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Functional Significance of Arrangement of Neurones in Cell Assemblies*

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Summary. An account is given of the columnar arrangement in the cerebral cortex that has been discovered for neurones having a similar receptivity. This has been observed in the somaesthetic cortex for neurones with similar modality sensitivities and in the visual cortex for neurones with similar directional sensitivities. The anatomical basis is discussed. In the motor cortex also there is an arrangement in clusters of pyramidal cells that are responsible for particular movements.

The functional significance of this organization in clusters in the cerebral cortex is discussed in relationship to the problem of securing a reliable performance despite the irregular background discharge of the individual neurones. It is proposed that reliability is secured by the in-parallel arrangement of neurones with similar receptivities in the clusters. The neurones of a cluster tend to converge onto common target neurones, which, as it were, read out the summed performance of the cluster from moment to moment. Recent work on the cerebellum also discloses that there is an arrangement of Purkyně cells in clusters with somewhat similar receptive fields and that their axons tend to converge onto neurones of the cerebellar nuclei (fastigial nucleus), which likewise are arranged in functional clusters.

The general concept emerges that the arrangement of neurones in clusters both in the cerebrum and in the cerebellum, achieves functional significance not only in giving opportunity for amplification and integration of incoming signals and for their sharpening by surround inhibition, but it is also important in the output performance. Signals are lifted out of noise by the spatial summation deriving from the many similarly performing neurones that project by their axons to the same cluster of target neurones; and this orderly projection can go on sequentially through all the complexities of on-going actions initiated by some input.

Key words: Cerebrum — Cerebellum — Neuronal Clusters — Reliability.

Zusammenfassung. Die Arbeit gibt eine Übersicht über die säulenartige Ordnung von Neuronen mit ähnlichen Funktionen in der Großhirnrinde und vergleicht diese mit entsprechend gruppierten Neuronpopulationen im Kleinhirn. Die Zellsäulen bilden senso-motorische *Funktionseinheiten von Neuronengruppen.*

Im somatosensiblen Cortex meldet jede Zellsäule jeweils die gleiche Sinnesmodalität, in der Sehrinde die gleiche Raumorientierung von Konturen. Der motorische Cortex enthält ebenfalls senkrechte Zellsäulen von Pyramidenzellen, die spezifische Bewegungen auslösen.

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* Prof. R. Jung to his 60th birthday.

Die Säulenordnung der Hirnrinde wird als Parallelschaltung von Neuronen ähnlicher Funktion in einzelnen Gruppen gedeutet. So entstehen geordnete kollektive Neuronenleistungen trotz unregelmäßiger Hintergrundsentladung der einzelnen Nervenzellen.

Mehrere Neurone eines Kollektivs konvergieren jeweils auf ein *Integrationsneuron* (*target neurone*), dessen Entladung die summierte Leistung der Zellsäulen in zeitlicher Abfolge wiedergibt.

Neuere Untersuchungen am *Kleinhirn* zeigen eine ähnliche Kollektivordnung der Purkinje-Zellen mit Gruppen von ähnlichen receptiven Feldern. Diese Purkinje-Axone konvergieren auf Neurone der Kleinhirnkerne, z. B. den Dachkern, der ebenfalls funktionell geordnete Neuronenkollektive enthält.

Allgemeine Folgerungen. Die kollektive Gruppenordnung der Neurone kann sowohl im Großhirn wie im Kleinhirn neben einer *Verstärkung und Integration einlaufender Signale* und einer *Kontrastverschärfung durch Umfeldhemmung* vor allem durch *räumliche Summation vieler ähnlich arbeitender Neurone* bedeutsame Signale aus dem Rauschpegel herausheben. Dann können die Axone dieses Zellkollektivs ihre gesamte Information auf die Integrationsneurone projizieren. Die Projektionen der neuronalen Funktionseinheiten verlaufen in mehrfachen Sequenzen und Stufen komplexer sensomotorischer Erregungskonstellationen, die durch eine afferente Eingangsmeldung ausgelöst werden.

Schlüsselwörter: Großhirn — Kleinhirn — Neuronengruppierungen — Projektionssicherung.

In 1957 Mountcastle made a systematic study of the modality and the specific responses of single neurones of the cat somaesthetic cortex. When the microelectrode was inserted perpendicular to the cortical surface, cells were encountered at successive depths, and the great majority belonged to the same modality subgroup. In one such track the cells responded to a superficial cutaneous stimulus, in another to movement of hairs, and in yet another to mechanical deformation of deep tissues such as fascia or joints. Mixed responses were rare. Mountcastle therefore postulated that there is a columnar arrangement of neurones having a similar modality specificity. These columns are arranged in an interdigitated mosaic that forms sub-patterns within the somatotopic representation on the somaesthetic cortex. Investigations on the somaesthetic cortex of the monkey (Powell and Mountcastle, 1959; Mountcastle and Powell, 1959) extended the evidence for the columnar arrangement, but it was pointed out that this discrete pattern of activity pertains only to the initial repetitive response of the cortical cells.

Study of the receptive field for a cortical cell in the centre of a cutaneous sensory column reveals that a cutaneous zone of maximum effectiveness on that cell grades into a surround of progressively less action that passes over to a more remote inhibitory surround. There is evidence that, at each of the relays on the pathway from the periphery to the cortex, there is a focussing of action by this surround inhibition. Presumably this processing of sensory input in successive relays is important in giving the specific columnar inputs.

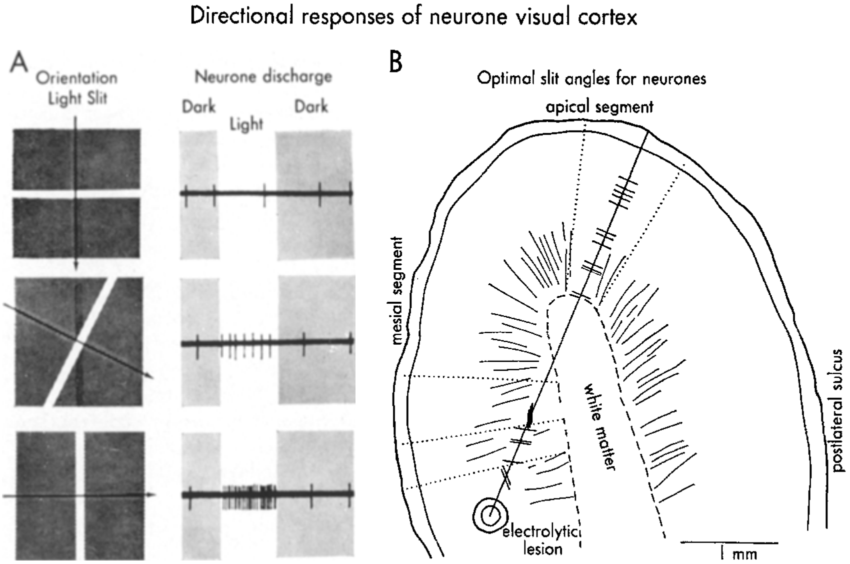


Fig. 1 A and B. *Columnar arrangement of visual cortex neurones with specific orientation.* In A the light slit is shown oriented in three different directions on the dark field and it sweeps across the field as shown by the arrows. The discharges of the neurone in the visual cortex are seen to be optimally evoked by the vertically oriented slit, the horizontal slit having zero action. Altogether the discharges of 21 neurones were observed in B along the microelectrode track through the visual cortex of the cat. The optimal direction of the light slit is indicated by a line for each of the neurones.Boundaries of columns are indicated by dotted lines (modified from Hubel and Wiesel, 1962)

A finer grain in the columnar arrangement was discovered by Hubel and Wiesel (1962) in the primary visual cortex by utilizing the directional sensitivity on the individual cortical cells. For example in Fig. 1 A the response to a moving band of light is seen to be greatest when the retina is swept by a vertical band and zero when it is horizontal. In Fig. 1 B the optimal direction of the light band is shown for many cells along a single microelectrode track. From its insertion until the white matter was reached, several cells were investigated and all showed exactly the same optimal orientation of the retina. By contrast, on the further side of the white matter the track was cutting across the vertically orientated columns of the cortex and there were three different optimal orientations. The corresponding columns are indicated by dotted lines. From such investigations it has been established that in the visual cortices of cat and monkey there is a fine mosaic of columns each with many cells of identical receptiveness (Hubel and Wiesel, 1962, 1963, 1965, 1968). As

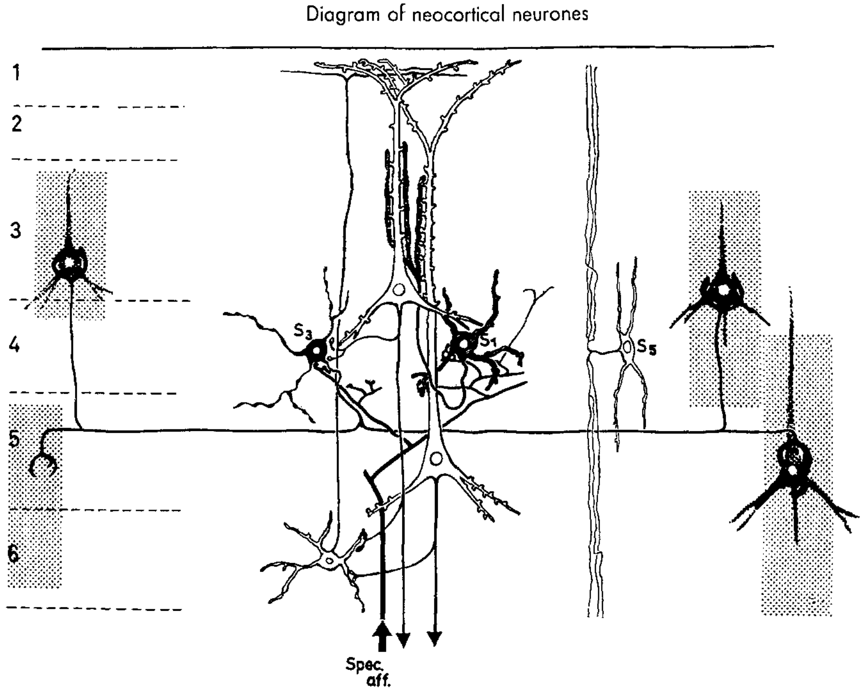


Diagram of neocortical neurones

Fig. 2. *Semidiagrammatic drawing of some cell types of the cerebral cortex with interconnections as discussed in the text.* Two pyramidal cells are seen centrally in lamina *3* and *5*. The specific afferent fibre is seen to excite a stellate interneurone S_1 (hatched) whose axon establishes cartridge type synapses on the apical dendrites. The specific afferent fibre also excites a basket type stellate interneurone, S_3, that gives inhibition to pyramidal cells in adjacent columns, as indicated by shading. Another interneurone is shown in lamina *6* with ascending axon and S_5 is an interneurone also probably concerned in vertical spread of excitation through whole depth of the cortex (modified from Szentágothai, 1969)

with the somaesthetic area, this mosaic pattern of irregular form is superimposed on the projection of the retinal map upon the visual cortex. The columns have a cross sectional area of a fraction of a square millimetre, which is of the same order as estimates for the somaesthetic cortex. The visual areas II and III are also organized in columns for the various specific spatial characteristics of complex and hypercomplex cells (Hubel and Wiesel, 1965).

The morphological basis for the columnar arrangement in the primary afferent cortices has been described by Ramón y Cajal (1911), Colonnier (1966) and Szentágothai (1969). In Fig. 2 specific afferent fibres synaptically excite stellate interneurones (S_1) whose axons ascend towards the cortical surface forming a sheath around the apical dendrite of each pyramidal cell. These intensely ramifying vertical axons with the enclosed dendrite form what Szentágothai calls a synaptic cartridge because of the close synaptic association of these axonal branches with the dendritic spines of the apical dendrites. A related type of neurone (S_5) has profuse axonal branching running in both directions strictly perpendicular to the cortical surface that was originally described by Ramón y Cajal. The dominant vertical orientation and the dense branching structure of these axons would provide for the intensive transfer of primary afferent inputs to columns of cells. Functionally this structural arrangement can be considered as a local amplifying device whereby input by each afferent fibre is greatly augmented by relay through vertically orientated stellate cells, which may trigger activity in other stellate cells as well as in the pyramidal cells via the synaptic cartridges, and these cells in turn excite locally by axon collaterals. S_3 is a stellate cell with a transversely directed axon that sets up a surround of inhibited cells.

While these investigations were being carried out on the cluster arrangement of neurons in columns for specific afferent inputs, complementary investigations were being made on the motor output from the cerebral cortex and were providing evidence also of a columnar arrangement of the pyramidal cells whose axons form the pyramidal tract. Landgren, Phillips and Porter (1962) and Phillips and Porter (1964) found that, when using surface stimulation of the cerebral cortex and recording intracellularly from motoneurones, there was evidence of an arrangement of the pyramidal cells in clusters which were defined by the similarity of their motoneuronal projection. The general concept emerged that the pyramidal cells of the motor cortex were arranged in a multitude of clusters that had a cross section of the order of 1 mm^2.

Unfortunately, surface stimulation was too "blunt" a technique for the fine delineation of the clusters. It remained for Asanuma and his colleagues to develop the technique of microstimulation via a microelectrode that was inserted at various depths in the motor cortex and used for passing the stimulating current (Asanuma and Sakata, 1967; Welt, Aschoff, Kameda and Brooks, 1967; Asanuma, Stoney and Abzug, 1968; Asanuma and Rosén, 1972; Rosén and Asanuma, 1972). This refined work corroborated the concept that pyramidal cells of similar function were arranged in clusters and gave reliable topographic mapping of the pyramidal cells that acted upon a particular muscle (Fig. 3). The motor cortex therefore resembles a mosaic pattern made up of many clusters of pyramidal cells. Each cluster appeared to be arranged in a column with a cross-sectional area of about 1 mm^2 in the cat's motor cortex (Asanuma and Sakata, 1967).

Furthermore, Asanuma, Stoney and Abzug (1968) combined this cortical stimulation with the technique of Mountcastle in which they used peripheral adequate stimulation of receptors and recorded from the individual neurones of the motor sensory cortex. In this way they found that the afferent input to cortical pyramidal cells often related to the muscle to which this cell projected. Thus the experimental evidence was provided for a reflex loop concept of cortical action, and this concept was further developed by Asanuma and Rosén (1972) and Rosén and Asanuma (1972) in their most elegant work on the monkey cortex, as may be illustrated in Fig. 3.

Several experimental investigations have therefore provided convincing evidence that there is a columnar arrangement of clusters of pyramidal cells in various regions of the cerebral cortex; areas 1, 2 and 3 of the somaesthetic cortex; areas 17, 18, 19 of the visual cortex; and the motor cortex. Furthermore, from the anatomical evidence the general idea emerges that the columnar arrangement of neurones in the cerebral cortex is an amplifying and discriminating device. As a consequence, even minute inputs can be amplified in columns which are isolated because of the surround inhibition (cf. Fig. 2; Mountcastle, 1957; Mountcastle and Powell, 1959; Pogio and Mountcastle, 1963; Hubel and Wiesel, 1965; Colonnier, 1966; Szentágothai, 1969). However, a further concept comes out of the work of Asanuma, Stoney and Abzug (1968), Asanuma and Rosén (1972) and Rosén and Asanuma (1972), namely that there is a meaningful reflex relationship through the cerebral cortex. Of course it must be recognized that there are very complex superimposed factors, but the essence of their concept is that contact with the skin area activates pyramidal cells in columns of the motor cortex that project to motoneurones that cause movement towards the area of skin stimulation (cf. Fig. 3), as, for example, is observed in the grasp reflex or in the initial phase of placing reactions.

In addition to these functional considerations it is essential to take account of the basic conditions of cell responses in the central nervous system. When observed by microelectrode recording techniques in the unanaesthetized animal, it is found that almost all cells under resting conditions have a background discharge of a rather irregular kind. It is upon this background that stimulation of receptor organs has to produce an unmistakable reaction of the cell under observation if reliability is to be achieved in the performance of the nervous system. In the experiments of Mountcastle (1957) and Hubel and Wiesel (1962, 1965) the stimuli were strong and simple as well as having stereotyped patterns of onset and offset, etc. The cells that they observed certainly disclosed reliable performance. However, under conditions of normal activity of the animal there would be much more variety and limitation in the strength and duration of the receptor organ stimulation as well as very complex spatiotemporal patterns of such stimulation. We should consider,

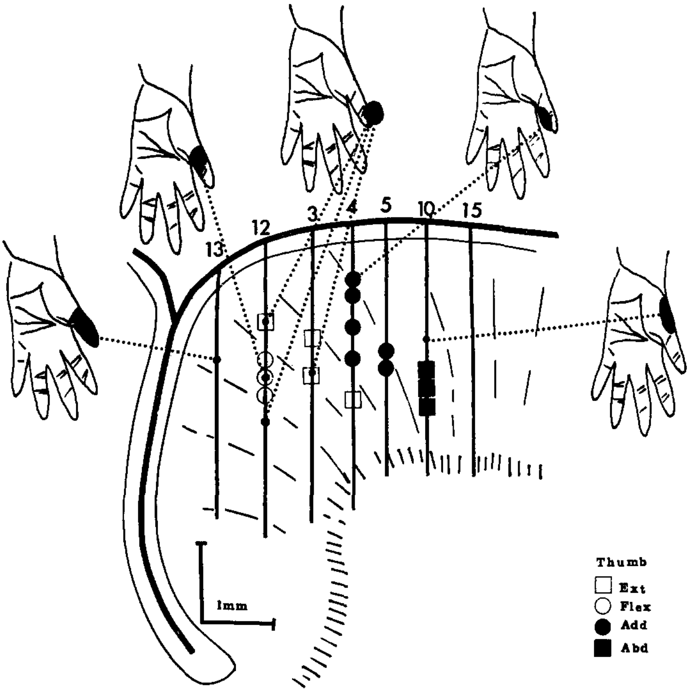


Fig. 3. *Reconstruction of electrode tracks and cell locations.* Electrode penetrations are indicated by numbers and passed through efferent zones projecting to various thumb muscles. The peripheral motor effects on the thumb produced by intracortical microstimulations of 5 μA strength at various locations are indicated by symbols, as identified in lower right corner. Positions of cells encountered along the track are indicated by dots, and dotted lines join these points to the figurines of the monkey's hand on which are indicated the receptive fields as determined by adequate stimulation (Asanuma and Rosén, 1972; Rosén and Asanuma, 1972)

for example, the fine exploring movements of the hand in man and monkey or of the forepaw of the cat. Under such conditions amplification by the synaptic cartridge arrangement on pyramidal cells (Fig. 2) could be most important in giving reliable responses to transient slight stimulations.

However, there is another way of looking at this problem of reliability and that concerns the manner in which there is a "read-out" of what any particular cell is doing from moment to moment. It is of course accepted that this "reading-out" process is accomplished by the cell projecting to other cells and acting upon them synaptically either in an excitatory or an inhibitory manner. The further concept can be developed that convergence upon a target neurone by the several cells of a cluster

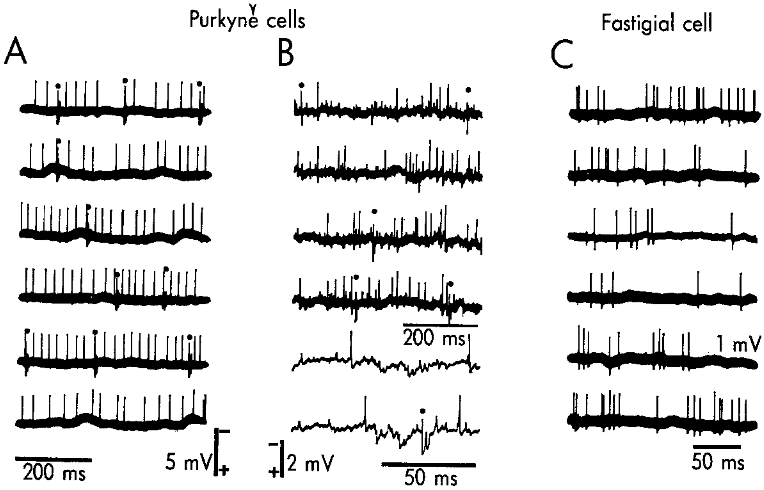


Fig. 4A—C. *Specimen records of spontaneous firing of single Purkyně cells* (A, B) *and of a fastigial neurone* (C) *in the unanesthetized cat cerebellum*. The Purkyně cell spike potentials evoked by climbing fiber impulses are marked by dots. Note the irregularity of the discharges

would greatly enhance the reliability of the "read-out". In fact this may turn out to be the essential feature deriving from the aggregation of neurones in clusters. The action of a single neurone probably tends to be lost in the noise of the general on-going activity of the nervous system. The in-parallel projection of motor pyramidal cells activated similarly in a cluster will probably be required to give the convergence onto target motoneurones, before these are excited sufficiently to discharge and so to bring about significant movement.

When we come to consider the mode of operation of the cerebellum as a neuronal machine, it is imperative to recognize that there is a strong and irregular background firing, both of the Purkyně cells and of the nuclear cells to which they project. Specimen examples of this firing can be seen in Fig. 4. Inputs to the cerebellar Purkyně cells that result from cutaneous (Eccles, Sabah, Schmidt and Táboříková, 1971, 1972) or muscle receptors (Ishikawa, Kawaguchi and Rowe, 1971) modulate this firing up or down, but such is the basic irregularity that the effects may not be evident in single traces. The averaging of many such responses is required in order to give reliability to the observations (Fig. 5). Such sequential averaging, as by the computer in Fig. 5, cannot be used to achieve reliability under conditions of normal activity where reliability is a requisite in each single operation of cerebellar control of motor performance.

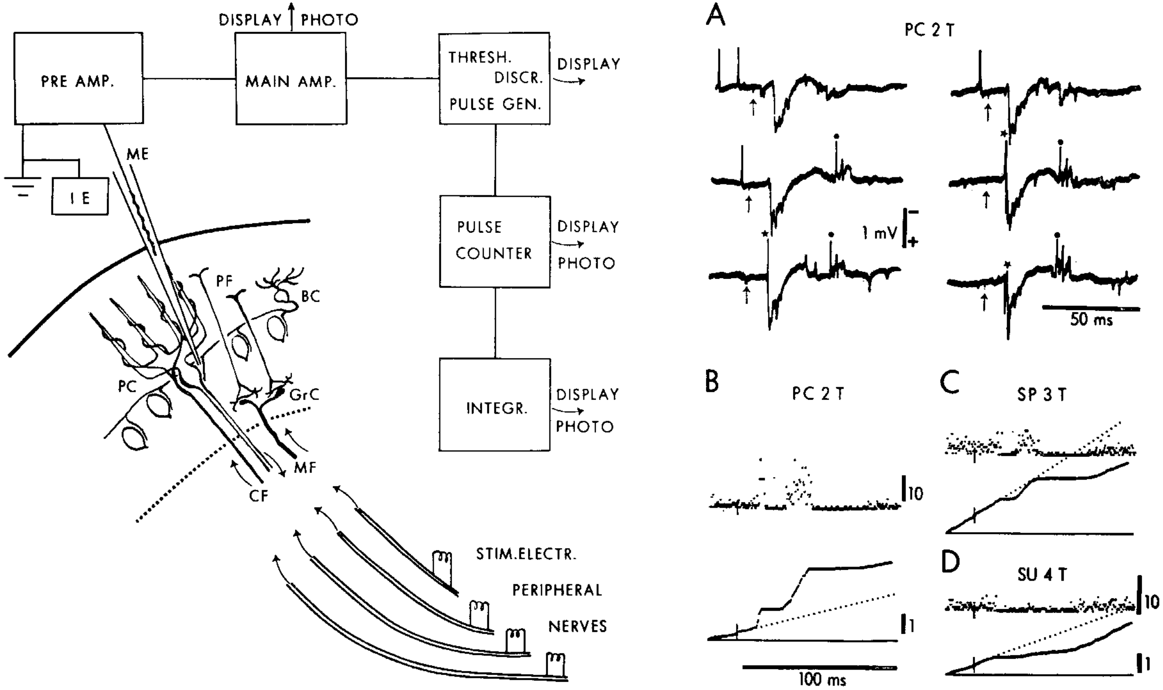


Fig.5A—D. *Recording of histograms of Purkyně cell responses to afferent volleys.* Diagram showing microelectrode *ME* in position for recording from a Purkyně cell *PC*. There is a climbing fiber, *CF*, and a mossy fiber, *MF*, with synapses on granule cells, *GrC*, whose axons are the parallel fibers, *PF*, of the molecular layer. Other Purkyně cells are shown only in outline of the somata. The basket cell, *BC*, gives inhibitory synapses to the *PC* somata. The potential fields recorded by *ME* against an indifferent grounded electrode, *IE*, on the head of the animal, are fed into a preamplifier (*PRE AMP*). The other recording features are described in the text. Also shown are four limb nerves with stimulating electrodes. A Specimen records of microelectrode recording from a Purkyně cell in the medial part of the Pars Intermedia, Lobule IV, the plantar cutaneous (*PC*) nerve being stimulated at twice threshold at the arrow. In B there is a PSTH and a CFD for 128 of these responses. Note in A the early discharge induced by a mossy fiber input in three traces (superposed stars), and in four the later CF induced discharges identified by superposed dots. C and D give PSTHs and CFDs for responses evoked by single volleys in two other cutaneous nerves, superficial peroneal (*SP, 3 T*) and sural (*SU, 4 T*). Same calibration for B, C and D. Pentothal anesthesia

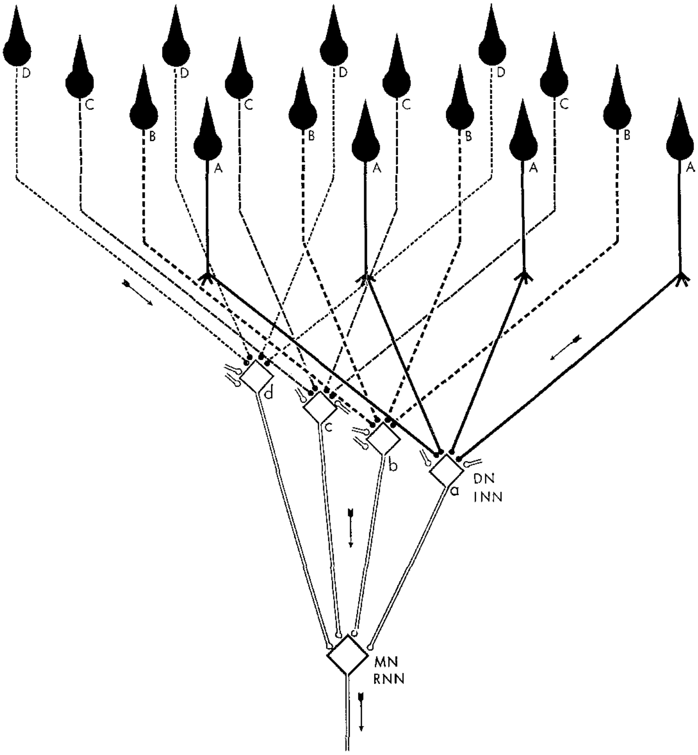
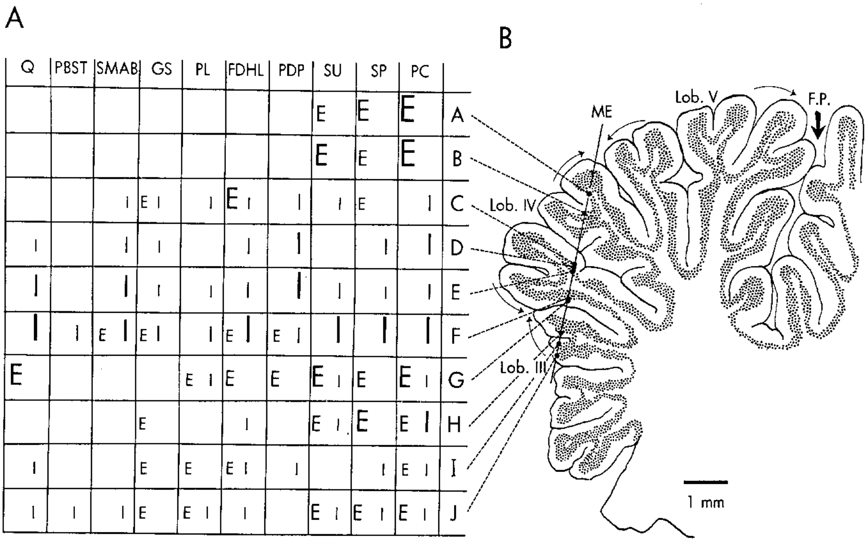


Fig. 6. *Diagram showing convergent operation of Purkyně cells.* An array of 16 Purkyně cells in 4 groups, *A*, *B*, *C*, *D*, project to 4 target neurones, a, b, c, d, that in turn project to one neuron next in the transmission line. The target neurons can be, for example, Deiters' neurones or interpositus nucleus neurones, *DN* or *INN*, the former projecting to motoneurones, *MN*, the latter to red nucleus neurones, *RNN*. The existence of other branches of the first transmission lines is indicated. It is to be noted that the diagram is highly schematic, and completely neglects all the overlapping connectivities that there would be for the original 4 groups, *A*, *B*, *C*, *D*. The Purkyně cells are all inhibitory, hence are symbolized in black as also are their synapses. All other cells and transmissions are excitatory, and are shown open

This investigation by the averaging of a large number of responses of a single cell can be regarded as a paradigm of the solution adopted in the nervous system for utilizing unitary signals of great variability in temporal pattern in order to convey precise communication. Physiologically this is of course done by having many cells in parallel converging upon neurons which, in turn, respond to the integration of these convergent bombardments. Fig. 6 represents an attempt to show diagrammatically the convergence of Purkyně cells upon target neurones on which there would be summation of inhibitory action (cf. Eccles, Ito and



Q	PBST	SMAB	GS	PL	FDHL	PDP	SU	SP	PC	
							E	E	E	A
							E	E	E	B
		I	E I	I	E I	I	I	E	I	C
I		I	I		I	I		I	I	D
I		I	I	I	I	I	I	I	I	E
I	I	E I	E I	I	E I	E I	I	I	I	F
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Fig. 7A and B. *Responses of 10 Purkyně cells along a single microelectrode track.* A is a table showing in symbolic form the responses for each of the 10 cells to 10 hindlimb afferent volleys. The convention is adopted of showing sizes of excitatory (*E*) and inhibitory (*I*) responses evoked by the mossy fiber with four sizes of letters indicating approximately the four sizes of the responses. Note that only the short latency *ME*-evoked responses are plotted. The blank sqnares correspond to the tests in which these responses were zero. B gives tracing of parasagittal section through the medial zone of pars intermedia. The microelectrode track is drawn in and on it are marked the locations of the 10 Purkyně cells. *FP* shows fissura prima and lobules *V*, *IV* and *III* are also indicated (Eccles *et al.*, 1971b)

Szentágothai, 1967, Chapts. XIII and XIV). Thus the four cells of row A converge on one target neurone (a), which could be a neurone of the Deiters' or the interpositus nucleus, and similarly for the 4 cells of rows B, C and D to target neurones b, c and d respectively. Furthermore, this diagram shows that these target neurones in turn converge on the cell next in series, which could be a motoneurone or a red nucleus or a VL thalamus neurone. Hence the sixteen Purkyně cells have their discharge patterns averaged by this cell. Since the actual convergence numbers have been calculated to be 20 to 50 for each relay with perhaps 10 as the lowest figure (Eccles, Ito and Szentágothai, Chapts. XIII and XIV), the actual integrational level is certainly over 100 for the two relays in series as in Fig. 6. It is further to be noted in Fig. 6 that the branching of each axon introduces divergence as well, so that there is widespread dispersal in the communication pathway from any one cell. The diagram does not illustrate any of the complexities of cross connections that would arise in this way, nor does it attempt to symbolize the various intensities of synaptic action at each relay.

When attempting to assess the mode of operation of patterns of neuronal connectivity, it is important to recognize that Fig. 6 represents a highly idealized situation. In the cerebellar cortex there is much more complexity and apparent confusion of input pattern than occurs in the orderly maps of the somaesthetic and visual cortices. However, there is evidence for the arrangement of Purkyně cells in clusters, but these must be more loosely defined than for the cerebral cortex because the essence of cerebellar performance is integration by convergence of many different inputs, both in respect of spatial origin and of modality. This is in fact observed when the impulse discharges are recorded for individual Purkyně cells. For example, in Fig. 7B a microelectrode track is shown in a tracing of a parasagittal section of the anterior lobe of the cerebellum. Along this track there are marked the locations of ten Purkyně cells whose impulse discharges were recorded extracellularly as unitary potentials (cf. Fig. 5). The standard procedures gave PSTHs and CFDs for each cell in response to a variety of afferent volleys. The observations on the MF-evoked response of the ten cells are shown in convention of coding in Fig. 7A, where four sizes of the letters E and I symbolize approximately the intensities of the respective E and I effects. It will be noted that sometimes the response has an E-I sequence.

The responses of the 10 Purkyně cells along the single track in Fig. 7 can serve as a paradigm of our findings in general. The predominant cutaneous excitatory input to cells A, B and H is typical for many cells. It is less common for muscle afferents to dominate the input, but this occurs for cells C and E. A mixed input from cutaneous and muscle afferents is illustrated in cells F and G and also in cells I and J. The dominant inhibition in cells D, E and F is not uncommon, but it can be presumed that other untested inputs will be excitatory, a role in which the cerebral cortex is very prominent.

The term cluster can evidently be applied to cells such as A and B of Fig. 7 but it may be surprising to apply it to cells such as F and G where there are such differences in their responses. The justification lies in the fact that they have much the same receptive fields, the differences in responses depending on the relative sizes of the excitatory and inhibitory effects that a mossy fiber input achieves by operation through the neuronal circuits in the cerebellar cortex (cf. Eccles, Ito and Szentágothai, 1967, Chapt. XII).

It must be appreciated that our experimental procedures allow a sampling of only a few cells of any particular cluster; nevertheless, from our observations on almost 1000 Purkyně cells in about 100 experiments (Eccles, Faber, Murphy, Sabah and Táboříková, 1971a, 1971b; Eccles, Sabah, Schmidt and Tábořiková, 1971, 1972), we have derived the general impression that cells with related receptive fields tend to be aggregated in clusters as indicated in Fig. 7, and that in the anterior lobe there are several such clusters receiving input from the cutaneous mechanoreceptors of the hindfoot in lobules III and IV and from the forefoot in lobule V.

The arrangement of Purkyně cells in clusters is of importance in the events subsequent to the impulse discharges from Purkyně cells. It would be expected that the axons of adjacent cells would tend to converge onto the same target neurones, where there occurs the first stage in the integration of the output from the cerebellar cortex. If there is not a highly specific projection from Purkyně cells to these neurones, i.e., if there is a randomization in the projection, there will be a smudging in the transmission process with a consequent irretrievable loss of information. Preliminary studies of the responses of the principal target neurones (the fastigial cells) have shown that there is a very effective transmission of integrated information (Eccles, Sabah and Tábořiková, 1972), and it is suggested that in the first place this is accountable to the colonial arrangement of Purkyně cells.

A clear picture of arrangement in clusters emerges in the more compact fastigial nucleus as tested by cutaneous mechanoreceptors of the footpads of fore and hindlimb (Eccles, Sabah and Tábořiková, 1972). Here there are observed some clusters where the cells have dominant input from hindlimb, others where there is dominant forelimb input, and others where there is mixed fore and hindlimb input. When these clusters are explored by a series of microelectrode tracks they are seen to interdigitate in an irregular manner somewhat reminiscent of the descriptions for the columnar arrangements in the cerebral cortex. In general the neurones of the fastigial nucleus display responses that bear witness to the convergence onto them of Purkyně cells that are similar with respect to inputs from peripheral receptors. It must be postulated that a cluster of Purkyně cells, as defined above, establishes some correspondence in its projection onto the nuclear cells. The integration achieved in the cerebellar cortex by convergence of various inputs onto Purkyně cells is conserved and even appears to be developed further in the projection to the fastigial nuclei where there is convergence of different clusters of Purkyně cells onto individual nuclear cells.

The general concept emerges that the arrangement of neurones in clusters both in the cerebrum and in the cerebellum, achieves functional significance not only in giving opportunity for amplification and integration of incoming signals and for their sharpening by surround inhibition, but it is also important in the output performance. Signals are lifted out of noise by the spatial summation deriving from the many similarly performing neurones that project by their axons to the same cluster of target neurones; and this orderly projection can go on sequentially through all the complexities of on-going actions initiated by some input.

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