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THE NEURON NETWORK OF THE CEREBELLAR CORTEX AND ATTEMPT
AT ITS MODELLING BY COMPUTER SIMULATION

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Speculative attempts at understanding the functions of the neuron network of the cerebellar cortex on the basis of its structural (connectivity) properties (Szentágothai, 1963, 1965) have been shown by subsequent physiological analysis as a justified approach to the operative features of neuron networks, and have led to quasi-realistic structure-function syntheses on operative features of the cerebellar cortex (Eccles et al., 1967). Considering the average distances bridged by the main types of intracortical connexions the smallest field of the cerebellar cortex that can be considered as some kind of elementary integrative unit is in the order of 1 mm^2 . The number of neurons/ mm^2 surface being around 650000 in the cat cerebellar cortex, the number of elements that has to be considered in an attempt at understanding the operations of the smallest part of the network - with excessive simplifications - is still several ten-thousands of neurons. Computer simulations of the earlier speculative neuron network models have been undertaken (Pollionisz, 1970, 1971) on the basis of the known physiological properties of the several types of neurons. Not knowing the exact numerical relations of various neuron types, and having only extremely crude notions about the geometric distributions and densities of the neurons, excessive - and as we know now unjustified - simplifications have been made in the structural (connectivity) relations of the model. A recent systematic quantitative study of the cerebellar cortex (Palkovits et al., 1971 a,b,c) enables us now to make the model of the neuron network more realistic:

(1) In structural respects by taking into account (1.1) the real numerical relations and densities of all neuron types; (1.2) the real geometrical positions of the Purkinje cells with the successive lateral shift of

the dendritic trees if longitudinal rows (with respect to folium axis) are considered, and its consequence that only every 5-6th Purkinje cell comes again to stand approximately in register; (1.3) the corrected average length of the parallel fibers (2 mm); and (1.4) that the average parallel fiber establishes synapses only with every 5th (more exactly with every 5th-6th) of the Purkinje cells the dendritic trees of which it penetrates.

(2) The new simulation model investigates the transformation of arbitrarily assumed input patterns (through the mossy fiber channel) in a number of successive fractions of time, as they traverse the neuron chain, and tries to display them visually by cinematography in the form of "animated pictures". The model considers the several neuron types of the cerebellar cortex as lying in successive separate planes. These neuron fields (one for each type of neuron) can thus be considered as matrices, in which the neurons represent the matrix elements. The stimulus patterns traversing the several fields can be described as simple binary matrices.

As an arbitrary input pattern a "spot"-like mossy afferent excitation pattern is considered having a generally symmetric Gaussian distribution within a matrix of 142×114 mossy terminals. While the threshold in the first step of transform (first synapse) - from mossy terminals to the granule cells - has been considered as fixed in earlier simulation models (Pellionisz, 1970), the new model to be presented takes into account Golgi cell inhibition assumed to be able to "select" the appropriate threshold of the mossy terminal-granule cell synapse according to the local density of the input. Advantage is taken here from a structural feature of this synapse, which is almost unique in the nervous system, the granule cell has 4-5 dendrites (on the average), all of which are engaged in synaptic contact with one mossy terminal of different origin. It is thus "a priori" probable that each granule cell has four (or five) possible thresholds (for the sake of simplicity only the four threshold granule cell is considered)

i.e. the granule cell may be excited either by the simultaneous arrival of impulses in 1, 2, 3, and 4 of its mossy contacts. Since each mossy-granule cell synapse (the so-called cerebellar glomeruli) has an inbuilt inhibitory mechanism in the form of the Golgi neuron endings, it would not be unreasonable to assume that lacking Golgi inhibition stimulation from one of its mossy contacts would fire the granule cell, and that depending from the strength of Golgi inhibition the granule cell needs the simultaneous arrival of impulses in 2, 3, and 4 (possibly 5) of its mossy contacts. This possibility has not been considered earlier as the Golgi axon-granule dendrite contacts have been considered as non-convergent. The recent quantitative studies on numerical relations of various neuron types (Palkovits et al., 1971 b) have now shown that there are at least three times as many Golgi cells as assumed earlier, so that a convergence of the axon branches of around three different Golgi cells can be assumed to exist at the level of each cerebellar glomerulus. Hence three different levels of inhibition can be imagined, which would give four different thresholds of the granule cell if the "non-inhibited" state were included.

This somewhat daring assumption would lead to the rather fascinating functional result (shown in Fig. 1) that the activity level of the granule cells (=parallel fiber system) could be kept between the levels of 30-70% (of the total granule cell population) between the inputs through 8-92% of the total mossy afferent population. The existence of such "stabilising mechanisms" in order to keep the function of neuron networks within certain limits, irrespective of the net amount of input, had to be postulated since long ago.

The computer simulation model tries to take account of the two possible modes of stimulation of the Golgi cells, either directly through the mossy fibers or indirectly over the parallel fibers. Also the collateral inhibition of Purkinje cells by the basket neurons can be now approached by modelling in more realistic manner, due to new quantitative data on the relative number and distribution of these neuron types.

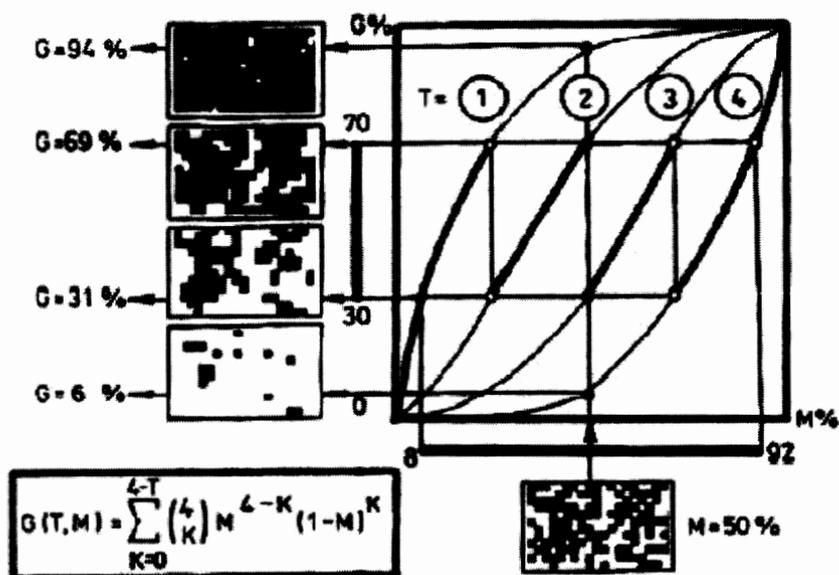


Fig. 1. Diagram illustrating hypothetical transfer characteristics from a mossy afferent population (M) to a population of granule cells (G). It is assumed that Golgi cell inhibition can increase the basic threshold T_1 gradually to T_2 , T_3 and T_4 . The inset pattern diagrams show how a random mossy input pattern of 50% saturation would be transformed into various granule cell excitation patterns according to the four possible thresholds.

Most exciting new perspectives for modelling are opened by the unexpected finding that only every 5th-6th of the Purkinje cell dendritic trees, penetrated by the parallel fibers, receives a synaptic contact (Palkovits *et al.*, 1971 c). This is particularly fascinating in view of the fact that the dendritic trees of only every 5th-6th of the Purkinje cells come again into register in the longitudinal axis of the folium (i.e. in the direction of the parallel fibers). This may be pure coincidence but it may also lead to quite new and hitherto unexpected features of neuron networks.

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