1 Learnable mappings in movement control

inverse kinematics Given an end-point somewhere in space, compute (or 'plan') the (series of) joint angles necessary to move to that point.

forward kinematics Given known joint angles, compute (or 'know') where in space the jointed end-effector is located or will be located.

inverse dynamics Given what is known about how a jointed end-effector moves, compute the proper amount of force necessary to move the end-effector in the desired manner.

forward dynamics Knowing how some weighted object will move based on knowledge of the amount of force necessary to move that weight.

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The 'center-out' task will serve as an example to illustrate the unique abilities of learned mappings that 'solve' specific kinematic and dynamic control problems. Figure 1 depicts the top-down view of a person given the task of moving a pole-object, for example either a light-weight broom-handle or heavy-weight metal pipe, held vertically (shown as the dark-filled circle), from a central point outward to one of many possible points in a circle drawn on the ground, while holding the pole-object vertical. The arm is two-jointed and the end-effector is the hand (not shown) gripping the pole-object.

Assume the person is told to close their eyes. Having learned (in life) the forward kinematics of where their hand is, or will be, located in space given their current arm position (as measured by proprioceptive signals from the joints) would allow a second person to move the person’s hand to some other point in space, and still that person will subsequently be able to move their hand (either holding a pole-object or not) to one of the points on the circle while keeping their eyes closed, and accomplish the task with some accuracy. None of the other learnable mappings allow this.
Now assume the person (eyes open) is holding the broom-handle pole-object, and is told to move the object from the center to some point on the circle, and to do this as quickly and accurately as possible. Being able to learn inverse dynamics allows the person, over repeated trials, to very accurately move the pole to any specified point, by learning exactly just the right amount of force to use to start and stop movement. None of the other learnable mappings allow this.

Lastly, assume this time the person is given the heavy metal pole object and told to perform the same task. Having learned (in life) how a heavy object, like a metal pipe, would move, due to its weight, compared to a light object like a broom stick, allows the person to make a fairly accurate judgement about how much force to use to move this new object in the center-out task. None of the other learnable mappings allow this.
2 Inverse kinematics models

The inverse-kinematics model DIRECT will be used to illustrate how, in the case of voluntary arm movements, such a NN-model can learn to guide movement to perceived points in space. The model architecture is shown in figure 2.

![Diagram of the DIRECT architecture for learning inverse kinematics.](image)

Figure 2: The DIRECT architecture for learning inverse kinematics.

Note first that the system is able to 'see' (perceive) points in space with a 'camera', and to reach to a point with a motor-controlled three-jointed manipulator with end-effector. The system undergoes a training process whereby essentially it learns to estimate a generalized inverse \( J^{-1} \) of the Jacobian matrix \( J(\theta) \). That is, in this system, the relationship between spatial velocity \( \dot{x} \) of the end-effector and joint-angle velocity \( \dot{\theta} \) of each joint of the manipulator is given by Equation 1. Equation 2 is a solution for obtaining the joint-angle rotation vector that moves the end-effector at a desired spatial velocity.

\[
\dot{x} = J(\theta)\dot{\theta} \quad (1)
\]
\[
\dot{\theta} = J^{-1}(\theta)\dot{x} \quad (2)
\]

The system training process is composed of tens of thousands of perception-action cycles of perceiving different points in space, and attempting to reach
to those points. The endogenous random generator (of joint-angle commands) is the source for each cycle. During one such cycle, the system internals undergo the following control loop. The camera 'subsystem' outputs two vectors of body-centered coordinates: one for the (perceived) position of the target, vector TPVs, and one for the present position of the end-effector, vector PPVs. The motor 'subsystem' outputs vector PPVm representing where it thinks the end-effector is located (also in body-centered coordinates). PPVs and PPVm are passed through a NN-based mapping function PPMm to create a spatio-motor present position vector PPVsm. PPVsm is subtracted from TPVs to create the spatial direction vector DVs. This difference operation is the crux of the servo behavior of this system. Next DVs is passed through another NN-based (associate Hebbian learning) position-direction mapping function PDMms which results in creation of a motor direction vector DVm. DVm is used to create the motor present position vector PPVm, which guides physical movement of the manipulator, which is perceived by the camera, closing the loop.

The directional mapping block PDMms contains the estimate of the inverse Jacobian $J^{-1}$, ie. the key transformation. Micci-Barreca and Guenther (2001) describe an alternative model of DIRECT that replaces this block with an algorithm the creates a pseudoinverse matrix that efficiently samples both joint-angle space and the spatial domain. This variation was motivated by the fact that DIRECT learns by uniformly sampling joint-angle space, which does not produce a uniform sampling of the spatial domain. Put simply, DIRECT may not always reach to every part of it’s ‘world’ in a uniform way, thus there may be points in space that it has not learned to reach. The difference between the two models is exposed by a measure described by Yoshikawa (1985) called the manipulability ellipsoid (ME), which measures the amount of joint rotation required to move an end-effector along different spatial directions. More specifically, it reveals a preferred axis of spatial movement, evident in end-effector trajectories during movement. The Micci-Barreca and Guenther model is in better agreement with experimental data on the curvature of hand-reaching movements than the DIRECT model. However, unlike the DIRECT model, its mapping mechanism (based on direct matrix operations) is not biologically plausible.

Both models work for redundant manipulators. This is to say that they work for manipulators having more degrees-of-freedom (DOF), ie. joints, necessary to reach a point in space. A non-redundant manipulator has no more DOF than required. Putting your elbow in a cast reduces your arm from redundant to non-redundant for 2D movements. Because the Micci-Barreca and Guenther model is based on using explicit information on the geometry of the arm, it will not work for a non-redundant manipulator, whereas the DIRECT model does because it learns the geometry, and can relearn if the DOF changes. Also, because the Micci-Barreca and Guenther model is based on a pseudoinverse, it may generate excessive joint velocities near singularities, as well as produce undesired (contorted and not ‘life-like’) arm configurations.
3 Electrophysiological cell types

The cell types found in area 4 of motor cortex and area 5 of sensory cortex are electrophysiologically well characterized. Typically, this has been done by taking electrode measurements of primate cortex while it is conducting some form of the voluntary movement 'center-out' task. The basics of this task were introduced in the answer to question 1. Expanding on that description, the 'pole object' is replaced by a mechanized manipulandum capable of exerting a resistive force ranging from zero to immovable. Also, the position of the manipulandum is typically measured and used to control a cursor on a computer screen, where the targets are generated under experimental control. This experimental setup allows exploration of direction and force variables.

The following is a list of the how cell types of area 4 and 5 are differentiated and characterized as relating to a voluntary movement task such as the center-out task:

- Whether and when the cell shows phasic activity (quick rise then fall)
- Whether and when the cell shows tonic activity (sustained activity)
- If activity is correlated with the time of reaction to the task stimulus (abbreviated RT, reaction time)
- If activity is correlated with the time of movement of the manipulandum (abbreviated MT, movement time)
- Whether activity is associated with movement direction (ie. position)
- Whether activity is associated with load (ie. force)

Given this information, at least six types of cells have been differentiated and characterized, and the following is a table which attempts to organize the data:

<table>
<thead>
<tr>
<th>Name of cell type</th>
<th>direction</th>
<th>load</th>
</tr>
</thead>
<tbody>
<tr>
<td>area 4 phasic RT</td>
<td>RT++ MT+</td>
<td>-</td>
</tr>
<tr>
<td>area 4 phasic MT</td>
<td>RT+ MT++ HT+</td>
<td>-</td>
</tr>
<tr>
<td>area 4 tonic</td>
<td>MT++ HT++</td>
<td>RT+ MT+ HT+</td>
</tr>
<tr>
<td>area 4 phasic- tonic</td>
<td>RT++ MT++ HT++</td>
<td>RT+ MT+ HT+</td>
</tr>
<tr>
<td>area 5 tonic</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>area 5 phasic</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

The 'direction' and 'load' columns indicate whether the behavior of the given cell type is strongly, mildly, or weakly (shown as ++, +, and - signs) modulated by the direction and load experimental variables. The strength sign coincides with the approximate time in the experiment when observed (RT is 'reaction time', MT is 'movement time', and 'HT' is 'hold time').

The extended-VITE (Vector-Integration-To-Endpoint) model, diagrammed in Figure 3, of voluntary movement and proprioception offers a functional description of these six cell types. The model operates in a similar manner as
the DIRECT model described in the answer to question 3, in that, basically, motor output is a function of the difference between a perceived position vector and a target position vector, but gated by a GO signal (such as from the basal ganglia). Additionally, the extended-VITE model incorporates proprioceptive processing and force generation (making it a models of kinetics in addition to kinematics).

The six cell types listed in the prior Table are incorporated into the extended-VITE model, and the next Table lists a mapping (refer to Figure 3) to model neurons. The cell type behavior profiles as described earlier (in the Table) are all accurately simulated by the model.

<table>
<thead>
<tr>
<th>Cell type</th>
<th>E-VITE</th>
<th>Acronym expansion</th>
</tr>
</thead>
<tbody>
<tr>
<td>area 4 phasic RT</td>
<td>IFV</td>
<td>inertial flow vector</td>
</tr>
<tr>
<td>area 4 phasic MT</td>
<td>DVV</td>
<td>desired velocity vector</td>
</tr>
<tr>
<td>area 4 tonic</td>
<td>OPV</td>
<td>outflow position vector</td>
</tr>
<tr>
<td>area 4 phasic-tonic</td>
<td>OFPV</td>
<td>outflow force position vector</td>
</tr>
<tr>
<td>area 5 tonic</td>
<td>PPV</td>
<td>perceived position vector</td>
</tr>
<tr>
<td>area 5 phasic</td>
<td>DV</td>
<td>difference vector</td>
</tr>
</tbody>
</table>

The major weakness of the model, it is claimed, is that it does not fully account for the properties of muscles, specifically the intrinsic damping force of muscle. However, it seems that, at a future date, the extended-VITE model could incorporate such properties through proper simulation of the Ia and II afferents and motoneuron efferents.
4 Roles of cerebellum and basal ganglia

Figure 4: Sensory-motor pathways through the cortex are activated by sites within motor thalamus. These sites are normally tonically inhibited by the basal ganglia, thus "closing the gate" on those pathways. DCN activates other sites in motor thalamus which themselves activate sensory-motor pathways, but DCN is tonically inhibited by cerebellar cortex, thus those pathways are also "normally gated closed".

Figure 4 diagrams the connectivity of the "normally closed" gating mechanism of the basal ganglia and the cerebellum. Sensory-motor pathways through cortex are activated by sites within motor thalamus. Certain sites are normally tonically inhibited by the basal ganglia, thus "closing the gate" on those pathways. The deep cerebellar nuclei (DCN) activate other sites in motor thalamus which themselves activate sensory-motor pathways. But DCN is tonically inhibited by cerebellar cortex, thus those pathways are also "normally closed" gated. Because motor thalamus make excitatory projections to motor cortex (area 4), the basal ganglia effectively directly inhibits motor cortical activity, and selectively removes this tonic inhibition in a phasic manner. The cerebellum does not have direct control over motor cortical activity. However, it indirectly excites motor cortex in a phasic manner manner by releasing DCN excitatory connections to motor thalamus.

The basal ganglia act to withhold activation of possibly many plans formulated in motor cortex until cortex has selected the best plan of action for the environmental context (fight? or flight?). Thus, direct inhibition of gates makes sense in that once a plan is formulated, and the gate is opened, it is 'off-to-the-races' with no delay. Concurrent with the outcome of whatever action is selected may be some expectation of reward. A dip occurs in dopamine activity (DA) broadcast to the basal ganglia (and many other sites) if no reward occurs, whereas DA activity remains at its baseline if the reward occurs. A burst of DA activity may follow an action if that action generates an unexpected reward.

The computational role of the cerebellum is to modulate the transformation of sensory-motor activity. This is in keeping with the manner by which the
cerebellum opens normally closed gates: phasic release of inhibition of the DCN acts to 'inject' specific excitatory motor activity into the sensory-motor stream, eg. modulate. The specificity in modulation is rooted in the selective nature of climbing-fiber discharges to cerebellar cortex. That is, only those Purkinje cells specifically involved in the task need undergo 'teaching'. Contrast this with the comparatively broad-based DA teaching signal to the basal ganglia, where selective tuning is not required.
5 Hybrid picture of cerebellum

The anatomical and physiological elements of the Marr-Albus perspective of a hybrid picture of the cerebellum are shown in Figure 5. These elements will be described before introducing the adaptive timing elements.

Figure 5: The fundamental cerebellar circuit necessary to satisfy the Marr-Albus theory.

Considering the circuit of Figure 5 from a system data-flow perspective, input enters from two points: the mossy fibers, and the climbing fibers. Mossy fibers carry sensory input from the periphery (various receptor organs in muscles, joints and skin), as well as information from the cerebral cortex, the vestibular system and the reticular formation. The information carried by the climbing fibers is believed to indicate the ‘error’ between the intended and the executed movement. Output from the system is from the deep cerebellar nuclei, which project to motor cortex.

Now consider the internals of the system. Assume all synaptic contacts are excitatory unless mentioned otherwise (in Figure 5, inhibitory contacts are labelled with a negative sign). The mossy fibers project to a layer of granule cells, undergoing what is believed to be an expansion recoding operation, allowing greater and simpler pattern recognition capability. The output of this ‘recoding’ is the parallel fiber layer, which makes excitatory contact to Purkinje, stellate-b, and basket cells. The Purkinje cells act in the manner of perceptron with adaptive weights. The stellate-b and basket cells project to the Purkinje
cells, making inhibitory contact, thus implementing negative weight adjustment capability. The parallel fiber synapses make excitatory contact, but it is believed that the positive weights tend to be reduced with learning, rather than increasing. However, it is very important to note here that the adaptive timing element of this hybrid circuit, considered later, operates on the Purkinje cell synapses.

Golgi cells, taking input from both the mossy fibers and the parallel fibers, make inhibitory contact with the granule cells, to roughly 100,000 cells at a time, and this network is believed to be vital to performing the sparse combinatoric recoding of the active mossy fiber input ‘vector’, where two similar mossy fiber activation vectors give rise to highly dissimilar parallel fiber activation vectors. The Golgi-granule network also plays an ‘attentional’ role, shutting down areas of cerebellum not currently active for a particular movement.

The climbing fibers make contact on a nearly one to one basis with the Purkinje cells. Climbing fiber activity tends to temporarily shutdown Purkinje cell activity. Purkinje cells output to cerebellar nuclear cells, making inhibitory contact. They also make feedback connections to other Purkinje cells, basket cells, stellate cells and Golgi cells.

This machinery is enough to achieve certain competencies. The sparse combinatoric recoding function is able to reveal information that is only implicit in the vector of mossy fiber inputs. The type of information entering the mossy fibers is by nature in general very similar, and it is the subtle relations between inputs that is of importance. This is implicit information, and the recoding function makes these subtle differences explicit.

This same machinery is also partly responsible for ensuring that a new control action is learned only in those motor control channels that are capable of acting to preempt the error. The other necessary ingredient is the near one-to-one correspondence between climbing fibers and Purkinje cells. Given that a Purkinje cell is receiving some explicit piece of information from the world, and given that CS-UCS pairing is taking place between the mossy fiber (CS) data and the climbing fiber (UCS) data, and given that the Purkinje cells drive (indirectly) a motor control channel, all this functionality combined solves the credit assignment problem. Put simply, the circuit is setup to support a lot of $CS \rightarrow UCS \rightarrow CR$ pairings.

For the other half of this hybrid picture of the cerebellum, consider the adaptive timing mechanism of Fiala et al. (1996). The focus of this mechanism is intracellular, at the Purkinje cell dendritic spine (synapse to parallel fibers). The critical mechanisms are 1) the climbing fiber triggered, glutamate sensitive, AMPA receptor which raises membrane voltage, thus setting-off the next mechanism... 2) the voltage-triggered $Ca^{++}$ channel, which dumps calcium intracellularly during the US, and 3) the parallel fiber, glutamate triggered, second-messenger receptor, which, when $Ca^{++}$ is present, sets forth a cascade which dephosphorylates the AMPA receptor, reducing its efficacy, that is, inducing LTD. (whew!) This functionality allows the learning of interstimulus interval timing ranging from 100ms to 4s, thus extending the temporal window within which CS-UCS pairing can occur (to learn and perform control actions).
This adaptive timing mechanism also ensures learning of control actions (aka CRs) that slightly lead what would otherwise be an error (aka UCR).

It is difficult to say whether this hybrid machinery allows a distributed practice regime, or allows procedural memory stabilization over long intervals. Both of these are difficult to test. However, this same cerebellar model (adding output-to-input recurrence) has been used to construct a model of cerebello-cortical interactions in the learning and performance of the fixed sequence "chunks" that characterize skilled performance.

Lastly, I should mention that the other competencies (a-d), described earlier, because their functionality does not conflict, allows at least that set of competencies to operate simultaneously.
6 Representation of movement direction in motor cortex

6.1 a

The center-out task was described in the answers to questions 1 and 3 of this exam. However, two elements relevant to the classic experiments of Georgopolous must be highlighted. Firstly, the Georgopolous experiments concentrated on direction of movement only. The experiments did not include force as a variable. Secondly, the setup was such that the targets, and hence the directions of movement, where broken into eight different points equally spaced points around a full circle.

What they discovered in their sets of recordings from motor cortex during this task was that cells appeared to have a preferred direction, firing maximally in that direction, and tapering-off in a Gaussian manner (fitted with a cosine function, hence "cosine-like") for the directions on either side.

The firing rate calculation used to determine the preferred direction was determined from the total time from the appearance of the target to the completion of movement, thus they concluded that cells were coding direction of movement and not the end-point. This is not a sound conclusion, as within that window of time could be distinctive cell firing activity that could be coding other information.

6.2 b

Equation 3 is an expression for the population vector, as originally formulated by Georgopolous.

\[ P(M) = \sum_{i=1}^{n} w_i(M)C_i \]  

Where...

\[ w_i(M) = d_i(M) - b_i \]
\[ d_i(M) = b_i + k \cdot \cos(\theta_{MC}) \]

<table>
<thead>
<tr>
<th>Term</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>d</td>
<td>cell discharge rate</td>
</tr>
<tr>
<td>b</td>
<td>resting level (cell-specific)</td>
</tr>
<tr>
<td>k</td>
<td>cell-specific regression coefficient</td>
</tr>
<tr>
<td>C</td>
<td>cell’s preferred direction (angle of peak discharge rate)</td>
</tr>
<tr>
<td>M</td>
<td>direction of reaching</td>
</tr>
<tr>
<td>( \theta_{MC} )</td>
<td>angle between the preferred direction of cell C and the direction of reaching M</td>
</tr>
<tr>
<td>w</td>
<td>magnitude of the cell’s vectorial contribution</td>
</tr>
</tbody>
</table>
Every cell contributes something to each possible direction, so the "population vector" is just a sum of each cells discharge rate (magnitude) while pointing in the movement direction with angle of that cell’s preferred direction, for every cell in the population. A population vector was supposed to represent the direction of movement. It was successful in providing an unambiguous and reliable estimation of movement direction, but did not provide any insight into how movement coordinates are transformed.

6.3 c
Scott and Kalaska decided to see if the population vector for a given direction remained the same for two different arm postures. They merely had the monkey do the normal Georgopolus-like center-out task, and then the same task but having to twist (or the fancy term, ‘abduct’) it’s arm. They found that the population vectors were not the same, and so concluded that motor cortex does not encode hand trajectory in spatial coordinates. I agree with them on this, but do not feel that this data gives insight into whether motor cortex encode in motor coordinates. This particular experiment does not reveal that.

6.4 d
A good part of the Todorov/Georgopolous-Ashe argument is wrapped-up in a lot of mathematical hugabolu intended to phase everybody else. However, Todorov needs to acknowledge the observation of velocity and direction sensitive cells in motor cortex, rather than assume that motor cortex performs low-level force control of muscles. Population vector analysis cannot settle this dispute alone, as it is necessary to look at the details of motor cortex cell activity.

6:00AM note to Prof. Bullock: Each of the figures in this doc was created by myself just for this exam. I mention this only in the hopes of getting a little credit for the mental effort taken in deciding what to include in each figure, and the attention to accuracy.