1. **Distinctive contributions of three learnable mappings in movement control.**
Write a brief explanation of the meaning of the following terms as used in studies of sensory-motor control: inverse kinematics, forward kinematics, inverse dynamics, forward dynamics. Then use a labeled figure and concrete control example to ground a discussion of how the abilities to learn forward kinematics (via neural net function approximation), to learn inverse dynamics, and to learn forward dynamics could each separately improve the performance of a voluntary movement system. That is, explain how each can provide an enhancement that the others cannot, in principle, provide. Finally, choose one of these types of mappings and explain whether and why you do or do not think the cerebellum mediates learning of that type.

**Kinematics** refers to the study of motion without reference to forces. Velocity and Position are kinematic velocities. **Dynamics** refers to the study of force-time patterns implicated in observed motions. The **forward kinematics problem** refers to the prediction of end effector motion from motions of the individual joints – for example, learning how wrist, shoulder and and elbow movement jointly affect hand movement. The **inverse kinematics problem** for a jointed effector refers to finding the adequate joint motions to produce desired motion of the end effector. The **forward dynamics problem** for a rigid body refers to predicting motion from the knowledge of applied forces. The **inverse dynamics problem** refers to finding adequate forces to produce a desired motion. When models of the motor system are built, they may aim to solve any number of the above problems.

One model which focuses on a solution of the forward dynamics problem is described in Wolpert et al. (1998). Wolpert uses self-organizing competitive forward dynamics models to learn how to predict future future system states given a motor command and a present system state. The predicted future state can be delayed an appropriate amount of time and compared with the actual future state, such that forward models can be accurately tuned for different situations. A solution such as this one is useful for two primary reasons. First learning a forward dynamics model of the arm allows the use of the arm without visual or even proprioceptive feedback, because the efferent motor commands can be used to generate an “expected state” from the forward model alone. In addition, a forward model can be paired with an inverse model, and as such learning the forward-inverse pairing and its role in an individual context can be determined during motor learning. Such a forward model can be useful also in generating fast movements, when feedback from sensory systems would be too slow. Finally, error signals can be estimated more quickly through use of a forward model, allowing fast correction without use of sensory feedback.
Solving the forward kinematics problem means that you know how moving individual joints leads to the movement of an end effector. One model that utilizes the solution to this problem is the DIRECT model. Although it functions primarily through the use of visual feedback, solving the inverse kinematics problem, it also learns solutions to the forward kinematics problem, which can be used when, for example, blind reaches are made. In a blind reach, there is no visual feedback that is available, but it is still possible to plan, to some extent, trajectories in space, if one can predict the future location of the end effector. In fast movements, where visual feedback is too slow to be useful, the forward kinematics model can predict the role of motor actions and give feedback to the inverse kinematics system, to generate future movements. For further details of DIRECT functioning, see Problem 2.
One model that utilizes inverse dynamics is that of Spoelstra et al. Their inverse dynamics model (IDM) uses errors sensed by the spinal reflex circuitry as a teaching signal, and learns how to associate this with the system state defined by the trajectory generator and spindles, in order to provide corrective feedforward control signals. Inverse dynamics models know the forces needed to generate particular movements, and these considerations are necessary when considering models that operate on objects that have mass. In Spoelstra's model, the Inverse Dynamics Model learns the dynamic properties of the plant and spinal circuit, thus enabling feedforward control of trajectory generation.

The cerebellum may be involved in considerations of forward dynamics. Evidence from this comes primarily in the form of case studies from subjects without healthy cerebellums. For example, healthy subjects who lift an object can anticipate the force that will arise from the added load. This is due to the use of a forward dynamics model, predicting the forces necessary to lift an object. Such anticipatory couplings between load and grip force are not seen in subjects with cerebellar lesions (Desmurget and Grafton, 2000). In addition, subjects with cerebellar lesions display ringing motions which would arise from the use of only sensory feedback, and no feedforward anticipatory model. Also, tracking deficits associated with cerebellar ataxia appear to be related to a weak or absent forward model.
Forward Kinematics (highlighted)
2. **Inverse kinematics models.** One of the basic problems in sensory-motor theory is how information about the location of perceived points in space is used to guide voluntary actions that are directed toward such points in space. If issues of force are ignored, then this issue can be thought of as purely a problem in kinematics, and as such is often formulated with a focus on inverse kinematics. Use any published NN-based inverse kinematics model of your choice to illustrate how this problem has been approached from a neural network perspective in the case of voluntary arm movements. First, use diagrams, equations, and prose to describe the basic architecture (i.e., circuit plus all key operations) of the model. Next, critique the chosen model from three different perspectives. First, does the model work for both non-redundant and redundant manipulators? Clarify terms and explain why or why not. Second, from the perspective of efficiency: Does the architecture provide a lot of behavioral competence relative to its complexity? Explain the rationale behind your assessment. Third, from the perspective of neurobiology: is the overall strategy embodied by the design consistent with biological data? Are the mechanistic details likely to be correct, given current data? Then briefly specify a plausible alternative model. This should be some architecture (not necessarily a published proposal) that differs in at least one important and testable way from the model you chose. Clearly identify the testable difference.

An example of an inverse kinematics model is the DIRECT model, developed by Bullock et al in 1993. It is an extension of the VITE model, developed in 1988, and is concerned with reaching movements towards a target, or end-effector position. The problem is made difficult because there are redundant degrees of freedom in joint space. DIRECT solves this problem by learning inverse differential mappings as part of a spatial-motor map.

DIRECT works in two distinct stages. First, the weights need to be trained, and this is done in a “motor babbling” phase. Motor babbling is used to sample the space of spatial and motor mappings. In particular, an Endogenous Random Generator is utilized to set random initial joint configurations and movements through joint space, which are then learned in a self-organized fashion. In this fashion, it is possible to learn both forward and inverse kinematics, that is, spatial to motor and motor to spatial mappings.

After learning has taken place, motor babbling ceases, and reaching movements may be simulated. The DVs direction in space vector is computed from the TPVs (target position in space) and PPVsm (present position vector in spatial coordinates). The PPVsm is computed from visual observation of the end effector when possible, and otherwise from the forward kinematics model. The DVs vector, once obtained, is then converted to motor coordinates by the position-direction map, into DVm, a direction vector in motor coordinates, which is integrated to form a movement.
The inverse kinematic mapping consists of mapping the DVs vector to the PPVm, the motor position vector. During motor babbling, the TPV represents the present position of the arm, and the PPVsm represents the position at a short time prior, due to the delay in visual feedback. Thus, the system can learn to map a DVs to a PPVm, that is, the necessary direction to move to reach the present motor position. After this is learned, the DVs represents the desired direction of movement, and is transformed in the position-direction map into joint coordinates. This is performed using spatial trajectory transformation with direction mapping (STD), which will give a one-to-many mapping of spatial directions to joint angles, any linear combination of which will be a solution to the problem at hand. To verify this, suppose that \( \dot{x} = J(\theta) \dot{\theta} \), where \( \dot{x} \) is the 3D-spatial velocity and \( \dot{\theta} \) is a joint space velocity vector, where \( J(\theta) \) is the Jacobian. This can be approximated as a linear system, and thus the superposition principle holds. Also, because the inverse of the Jacobian does not exist, it is clear that there is no unique solution to this system, and thus a one-to-many mapping is needed. The spatial-to-motor mapping represents a pseudoinverse style solution to this problem.

A nonredundant manipulator is a motor device that can perform a given task with only one configuration, for example, a joystick has only one way to move to a given location. A redundant manipulator, on the other hand, has multiple ways to approach a given task. A multi-jointed arm, for example, can reach to a point using an infinite number of configurations. The DIRECT model can be successfully trained in either situation. The motor equivalence problem is solved by the position-direction map, which learns positions for motor situations while the ERG is functioning through the use of an
outstar. As a result of the superposition principle, DVm's will still add to move in the
correct direction, even in the presence of redundancy.

The DIRECT model provides for a large degree of behavioral competence. It is
capable of reaching movements using many variants – blind reaches, reaches with
constrained joints, and reaches with visual feedback (both normal and distorted). Once
training has taken place, all of these reaches may be simulated, and the results are
representative of psychophysical data. The model cannot, however, account for
considerations of force. Even so, the model is relatively simple – a few different maps
and vectors are used to represent many different stages, and as such, given the complexity
of the output reach trajectories, it seems to be a very efficient model.

The DIRECT model did not have as a goal the explanation of neurobiological
data. Even so, many of the consequences of its design lead to similar patterns of
activation in the various cells of the model. DIRECT contains modules containing the
direction of motion in both spatial and motor coordinate frames. In M1 there are cells
which are broadly tuned to movement direction (Georgopoulos, etc), which is consistent
with this representation. In addition, it is well known that stimulation of a single motor
cortical cell activates multiple muscles, which is again consistent with the preferred
direction coding, particularly with redundant manipulators.

DIRECT converts a direction vector to motor space and integrates it to move
along a trajectory to a target (STD). An alternative to this STD is Spatial Trajectory
Formation with Position Mapping, or STP. In this case, there is also a one-to-many
mapping of 3D spatial positions to joint angle configurations, but it is a nonlinear
function, and thus the principle of superposition no longer holds. The function
\( x = f(\theta) \) now has multiple solutions \( \theta \) which are not necessarily adjacent to the
current position in joint space. Thus, to use this STP strategy, it is necessary to search
through all solutions, which is a time-consuming process, and not easily learned. One
could test both the time to learn and the accuracy using a STP strategy versus STD.
3A. **Circuit model spanning multiple electrophysiological cell types.** Motor system physiologists often classify cells based on the time course of their spiking immediately before, during, and immediately after, movement. Terms like ‘phasic RT’, ‘tonic’, ‘burst’, ‘pauser’, etc. are often used. Another important dimension for classification is whether the pattern of cell discharge is solely a function of kinematic task variables, such as the direction of movement – or whether it also depends on kinetic task variables, such as the amount of force needed along a particular direction to launch or brake the movement, or to hold a posture under load. A key goal for neural network theory is to formulate testable explanations of the network bases of these cell properties, e.g. , how a phasic MT cell’s burst is terminated by network computations, or what physical pathway enables a central cell’s activity to be a function of the force being used to produce a movement. Choose one, or two tightly interlinked, non-cerebellar supra-spinal brain areas (e.g., motor cortex, or the basal ganglia, or the brainstem saccade generator) for which there is a significant inventory of physiologically identified cell types which have been reliably observed in more than one laboratory. Carefully describe at least 4 clearly distinct and replicable cell types, with a brief but clear statement of at least one task in which the distinctive characteristics can be observed. Then choose some circuit model, describe it with the help of diagrams, and explain how its computations are purported to provide an explanation of the functional characteristics that distinguish the chosen cell types. Next, find and carefully describe at least two model weaknesses (whether omissions or commissions) that you assess to be important. Be sure to justify your characterization of the weaknesses.

One area which gives rise to a large number of stereotyped cells is Area 4 of motor cortex. These stereotyped cell types have been observed primarily in the laboratory of Kalaska (1989), but have been replicated in a number of other labs (reported in Bullock et al., 1998). These patterns of activity may be recorded by using a center-out style task, as utilized prominently by Georgopoulos and colleagues throughout the 1980s. While Georgopoulos used essentially...
massless manipulanda in his experiment, Kalaska and colleagues progressed towards using manipulanda of varying forces, isometric tasks and inertia. In this fashion, Kalaska was able to examine whether the recorded cells were sensitive to kinetic or kinematic properties. Bullock et al (1998) proposes a model that uses these firing patterns as building blocks of a larger reaching model.

The center-out task consists of, canonically, a monkey controlling a lever, holding it at a center position until a light comes on at one of eight peripheral locations. This task can be broken into epochs in time – an initial holding time at the center (CHT), reaction time between light onset and movement onset (RT), movement time before hitting the target (MT), and time holding at the target (THT).

Phasic RT Cells (a, in diagram) fire a quick burst of activity during RT, and are comparatively quiescent the remainder of the trial. They are relatively invariant with respect to load. Bullock et al equate these to the inertial force vector, or IFV component of their model. Phasic MT Cells (b) also consist of a phasic burst of activity, although this is a longer burst than that of the Phasic RT Cells. Moreover, this burst takes place essentially at the onset of movement and persists throughout the MT period. These cells are not strongly modulated by forces or loads in different directions. These phasic MT cells are utilized at the desired velocity vector (DVV) stage by Bullock et al.

Tonic cells (c) are active at a higher tonic rate during MT, with little or no phasic component. They stay active even during the THT and are greatly modulated by the load present. They are used as the outflow position vector (OPV). Phasic-tonic cells (e) have a phasic response during the end of RT/beginning of MT, but then a higher tonic firing rate lasting throughout the THT. These are used as the outflow and force position vector stage. These cells are sensitive to external loads.

The model developed by Bullock et al (1998) is an extension of the VITE model. At its core, it integrates a direction vector over time to form a trajectory. It is quite different from the initial VITE
architecture, however, because it accounts for the presence of forces and matches profiles of internal elements to physiologically measured types of cells. Within area 4, there is a multicomponent motor command that simultaneously specifies desired position and load-compensating forces, as opposed to simply desired position.

An arm movement difference vector (DV) is computed in parietal area 5 from a comparison of a target position vector (TPV) with a representation of current position called the perceived position vector (PPV). The DV command may be activated, or primed, prior to its overt performance.

The PPV is also computed in area 5, where it is derived by subtracting spindle-based feedback of position error, which is routed to area 5 via area 2, from an efference copy of an outflow position vector (OPV) from area 4.

The primed DV projects to a desired velocity vector (DVV) in area 4. A voluntarily scalable GO signal gates the DV input to the DVV in area 4. By virtue of the scaled gating signal, the phasic cell activity of the DVV serves as a volition-sensitive velocity command, which activates lower centers including gamma-dynamic motoneurons. The DVV is related to the phasic-MT cells seen in area 4. We would expect these to be insensitive to force, because the desired velocity should not change in the face of a load.

The DVV command is integrated by a tonic cell population in area 4, whose activity serves as an outflow position vector (OPV) to lower centers, including alpha and gamma-static motoneurons. This area 4 tonic cell pool serves as source of the efference copy signal used in area 5 to compute the perceived position vector (PPV). As the movement evolves, the difference vector (DV) activity in area 5 is driven toward baseline. This leads to termination of excitatory input to area 4 phasic cells, and thus to termination of the movement itself. Again considering the role of phasic-MT cells, it makes sense that the DVV would slowly decline to zero as the target is reached, which is the case in these cell types. The area 4 tonic cells are modulated by force, as is the OPV signal. This should be modulated by a load because generating an accurate estimate of the present position needs information about the force on the end effector. This tonic outflow position vector must be scaled by force so as to integrate the desired velocity vector to a greater or lesser degree, thus generating the appropriate output.

A reciprocal connection from the area 5 PPV cells to the motor-cortical tonic cells (OPV) enables the area 4 position command to track any movement imposed by external forces. This reciprocal connection also helps to keep spindles loaded and to avoid instabilities that would otherwise be associated with lags due to finite signal conduction rates and loads. It is also consistent with the interpretation of tonic area 4 cells being modulated by force. This force modulation also explains why tonic area 4 cells should persist after reaching the target location.
Phasic-tonic force-and-position-related (OFPV) cells in area 4 enable graded force recruitment to compensate for static and inertial loads, using inputs to area 4 from cerebellum and a center that integrates spindle feedback. These area 4 phasic-tonic corticomotoneuronal cells enable force of a desired amount to be exerted against an obstacle without interfering with accurate proprioception (PPV), and while preserving a target posture (TPV) should the obstacle give way. The phasic input is reflected from the IFV, and the tonic input from the OPV, and together these should be strongly modulated by force. This is reasonably because the OFPV is the final stage before movement (in the model) and forces certainly have an effect on the activity of spinal motor neurons. Additionally, the tonic activity from OPV is highly modulated by force.

The Inertial Force Vector (IFV) represents a force vector that is necessary to displace the object from its initial resting point. Bullock et al describe this as a signal computed from cerebellar input, which is added to the OFPV. This phasic activity is only overcoming the inertia, and it thus makes sense to connect it to the Phasic RT.

One large weakness of this model is that it does not take into account considerations of alternate coordinate systems. It plans trajectories in motor space, but this is probably not how trajectory planning takes place in real life. Examples of this come in studies of, for example, handwriting with feet, in which the maps in space are more or less preserved over completely different motor units. An additional representation of spatial trajectory formation would be necessary in this case to solve these problems.

Rapid movements are also difficult to enact, because feedback from sensory systems needs a certain delay. One solution for this would require a forward kinematics (and even dynamics) model, perhaps in the cerebellum, which could provide a signal similar to IFV to augment the final feedforward signal.
4. **Nature of the representation of movement direction in primary motor cortex.**

a. What is the center-out task and how was it used in the classic experiments of Georgopoulos and colleagues? What were the results of the cell recording studies for this behavioral task? What was the basis for the early conclusion that cells were coding the direction of a movement and not its endpoint? Was this basis sound?

b. Write down an expression for the population vector as originally formulated by Georgopoulos. Explain in detail what each of the variables means. What was the early interpretation of this population vector (i.e. what global parameter of movement was it supposed to represent)? How successful was it, and was its measure of ‘success’ taken to demonstrate anything about the coordinate system in which motor cortex represents movements?

c. Describe how the experiments of Scott and Kalaska (1995; 1997) differed from prior center-out experiments in terms of changed independent and / or dependent variables. With these experiments in mind, discuss the main difference between a motor-coordinate interpretation vs. a spatial (Cartesian) interpretation of motor cortical cell activity, with special attention to whether the Cartesian preferred directions (PDs) of cells are invariant across the workspace. Of the two interpretations, which do you find offers a better understanding of the results of these experiments? Why? If you prefer the motor-coordinate interpretation, can this same interpretation explain the original center-out results? How? Give your reasoning.

d. Suppose, as many experimentalists have argued over the last 25 years, that motor cortex is not homogeneous in its cell types. In particular, suppose that it contains cells that are tuned to spatial variables and cells tuned to motor variables, and that among the motor variables reflected in cell discharges are both kinematic and kinetic variables. Then use this perspective as a basis for evaluating the arguments of Todorov (2000; hint: besides class notes, you might want to consult the published dispute between him, Georgopoulos, and Schwartz). Can population vector analysis help settle this dispute? Why or why not?

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**a.** The center-out task used by Georgopoulos and colleagues throughout the 1980s consisted of a monkey making reaching movements, either using a manipulandum or using his hand to push a lighted button. In the early studies, monkeys were instructed to keep a manipulandum centered in a plane until the presentation of a light in one of eight discrete locations. After the presentation of this light, the monkey moved the manipulandum to the lighted area, held it until receiving a reward. In the 3-D case, lighted buttons were placed equidistant from a center location, such that they form the corners of a cube. Once more, the monkeys were instructed to press and hold the center button, and then move to a lighted button and hold until receiving a liquid reward. In
each case, cells were recorded with an adequate sampling of all movement directions a
number of times.

Cells were differentially active during movements toward certain locations, and
these locations did not appear to correspond to any of the eight given movement
directions. A preferred direction could be calculated, and the responses to cells appeared
to fit a cosine tuning curve, such that angles of movement near the preferred direction of
movement. The authors conclude that these cells are coding for movement direction
because there is an orderly relationship between movement direction and firing rate.
Additionally, they believe that the endpoint is not coded for because motor cortical cells
in general do not fire explicitly for one of the eight tested directions.

While this is not terrible reasoning, it would have been trivially simple to test
whether or not this is the case, and they did not perform these trivial tests. In particular,
the monkey could have been trained to move in a given direction but then move to a
different target. Alternatively, the monkey could have been trained to move randomly,
and the direction vector could have been computed empirically over time and compared
to the temporal firing rate of neurons. Later experiments, however, using parallel
reaching movements (Caminiti et al 1990) did dissociate endpoint from movement
direction, and verified the population level direction coding assumed by Georgopoulos,
although single cells were no longer tuned to the same directions.

b.) The population vector refers to a mechanism that is used to reconstruct the overall
movement from the activity of the individual cells. This is done by adding scaled vectors
together, where the vector direction relates to the preferred direction of a given cell, and
the scaling is related to the firing of the cell. In particular, the population vector can be
specified mathematically as the following. $D$ is the total firing of a cell, $b_0$ is the
tonic cell activity, and $b_k$ represent scaling coefficients found via linear regression,
such that $(b_x, b_y, b_z)$ represent the preferred direction of the cell. The present
movement direction is given by $(m_x, m_y, m_z)$, and the total cell activity may be
expressed as the dot product of these two vectors:

$$B \cdot M = b_x m_x + b_y m_y + b_z m_z$$

and thus may be expressed in terms of the cosine of the angle between them:

$$B \cdot M = |B| |M| \cos(\theta)$$

This cosine function gives clues as to an optimal weighting function for firing rates when the preferred directions are weighted
and summed. The population vector itself is given by $P = \sum_i C_i \cdot W_i$, that is a sum of
the scaled unit vector of each preferred direction scaled by some function of its neural
activity. This function may simply be $D - b_0$, the firing rate above baseline.

This approach modeled the direction of movement, and as the population vector
approach was successful in the computation of the direction of hand movement. The
coordinate system was not, however, explicitly discussed in these articles, and it is implicit that the direction is coded for in an appropriate coordinate space. The coordinate space considered, however, is with respect to the position of the hand, but no experiments were carried out to verify if this was in fact the coordinate frame in which movements were coded.

c.) The research of Scott and Kalaska was quite similar to that discussed in the work of Georgopoulos, but they made slight variations. Notably, they changed the posture at which the center out task was performed, by introducing a barrier that changed the range of motion for the arm. Both with and without the barrier, the trajectories of the end effector were identical, however in motor coordinates, there were vast differences between the two tasks. If the population vector approach codes for the movement of the hand in hand-centered coordinates or spatial coordinates, then it should yield identical results for both of these tasks. If, on the other hand, the population vector is tied to motor coordinates, then one would expect poor predictions from the population vector.

The results of Scott and Kalaska demonstrated that the population vector was sensitive to motor coordinates, and most likely did not encode preferred directions in motor coordinates. The motor-coordinate interpretation of preferred direction makes more sense in this situation, and it is also consistent with the original results of Georgopoulos. Because the initial center-out tasks were performed with the same motor coordinates each time, and because of the specific choice of motor coordinates, there is a high degree of correlation between the motor coordinates and the Cartesian coordinates.

d.) The motor cortex, as viewed by many is composed of different types of cells. The work of Kalaska has identified many different types of cells in motor cortex, which are sensitive to different kinetic properties of reaching movements, for example. This stands in opposition to the explanation given by Todorov. Todorov believes that motor cortex controls the muscles directly, and that the properties of muscles must be viewed in light of their visco-elastic properties, which vary according to the present state of the muscle. Thus, he claims, the properties of motor cortical neurons may be viewed as consistent with the overall impression that populations of neurons in the brain are used to code higher order movement properties.

Todorov's hypothesis is inconsistent with the notion that cells in M1 are inhomogeneous. If indeed they all control particular muscle groups, then it is not clear how some code for kinetic properties and others kinematic properties. Moreover, the findings of Georgopoulos that individual cells are tuned to particular movements would not be supported by Todorov's approach, but then again, they are not supported by the work of Scott and Kalaska either. If each cell is considered to be tuned to a direction in
motor coordinates, then it is unclear whether or not Todorov's hypothesis holds true, although it is much more plausible, because he holds that muscles are controlled by cortical cells, and muscle activity is much more likely to be correlated to activity in joint space than in Cartesian space. Even so, the complicated nonlinear dynamics of the muscles do not lend themselves to clearly visible encoding in the brain, as is suggested by the work of Georgopoulos.
5. **Hybrid picture of the cerebellum.** Consider the neural machine that emerges from combining the Marr-Albus perspective with the adaptive timing perspective of either Fiala et al. (1996) or of Medina, Garcia, Nores, Taylor & Mauk (2000), but not both. That is, consider the cerebellum as a device for filtering masses of mossy fiber signal traffic in search of information that may be useful in triggering appropriate control actions at appropriate times in the near future. Use a circuit diagram and other graphics to anchor your discussion of whether and how the cerebellum can simultaneously:

a. Reveal information that is only implicit in the vector of mossy fiber inputs;
b. Extend the temporal window within which this information can be used to learn and perform control actions;
c. Ensure that control actions are scheduled so as to slightly lead the time at which an error (or other unwanted event) would occur in the absence of the control action;
d. Ensure that a new control action is learned only in that small subset of cerebellar output channels (among the millions of output channels) that are capable of acting to preempt the error; i.e., how does the cerebellum solve the credit assignment problem?

f. Allow an interleaved practice regime (switching back and forth among practice sessions with various tasks) to refine motor skill memories by shaking off spurious correlations and by moving procedural memories onto more task-unique pathways; and thus allow the formation of procedural memories that can be stable over long intervals of disuse.

For each property a-f, state clearly how model-highlighted features of the anatomy (connectivity) and physiology (sign of action of afferents, cellular processing, and functional dependencies of synaptic plasticity) act cooperatively to yield the specified property. Be sure to clarify whether the model combination you chose really does simultaneously achieve the full set of competencies a-f. If it does not, explain why it fails.

The hybrid picture of the cerebellum refers to the general processing power of the cerebellum by both filtering massive amounts of information and learning important characteristics of this information, such as its timing.

(a) The cerebellum can indeed learn information implicit in the mossy fibers. This is done, according to Marr-Albus theory, through the expansion of mossy fibers to the granule cells. Mossy fibers project to...
the granule cells, as can be seen in the diagram – but there are as many granule cells in
the cerebellum as there are cells in the remainder of the brain. Thus, there are many,
many more granule cells than there are cells giving rise to parallel fibers in the brain.
The expansion recoder idea proposal is that the cerebellum performs a sparse
combinatoric recoding of the active mossy fiber input vector, which pulls apart very
similar patterns in the mossy fibers and represents them as distinct patterns on the parallel
fibers. These patterns are then learned at the Purkinje Cells, through mechanisms that
will be developed in further sections. What is crucial, however, is that the model of Fiala
(1996) is capable of encoding timing without the use of the parallel fiber encoding. This
is, in fact, true, and as such it is possible to learn the implicit information on the mossy
fibers.
(b) The cerebellum can use this information not only immediately, but over an extended
temporal window such as to learn associations with other events. This is accomplished
with the model of adaptive timing proposed by Fiala (1996). Before delving into the
model, it is necessary to understand the circuitry further. Teaching signals arrive at
Purkinje Cells via the climbing fibers. These teaching signals consist of, for example, the
Unconditioned Stimulus, in a classical conditioning paradigm. The Unconditioned
Response is a Purkinje Cell pause, and the Conditioned Stimulus is thought to reside
along the parallel fiber pathway. The Fiala model is capable of explaining how the
cerebellum may learn not only the appropriate parallel fiber pattern, but also the timing
between the presentation of the parallel fiber pattern and the unconditioned stimulus.

This extended temporal window is present as a result of varying peaks of internal
Calcium spikes, which arise from variable densities of MGlur1 density along Parallel-
Purkinje spines. In particular, the presentation of the CS sets off a second messenger
pathway that leads to different Calcium concentrations depending on receptor density,
and this internal concentration of Calcium allows LTD of the Parallel to Purkinje
synapses upon presentation of the US within a window of time after CS presentation.
The mechanism by which this LTD acts seems to involve both the phosphorylation of
AMPA receptors (or their endocytosis off the membrane and into the cell itself) and
Calcium-dependent Potassium Channels. Together, these are able to effect LTD in the
Parallel-Purkinje synapses along the relevant spines. Later, when these spines are
activated by the same Parallel fiber pattern (that is, the same CS), the Purkinje cell is
differentially inactive as a result of this LTD, and proceeds to pause at the appropriate
time (modulo the specifics of endogenous Calcium concentrations).
(c) The cerebellum also successfully learns to present a UR slightly before a US is
expected, so as to prevent the unpleasant effect normally associated with the US. The
Fiala model is capable of handling this because the Calcium spikes described earlier are
not instantaneous. Rather, even after Calcium has peaked, which is associated with a
time lag that is shorter than the correct interval between CS and US, there is still transient Ca++ that resides for a short amount of time, and thus, LTD will occur on these spines as well. The result of this is that as long as Calcium is present inside Purkinje cells, LTD will occur, thus leading to timing which is slightly earlier than the expected time.

(d) The cerebellum is able to solve the credit assignment problem because there is a one to one ratio between climbing fibers and Purkinje cells. Because the climbing fibers contain the learning signal, they will only convey this to the relevant Purkinje cells. Similarly, the Fiala model demonstrates how only spines on the Purkinje cell that receives the learning signal will undergo LTD. Thus, the relevant Purkinje cell will learn to pause, without affecting any other Purkinje cells. Because the Purkinjes are the output cells of the cerebellum, these will have the ultimate effect on the control action.

(e) An interleaved practice regime will be able to refine motor skills because of the interactions between the Parallel fibers and Purkinje cells. As we know from the functioning of the Fiala model, only the relevant Purkinje synapses will be altered, and moreover this will happen on very specific dendritic spines. The expansion recoding will produce different parallel fiber patterns, and thus the only learning that will take place in both cases is when the same Purkinje cell makes the same mistake, due to the same input but at varying times. This will functionally never be the case, and thus an interleaved practice regime will be successful.

(f) The formulation of procedural memories that will remain stable after periods of disuse depends on the form of plasticity taking place at the Parallel-Purkinje pathways. The Fiala model discusses the long term depression that takes place at these synapses, which is where that form of procedural learning will be learned. While the timing may take place, if the depression fades over time, then this system will not be successful. It is unclear whether this system will be capable of such long term procedural memories. As discussed in Fiala et al (1996), Parallel fiber activity alone can lead to LTP, which will result in forgetting these mappings. Even so, the exact pattern of parallel fiber activity is unlikely, and thus the entire pattern may take a long period of time to decay back to its initial state.
6B. **Distinctive roles of cerebellum (CBM) and basal ganglia (BG).** Use diagrams to illustrate the anatomical and the physiological bases for the hypothesis that both the cerebellum and the basal ganglia provide ‘normally closed gates’ that can be ‘opened’ to selectively facilitate contextually appropriate actions. Be sure to also mention how the basal ganglia and the cerebellum differ in the sign of their effect on the ‘motor’ (i.e., basal ganglia- or cerebellum- recipient) nuclei of the thalamus. After thus summarizing the empirical case, present computational arguments regarding how the BG gates should differ in their basic functions from the CBM gates, and thus why both kinds of gates are needed in any animal with a complex behavioral repertoire. As part of your discussion, be sure to assess whether your computational argument helps explain the differences between the natures of the teaching signals that appear to operate in the two systems: dopamine bursts and dips in the striatum vs. climbing fiber discharges in the cerebellar cortex. To simplify your answer, you may focus solely on hypothesized roles of BG gating vs. CBM gating of excitation of cell types in motor cortex (or, if you prefer, within the oculomotor system).

![Diagram of basal ganglia and cerebellum](image)

The basal ganglia and cerebellum are both postulated to have roles as “normally closed gates” in the motor pathway. A normally closed gate is an inhibitory connection that is almost always on – relaxing the inhibition has the effect of allowing a certain movement to transpire, letting it through the gate.

The basal ganglia plays a role in motor planning through action on the motor thalamus, also known as the ventrolateral thalamus. The Globus Palladus, which as can be seen above takes inputs from the Putamen and the Subthalamic Nuclei, inhibits the VL thalamus, which itself proceeds to excite motor cortex. Recordings of the GPi, which is the specific portion of the Globus Palladus that inhibits that motor thalamus have indicated that it has an extremely high tonic level of activation. Thus, because a strongly active component is inhibiting motions, we may think of this as a normally closed gate.

Likewise, the cerebellum acts as a normally closed gate. The Purkinje cells, much like the GPi, have a high tonic level of activation. These cells inhibit the deep cerebellar...
nuclei, which then excite the motor thalamus (different nuclei of the motor thalamus, however). Important to note is the sign of the activation and the role it plays in these normally closed gates. The basal ganglia have a constant inhibitory effect on the thalamus, punctuated by bursts of inactivity. The cerebellum has the opposite property, that is, a consistent lack of excitation of the motor thalamus, punctuated by bursts of activity. There is empirical evidence for this distinction as well, because disorders of the basal ganglia lead to difficulty generating movements – that is the punctuations of inactive moments cease, and the motor thalamus is constantly inhibited. Cerebellar disorders, however, lead to a lack of coordination, but never lead to difficulty generating movements. This is consistent with the notion that the thalamus is being presented with a quiescent input from the deep cerebellar nuclei, and are no longer punctuated by activity, which would lead to modulatory movements.

The basal ganglia then, is considered to be important in movement selection, while the cerebellum is considered relevant to movement modulation. This makes sense from their structure, because restricting all but a few movements is selecting the relevant movements, whereas declining to add all but a few movements is modulating relevant movements. Complex motor tasks will need both of these – it is important to gate unwanted movements, such that parallel plans may be represented simultaneously. Similarly, complex motor tasks necessitate the fine-tuning that is provided by modulatory movements. For example, well-timed reactions may be needed to learn specific procedural tasks – such coordination cannot be provided by a simple movement selection mechanism.

These normally closed gates have very different roles in the motor cortex, as are exemplified by the extended VITE model of Bullock et al. In this model, the output from the basal ganglia (the ventrolateral thalamic nuclei innervated by the basal ganglia, in fact) can be thought of as the GO signal. This GO
signal is then multiplied by the DV and integrated to form the OPV, or the outflow position vector. Thus, if the GO signal is not presented, the movement will not be able to take place. The basal ganglia outputs themselves gate topographically organized zones in laminar target areas, thus enabling the selection of entirely different movements by simply gating different regions of cortex, and thus different circuits. This system is learned through the use of phasic dopamine signals. More dopamine than usual is released after an unexpected reward, less than usual after an unexpected reward, and a tonic amount during expected circumstances. These diffuse projecting dopamine signals, combined with the gating signals are necessary for learning, and cells within the basal ganglia express dopamine receptors. By interacting with the local signaling pathways, dopamine signals may guide learning and performance. In particular, when things are going as expected, the dopaminergic signal is constant, allowing for integration of the GO signal, and thus movement to take place. If this movement no longer provides the expected reward, then a dip in dopamine will cease the GO signal and thus the integration of the movement.

Cerebellar activity is thought to play a modulatory role in the motor cortex, particularly by influencing the inertial force vector, or IFV. This augments the OPV selected by the basal ganglia at the final step before movement generation, and works in short, phasic bursts. This is parallel to the functioning of the cerebellum itself, in particular with respect to how it learns. When the climbing fiber discharges, this causes an alteration in Purkinje Cell firing, a break in the normally closed gate, and thus a modulatory signal in response to an error. This phasic burst is quite different from the constant dopamine signal provided when things are going as is expected. Thus, these two systems use distinct teaching methods which are well suited to their individual demands.