the previous time step. The procedure was then repeated with this new list of neuronal units. This process was iterated until the MT units that led to the motor reference event were identified. By using this method, backtrace networks were
generated that were comprised of 377 turns to the left and 280 turns to the right. These backtraces represent a direct causal chain of neuronal units through the network from sensory input caused activity, which drove the motor neurons. After learning, visual input caused DCN activity, which then drove motor neurons before any error signal from IO (Fig. 9, which is published as supporting information on the PNAS web site). These changes were brought about by alterations in synaptic efficacy in which depression at the PC synapse caused disinhibition of DCN neuronal units resulting in DCN activity that drove motor activity. To a lesser degree, potentiation at the DCN synapses also increased the DCN response to visual cues (Fig. 10, which is published as supporting information on the PNAS web site).

We also examined the changes in synaptic weight due to experience-dependent plasticity changes based on our delayed eligibility trace learning rule. Depression at PC synapses was primarily responsible for velocity control (Fig. 6) and turning (Fig. 10). Motion cues indicating the proximity of a cone, whether on one side or the other of the visual field, triggered braking behavior. Moreover, when comparing synaptic weight changes in response to the different courses, the number and strength of the connections were changed to a greater extent in the case of the sharp course as compared with the gradual course (Fig. 6), correlating with the BBD’s overall lower speed on the sharp course (Fig. 7). Weight changes responsible for the control of turning (Fig. 10) had a pattern consistent with the MT responses shown in Fig. 5. Cerebellar potentiation and depression coupled with the proposed reflexive error signal from IO and the delayed eligibility trace learning rule were sufficient to adjust the weights in accordance with what is known about synaptic learning rules in the cerebellum (21).

Discussion

To test a general-purpose motor-learning algorithm, we constructed a BBD whose behavior was controlled by a synthetic neural model containing a MT and a cerebellum. This BBD was capable of learning a visuomotor task in the real world under varying conditions. We found that both the turning and braking reflex responses could be predicted and activated at the appropriate time and magnitude to prevent near-collisions with obstacles. Predictive cerebellar activity resulted in smooth motor responses that precluded awkward reflex responses and collisions, supporting a recent theory of cerebellar function (1). The BBD methodology allowed us to sample the detailed real-world responses of the device’s nervous system at all levels during the experiments.

In the path-following task presented here, the delayed eligibility trace learning rule allowed the BBD to develop adaptive motor control under varying conditions. Delays on the order of 2 and 4 sec resulted in successful behavior (Fig. 3). When delays were shorter than 2 s or longer than 4 s, the BBD did not perform better than nonlearning subjects on this task, supporting the need for a delay of appropriate duration. A delay of 4 s was sufficient for development of successful motor behavior under different course conditions (Fig. 4), and motor learning could generalize from one environmental situation to another (Fig. 8).

Note that we shifted the eligibility window onset to well beyond the 100-ms window onset inferred from eyeblink conditioning studies (20); this chosen window was optimal for the visuomotor

Fig. 5. Neuronal unit responses to different movements of neuronal units in the MT. Contour plots show the borders of MT neuronal unit activity before turning. The borders were found by tracing back from a motor unit that was active during a movement to the MT (see Results for details on the backtrace). The contours for the gradual, middle, and sharp courses are shown in red, green, and blue, respectively. Each contour depicts the MT neuronal units whose activities were above the 90th percentile. (A) MT responses during turns to the left (377 turn responses). (B) MT responses during turns to the right (280 turn responses).
task carried out by the BBD. Although our model had only one delay associated with the cerebellar synapses, we would predict that, if our proposed mechanism is validated, a behaving animal’s cerebellar circuits would have multiple delays. In that case, interaction of the organism with different demands in the environment would facilitate the selection of the appropriate delays and cerebellar circuits.

We analyzed patterns of neuronal activity in the simulated MT, which developed as a result of experiential learning and caused appropriate motor responses. These findings agree with recent results, suggesting that MT signals are implicated in cerebellar motor learning (14). In contrast to the present analysis, various models of MT have been carried out on computer simulations that were uncoupled from the environment (22–24). In addition, our model of MT was based on the suggestion that the visual system makes use of visual blur or streaking for determining motion direction (15, 16). By using streak information and combining a standard crosscorrelation motion-sensing algorithm (17, 25) with orientation-selective units, neuronal units in MT responded to visual motion and triggered appropriate motor responses under our experimental conditions. These elements were computationally efficient and unambiguous and may offer advantages over more computationally demanding models of motion processing (26, 27).

Inasmuch as all aspects of the neural model were accessible as the BBD performed its tasks, the backtrace procedure (7) could be used to extract the causal chain of neuronal elements that led to a behavioral event. Using this approach, we could observe the specific patterns of neuronal activity in our simulated MT that led to motor responses. These patterns were specific to the direction of apparent motion (i.e., down vs. up and left vs. right) and to the sensory-receptive field (Fig. 5). It is important to note that these responses were selected by the device through experience-dependent changes in synaptic plasticity, which were based on the ability of MT and the cerebellar responses to predict motor errors.

We were also able to observe the actual synaptic strength changes that subserved this experience-dependent learning, and the synaptic weight patterns gave further insight into the mechanisms underlying behavior. Weight changes corresponding to particular receptive fields were stronger when more control was necessary (Sharp vs. Gradual in Fig. 6). We demonstrated that the combination of strong depression at the PC synapses and potentiation to a lesser degree at the DCN synapses was sufficient for successful learning of the visuomotor task under a variety of conditions.

Adaptive behavior depends on nervous system morphology and dynamics as they interact with the phenotype and the environment. The BBD presented here was designed to take advantage of these attributes and also provide insights into motor control and visual perception. It will be of interest to determine whether the learning rule described here has applications in animal systems. In any case, the methodology may be useful as groundwork for the development of a general-purpose motor-learning system for machines.

Materials and Methods

The BBD (Fig. 2A) is built on the Segway RMP, a commercially available robotic version of the Segway Human Transporter (HT). The device received sensory input from a color camera, a laser rangefinder, and banks of short-range IR proximity sensors that were mounted low around the device to detect nearby objects (28). An aluminum chassis on the commercial base contained a cluster of six compact Pentium IV personal computers (EZgo; Atoz Technology, Taipei, Taiwan) and enough battery capacity to operate for ~45 min.

Fig. 1 shows a high-level diagram of the simulated nervous system, including the various neural areas and the arrangement of synaptic connections. Each area contains neuronal units that can be either excitatory or inhibitory, each of which represents a local population of neurons (29) in which the mean firing rate variable of each unit corresponds to the average activity of a group of ~100 real neurons during a time period of ~40 ms. For more details, see Supporting Materials and Methods and Tables 1 and 2, which are published as supporting information on the PNAS web site.

The simulated cerebellum had precerebellar nuclei (PN) that received input from visual cortical areas (MT→PN in Fig. 1) and output to the cerebellum (PN→PC and PN→DCN in Fig. 1), a cerebellar cortex containing PCs that inhibited DCN for turning and velocity (PC→DCN in Fig. 1), and an IO that simulated climbing fiber input to the cerebellum (IO→PC and IO→DCN in Fig. 1). Note that, for computational reasons and the lack of data regarding granule cell function (30), we omitted the granule cell layer from our model and have the PN [e.g., nucleus reticularis tegmenti pontis (31)] project directly to PC and D CN in the model. Other cerebellar models have made similar assumptions (32).

The device had three basic innate behaviors: continue moving forward, avoid large obstacles, such as walls or people, and avoid head-on collisions with the cones. In the continue behavior, the device moved forward in a straight line at a maximum of 1.25 m/s unless the head-on behavior, avoid behavior, or activity of the neural simulation caused the device to slow down and/or turn. When the neural simulation intervened, motor neural areas were converted into wheel commands (Supporting Materials and Methods and Fig. 11, which is published as supporting information on the PNAS web site). Motor neural areas could be activated by IR detector input or by visuomotor pathways. Continue is the default behavior for the simulation.

The laser range finder on board the Segway BBD (SICK Vertriebs, Dusseldorf, Germany) detected obstacles up to 20 m away in a 180° arc that was 76 cm high, which was above the height of the cones marking the course. If an object was detected within 1 m of the device, an avoid behavior was initiated and the device would rotate in place until the laser detected no obstacles closer than 1 m. After the avoid behavior was complete, the device initiated the continue behavior. In general, when the device completed a lap on the course marked by cones, it would typically be close to a wall; avoid caused the device to turn around ~180°, and it then proceeded along the course in the opposite direction.

If the IR proximity detectors signaled the presence of cones directly in front and within 6 inches of the device, the head-on behavior was initiated, and the device backed up until it was clear of the cones. After clearing the cones, the continue behavior was initiated, and the IR detectors or the visuomotor system would typically trigger a neural motor response to maneuver away from the cones and proceed down the course.

Synaptic Plasticity and the Delayed Eligibility Trace Learning Rule.

Synaptic strengths were subject to modification according to a synaptic rule that depends on the pre- and postsynaptic and IO activities. Details of changes in neuronal unit activity and parameter details can be found in the Supporting Materials and Methods. The following equations are based on these details.

Synaptic changes are given by

\[ \Delta c_{ij}(t + 1) = \eta_i(t) \text{trace}_{eligibility}(t) \cdot (IO_j(t) - 0.02), \]

where \( c_{ij} \) is the connection strength from unit \( i \) to unit \( j \), \( s_i(t) \) is the activity of the postsynaptic unit, \( IO_j(t) \) is the activity of the IO unit corresponding to unit \( j \), \( \eta_i \) is a fixed learning rate, and \( \text{trace}_{eligibility}(t) \) is the eligibility trace of synapse \( j \). The eligibility trace (see below) determines the amount of efficacy change at a specific synapse for a given time. This learning rule supports
both potentiation and depression at PC and DCN synapses (21). When \( \eta \) was negative (e.g., in PN→PC synapses), the learning rule induced depression when the IO was active above a baseline firing rate and potentiation when IO was below baseline (33). Note that this learning rule supported extinction of learned responses when the error from the IO was absent (20, 34).

In the model, the change in synaptic efficacy was based on the delayed eligibility trace rule, according to which an eligibility trace \( \text{trace}_{\text{eligibility}}(t + 1) \) determined the amount of synaptic change at that synapse when eligible:

\[
\text{trace}_{\text{eligibility}}(t + 1) = \begin{cases} 
0 & \text{if } t < \text{delay}, \\
 s(t - \text{delay}) & \text{if } s(t - \text{delay}) \geq \sigma, \\
0.9 \cdot \text{trace}_{\text{eligibility}}(t) & \text{otherwise}
\end{cases}
\]

where \( s(t) \) is the presynaptic input to the synapse at time \( t \), \( \sigma = 0.15 \), and \( \text{delay} \) is a time offset from the previous simulation cycle. (Note that once \( s(t - \text{delay}) \geq \sigma \) was used to trigger synaptic eligibility, more input was ignored until \( \text{trace}_{\text{eligibility}}(t + \Delta) < 0.1 \), where \( \Delta \) is the time offset after delay). When presynaptic input exceeds a threshold, the synapse becomes eligible for modification after a set delay, at which time the eligibility declines exponentially. The delay was varied to investigate the effect of different delay periods. Delay periods investigated were 0, 2, 4, and 8 s.

Vision and Motion Processing. Visual information was provided to the Segway BBD by a charge-coupled device camera that captured images at 30 frames per s. Details describing visual preprocessing can be found in Supporting Materials and Methods. Neuronal units that responded to the presence of red–orange color provided visual input into the neural simulation (Fig. 1). Streaks and blurring of the visual image in the BBD were realized by a combination of neuronal persistence and reciprocal connections between visual neural areas. Horizontal and vertical edges and direction-selective responses were derived from the blurred visual image. Activation of a neuronal unit in simulated MT was a result of coincident activity of an orientation-selective unit with a direction-selective unit. For example, an MT-Down neuronal unit at a given receptive field was active when a vertical orientation neuronal unit and a downward motion-selective unit were coactive at the same receptive field (see Supporting Materials and Methods and Tables 1 and 2 for more details).

Motor Output. Motion of the Segway RMP is controlled by velocity (m/s) and turn rate (°/s) commands. At a given turn rate, the radius of the turn is a function of velocity; i.e., a turn rate with zero velocity results in the RMP turning in place, and the same turn rate at a high velocity results in a wide turn. The RMP turn rate was set based on the Motor-Turn activity (e.g., activity on the left resulted in a turn to the right). Motor-Turn activity was affected by IR input by way of the inferior olive (IO-Turn→Motor-Turn in Fig. 1) and by visual input by way of the cerebellum (DCN-Turn→Motor-Turn in Fig. 1). The speed of the device was controlled based on the activity of the Motor-Velo area. When there was no motor activity, the RMP speed was set to a maximum of 1.25 m/s. The Motor-Velo area slowed down the RMP based on the number of IR detectors signaling an obstacle; that is, the more IR detectors that were activated, the slower the velocity. Motor-Velo activity was affected by IR input by way of the IO (IO-Velo→Motor-Velo in Fig. 1) and by visual input through the cerebellum (DCN-Velo→Motor-Velo in Fig. 1).

We thank B. Krekelberg for suggesting visual blurring as a motion cue; J. Gally for useful suggestions and discussion; and J. Snook, D. Moore, and D. Hutson for their contribution to the BBD design. This work was supported by grants from the Office of Naval Research, Defense Advanced Research Projects Agency, and the Neurosciences Research Foundation.