Computer simulation of the information preprocessing in the input of the cerebellar cortex

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1. Introduction

Since the classical studies of Ramon y Cajal (1911) extensive work has been carried out in order to reveal the neuronal organization of the cerebellar cortex. The morphology has been elucidated in many particularly also ultrastructural details by neuroanatomists (Fox *et al.* 1954, 1962, 1967; Szentágothai and Rajkovits, 1959; Gray, 1961; Hámori, 1964; Hámori and Szentágothai, 1964, 1965, 1966) and tentative circuit diagrams have been suggested (Szentágothai, 1963, 1965). The physiological properties of different types of neurons have been established electrophysiologically (especially by Eccles and his collaborators, 1964, 1966). As a result of these studies considerable progress was attained also in the interpretation of the function of the cerebellar neuronal circuits which has led to the possibility of some structuro-functional synthesis of the cerebellar network. (Eccles *et al.* 1967a.)

All these efforts have paved the way for preliminary attempts at computer simulations of the cerebellar neuron network (Pellionisz, 1970). By simulation of cerebellar neuronal fields of restricted but nevertheless substantial size (in the order of 10^4 neurons) one could get some insight into the holistic activity of whole fields of the cerebellar cortex. In our first step at modeling the cerebellar circuits neurons were considered as McCulloch-Pitts type elements, and the transfer of an arbitrary random excitation pattern arriving simultaneously through the mossy fibers was simulated.

In this paper the simulation of the transfer of excitation patterns is applied with the objective of a further analysis of the mossy fibre input. First, in order to explain the structural basis of this approach, a short review of the neuronal arrangement of the cerebellar granular layer will be given. As this layer receives all the mossy fibre input, any volleys of information (before entering the higher layers of the cerebellar cortex) undergo a certain kind of preprocessing in this remarkably simple and regular neuronal structure. Looking at this structure the first obvious question that comes to one's mind is: What may be the functional significance of this preprocessing? In the first part of this paper it will be shown how this question might be answered by analyzing the transfer of excitation patterns in the model neuron circuit. The second part is to demonstrate that even complex physiological events can be readily explained by this approach: The electrophysiologically observed "pattern sensitive" inhibition of the Golgi cells (Precht and Llinás, 1969) will be interpreted by computer simulation of excitation patterns.

2. Neuronal organization of the cerebellar granular layer

It would be far beyond the scope of this paper to discuss in full details the structure of this neuron arrangement. The reader is, therefore, referred to the anatomical literature and the recent comprehensive treatment by Eccles *et al.* 1967 a. Characteristic features of the architecture of the granular layer are shown in the Fig. 1. The inputs to the layer are the mossy fibres (MF) that upon entering the layer branch several times and develop presynaptic expansions, each giving rise to a complex synaptic apparatus, to a so-called "cerebellar glomerulus" (GL). The space is densely packed with very small granule cells (GR) having 3—5 dendrites each. Their axons constitute the output lines of the layer. They ascend to the molecular layer, where they bifurcate in *T*-shape manner to give rise to the parallel fibres (PF). The terminals

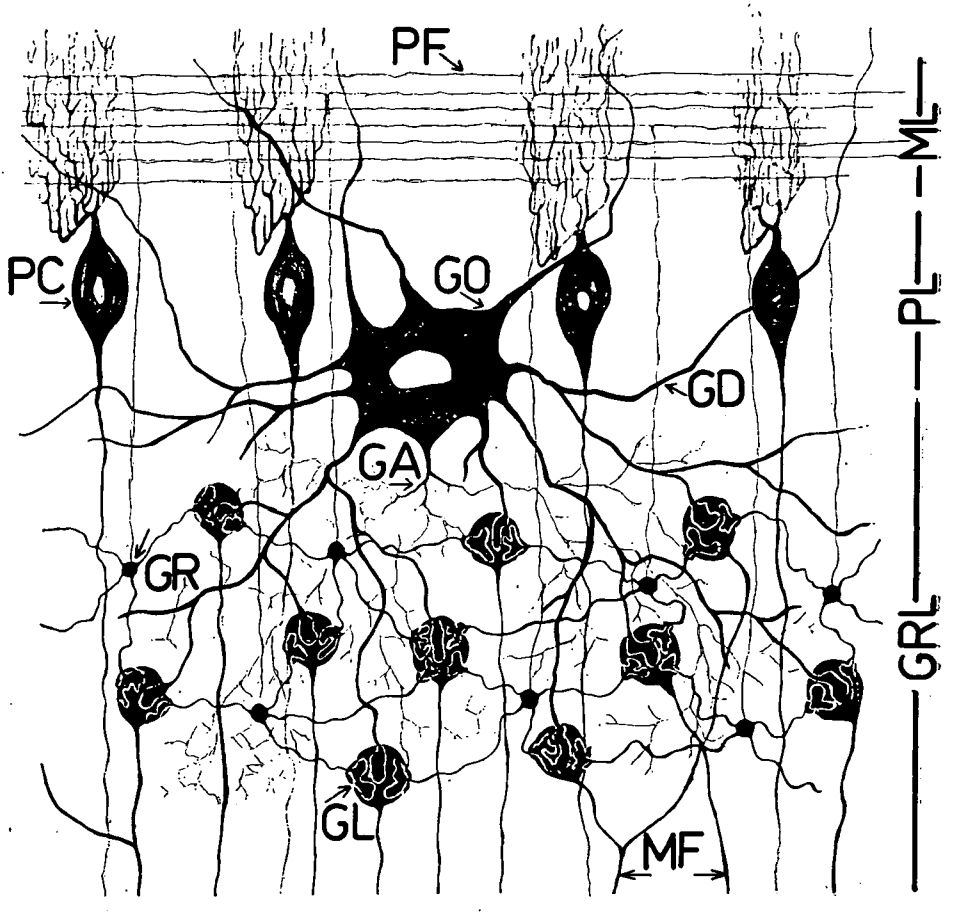

Fig. 1. Simplified, schematic view of the cerebellar architecture. Lamination of the cortex is indicated at right: GRL: granular layer; PL: Purkinje cell layer; ML: molecular layer; MF: mossy fibres; GL: cerebellar glomeruli; GR: granule cells; GO: Golgi cell; GD: Golgi cell dendrites; GA: Golgi axon; PC: Purkinje cell; PF: parallel fibres.

of the mossy fibres in the glomeruli establish excitatory synapses with the granule cell dendrites. A glomerulus receives always only one mossy fibre terminal. The mossy fibres synapse in the glomeruli also with the descending dendrites (GD) of the Golgi cell (GO). The axonal terminals of the Golgi cell (GA) descend also into the glomeruli, and exercise a postsynaptic inhibitory influence on the dendrites of granule cells. (Golgi cells have excitatory synapses also with the parallel fibres, this indirect input, however, will be neglected in the model for the time being.)

3. Pattern-transfer in the mossy fibre-granule cell neuronal net

In order to model the function of the structure, a connectivity chart has to be deduced first. Fig. 2 shows a simplified model of the connectivities among mossy fibre terminals (glomeruli) and granule cells, by placing all these neurons into a two dimensional field. The mossy fibres entering the layer end in a glomerulus each. Granule cells are assumed to have four dendrites, which enter into glomeruli situated around the granule cell. The functioning of this system can be visualized (Pellionisz, 1970) by considering a pattern of the excited glomeruli at a particular instant, and computing the transfer of this excitation pattern to the granule cells, if they are considered McCulloch-Pitts elements.

In Fig. 2 the glomeruli, considered to be excited at a particular instant, for example, are shown in black. Let us assume that the threshold of the granule cells be 3, i.e. simultaneous excitation of three of the four glomerular synapses would fire the granule cell. The granule cells excited under these circumstances are also shown in black. In this way, the pattern of excited glomeruli is easily transformed into a granule cell excitation pattern. But as nobody knows the real threshold of the granule cells, all the four possibilities have to be considered (each granule cell having four synaptic sites, of unitary function each, it has obviously four possible thresholds, i.e. if no other influence were exercised upon the granule cell). The transfer for all the four possible thresholds are shown in Fig. 3. A randomly generated pattern of active glomeruli are shown here and the transfer into excitation patterns of granule cells if their threshold is supposed to be 1, 2, 3 or 4, respectively. From these patterns one gets the visual impression that — independently of the threshold — as a result of the pattern-transformation a

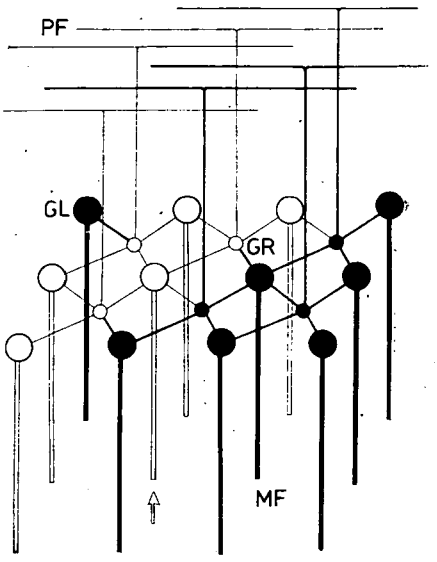

Fig. 2. Model of the mossy fibre-granule cell neuronal connexions. MF: mossy fibres; GL: glomeruli; GR: granule cells; PF: parallel fibres. Mossy fibres (and glomeruli) supposed to be excited in a particular instant are shown in black. If the granule cells are considered threshold elements, granule cells, shown in black are excited (granule cell threshold is assumed to be 3). Note, that the state of the mossy fibre marked with arrow is irrelevant (c. f. p. 160).

concentration of the excitatory spots emerges. At the granule cell threshold of 1 or 4, however, the result of the transfer is an almost entirely black (or white) pattern. The granule cell threshold, therefore, seems very unlikely to be 1 or 4; it is most probably 2 or 3. This preprocessing, however, can be interpreted not only as a visual impression but can be considered from a theoretical aspect as well:

Note, that in Fig. 2 the mossy fibre, marked with arrow, carries *no information* under the existing conditions: i.e. no matter, whether excited or not, the granule cell pattern would remain the same. That means, that there is a *redundancy* in the functioning of the mossy fibre-granule cell cerebellar input channel, which provides an increased reliability in this input. The error-suppressing effect of this redundant transformation can be numerically estimated:

Determine the probability that an erroneous activity of a single mossy fibre terminal (i.e. an excited state instead of non-excitation, or vice versa) *does not effect*

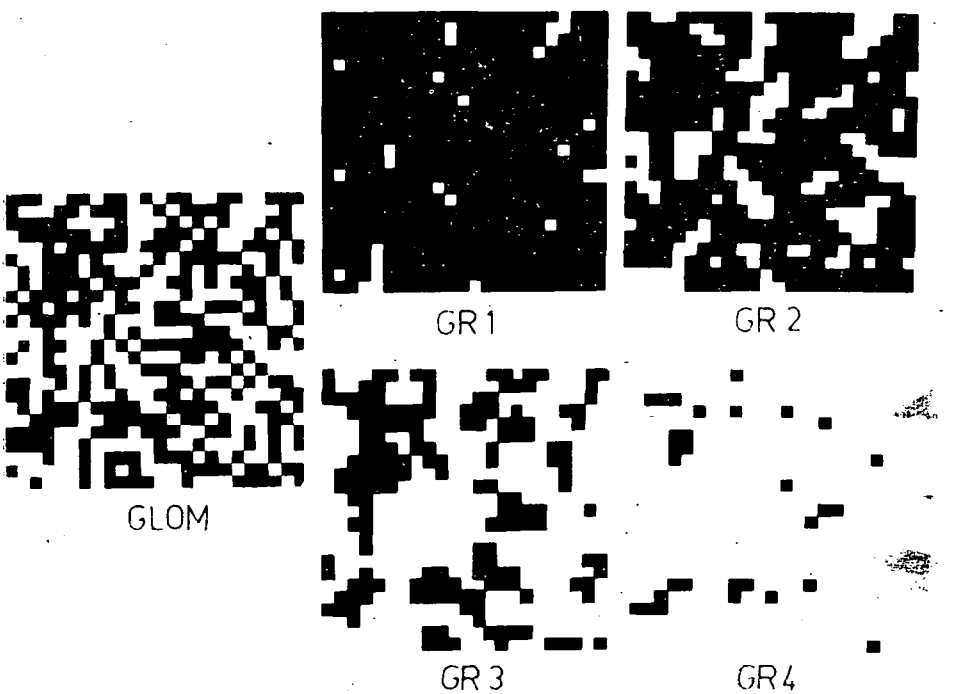

Fig. 3. Transfer of a randomly generated excitation pattern of 24×24 glomeruli (GLOM) to patterns of excited granule cells if their threshold is considered, 1, 2, 3, 4 in GR 1, GR 2, GR 3, GR 4 respectively. Black squares represent excited neurons.

any change in the granule cell excitation pattern. Consider that every mossy fibre terminal (glomerulus) is connected to four granule cells in the model, and these cells in turn are connected to eight other mossy fibre terminals (see Fig. 2). Thus each erroneously activated mossy terminal has $2^8=256$ different possible pattern-environments. The granule cell patterns have been computed for all the 256 possible cases at 1, 2, 3 or 4 values of the granule cell threshold. At 1 or 4 values of the

granule cell threshold, no change in granule cell excitation pattern would occur in 161 cases if the state of the central mossy fibre terminal were changed to 1 from 0 or vice versa. At 2 or 3 values of the threshold the output pattern is indifferent to a single change in the input pattern in 47 cases. Therefore, if the probability of all the possible patterns is considered equal, the probability, that a single error of a mossy fiber terminal will not be carried on to the granule cell pattern is 0,63 (at 1 or 4 values of the threshold) and 0,18 (at 2 or 3 values of the granule cell threshold). The 0,63 probability of the error suppressing largely limits the capacity of the mossy fibre channel, and in addition, very asymmetrically: the threshold of 1 favours low activity-level in the mossy fibre patterns, the threshold of 4 favours the highly excited patterns. As there is no reason to postulate such asymmetry in the functioning of the pattern transfer, the 1 or 4 threshold seems again unprobable, as long as Golgi inhibition is not introduced. This case is discussed in a following study (Szentágothai and Pellionisz, 1971).

It is worth mentioning, that besides the redundancy of the transform itself, there is another kind of redundancy in the flow of information: the *redundancy in the neuronal structure.* In the model the number of glomeruli and granule cells are considered equal, consequently the numbers of the possible input- and output patterns are identical, both being 2^n (if n is the number of the elements in the pattern).

In the real cerebellar granular layer, however, there are about 27 times as many granule cells as there are glomeruli (Palkovits *et al.* 1972) and, therefore, there can be approximately 2^{27n} output patterns, while the number of the possible inputs is 2^n. Considering, that every glomerulus pattern determines one and only one granule cell pattern (if the granule cell threshold is fixed) the structural redundancy is enormous.

Both considerations lead to the notion that the granular layer might play an error-suppressing role in the mossy fibre input of the cerebellar cortex. It is worth while to draw attention to the fair agreement between a real neuronal structure and theoretical studies (Neumann, 1956) dealing with formal neuronal networks, in which information restoring organs in such networks had been postulated.

4. Model of the pattern-sensitive Golgi cell inhibition in the granular layer

In this Chapter an experimental observation of complex interaction events in the mossy fibre input will be demonstrated and explained by computer simulation of the excitation pattern transfer.

In experiments performed by Precht and Llinás (1969) mass activity of granule cells had been recorded by microelectrodes introduced into the floccular area of cat's cerebellum. The field potenctial of great many granule cells could be evoked by electrical stimulation both of the ipsilateral and of the contralateral VIIIth nerve, since there is an overlapping mossy fibre input to this area of the granular layer from both the ipsi- and contralateral VIIIth nerves.

If the test stimulus was preceeded by an identical conditioning volley, the second granule cell field response was drastically reduced. This phenomenon is attributed to a Golgi cell inhibition exercised upon the granule cells (see Fig. 1) and it is in good accordance with the morphological observation by Hámori and Szentágothai

(1966) that Golgi cells have fairly large direct inputs from the mossy fibres. (Subsequently these connexions have been also confirmed electrophysiologically by Eccles *et al.* 1967a.) Figs. 4, 5, 6 show experimentally measured field potential recordings (EXP) (by Precht and Llinás, 1969), and the simulated results (SIM) (see Figs. 8, 9, 10). In Fig. 4 A shows the field potential evoked by single ipsilateral stimulation of the VIIIth nerve. In AA the response had been conditioned by an identical

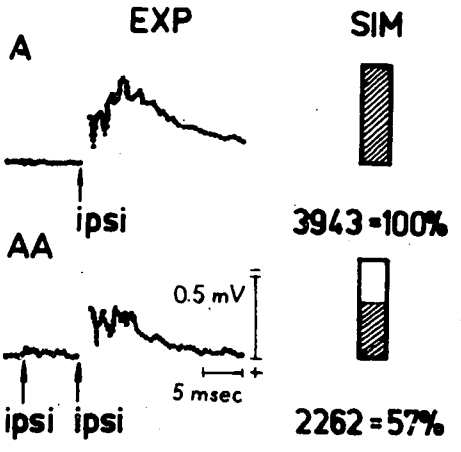

Fig. 4

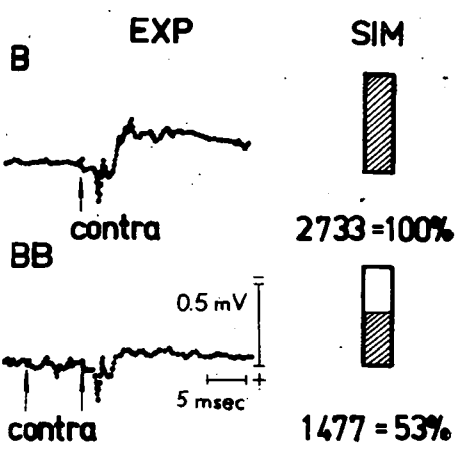

Fig. 5

Composite diagram of experimental recordings (EXP, after Precht and Llinás, 1969) and computer simulated results (SIM) of homonymous ipsilateral VIIIth nerve stimulation. A shows granule cell field potential evoked by single stimulation. In AA the stimulus was conditioned ipsilaterally; the response is considerably reduced. Arrows show the location of the stimuli. Simulated results indicate the number of active granule cells in the simulated pattern (c. f. Fig. 8).

Responses at homonymous contralateral stimulation (c. f. Fig. 4). In B the granule cell field was evoked by single contralateral impulse; in BB a double contralateral impulse was applied: shown as Fig. 4.

preceeding stimulus. Records A and AA are averaged from 16—16 responses. AA shows the response to the second stimulus exclusively as the first response has been subtracted from this record.

Similarly, Fig. 5 shows the responses to homonymous contralateral stimulation. In B the field potential was evoked by single contralateral stimulus, in BB the response had been conditioned also contralaterally. The amplitudes of the second responses in Figs. 4 and 5 are considerably reduced.

At heteronymous stimulation, however, when the ipsilateral stimulation had been conditioned by preceeding contralateral stimulus (or vice versa) the second response showed only a slight decrease: In Fig. 6 BA shows the *only slightly reduced* granule cell field potential response to ipsilateral VIIIth nerve stimulation (conditioned by contralateral stimulus), AB shows the response evoked by contralateral stimulus if the conditioning stimulus was applied ipsilaterally.

This unexpected phenomenon, labelled as "pattern sensitive Golgi cell inhibition" will be modelled and an attempt at its explanation will be made by simulat-

ing the granule cell excitation patterns emerging upon different combinations of stimulation. The model might reveal in very highly schematized form *patterns* that, if existing, would be hidden from microelectrode recording, in which only the average activity-level of a pattern can be measured.

The model considers a two-dimensional field, consisting of 100×100 glomeruli and 100×100 granule cells, in a configuration as shown in Fig. 2. First a pattern-pair of the excited glomeruli is generated by a computer according to the ipsi- and contralateral stimulation. Then the granule cell patterns are computed from these input patterns, without and with considering the effect of Golgi inhibition.

It is supposed that the 10^4 glomeruli are innervated exclusively by two (an ipsilateral and a contralateral) bundles of mossy fibres. In order to try to imitate the realistic innervation of a field of glomeruli by a single mossy fibre bundle, let us assume a quasi-random distribution of the glomeruli excited for example by the ipsilateral mossy fibre bundle as follows: (Fig. 7)

1. The field of 100×100 glomeruli is divided into 100 subordinate quadrangular areas, containing 10×10 glomeruli each.
2. In each subordinate area either 30 or 70% of the glomeruli can be fired by stimulating one of the two mossy fibre bundles (B and A in Fig. 7).
3. About 50% of the subordinate areas are of 70% activity (dominant areas, marked by A), but the distribution of the dominant areas is random.

As every glomerulus can be thrown into action in the model either by ipsilateral or by contralateral stimulation, the patterns of glomeruli in Fig. 8 A GLOM and in Fig. 9 B GLOM have to be complementary to each other.

Fig. 8 shows the patterns set up in the model by ipsilateral stimulation. A GLOM shows the pattern of exited glomeruli at ipsilateral stimulation, and A GRAN shows the pattern of granule cells transformed from A GLOM assuming a granule cell threshold of 3. The number of active granule cells corresponding to the amplitude of the field potential in the experiment is shown in Fig. 8 (compare with Fig. 4). Similarly in Fig. 9 B GLOM shows the glomerulus activity pattern evoked by contralateral mossy fibre

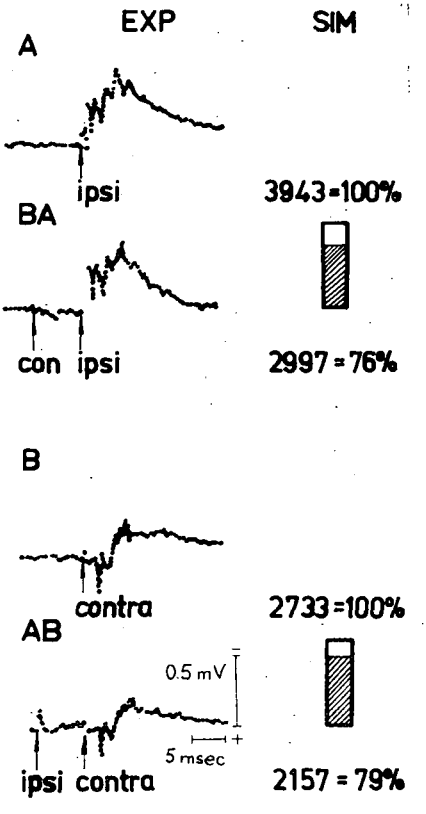

Fig. 6. Recorded (EXP) and simulated (SIM) granule cell responses at heteronymous stimulation of the VIIIth nerve. If the ipsilateral stimulation was conditioned contralaterally (BA) the second response is only slightly reduced compared to A. Similarly the granule cell field potential evoked by contralateral stimulus (B) decreases only slightly if an ipsilateral conditioning impulse is applied (AB).

activation, and B GRAN represents the transformed granule cell pattern (compare with Fig. 5).

The inhibition of mossy fibre-granule cell relay by the Golgi cells upon repeated stimulation, either ipsilaterally or contralaterally, was taken into account in this model as follows: The inhibitory Golgi cells (Fig. 1) show a territorial arrangement in the granular layer, which territories do not overlap significantly (Eccles *et al.* 1967 a). Each Golgi cell controls the mossy fibre-granule cell relay approximately in its own territory i.e. where its dendrits receive their excitatory inputs from the mossy fibres. Accordingly, the modelled neuronal field is divided into 5×5 rectangular territories (Fig. 7) corresponding to a Golgi cell each and comprising 4 neighbouring subordinate areas.

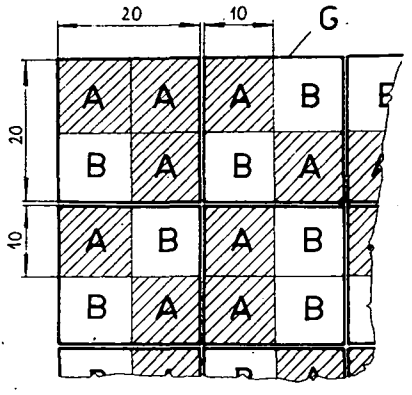

Fig. 7. Schematic diagram of a part of the 100×100 glomerulus pattern, generated by the computer so as to imitate the realistic excitation patterns emerging at for example ipsilateral stimulation. The field is divided into subordinate areas of 10×10 glomeruli. In these areas the average glomerulusactivity is randomly 70% (dominant areas, A) or 30% (B). Every Golgi cell owns four subordinate areas (G).

The Golgi cells are supposed to be thrown into action by the mossy fibres if in the majority of the 4 subordinate areas the glomerulus activity is dominant. The Golgi cells, after having been activated by a mossy fibre volley, will in turn inhibit the glomeruli in their territories for a short time. When the next glomerulus pattern appears during this period of inhibition the activity of glomeruli in these territory will be reduced (to an assumed 10%).

In Fig. 8 AA GLOM and in Fig. 9 BB GLOM shows the glomerulus-patterns evoked by the *second* stimulus at homonymous (ipsi- or contralateral) stimulation. In these patterns the most active areas of the previous A or B pattern are largely blotted out. Therefore, in the granule cell responses transformed from these patterns (in Fig. 8 AA GRAN and in Fig. 9 BB GRAN) the full number of the active granule cells is remarkably smaller (also indicated in the corresponding Figs. 4 and 5).

Upon heteronymous stimulation, however, the second response is inhibited by Golgi cells activated by the *inverse* excitation pattern: accordingly not the most active, but inversely the *least* excited areas will be suppressed by the Golgi cell inhibition. See in Fig. 10, where AB GLOM shows the response to the second B stimulus, conditioned by a previous A stimulus, and in BA GLOM vice versa. The number of the activated granule cells, therefore, is only slightly decreased in AB GRAN (Fig. 10) as compared to BB GRAN (Fig. 9) or in BA GRAN (Fig. 10) as compared to AA GRAN (Fig. 8). (See also Fig. 6.)

The results of the model can be summarized in saying that by a computer simulation based on the micromorphology of the cerebellar granular layer it can be explained why the Golgi inhibition is more effective upon homonymous stimulation then upon heteronymous pairing of the stimuli.

It has to be emphasized that in spite of the quantitative data, the model must

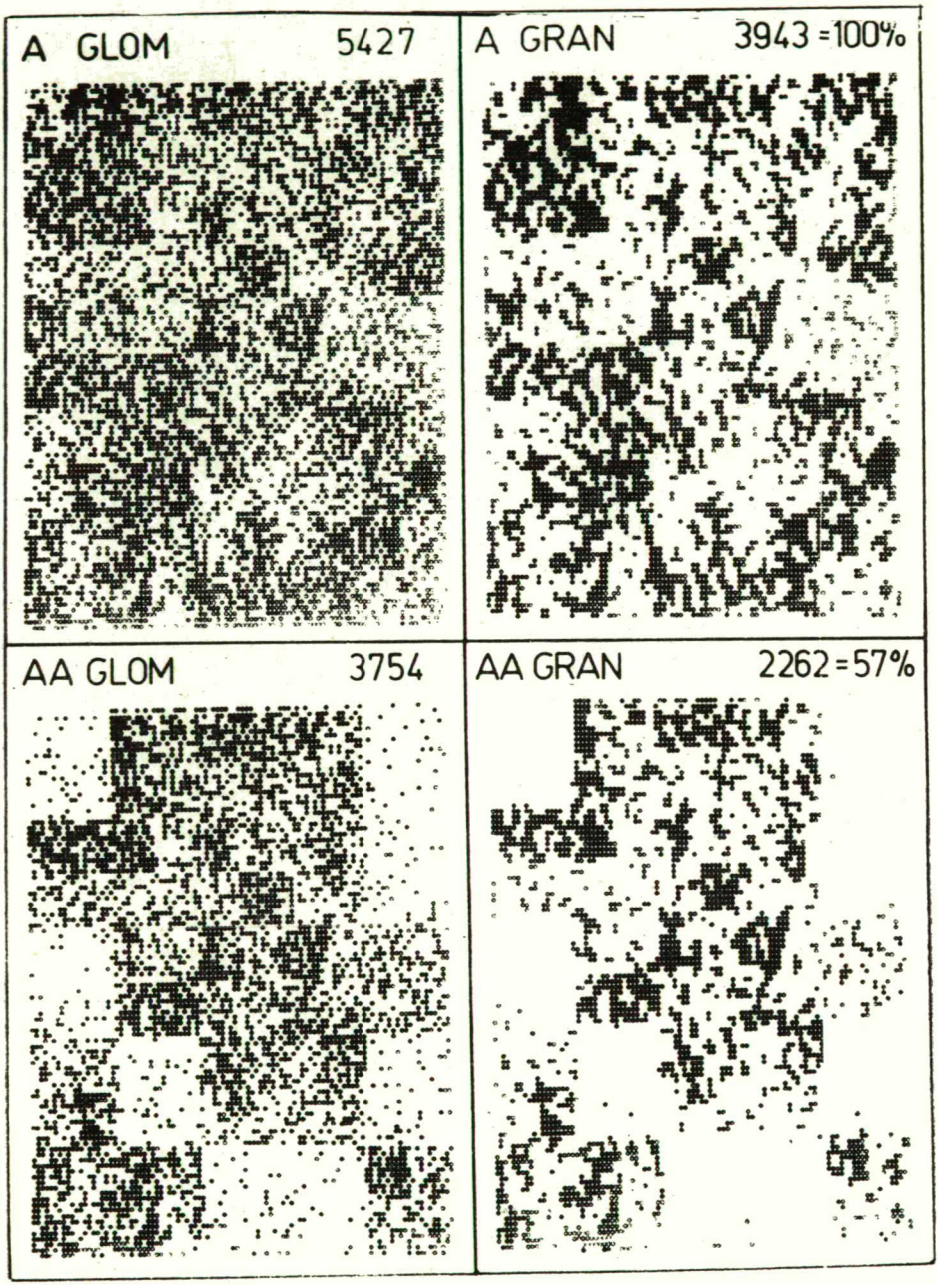

Fig. 8. Computer simulation of glomerulus- (GLOM) and granule cell (GRAN) excitation patterns at homonymous ipsilateral stimulation. (Black asterisks represent excited glomeruli or granule cells.) Responses to single ipsilateral stimulation are shown above (A), the second responses at double ipsilateral stimulation the previously most active spots in AA GLOM (and therefore in AA GRAN) are drastically inhibited by the Golgi cells. The number of the excited neurons in the patterns are also indicated (c. f. Fig. 4).

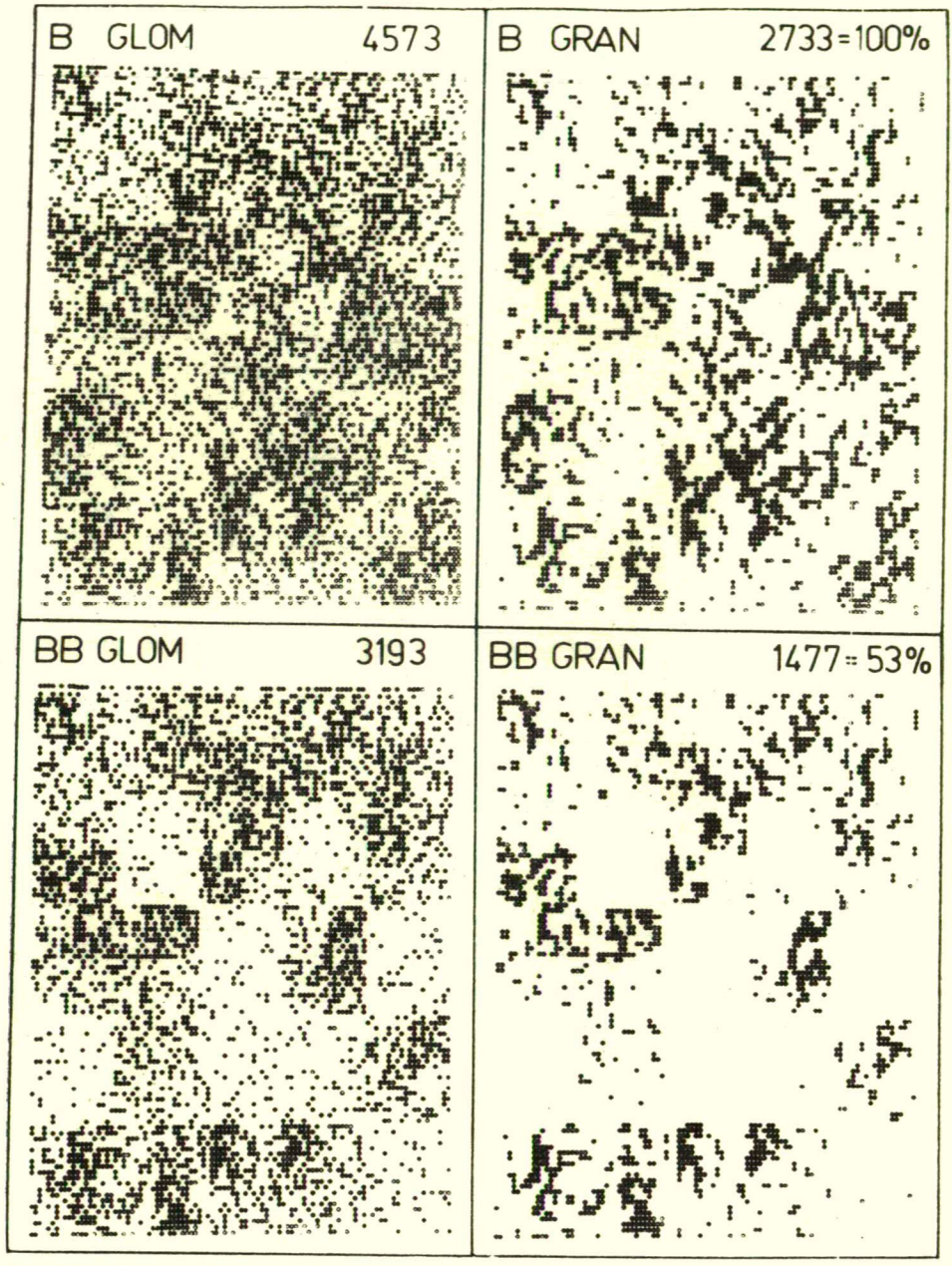

Fig. 9. Modelled excitation patterns evoked by homonymous contralateral stimulation (c. f. Fig. 9). B GLOM shows the response to single contralateral stimulation (it is the inverse pattern of A GLOM). B GRAN is computed from B GLOM by the threshold 3. At contralaterally conditioned contralateral stimulation the response is BB GLOM and BB GRAN. Note the largely reduced second responses (c. f. Fig. 5).

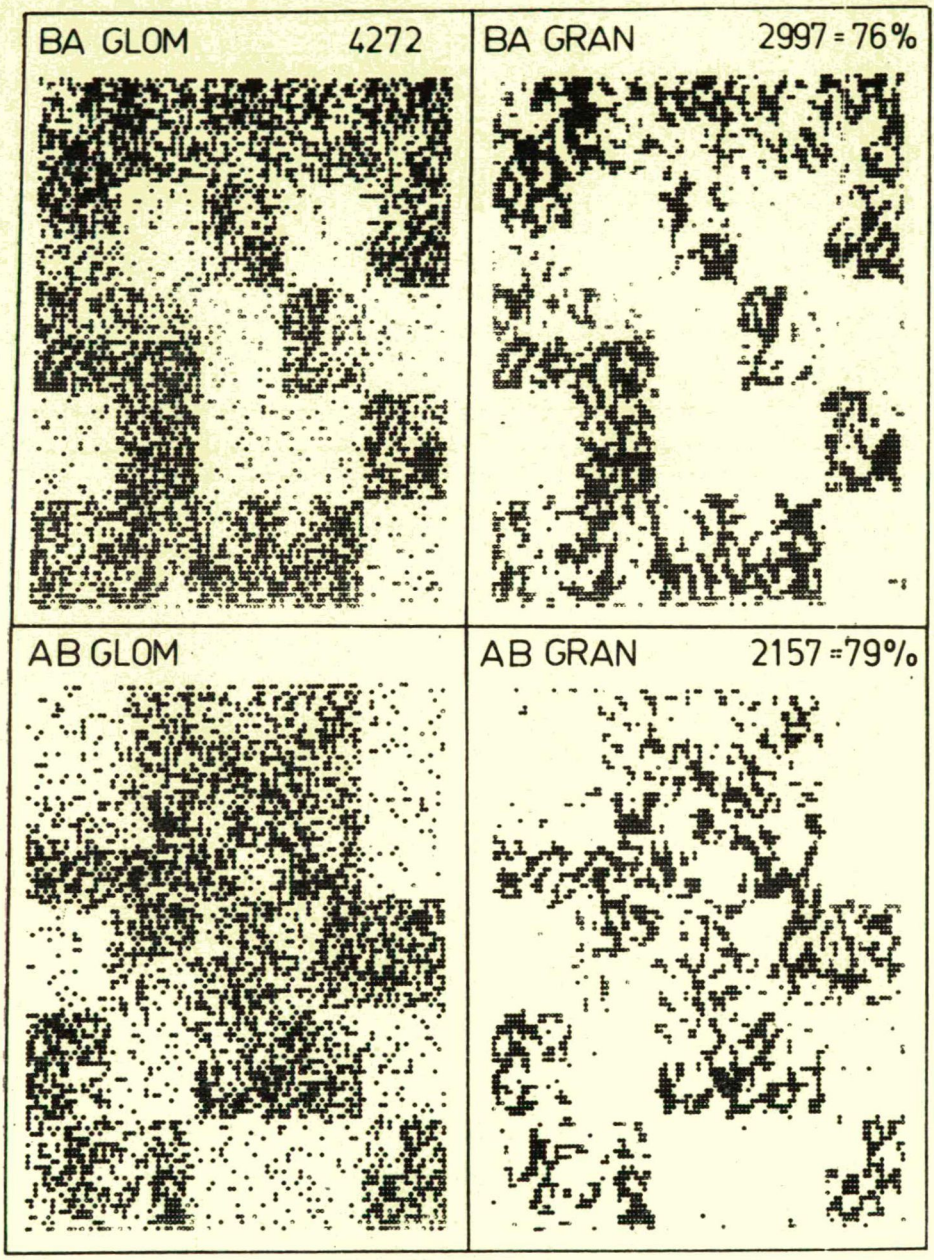

Fig. 10. Simulated patterns evoked by heteronymous VIIIth nerve stimulation. BA GLOM shows the response to ipsilateral stimulus conditioned contralaterally. The Golgi inhibition is activated by the conditioning impulse, therefore the pattern is inhibited in the least active areas. Accordingly in the transformed BA GRAN pattern the number of active granule cells is only slightly reduced as compared to A GRAN and AA GRAN. Similarly AB GLOM is the pattern of excitation at contralateral stimulation, previously conditioned ipsilaterally (c. f. Fig. 6).

not be considered as a quantitatively precise description of the physiological events but rather as a qualitative explanation of an unexpected experimental result. This remark is necessary since this model has several free parameters (as models generally do) and any variation in their values (for example in the threshold-values) can effect numerical deviations in the results. The qualitative result, however, is fairly indifferent to threshold-variations. The whole simulation has also been carried out for example with a 2 value of the granule cell threshold. In this case the results are slightly modified, however, the much smaller effectiveness of the inhibition at heteronymous stimulation has remained qualitatively identically demonstrated:

Granule cell threshold=3

response	ipsilateral	contralateral
stimulation		
homonymous	57%	54%
heteronymous	74%	78%

Granule cell threshold=2

response	ipsilateral	contralateral
stimulation		
homonymous	66%	65%
heteronymous	76%	78%

5. Acknowledgement

The simulation has been performed on a computer of ODRA 1013 type. The time required has been granted by the Chair of Numerical and Computer Mathematics fo the Roland Eötvös University, Budapest. It is gratefully acknowledged to the Head of the Chair: Dr. J. Mogyoródi.

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(Received August 15, 1970)