Department of Anatomy, University Medical School, Pécs
(Director: Prof. J. Szentágothai)

ASSOCIATIVE CONNECTIONS ESTABLISHED BY PURKINJE AXON COLLATERALS BETWEEN DIFFERENT PARTS OF THE CEREBELLAR CORTEX

J. Frezik

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Introduction

The existence of associative connections between relatively distant regions of the cerebellar cortex (Dow and Moruzzi; 3) is generally assumed especially by physiologists. Exact anatomical information is, however, lacking as to the types of neurons and pathways that might be involved in such associative connections. There is of course ample opportunity for relatively direct extracerebellar pathways, especially over vestibular nuclei and the brain stem reticular formation which both have cerebellofugal as well as cerebellopetal connections, but obviously these are not such types of connections that are usually meant under intercortical cerebellar association systems. Another not quite direct though intracerebellar association system could be conveyed over the cerebellar nuclei if the assumption of corticopetal fibres arising from these nuclei and terminating in the cerebellar cortex as climbing fibres would hold true (Carrea, Reissig and Mettler; 2). It has, however, been shown recently (Szentágothai and Rajkovits; 11) that the climbing fibres are terminations of the olivocerebellar system and there are no fibres returning from the cerebellar cortex. — If there are, therefore, true association systems, we have to find their direct origin in the cerebellar cortex itself. From the neuronal elements of the cortex three neuron types might be supposed to establish associative connections with more remote regions of the cerebellar cortex, (i) basket cells; (ii) Golgi II type neurons, and (iii) collaterals of Purkinje neurons. The outer star cells of the molecular zone with their short axons ramifying in immediate neighbourhood of the cell body can safely be discarded, as well as also the axons of the granular cells — the parallel fibres — which, according to the investigations of Fox and Barnard [4], have a maximum length of about 3—4 mm. According to unpublished investigations by Szentágothai [10] on the degeneration of basket cell axons after superficial longitudinal incisions of cerebellar folia, the maximum length of these connections does not exceed a few millimeters so that they cannot supply any associative contacts with regions more distant than some part of the immediately adjacent folium.

Although CAJAL [1] described some Golgi cells whose axon might reach regions of the cortex rather remote from the cells of origin, neither CAJAL himself nor any other author has given more detailed description or illustration of such neurons. LANDAU [6] described under the term "synarmotic cells" some Golgi II type cells which are supposed to bridge two opposite sides of the same folium, but these distances are still far too small to be considered even as a medium range association. Thus we are left with the recurrent collaterals of the Purkinje neurons most exactly described by CAJAL and several other authors. There is a single observation available in the whole literature, that by JANSEN [5] according to which, as jugded from Marchi degeneration, the Purkinje collaterals may reach the third neighbouring folium in the rabbit. This is of course not a long distance association connection, but taking into account the fallacies of the Marchi method when applied to such questions, there is a fair probability that such connections might prove much longer if investigated with appropriate modern methods using axon degeneration. It seemed therefore interesting to investigate the problem by the axonal degeneration method an account of which will be presented in the following pages.

Material and methods

Adult cats were used in the investigation. Under ether anaesthesia, in the posterior vermis, especially the lobule VII B of LARSELL [7], superficial cortical ablations were performed with the aid of the knife. In some cases smaller superficial and extended thermocoagulations were made. — In the hemispheres superficial lesions of the posterior part of the ansiform lobe were produced.

The animals were left to survive for 5 days postoperatively and then sacrificed by perfusion with neutral formol under ether anaesthesia. Adjacent and distant parts of the cortex were investigated in frozen sections stained according to the NAUTA—GYGAX [9] technique.

Results and conclusions

The degeneration of preterminal axon branches entering the cerebellar cortex even in its remote regions can easily be observed in Nauta preparations as seen in Fig. 3. The course of the degenerated preterminal fibres is very characteristic. They approach the layer immediately below the Purkinje cell bodies and participate here in a tangential plexus which can easily be recognized as the infraganglionic plexus of Cajal. Some of the degenerated elements switch over to another tangential plexus immediately above the Purkinje cells, at about the level of the horizontally running main dendrites of these cells. Thus this localization of the degenerated elements corresponds exactly to the supraganglionic plexus of Cajal. Though the termination by means of terminal knobs of the degenerated collaterals on the main dendritic branches of the Purkinje neurons could not be visualized, this characteristic course of the degenerated fibres shows beyond doubt that they are in fact

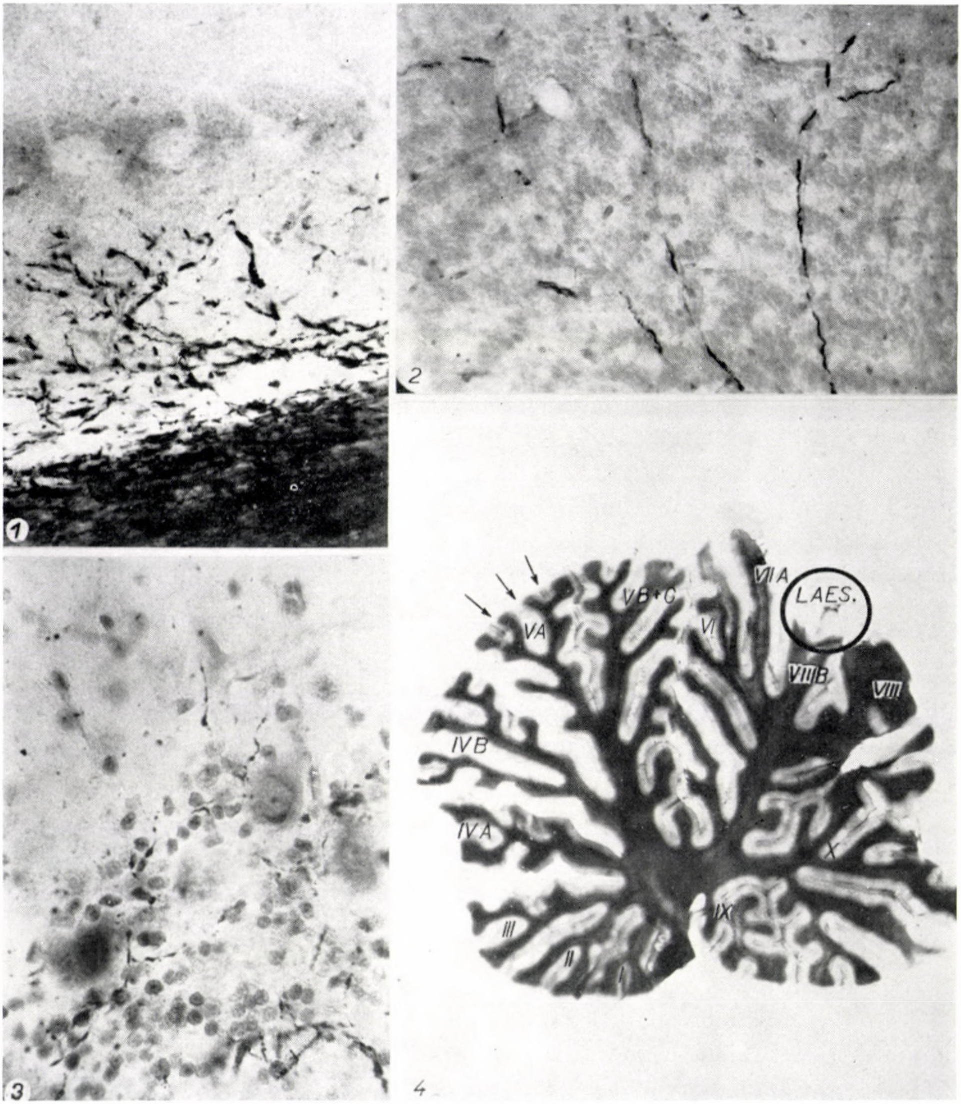

Fig. 1. Degeneration of mossy afferents in the cerebellum after lesion of spinocerebellar systems

Fig. 2. Preterminal degeneration of climbing fibres after olivary lesion (after Szentágothai and Rajkovits)

Fig. 3. Degeneration of recurrent Purkinje axon collaterals

Fig. 4. Superficial lesion (circle) of lobule VIIB causes degeneration of Purkinje axon collaterals as far as lobule VA (arrows)
All sections stained according to Nauta and Gygax

collaterals of the Purkinje cells which had been destroyed in the lesioned regions of the cortex. The signs of degeneration of mossy fibres being known from the investigations of MISKOLCZY [8], those of climbing fibres from the findings of SZENTÁGOTHAI and RAJKOVITS [11], neither of their characteristic patterns of degeneration could be mistaken for, or confused with, the degeneration seen in our material (Fig. 1, 2). However thoroughly we looked for any other type of axonal and preterminal degeneration even in folia immediately adjacent to the destroyed region of the cortex, no other type of degenerated fibres could be observed.

By carefully mapping in all cases the distribution of degeneration in the whole cortex, we could determine the distances and directions of associative connections established by Purkinje axon collaterals originating from the posterior vermis and some parts of the hemispheres. We cannot of course be certain whether the associative connections of other regions of the cerebellar cortex are similar to those which we have investigated.

The findings can be summarized briefly as follows. Associative connections in transversal direction are rather poor. Even extensive lesions on one side of the vermis yield degeneration symptoms not farther than 2—3 mm in transversal direction measured from the border of the lesion. Almost no degeneration symptoms can be seen in the paramedian lobe and none in the hemispheres. Conversely even large cortical lesions of the hemispheres do not yield any signs of degeneration in the vermis, not to speak of those in the opposite hemisphere. Our material is not sufficient, however, to make general statements concerning all parts of the hemispheres, not having investigated regions other than the posterior part of the ansiform lobe.

In sagittal direction associative connections established by recurrent Purkinje axon collaterals are remarkably more abundant and much longer than expected. The signs of degeneration are of course most abundant in the folia immediately adjacent to the lesioned region of the cortex, but they are only very gradually diminishing as one proceeds farther. We had expected that some connections might be found also in more distant folia belonging to the same main branch of the white matter. Much to our surprise after a superficial lesion of LARSELL's lobule VIIB, we could observe clear signs of degeneration in lobule VA of the anterior vermis which belongs to the anterior lobe and this to the anterior principal lamella of the white matter (Fig. 4). — Though the situation is less clear in the hemispheres, it nevertheless appears that associative connections are much longer in sagittal, than in any other direction.

Thus, investigation with the aid of axonal degeneration methods has revealed quite strong and long association systems between different regions of the cerebellar cortex. They appear to be established exclusively by the recurrent collaterals of Purkinje axons being thus of monosynaptic character. The poor associative connections in transversal direction, when compared with the fairly distant and rich connections established in the sagittal plane, are suggestive of a predominantly sagittal organization of the cerebellum for which numerous further observations also seem to speak.

Summary

Direct cortical association systems of the cerebellum have been investigated in the cat with the aid of the axonal degeneration (Nauta and Gygax; 9) method. — Associative connections more distant than to the immediately adjacent folium are established exclusively by the known recurrent collaterals of Purkinje axons. — The connections in transversal direction are rather poor in number and can bridge distances of not more than a few mm. In the sagittal plane the associative connections established by Purkinje axon collaterals are both fairly abundant and of quite unexpected length. Connections between non-neighbouring lobuli of the two principal lobes of the vermis have even been established.

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ASSOZIATIONSVERBINDUNG DURCH PURKINJESCHE AXONKOLLATERALEN ZWISCHEN VERSCHIEDENEN GEBIETEN DER KLEINHIRNRINDE

J. FREZIK

Es wurden die direkten Assoziationssysteme der Kleinhirnrinde von Katzen untersucht. Nach oberflächlicher Läsion des Larsellschen Lappens VIIB [7] ließen sich mit der Axondegenerationsmethode von Nauta—Gygax entartete Fasern nachweisen, die bis zu den vom lädierten Lappen in großer Entfernung befindlichen Blättern verfolgt werden konnten. Diese Assoziationsverbindung wird durch zurückbiegende Kollateralen aus Purkinje-Zellen hergestellt. In Querrichtung ist diese Verbindung ziemlich spärlich und überbrückt eine Entfernung von nur einigen mm. Sagittal ist sie jedoch recht stark und lang. Nach der Läsion des zum Vermis inferior gehörenden Lappens VIIB ließen sich auch im Lappen VA des Vermis superior degenerierte Fasern nachweisen.

АССОЦИАЦИОННАЯ СВЯЗЬ МЕЖДУ РАЗЛИЧНЫМИ ОБЛАСТЯМИ КОРЫ МОЗЖЕЧКА, СОЗДАННАЯ КОЛЛАТЕРАЛЯМИ ИЗ АКСОНОВ ПУРКИНЬЕ

Й. ФРЕЗИК

Автор исследовал прямые корковые ассоциационные системы мозжечка кошек. После поверхностного повреждения дольки VII B по Ларселю он при помощи метода дегенерации аксонов по Наута—Гигаксу выявил перерожденные волокна, которые удалось проследить до весьма отдаленных от поврежденной дольке пластинок. Данная ассоциационная связь создается коллатералями из клеток Пуркинье. В поперечном направлении эта связь довольно скудна, и соединяет расстояние только в нескольких мм, однако, в сагиттальном направлении она весьма сильна и длинна. После повреждения дольки VII B, принадлежащей к нижнему червю, в дольке V A верхнего червя также были обнаружены перерожденные волокна.

Dr. József Frezik, Pécs, Dischka Gy. u. 5. Hungary