Granule cells are irreducibly small (6-8 μm)

Figure 7.15
Largest cerebellar neuron occupies more than a 1,000-fold greater volume than smallest neuron. Thin section (~1 μm) through monkey cerebellar cortex. Purkinje cell body (PC) and nucleus are far larger than those of granule cell (grc). The latter cluster to leave space for mossy fiber terminals to form glomeruli with grc dendritic claws and space for Golgi cells (Go). Note rich network of capillaries (cap). Fine, scattered dots are mitochondria. Courtesy of E. Mugnaini.
Chapter 7

a granule cell’s output synapse is structured to reliably deliver a precisely timed message—privately (Nahir & Jahr, 2013). All 150,000 parallel fiber synapses onto an individual Purkinje cell tend to be wrapped by the same glial cell (Bergman glia), whose form mimics that of the Purkinje cell’s extensive dendritic tree (figure 7.1).

The different tasks of inner and outer cerebellar layers and their consequent different designs illustrate why there can be no generic neuron. In the inner layer, high-rate synapses improve S/N by pooling excitatory responses and sharpen timing precision with feedback inhibition—allowing a burst of information-rich spikes (figure 7.16). In the second case, spikes deliver this information by a synaptic design that facilitates a burst (figure 7.17). The first design reduces glial wrapping to enhance synaptic spill-over; the second design does the opposite. Now we can ask: what are the costs of these two designs?

Costs of different neuron designs

Energy costs by cell type

When the various energy costs are totaled, the individual Purkinje cell proves to be the most expensive neuron, and granule cell proves to be the cheapest.

Figure 7.18

Energy costs by cell type. Left: Purkinje cell is the most expensive neuron, and granule cell is cheapest. Right: Granule cell array is the most expensive, and Purkinje cell array is far cheaper. Glial cells are cheap individually and as arrays. Reprinted with permission from Howarth et al. (2012).
The central nervous system (CNS) reflex is three-dimensional in the sense that all directions of head rotation elicit specific compensatory eye movements. Vergence movements change the visual axes of the eyes in relation to each other when the point of fixation moves away from or toward the eyes. This is necessary to keep the image on corresponding points of the retina. Vergence movements are a prerequisite for fusion of the two images and for stereoscopic vision.

Convergence of the visual axes, which takes place when an object is approaching the eyes, depends primarily on the activity of the medial rectus muscles, with some contribution also from the superior and inferior recti (Fig. 15.2). Accommodation and pupillary constriction accompany convergence movements.

More about Voluntary Saccades and Scanning

When reading, we fixate a point on the line for an average of 250 msec (60–500) before the gaze is moved on by a saccade. How far the gaze moves before reaching a new point of fixation varies greatly. There is a tendency to fixate on long "content" words rather than on short "functional" words. Native readers of English perceive about 4 letters to the left and 15 to the right of the point of fixation.

A woman with inborn ophthalmoplegia (inability to move the eyes) had surprisingly small problems and was able to live a normal life. She apparently used quick head movements to compensate for the lack of saccadic eye movements (Gilchrist 1997), and was thereby able to scan the visual scene with sufficient speed and accuracy.

The Cerebellum Can Adjust the Vestibulo-Ocular Reflex to Changing External Conditions

The magnitude of the reflex response (not the response itself) to a certain rotational stimulus depends on signals to the vestibular nuclei from the cerebellum (Fig. 25.4). The Purkinje cells of the vestibulocerebellum receive primary vestibular fibers (ending as mossy fibers) that provide information about direction and velocity of the head movement. In addition, the same Purkinje cells receive information, via the inferior olive and climbing fibers, about whether the image is stationary or slips on the retina. A retinal slip indicates that the velocity of the compensatory head movement is too high or too low. The cerebellum is then capable of adjusting the excitability (the gain) of the neurons in the vestibular nuclei—that is, in the reflex center of the vestibulo-ocular reflex. Such adaptive change of gain of the reflex is presumably needed continuously during growth and in situations of muscular fatigue. Experiments in which animals wear optic prisms that deflect the light so that it appears to come from another direction than it really does, show the remarkable capacity for adaptation (learning) in this system.

Cerebellum stores sensorimotor contingency between vestibular signals and oculomotor response (VOR)
(Kandel & Schwartz & Jessell, fourth edition, Figure 42-7)
Traditional random-access memory (RAM)

Figure 3.3. Organization of a random-access memory. The selected memory location is shown by shading.
Sparse, distributed memory (SDM) (Kanerva, 1988)

Figure 3.4. Organization of a sparse distributed memory. The first selected memory location is shown by shading.
Figure 3.5. Address space, hard locations, and the set activated by $x$. $H$ is the (Hamming) radius of activation.
(Kandel & Schwartz & Jessell, fourth edition, Figure 42-7)
Cerebellum is not purely sensorimotor, but also stores cognitive contingencies

Strick, Dum & Fiez (2009)