How The Cerebellum Contributes to Behavior

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Accurate Movement is Deceptively Difficult

For the purpose of discussion let’s analyse a simple concrete skill: holding a delicate object in your jaw without crushing or dropping it. We take this skill for granted but without a cerebellum it would be impossible. Most animals can do this easily, even when the object is extremely fragile and valuable. Normally we are not aware of the difficulties involved with this skill because it’s normally a subconscious process.

This task is difficult because all of the parts of the system are dynamic and constantly changing and so it’s difficult to build a model of the system ahead of time. Muscles are difficult to model; it’s difficult to calculate how much force a muscle will produce. They are weakened by fatigue and depleted oxygen and glucose levels. Good nutrition and exercise will permanently strengthen a muscle. Muscles get damaged and heal. Sensory organs are also difficult to model; some are stochastic and others have highly non-linear response properties.

The external environment is impossible to model ahead of time. A useful model of the environment must be learned while alive and living in it and it needs to be continuously updated. The real world is full of unpredictable bumps and disturbances. Even things that should not change, like the laws of physics, can sometimes change in unexpected ways. For example an egg is filled with free floating fluid and that alters its angular momentum. At the extreme, accurate movement can be part of an adversarial competition. For example consider holding a kitten that does not want to be held and wiggles around trying to escape.

Clearly the brain is capable of quickly and accurately responding to disturbances. Furthermore with repeated practice animals can improve arbitrary motor skills. How have animals mastered accurate movement in the messy biological world?

Closed Loop Control in the Brainstem

Close loop control (also known as “Feedback Control”) is a guiding principle throughout the central nervous system. Closed loop control is a method of achieving a desired state by comparing it with the current state to determine which direction to move and how far. Closed loop controllers update their output every time the animal receive new sensory input, which allows them to quickly react to disturbances. The spinal cord and brainstem contain a multitude of closed loop controllers for controlling the body. They’re some of the phylogenically oldest circuits in the brain and they’re still intact and functional after 500 million years of evolution.

In our example: the brain controls the muscles on lower jaw bone with the goal of obtaining a desired level of force, velocity, or position; which is known as the “setpoint”. Sensory organs embedded inside of the muscle fibers inform the central nervous system of the muscle’s current state; which is referred to as the “sensory input”. By subtracting the sensory input from the setpoint the brain obtains a deviation; which known as the “error”. The brain uses the error to calculate a motor command that reduces the error. This calculation can be as simple as a scaling the error by a constant multiplier to produce a motor command. PID controllers, which are common in engineered systems, also use the derivative and the integral of the error over time to correct for sudden or systematic errors (respectively).

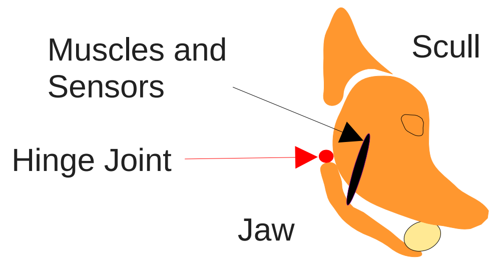

Figure 1: Schematic diagram of a fox carrying an egg in its mouth.

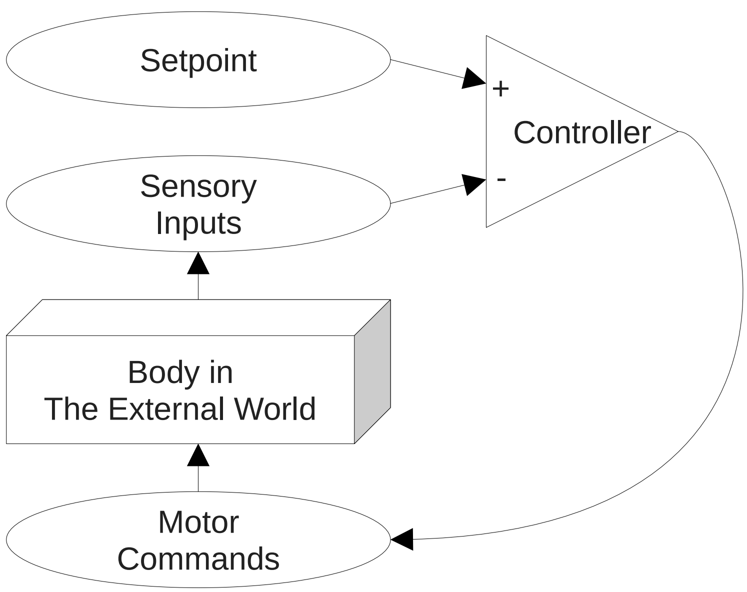

Figure 2: Schematic diagram of a closed loop controller.
Motor Commands = f (Setpoint – Sensory Inputs)

Closed loop controllers can be simple in their design. Many of the controllers in the spinal cord and brainstem are genetically determined (hardwired). They do not contain any explicit model of the world. They simply modulate their output until their sensory input matches their setpoint. In general, closed loop controllers work well but they can get stuck in oscillatory feedback loops if they try to move too fast. Over-correcting a mistake can lead to another larger mistake.

Multiple closed loop controllers can be combined to manage systems with multiple sensory inputs, in a scheme known as “Cascade Control”. Each distinct sensory input has its own controller and setpoint dedicated to it, and the controllers can connect to each other by sending their motor commands to other controller’s setpoints. In this way they form a hierarchy of controllers, with the higher tiers commanding the lower tiers, and the lowest tier sending commands to the actual motors. Cascade control allows the controllers to operate independently of each other and at different speeds from each other; and it allows the controllers to be fine-tuned and specialize for their domain. Cascade control allows many simple controllers to work together to create complex behavior.

For example, controlling a regular skeletal muscle involves three layers of control for the force, velocity, and position of the muscle. Sensory nerve endings embedded in the muscle measure each of these quantities. The controllers for a muscle are arranged as follows: the position controller adds its output to the setpoint of the velocity controller, which in turn adds its output to the setpoint of the force controller. The force controller acts directly on the muscle. The logic here is that the higher tier controllers act on the derivative of the measurement that they control.

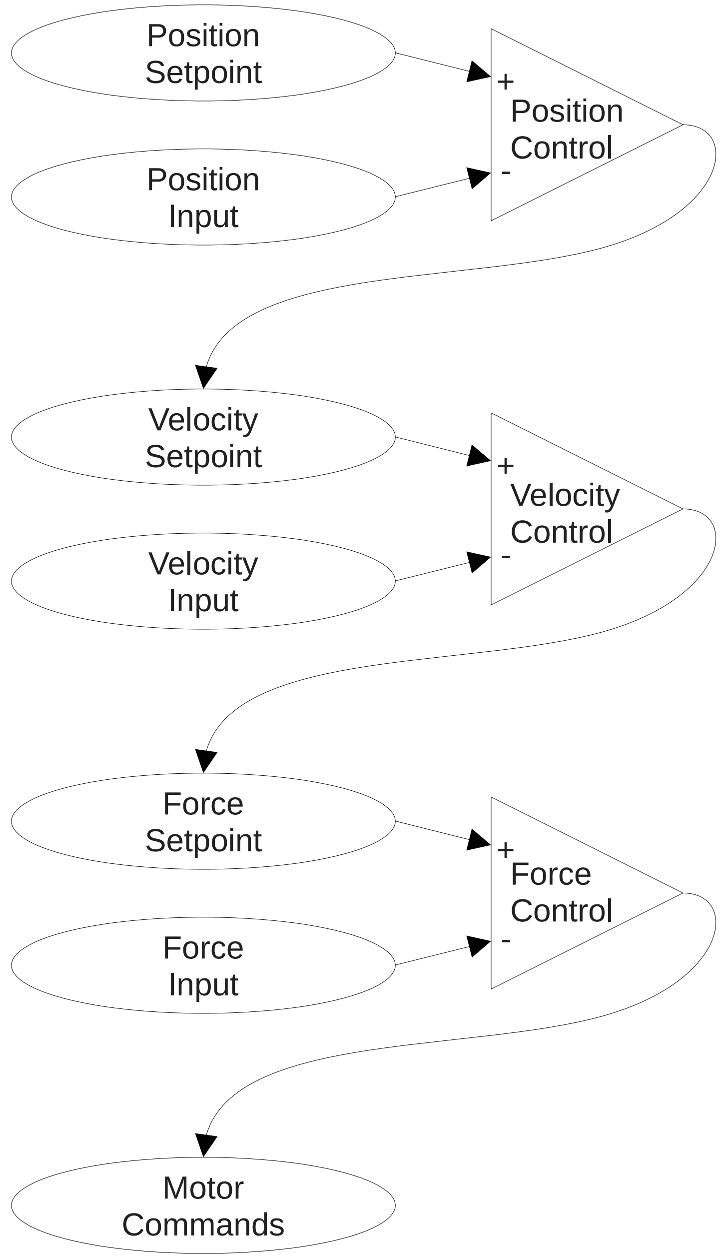

Figure 3: Example of cascade control for a skeletal muscle.

The Cerebellum as an Associative Memory

In the 1970's three scientists, named David Marr, Masao Ito, and James Albus, each independently discovered that the cerebellum uses supervised learning to implement an associative memory. An associative memory is a device that stores pairs of input and output values, and when it is presented with a known input it will return the associated output. Supervised learning is a class of learning algorithm in which a external "supervisor" provides the correct answer for the algorithm to learn from. The cerebellum associates sensory inputs and a copy of the motor commands with a value that the supervisor gives it. The cerebellum will recall that value in the same sensory and motor context. The cerebellum can memorize a vast number of these associations; it is in essence a very large look-up table. Ever since this discovery more than 50 years ago, scientists have been wondering what the cerebellar outputs represent. What is the supervisor having the cerebellum do?

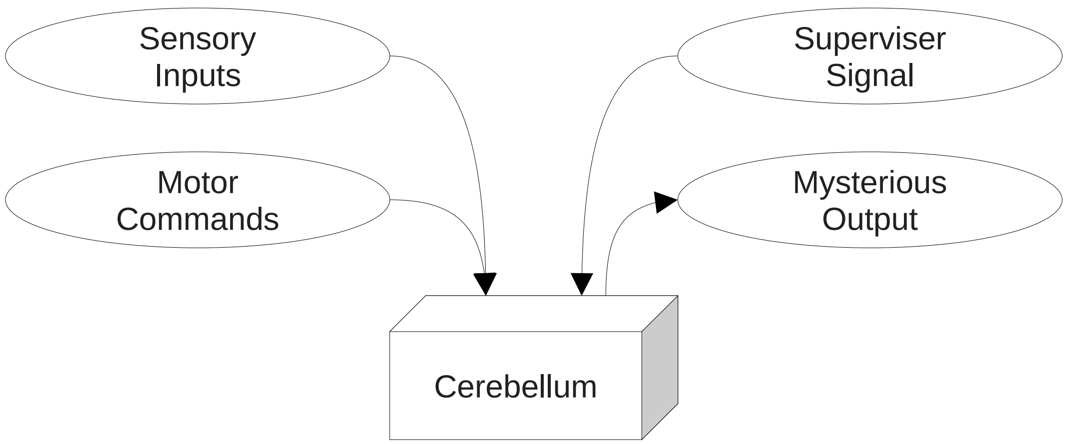

Figure 4: Known external connections of the cerebellum, as of the 1970's.

The Cerebellum as a Forward Internal Model

The cerebellum implements a forward internal model, meaning that it analyses the animal's current sensory inputs and motor commands to predict what sensory inputs it will see in the immediate future. The controller uses these predictions as an additional source of sensory input.

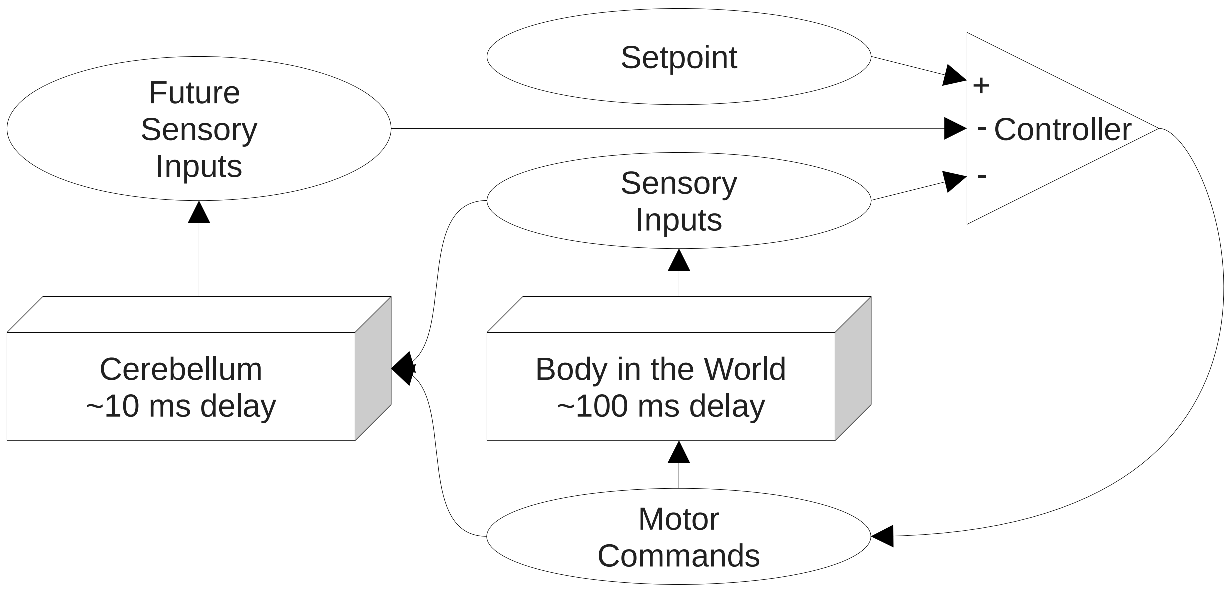

Figure 5: Schematic of the cerebellum and the brainstem

The cerebellum gives the controller a preview of what its actions are going to do. If the controller makes a mistake then the cerebellum informs the controller of its mistake and the controller can start issuing corrections immediately, without waiting for sensory confirmation that it made a mistake. For some tasks, by the time you get sensory feedback about a mistake it's already too late to fix it. Closed loop control is entirely reactive and is incapable of solving such tasks on its own.

Because the cerebellum reacts so quickly the controller can act quickly as well. The controller now participates in two different feedback loops, one through the real world and the other through the cerebellum. The feedback loop through the cerebellum has a very short latency which allows for very fast movements without accidentally over correcting or entering into unstable oscillations. The brain can go through many cycles of predictions and corrections as the action is unfolding.

To take full advantage of the cerebellum and make fast movements the controller needs to be tuned with a very high gain. This makes the system dependent on the cerebellum for accurate movement. The controller is then ill-suited to operate on it's own and if the cerebellum is disabled or damaged then the system will oscillate. Consider for example alcohol, which can temporarily disable the cerebellum and cause tremors and a loss of fine motor skills.

The cerebellum learns constantly. As long as the animal is awake and acting in the world, the cerebellum will receive a steady stream of inputs to learn from. It checks every prediction that it makes by waiting a fraction of second to see if the prediction comes true, and then it learns from its mistakes.

The cerebellum is not limited to modeling the body, it also learns about the external world as the body interacts with it. The brain is not limited to controlling the position of the body. The brain can control arbitrary sensory inputs. For example hitting a baseball requires controlling the position of the baseball bat in three dimensional space, a skill known as hand-eye coordination.

The Smith Predictor

Incidentially, 1957 Otto Smith invented the Smith Predictor which combines a closed loop controller with a forward model in a remarkably similar way as the combined brainstem and cerebellum. The Smith Predictor uses forward models to predict both the future sensory input as well as the length of the sensory-motor delay, which is needed in order to differentiate between unwanted disturbances and the intended effects of the motor commands. The Smith Predictor was invented in order to control industrial processes which have long delays in the sensory-motor feedback loop. However for safety reasons, industrial applications must not incorporate learning algorithms and the forward model is expected to be engineered ahead of time. Making forward models by hand is difficult and error prone, which limits the usefulness of the Smith Predictor for its intended applications.

Inverse Models

A competing theory is that the cerebellum is memorizing an inverse model. In this alternative theory the cerebellum memorizes the correct motor program to achieve a desired setpoint. This theory is appealing because it directly outputs motor commands, which makes the theory easy to understand.

The neuroscientific issue with this theory is that the cerebellum does not make the correct connections to implement it. The inputs to an inverse model are the current input and the desired input (the setpoint), and the output is the motor command. The cerebellum does not make these connections!

The computational issue with this theory is that, at a fundamental level, inverse models need to subtract the sensory input from the setpoint, and the cerebellum is very bad at doing subtraction. Using an associative memory (like the cerebellum) to solve a problem which contains subtraction will by necessity require memorizing a subtraction-table. Memorizing an inverse model requires remembering a motor program for every combination of distinct input and setpoint values, and number of such pairs grows quadratically with respect to the number of inputs and setpoints.

The forward model presented here does not implement subtraction. Instead it's combined with a specialized controller that implements the necessary subtraction. Memorizing a forward model requires remembering a sensory state for every combination of sensory inputs and motor commands. Since the number of motor commands is constant, the total number of things to be memorized grows linearly with respect to the number of distinct sensory input values.

Another way of analysing this computational issue is that: inverse models learn how to reach a setpoint, and they can not reuse that knowledge for reaching other setpoints. Forward models learn significantly faster than inverse models because they can be used to reach any setpoint, regardless of what the setpoint was when they learned the model.

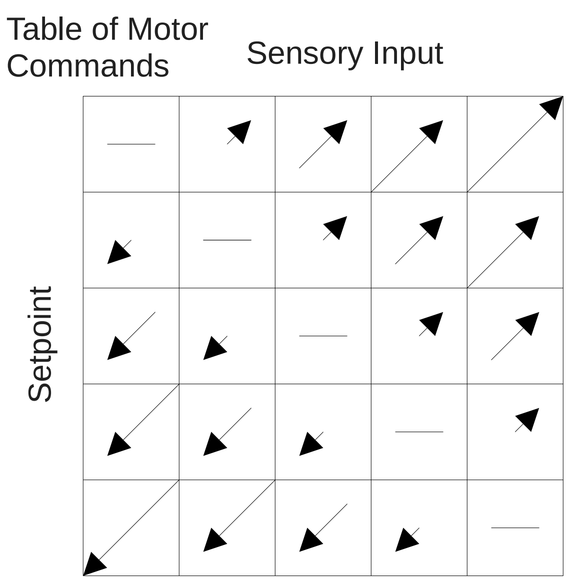

Figure 6: Inverse models memorize a motor command for every combination of sensory inputs and setpoints. This implicitly requires memorizing a subtraction table.

References

A THEORY OF CEREBELLAR CORTEX
David Marr (1969)
https://doi.org/10.1113/jphysiol.1969.sp008820

A Theory of Cerebellar Function
James S. Albus (1971)
https://doi.org/10.1016/0025-5564(71)90051-4

NEURAL DESIGN OF THE CEREBELLAR MOTOR CONTROL SYSTEM
Masao Ito (1972)
https://doi.org/10.1016/0006-8993(72)90110-2

Is the Cerebellum a Smith Predictor?
Miall, Weir, Wolpert, Stein (1993)
https://doi.org/10.1080/00222895.1993.9942050

Cerebellar forward models to control movement
John Stein (2009)
https://doi.org/10.1113/jphysiol.2008.167627

An internal model of a moving visual target in the lateral cerebellum
Nadia L Cerminara, Richard Apps, and Dilwyn E Marple-Horvat (2009)
https://doi.org/10.1113/jphysiol.2008.163337

How Basal Ganglia Outputs Generate Behavior
Henry H. Yin (2014)
https://doi.org/10.1155/2014/768313

Short latency cerebellar modulation of the basal ganglia
Christopher H Chen, Rachel Fremont, Eduardo E Arteaga-Bracho & Kamran Khodakhah (2014)
https://doi.org/10.1038/nn.3868

Evolution of behavioural control from chordates to primates
Paul Cisek (2021)
https://doi.org/10.1098/rstb.2020.0522

50 Years Since the Marr, Ito, and Albus Models of the Cerebellum
Mitsuo Kawato, Shogo Ohmae, Huu Hoang and Terry Sanger (2021)
https://doi.org/10.1016/j.neuroscience.2020.06.019

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Nora Feddal (2017)
https://www.flickr.com/photos/64942074@N03/32281891152

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https://pictures-of-cats.org/Loving-Cat-Pictures.html/sand-cat-and-her-kittens