Figure 1: A drawing by Santiago Ramón y Cajal of a Purkinje cell. [Picture taken from `http://en.wikipedia.org/wiki/Golgi's_method`]

The cerebellum as a perceptron

The cerebellum has a number of striking features; it has a more stereotypical structure than most brain area and this structure is conserved across species. It also has one of the brain's largest cells, the Purkinje cell, and its most numerous, the granule cell.

Purkinje cells have a distinctive structure with a huge, highly branched, but flat dendritic arbor, see Fig. 1; this allows an extensive connectivity with each Purkinje cell receiving inputs from around 100,000 other cells. In the cerebellum the Purkinje cell are lined up like pages in a book, with their arbors lying in parallel planes. They receive two excitatory inputs, weak inputs from parallel fibres, axons that run perpendicular to the planes of the Purkinje cell dendritic arbors, and a strong input from a climbing fibre, a single axon which winds around the Purkinje cell and makes multiple con-

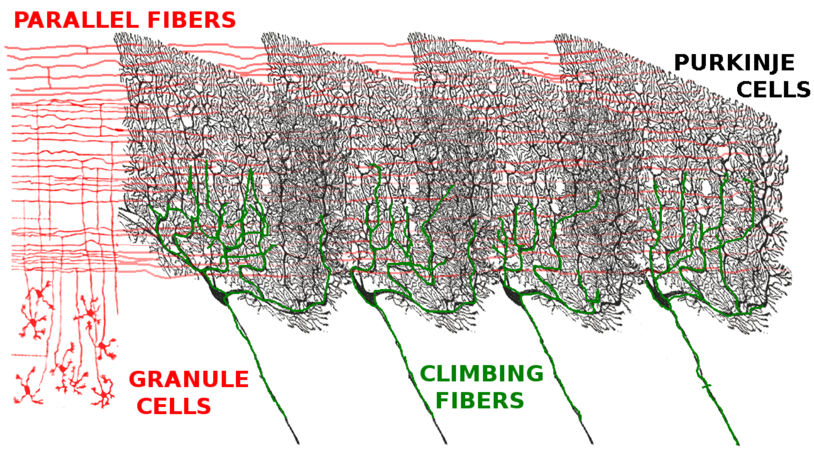

Figure 2: A cartoon of the cerebellar circuitry. A vertical axon rises from each granule cells, splits once and then extends horizontally in two directions making connections with multiple Purkinje cells. Each Purkinje cell has its own climbing fiber which winds up around it.

tacts with it, see Fig. 2.

Another peculiarity is that the Purkinje cell emits dramatically different types of spikes to different inputs. In response to multiple weak inputs from the parallel fibres it fires a normal spike, called in this context a *simple spike*; In response to single spike from the climbing fibre is fires a special spike, called a *complex spike*, with a leading spike, a number of small 'spikelets' and a sustained after-period of depolarisation; this is illustrated in Fig. 3.

It is still unclear exactly what the cerebellum does; what is known is that it is important for actions, fine motor control and proprioception; problems with the cerebellum are associated with ataxia, loss of fine motor control, poor motor learning and poor balance. There is a specific gait associated with cerebellar damage, one that exhibits a certain self-consciousness or vigilance is required for movement. According to most ideas about cerebellar function it is required for the calculation of fine motor signals [1], or for predicting the sensory or proprioceptive consequences of motor actions [2]; it is believed it encodes forward and backwards models of movement so that it predicts the consequences of motor commands, or calculates the motor command that will a particular movement.

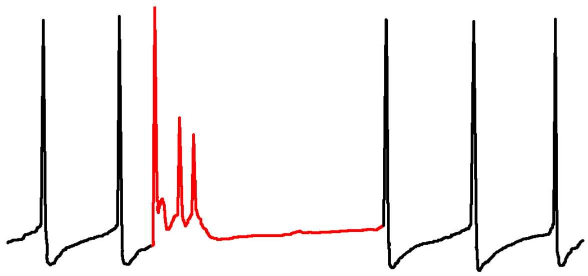

Figure 3: A complex spike. This drawing shows simple spikes in black and a complex spike in red. The complex spike is followed by a long refractory period during which spiking is not possible. This is a sketch, not an actual recording, but a typical time scale would have this refractory period 50 ms long.

Whatever exactly it does, it is widely believed, in accordance with the Marr-Albus model [3, 1], that the connections from parallel fibers to Purkinje cells acts as a perceptron. Thus, if y is the output of the Purkinje cell and, in this simple model, taking into account the fact Purkinje cells are inhibitory

$$y = -\sum w_i x_i \tag{1}$$

where the x_is are the activities in the parallel fibers and w_i is the strength of the synapse from the ith parallel fiber to the Purkinje cell. The idea in the Marr-Albus model is that the climbing fiber carries the error signal $d - y$ making the cerebellum an example of supervised learning.

References

[1] Albus, JS. (1971) A theory of cerebellar function. Mathematical Biosciences 10: 25–61.

[2] Gao J-H, Parsons LM, Bower JM, Xiong J, Li J and Fox PT (1996) Cerebellum implicated in sensory acquisition and discrimination rather than motor control. Science 272: 545–7.

[3] Marr, D (1969) A theory of cerebellar cortex. Journal of Physiology 202: 437–70.