Theories of the cerebellum

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- **Cerebellar circuitry**: Parallel and climbing fibre inputs to Purkinje cells. Influence on movement via cerebellar nuclei.

- **Marr’s theory and motor learning**: Purkinje cells receive cerebral teaching signals for movements via climbing fibres; contexts via parallel fibres. Parallel fibre synapses on P-cells modifiable when climbing fibre fires. Memory capacity of P-cells.

- **Albus**: LTD at parallel fibre synapses on P-cells, basket cells and stellate cells.

- **Gilbert**: Group of P-cells as the memorizing unit. Variable frequencies learned by P-cells (as opposed to binary outputs of Marr and Albus). How muscular actions are coordinated. Potential second teaching input to P-cells via the noradrenergic input.

- **D’Angelo and De Zeeuw**: Granular layer plasticity: potential role in cerebellar learning.

- **Rhythmic activity in the cerebellum**: possible role in “binding” of complex contexts and in temporal sequencing of movements.

- **Experimental testing of the theories**: LTD in cerebellum. Output of P-cells during learning of movements. On-beam synchrony in parallel fibres of cerebellum.

References
25. The use made by the cerebellum of the information that it receives from sensory organs

by G.S. Brindley, The Physiological Laboratory, University of Cambridge, Cambridge (United Kingdom)

There is already good evidence, from the effects of lesions, that the cerebellum is mainly concerned in voluntary movement and only slightly in reflexes. If its function in voluntary movement is no more than to fill in, according to a developmentally pre-determined set of rules, the messages sent down from the fore-brain each of which is just, but only just, informative enough to distinguish the desired movement from all other anatomically possible ones, there is no reason why the cerebellum should be a large organ. The size and complexity that it needs is not greatly increased if it be supposed that in constructing the detailed message telling the anterior horn cells what to do in the later phases of a movement, it makes use of sensory information about the success of the earlier phases to the very limited extent that is possible on a pre-determined code of rules. And no other non-plastic function that has yet been suggested for the cerebellum would, if performed by a computer, require many elements.

It is therefore suggested that the message sent down by the fore-brain in initiating a voluntary movement is often insufficient as instructions for all the anterior horn cells that take part in the movement even if elaborated as far as it can be according to fixed rules; it needs to be further elaborated by the cerebellum in a manner that the cerebellum learns with practice, and this further elaboration makes use of information from sensory organs. The cerebellum is thus a principal agent in the learning of motor skills.

Experiments were described that favour this hypothesis and help to indicate how information from sensory organs is used plastically.


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**Fig. 1.** Schematic diagram showing the connections of the neurons in the cerebellum. The parallel fibers run in a longitudinal direction along a cerebellar folium (shown on the left) and synapse with the dendrites of the Purkinje cells, which extend in transverse planes of the folium (shown on the right). The basket and stellate cells would synapse with a number of other Purkinje cells (not illustrated) in the same transverse plane. The directions in which nerve impulses travel are marked with arrows.
Figure 2. Organization of the limb premotor network and its regulation by cerebellar Purkinje cell (PC) inhibition. Neural stages in the limb premotor network are: N, cerebellar nuclear cells; T, thalamic relays; M, neurons in the primary motor cortex; R, neurons in the magnocellular red nucleus; P, pontine neurons; L, lateral reticular neurons.


Figure 4. Model of granule cell parallel fiber control of muscular coordination: (a) within each nucleus, there is a use-specific (modal) representation of somatic musculature; (b) the orientation of the myotome is in the coronal plane; (c) the orientation of the parallel fibers is also in the coronal plane; (d) the output of the parallel fiber beam of Purkinje cells falls on the nuclear representation of the myotome; (e) different uses of the muscles in a limb may be coded by different subsets of parallel fibers and their differential effects on the Purkinje cells (coordination of synergist muscles); (f) parallel fiber beams that span the nuclei in their Purkinje cell projection may influence two or more nuclei simultaneously (coordination of modes of movement).


Figure 8. Operation of the associative net: (a) initial state; (b) learning to associate an input pattern with an input pattern; (c) subsequently presenting a learned pattern; (d) subsequently presenting an unlearned pattern.


Figure 9. Solution in the associative net: (a) turning on neuron synapses with neuron associations, (b) two false positives when presenting an unlearned pattern.

5.3. The storage capacity of a Purkinje cell

The capacity of a Purkinje cell may be calculated very simply from the assumptions 5.2. Suppose the fraction of facilitated parallel fibre synapses is 0.7, and each learned event occupies \( n \) parallel fibres. Then \( x \), the expected number of events which may be learned before the total proportion of synapses used exceeds 0.7, is the largest integer for which

\[
(1 - \frac{n}{200,000})^x > 0.3.
\]

\( x \) has been computed for various values of \( n \), and the results appear in Table 6. It will be seen that the advantage of having a small number of fibres active in each learned event is an enormous increase in capacity: the Golgi cell arrangement of local as well as global constraints on the codon size begins to make good sense. If the minimum number of parallel fibres active in learned event is 500, the average number of responses stored by each Purkinje cell is probably in excess of 200.

Table 6. \( x \) is the number of events each occupying \( n \) parallel fibres that can be learned by one Purkinje cell, i.e. \( x \) is the largest integer for which

\[
\left(1 - \frac{n}{200,000}\right)^x > 0.3
\]

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<th>( n )</th>
<th>500</th>
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<th>5,000</th>
<th>10,000</th>
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<tr>
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<td>240</td>
<td>119</td>
<td>47</td>
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Fig. 8. Cerebellar Perceptron: \( P \), Purkinje cell; \( B \), basket cells; \( S \), stellate b cells. Each Purkinje cell has inputs of the type shown.

Fig. 3. Diagram showing the organization of the cells in a unit when it is memorizing by the jth signal transmitted by the climbing fibres. Identical signals bj are transmitted along the climbing fibres to the k Purkinje cells P1, P2, ..., Pk. There are Nj parallel fibres synapsing with the Purkinje cells in the unit, and the frequency of firing in the ith fibre is fi. Each parallel fibre makes only one synapse with one of the Purkinje cells in the unit. The inhibitory (basket or stellate) cells S1, S2, ..., Sn, only form synapses on Purkinje cells in the unit, and each parallel fibre makes one synaptic connection with only one of the inhibitory cells. The outputs a1, a2, ..., an of the Purkinje cells in the unit are summed by the cell C.

\[
\frac{r.m.s. \text{ signal of unit}}{r.m.s. \text{ noise}} = 0.5 \frac{\text{number of parallel fibres}(N_j)}{\sqrt{\text{no. of c.f. signals memorised}(P_i)}}
\]

Gilbert, P.F.C. Brain Res. 70, 1-18 (1974)

Gilbert, P.F.C. Brain Theory Newsletter 2, 36-38 (1976)

Figure 1. Microelectrode recording of a single muscle spindle Ia afferent during a voluntary finger flexion movement.

Panel A: Records from above: original nerve signal; instantaneous nerve impulse rate histogram; subject’s performance and tracking signal (dotted line); velocity and a schematic representation of the spike train. Note the strong component of 9–10 Hz discontinuities in this movement, and the strong correlation between unit firing and the individual discontinuities.

Panel B: Note the strong component of 8–10 Hz discontinuities in this movement, and the strong correlation between unit firing and the individual discontinuities.


Fig. 3. Map of 6- to 9-Hz cerebral connectivities. The SPM map represents spatial distribution of coherence with the left primary motor cortex as reference region. Only areas with $P < 0.05$ (corrected, one-sample t test) are shown.

