A speculative model of supervised learning in cerebellum.

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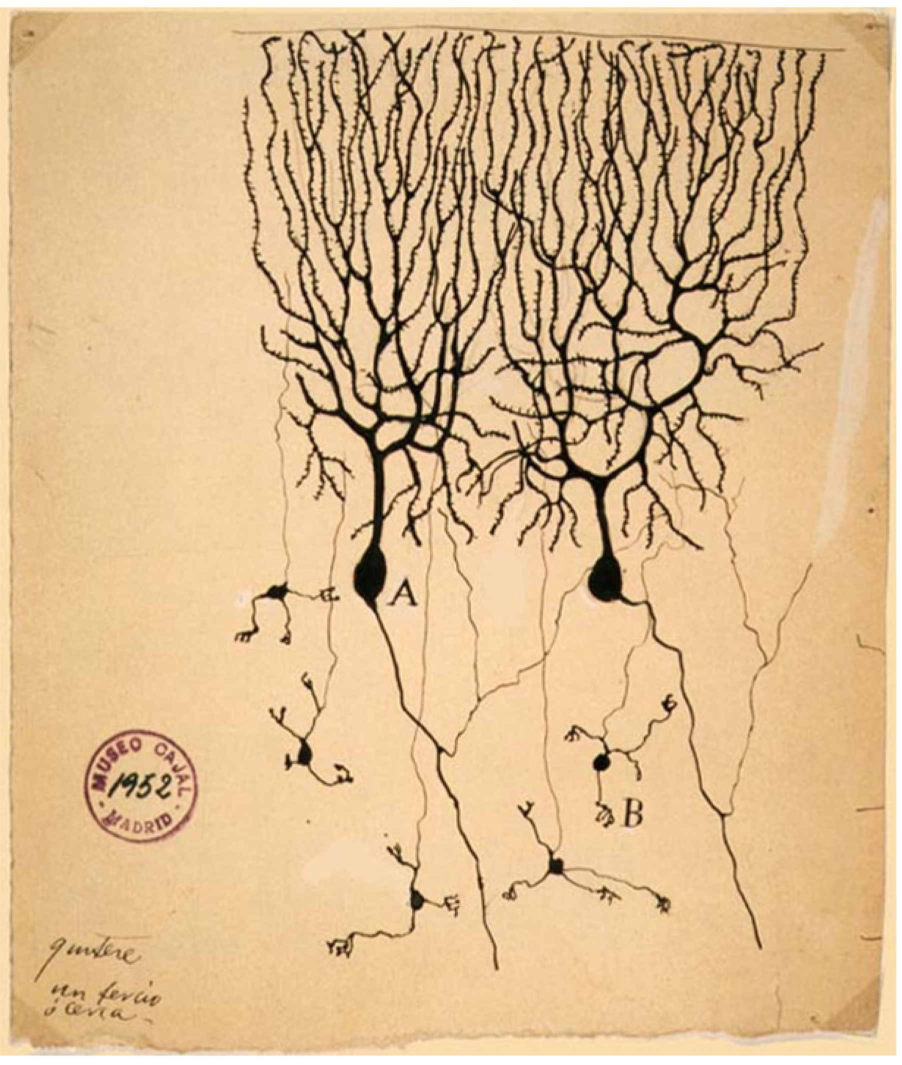
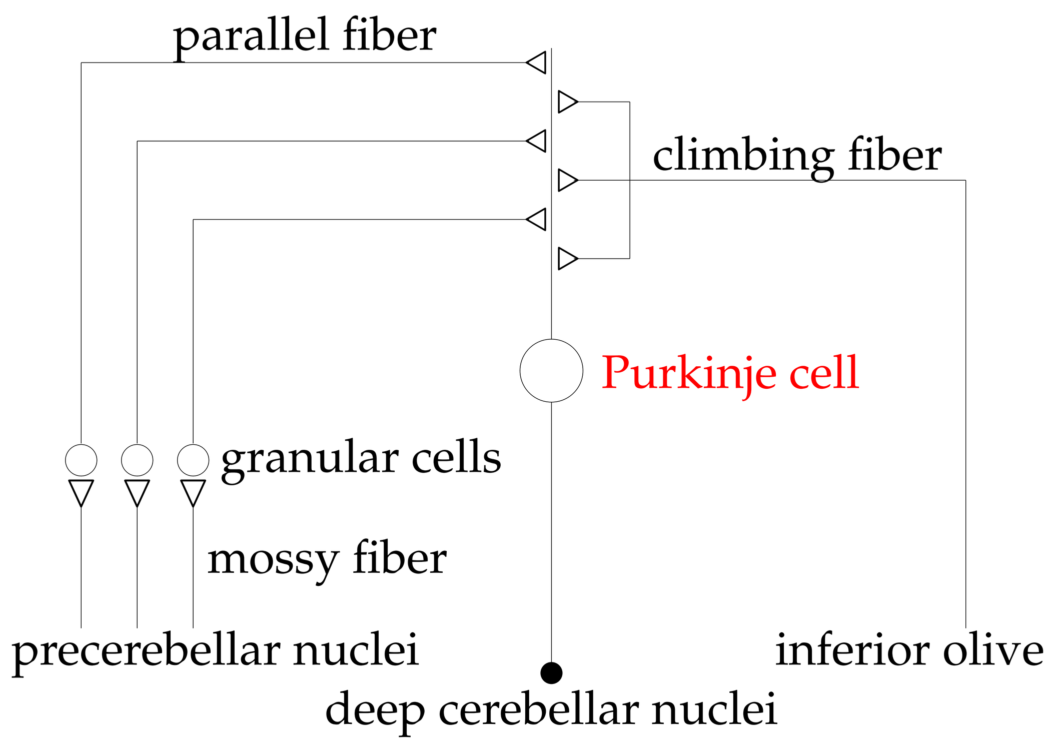
Abstract.
The cerebellum is thought to do supervised learning. This poster proposes that spike timing dependant plasticity and the sustained refractory period that follows the complex spikes the Purkinje cell fires in response to input from the climbing fiber could combine to allow the inferior olive to supervise learning.

Purkinje Cells

Purkinje cells are an important component in motor control and the pathway from the cerebellar cortex to the motor system passes through their inhibitory input to the deep cerebellar nucleus.



One of Santiago Ramon y Cajal's celebrated drawing of Golgi stained cells. **A**: a **Purkinje cell** from pigeon cerebellum, **B**: one of the many granular cells whose axons, the parallel fibres, constitute one of the two main inputs to the Purkinje cell.

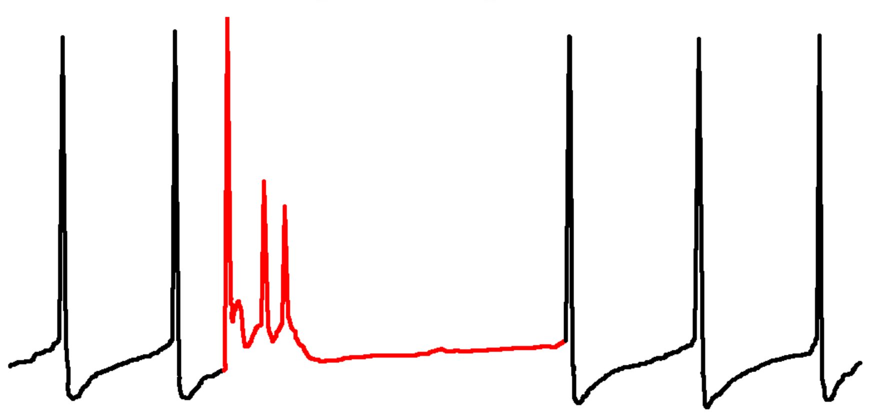


A highly simplified schematic of the **connectivity in the cerebellar cortex**.

- Multiple weak parallel fiber excitatory inputs from the precerebellar nuclei.
- A single strong excitatory climbing fiber input from the inferior olive.
- Purkinje cell are inhibitory and afferent to the deep cerebellar nuclei.
- This diagram simplifies connectivity and omits local inhibitory neurons.

Complex spikes

A distinctive feature of Purkinje cells is that they have two types of discharge. In addition to simple spikes they fire complex spikes in response to input from the climbing fibers. Complex spikes have an initial spike followed by a sustained depolarization and, often, a train of partial spikes.

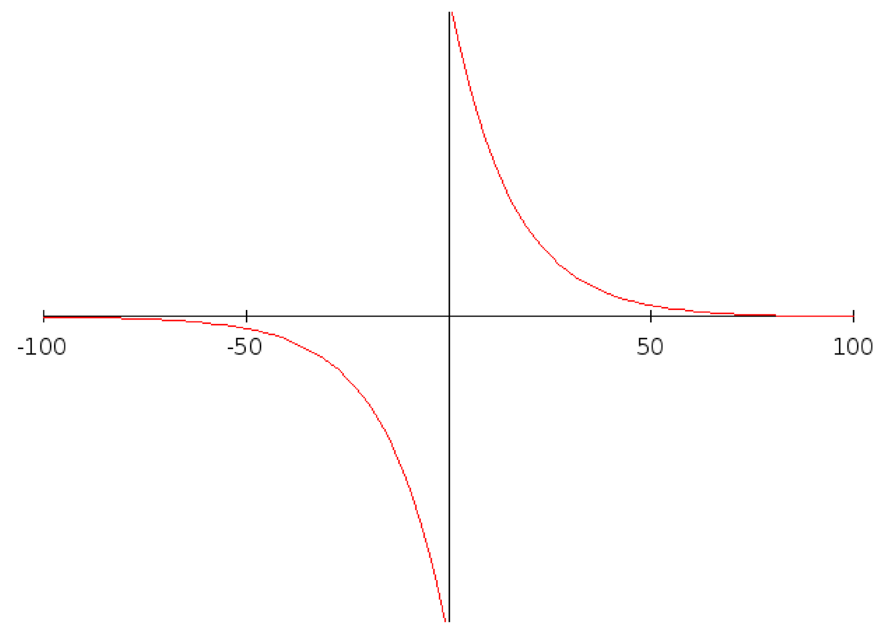


A complex spike. This drawing shows a simple spikes in black and a complex spike in red. The complex spike is followed by a long refractory period during which spiking is not possible. This is a sketch, not an actual recording, but a typical time scale would have this refractory period 50ms long.

Spike timing dependent plasticity

Typically, in STDP changes to synapse strengths depend on the time difference between pre-synaptic and post-synaptic spikes. In the classical STDP for excitatory cells:

- **causal** pre-synaptic spike precedes post-synaptic spike: synapse is strengthened.
- **acausal** post-synaptic spike precedes pre-synaptic spike: synapse is weakened.



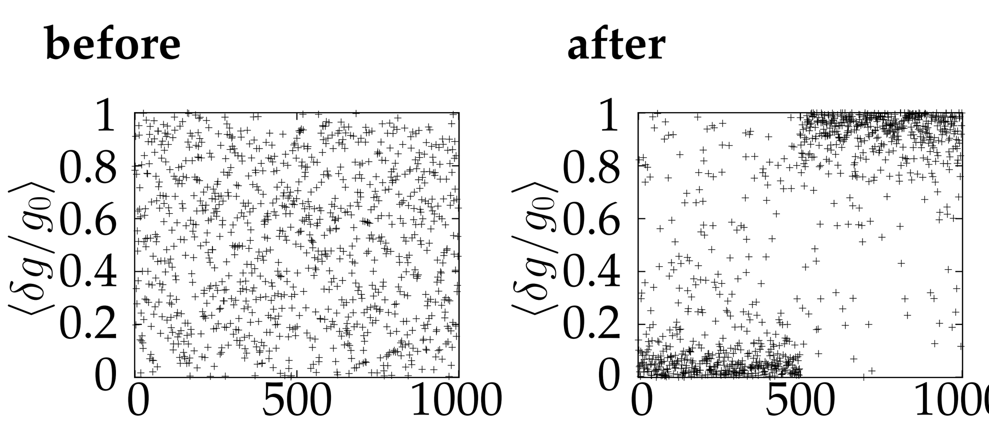
In classical STDP, based on the experimental observations of Bi and Poo (1998), changes to the synapse strength are additive and have an exponential profile. The graph shows a notional change against the difference in spike time (ms).

What does STDP do?

Song and Abbott (2001) gave an elegant demonstration of STDP's ability to extract structure in data. The used a simple network where 1000 spiking inputs feed-forward through STDP synapses to a single integrate and fire neuron. The inputs came in two groups with correlated activity in each group.

1000 input neurons
↓
An integrate and fire neuron

Over time the synapses of one group grows stronger and of the other, weaker.



Synapse strengths before and after. The synapses are divided into two groups, with the first 500 in one group and the rest in the other, the **before** graph shows the random initial conditions, the **after** graph, the distribution after $t = 5000$ s of simulated time. This reproduces a similar graph shown in Song and Abbott (2001).

- This is unsupervized learning and the ability to do unsupervized learning is one of the strengths of STDP.
- Learning is very slow, one group of synapses gradually wins out over the other, gaining control of the post-synaptic neuron.
- The 'winner' is chosen randomly based on small initial variation giving one group a greater tendency to control the post-synaptic neuron.

A proposal

It is proposed here that the learning role of complex spikes is to give a pause during which there is no post-synaptic spike. This will mean any pre-synaptic spikes will be in an anti-causal relationship with the initial spike of the complex spike. According to the standard STDP rule, this will cause long term depression.

Proposal again

In short, it is proposed that a standard STDP rule governs plasticity in synapses from the parallel fibres and local inhibitory neurons and this is exploited by error-correcting complex spikes to supervize learning.

A Song-Abbott model

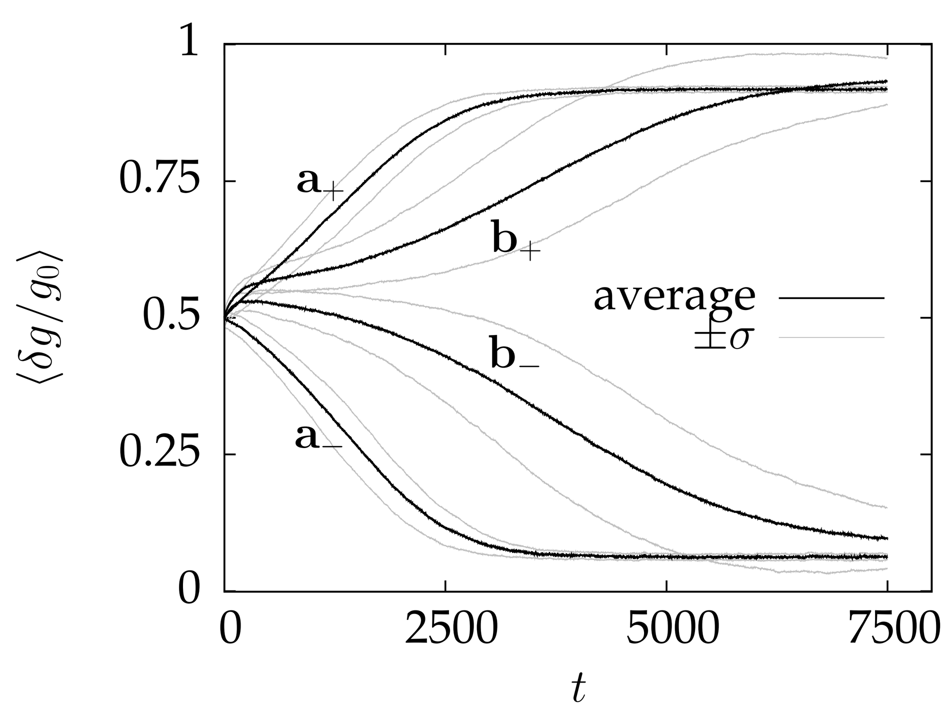
The Song-Abbott model can be used modified to illustrate this proposal.

1000 input neurons
↓
An integrate and fire neuron←climbing fiber

Here the climbing fiber produces a noisy spiking input, correlated to the spiking in one of the two groups. When it fires the integrate and fire neuron, which now models a Purkinje cell, also spikes and this spike is followed by an extended refractory period.

Results

- The climbing fiber succeeds in supervising the learning, in every one of a 100 trials the group with the climbing fiber is the one that ends up with very low synapse strengths.
- Supervised learning is also much much faster and the variations in learning rate are much smaller.



The curves for the supervised learning are marked $a_\pm$ with a_- indicating the group correlated to the climbing fiber. In the case of the unsupervised learning the group that wins out varies from trial to trial, but the average is taken across matching groups: $b_\pm$ mark the unsupervized learning groups, with b_+ the average for the group that ends up with the larger average value.

Positive conclusions

- The proposal works for the simple model!
- Perhaps this is even a useful way of thinking about supervized learning in the brain; it is possible that the complex spike with its extended pause in spiking may be a particularly direct example of a more widespread phenomenon where learning is supervised through the modulation of pauses in spiking.

Problems

The simple model is too simple to be taken seriously, it ignores the detailed structure of the cerebellum, the complicated dynamics of the Purkinje cells and the complexity of more recent models of spike timing dependent plasticity and calcium dynamics.

Bibliography

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