

## THE CEREBELLUM REVISITED\*

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25 years ago I thought that the cerebellum was the part of the brain most likely to be understood by direct translation of the anatomy into functional terms. To-day I am still confident, even if the schemes proposed in the meantime have proved to cover at best only very partial aspects of cerebellar function and sometimes are quite divorced from any realistic consideration of histology. I want to show in what direction my hopes go.

My own contribution to theory was based on considerations on the geometry of the cerebellar cortical neuropile and in particular on its peculiar translational symmetries. The result in a nutshell was expressed in Braitenberg and Atwood (1958) as the cerebellar cortex having something to do with transformations of time into space and vice versa, in other words, with the various aspects of the function of a clock. This idea is still around in its most general form, e.g. in recent papers by Pellionisz and Llinas (1979, 1980, 1982) but was met with well justified criticism when it was applied in detail to the coordination of rapid movements (Braitenberg, 1965) and especially to eye movements (Kornhuber, 1974). The most devastating observation is that parallel fibers, if they are interpreted as delay lines, as we had proposed, cannot produce delays much longer than 10 ms and hence seem of little use in the context of motor or sensory functions for which the cerebellum is held responsible. It is this observation, and not that vast body of later physiological data (Eccles, Ito and Szentagothai, 1967; Llinas, 1969; Thach, 1973; etc.) or new theoretical proposals (Brindley, 1964; Marr, 1969; Albus, 1971) which made the old idea obsolete. On the contrary, the physiology had provided direct evidence for assumptions implicitly or explicitly made in the timing theory (such as the excitatory relations between mossy fibers and granular cells, parallel fibers and Purkinje cells, climbing fibers and Purkinje cells), and the Brindley-Marr-Albus theory could very easily be combined with the idea of exact timing.

Personally, I am reluctant to give up an idea on neural computation which has the rare merit of providing detailed explanations of many morphological peculiarities in a piece of grey substance. The shape of dendritic trees of Purkinje cells, the connections of one parallel fiber with a long row of Purkinje cells, the absence of antero-posterior folds are in good accord with the idea of timing (Braitenberg, 1977) but make little sense in the light of any of the other theories. Can this interpretation of cerebellar histology be upheld in the face of new evidence and critical insights?

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\*Dedicated to M. Franz on his birthday 1982.



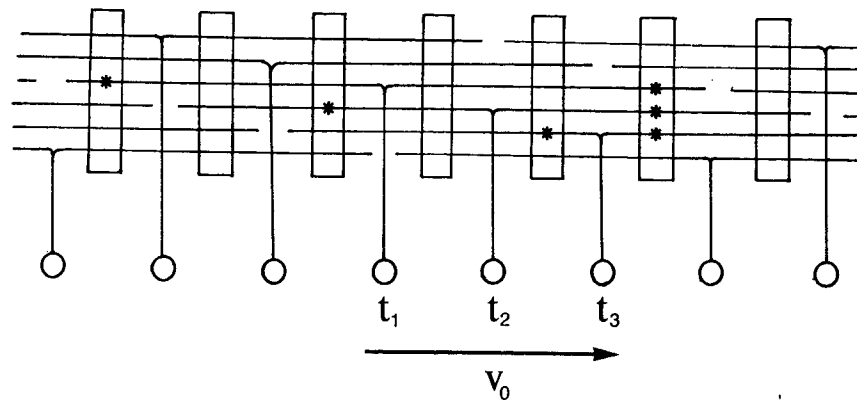


Fig. 2: A stimulus which sweeps along a folium of the cerebellar cortex will produce maximal summation on individual Purkinje cells (three stars) if it hits successive input points at times  $t_1, t_2, t_3$  corresponding to the velocity  $v_0$  of spike conduction in parallel fibers.

associated with one row of Purkinje cells. Let the input be point to point in a somatotopic map. Then, if something runs through the body at a velocity that makes the input sweep through the beam at a velocity equal to that of conduction in parallel fibers, the activity will summate maximally, because each new innervation will add to the travelling wave already set up by previous input. There will be less summation for smaller or larger velocities. A Purkinje cell along the beam will become maximally active when it is approached from either side by such a travelling wave at just the right velocity. This makes a velocity detector out of a beam of parallel fibers plus Purkinje cells. The output from the Purkinje cells may be fed back to control those variables that keep the velocity of whatever images sweep through the cerebellum at the desired value.

An interesting aspect of this new variant of a chronometric cerebellar theory is that it can account for the control of quite long sequences, up to a few tenths of a second in larger cerebella, if we imagine activity sweeping transversally through the cerebellar sheet from one end to the other (more than 10 cm in the human cerebellum). The duration of a few tenths of a second is characteristic of certain elementary episodes of motor control, such as syllables in language, saccades in visual or manual tracking (Stark, 1968). It is reasonable to suppose that the chaining of such elementary motor acts is controlled by the motor cortex, while the sequencing within the elementary episodes is the responsibility of the cerebellum.

Like in our previous theory, the inhibitory components of the cerebellar machinery (stellate, basket and Golgi cells) have been again neglected. Their role is most likely as Eccles, Ito, and Szentagothai have suggested, to isolate a beam from its neighbours by "lateral inhibition", and to keep activity in the molecular layer below a certain level by controlling the input to the granular layer. These are auxiliary mechanisms that are intuitively useful in the function which we ascribe to the cerebellum. Also, there is no mention of climbing fibers. The suggestion by Marr (1969) that they may serve as tutors for learning, is still the most appealing one.

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