The Cerebellum and Motor Learning: Marr's Theory of Cerebellar Cortex

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What Does the Cerebellum Do?

1. Classical conditioning.

   Thompson: rabbit eyeblink conditioning.

   Conditioning is abolished by cerebellar lesion, but can eventually be recovered even with cerebellum absent.

   Korsakoff's syndrome patients acquire the eyeblink response but can't remember the training procedure, which they underwent just the day before.

2. Real-time motor control.

   Fine-tuning the vestibulo-ocular reflex (VOR), an open-loop control system (just three synapses.)

   Recalibration of saccadic eye movements.

   Cerebellar lesions impair motor coordination, but movement is still possible even with no cerebellum.

3. Motor learning.

   Marr-Albus theory of cerebellar cortex.

Marr's Theory

- Marr suggested that the cerebellum is an associative memory.
- Input: proprioceptive information (state of the body.)
- Output: motor commands necessary to achieve the goal associated with that context.
- Compare with Marr's other cortical theories:
  - Hippocampus: learning was only temporary (for about a day) rather than permanent. Retrieval based on partial cues was an important feature.
  - Cortex: extensive recoding of the input thought to take place. Hippocampus was used to train the cortex during sleep.
  - Cerebellum: long-term memory, not a temporary buffer. Pattern completion from partial cues was not desirable. Strictly "table lookup."

Inputs to the Cerebellum

1. Climbing fibers.

   - These fibers originate in the inferior olivary nucleus.
   - The “training signal” for motor learning? Or the UCS for classical conditioning?

2. Mossy fibers: all other afferent input to the cerebellum.

   - Input from spinal cord, vestibular nuclei, and the pons.
   - Spinocerebellar tracts: cutaneous and proprioceptive information.
   - Much more massive input comes from cortex via the pontinue nuclei and then the middle cerebellar peduncle.
   - More fibers in the middle cerebellar peduncle than in all other afferent and efferent fiber systems of the cerebellum combined.

The Purkinje Cells

- Purkinje cells are the principal cells of the cerebellum.
- Largest dendritic trees in the brain: 200,000 synapses.
- Purkinje axons form the sole output of cerebellar cortex.
- Nearly all the output is to cerebellar nuclei, such as the interpositus nucleus.
- Purkinje cells make only inhibitory connections.

Input Processing

- If mossy fiber inputs made direct contact with Purkinje cells, the cerebellum would have a much lower memory capacity.
- Also, we don't want subsets of an input pattern to produce the same result as the whole pattern. Subsets must be recoded so that they look less similar to the whole.
- Solution: introduce a layer of processing before the Purkinje cells to make the input patterns more sparse and less similar to each other (more orthogonal.) Cf. role of dentate gyrus in the hippocampus.
- Mossy fibers synapse onto **granule cells.**
- Granule cells provide the input to Purkinje cells, via the **parallel fibers.**
- **Golgi cells** are inhibitory interneurons that modulate the granule cell responses to produce "better" activity patterns.
- Mossy fiber input patterns with widely varying levels of activity result in granule cell patterns with roughly the same level of activity, thanks to the Golgi cells.

The Golgi Cells

- Modulate the activity of granule cells.

- Descending dendritic tree samples inputs from the mossy fibers, which are the input to the granule cells. Provides for fast response to changing inputs.

- Ascending dendritic tree samples inputs from the parallel fibers, which are the outputs of the granule cells. Provides feedback control of the granule cell activity pattern.

- Axons descend and make inhibitory connections with the mossy fiber to granule cell synapses.

Constraints on Granule Cell Activity

α_m is fraction of active mossy fibers.

α_g is fraction of active granule cells.

N_m, N_g are numbers of mossy fibers / granule cells.

1. Reduce *saturation:* the tendency of the memory to fill up. We want $\alpha_g < \alpha_m$.

2. Preserve information. The number of possible patterns should not be reduced by the granule cell processing.

$$\alpha_g (\log \alpha_g) \geq \frac{N_m}{N_g} \alpha_m (\log \alpha_m)$$

2. Pattern separation: for two distinct patterns, the number of positions at which activity differs should increase as we go from mossy fiber patterns to granule cell patterns.

   Pattern separation is a decreasing function of α, so we again want $\alpha_g < \alpha_m$.

The Matrix Memory

- The weights: modifiable synapses from granule cell parallel fibers onto the Purkinje cells.
- The thresholding function: whether the Purkinje cell chooses to fire or not.
- Threshold setting: **stellate** and **basket cells** sample the input pattern on the parallel fibers and make inhibitory connections onto the Purkinje cells.
- These two cell types are treated as equivalent, but only because we don't know their real functions.
- Albus' contribution: synapses initially have high weights, not zero weights. Learning *reduces* the weight values.
- Since Purkinje cells are inhibitory, reducing their input means they will fire less, thereby dis-inhibiting their target cells.

Summary of Cerebellar Circuitry

Two input streams:

- Mossy fibers synapse onto granule cells, which in turn provide input to Purkinje cells via the parallel fibers.
- Climbing fibers synapse directly onto Purkinje cells.

Five cell types:

1. Granule cells (input pre-processing.)
2. Golgi cells (regulate granule cell activity.)
3. Purkinje cells (the principal cells.)
4. Stellate cells and ...
5. Basket cells sample the parallel fiber activity pattern and set the thresholds for Purkinje cells.

One output path:

- Purkinje cell axons project to the cerebellar nuclei.

A Higher Level View

- The cerebellum is divided into three principle regions:
  - Spinocerebellum: inputs from from spinal cord, and from visual and auditory areas.
  - Cerebrocerebellum: corticopontine inputs.
  - Vestibulocerebellum: for balance and eye movements.
- Both the anterior and posterior lobe of the spinocerebellum contain complete somatotopic maps of the body.
- Within each map there are actually multiple representations of the same body parts: **fractured somatotopy.**

Tyrrell and Willshaw's Simulation

- C program running on a Sun-4 workstation (12 MIPS processor, 24 Mbytes of memory.)
- Tried for a high degree of anatomical realism.
- Took **50 hours** of cpu time to wire up the network! Then, 2 minutes to process each input pattern.
- Parameters of the simulation:

  13,000 mossy fiber inputs
  200,000 parallel fibers
  100 Golgi cells regulating the parallel fiber patterns

  40 basket/stellate cells
  binary weights on the parallel fiber synapses
  1 climbing fiber for training
  1 Purkinje cell

- Memory capacity: 60–70 patterns can be stored with a 1% probability of a false positive response to a random input.

Tyrrell & Willshaw's Conclusions

- Marr's theory can be made to work in computer simulation.
- A few of his assumptions were wrong: binary synapses, for example.
- But the overall idea is probably right.
- Several parameters had to be guessed because the anatomical data is not yet available.
- The theory is also compatible with the cerebellum having a role in classical conditioning.

Buckingham, Barto, and Houk

- How does a cerebellar-model controller perform in a real-time control task?
- APG (adjustable pattern generator): a module that can generate an elemental burst command with an adjustable intensity and duration.
- Complex behaviors are controlled by groups of APGs.
- Use a non-linear spring-mass system defined by:

$$m\ddot{x} + b\dot{x}^{1/5} + k\,(x - x_{eq}) \;=\; 0$$

- This is a "sticky" system: motion stops when velocity falls below .005 m/s.
- Purkinje cells have two states: **low** and **high**.
- In order to reach a desired target position x_{eq}, the cell must switch states at the right time.
- It learns to do this by adjusting the weights on its inputs.