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PREFACE

To Professor ERIC KUGELBERG I offer my sincere gratitude for placing the facilities of his laboratory at my disposal and for the friendly and stimulating interest with which he has followed this work. His advice and generous support as well as the excellent relations prevailing in the department have been invaluable.

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Stockholm, January 1955.

LENNART WIDÉN

GENERAL INTRODUCTION

Until about 15 years ago the cerebellum was considered to be concerned solely with the regulation of motor function—"the head ganglion of the proprioceptive system"—which received, in addition to its cerebro-cerebellar connections, impulses only from proprioceptors of muscles, tendons, joints and labyrinths. The classical pathways of Gower and Flechsig were assumed to be the principal fibre systems for the transmission of spinal impulses to the cerebellum. The anatomical and physiological investigations of recent years, however, have necessitated a modification of this concept. Electrophysiological studies have shown that impulses from other groups of receptors also pass to this organ: tactile (SNIDER and STOWELL, 1942; ADRIAN, 1943), auditory (STOWELL and SNIDER, 1942), visual (STOWELL and SNIDER, 1942) and olfactory (HUGELIN, BONVALLET, DAVID and DELL, 1952). The cerebellar projection of impulses from muscle proprioceptors has also been confirmed with this technique (DOW and ANDERSON, 1942; GRUNDFEST and CAMPBELL, 1942; MOUNTCASTLE, COVIAN and HARRISON, 1952; CARREA and GRUNDFEST, 1954). Neuroanatomical studies have revealed the existence of additional pathways for impulses from the spinal cord to the cerebellum. Recently BRODAL (1953), who has carried out pioneering work in this field, defined anatomically not less than eight possible pathways between the spinal cord and cerebellum.

The possibility of a somatotopic as well as a functional localization in the cerebellum has long been discussed. The results of neuroanatomical studies have not always shown agreement with electrophysiological data. On the other hand, the latter have often been found to be at variance. Afferent pathways from the periphery and higher centres to the cerebellum as well as efferent pathways from the cerebellum have been studied in these investigations. A brief account of investigations on afferent projection systems from the periphery only will be given here.

DOW (1939) and DOW and ANDERSON (1942), who recorded the cerebellar responses to electrical stimulation of various nerves in the fore- and hindleg of decerebrate cats and of rats in nembutal anaesthesia, found no evidence of somatotopic organization in the cerebellar areas from which responses were obtained: the entire anterior lobe, lobulus simplex, pyramis and paramedian lobules. On the other hand, SNIDER and STOWELL (1942, 1944) have reported with physiological tactile stimulation the presence of discretely localized face, forelimb and hindlimb sensory areas in the cerebellar cortex of anaesthetized cat and monkey. The receiving areas for impulses of tactile origin were located in three parts of the cerebellum: one in the posterolateral half of the ipsilateral anterior lobe and two in the paramedian lobules. In each lateral half of the anterior lobe there was a projection of the ipsilateral half of the body surface in which the feet and vibrissae were the parts most conspicuously represented. In the lateral part of this area there was the representation for the feet, with the hindpaw most rostral, and in the medial part the trunk and head, with the hip most rostral, and posterior to this the shoulder region which overlapped the caudally placed head zone. The forefoot and hindfoot of one side were represented in both paramedian lobules, the forefoot having a stronger contralateral representation than the hindfoot. ADRIAN (1943), independently of these authors, reported in the cat and monkey definite topographical localization in the cerebellum for responses evoked by mechanical stimulation, such as touch, pressure, movements of joints and muscle stretch. WHITLOCK (1952), in a combined neurohistological and neurophysiological study of the avian cerebellum, found a definite somatotopic arrangement of the activated loci of the cerebellar cortex into tail, leg, wing and face tactile areas.

These experimental results of SNIDER and STOWELL, of ADRIAN, and of WHITLOCK strongly favour a somatotopically organized projection of the tactile afferent system to the cerebellum. This raises the question whether one of the known pathways between the spinal cord and cerebellum satisfies the requirements for a somatotopically arranged spinocerebellar projection for these tactile impulses. BRODAL (1949, 1953), who has studied this problem, concluded that the only system possible was the spino-lateral reticular nucleus-cerebellar. The lateral reticular nucleus receives ascending afferents from the lateral funiculus of the spinal cord which terminate in the nucleus where they are systematically organized, the fibres from the hindleg in the superficial parts and those from the foreleg in somewhat deeper parts. Those parts of the nucleus which receive spinal afferents project to the cerebellar tactile receiving areas. BRODAL was further able to demonstrate that those parts of the nucleus which project to the foreleg area in the anterior lobe are identical with those which receive spinal fibres from the foreleg. The electrophysiological studies of BERRY, KARL and HINSEY (1950) and BOHM (1953) have shown that the afferent impulses which enter the spino-lateral reticular nucleus-cerebellar system derive from coarse cutaneous nerves.

The importance of the part played by anaesthesia in mapping studies of specific sensory projection areas in the cerebral cortex has long been recognized. Very deep anaesthesia is often necessary. The effect of anaesthesia on the cerebellar responses evoked by electrical stimulation of various dorsal roots and peripheral nerves as well as by physiological stimulation of tactile end organs has been systematically studied by COMBS (1954). This author found no evidence of somatotopic localization in *unanaesthetized* preparations. On the other hand, in animals in *nembutal anaesthesia* a precise confirmation of foreleg and hindleg afferent localization was noted. COMBS' observations on the effect of anaesthesia on cerebellar localization may explain the somewhat controversial results of earlier workers.

With regard to functional localization in the cerebellum only the question of whether different sensory modalities have separate areas of representation in the cerebellum will be discussed. Also on this point the results of different authors have varied. DOW and ANDERSON (1942) found, in the rat, that impulses from proprioceptive receptors projected mainly to the pyramis, while "exteroceptive stimulation" (touch) evoked responses primarily in culmen. Accordingly, they considered they were able to demonstrate at least a degree of localization for these modalities. MOUNTCASTLE, COVIAN and HARRISON (1952) stimulated various peripheral nerves and found that stimulation of Group I and III fibres of a purely muscle nerve in the hindleg resulted in an anterior lobe localization of evoked potentials identical to that found with stimulation of a purely cutaneous nerve. Likewise, CARREA and GRUNDFEST (1954) found that the anterior lobe receiving area for impulses from cutaneous nerves in the foreleg and hindleg conveyed by the ventral spinocerebellar tract considerably overlapped that for impulses from muscle nerves conveyed by the dorsal spinocerebellar tract. Similar results were reported by COMBS (1954) in unanaesthetized preparations.

SNIDER and STOWELL (1944) have shown that the auditory and visual cerebellar projection areas are almost conterminous and occupy predominantly lobulus simplex and tuber vermis. Rostrally these projection areas overlap the tactile response areas for the face and partly that for the forepaws. The audiovisual area often extends to the paramedian lobules and consequently here also overlaps the tactile area. HUGELIN and co-workers (1952) have shown that also the third type of distance receptors, olfactory sensory cells, project to lobulus simplex as well as to both paramedian lobules and to pyramis. DELL and OLSON (1951) found that the vagus visceral afferent fibres have a cerebellar representation. This was located in the posterior part of the anterior lobe and the anterior part of lobulus simplex and overlapped the receiving areas for olfactory, auditory and visual impulses as well as that for tactile impulses from the face.

Thus the majority of the investigations would seem to indicate that there is considerable overlapping of the projection areas of different afferent systems.

The first purpose of the present investigation was to determine whether the afferent neurones distributed with the sympathetic outflow to the viscera have a cerebellar representation. This was found to be the case. A study was then made of the type of fibres mediating the afferent impulses and their spinal pathways, as well as the sensory modality they subserve. Since it was found that the splanchnic afferent fibres which mediate the cerebellar responses belong to the delta group, experiments were performed to determine whether delta fibres from other sources also have a cerebellar representation.

MATERIAL AND METHODS

Cats were used in all the experiments. Most of the animals were anaesthetized with intravenous nembutal. The level of anaesthesia was varied according to the experimental needs, the initial dosage being about 20—25 mg/Kg body weight. A few experiments were performed on decerebrate preparations. The animals were initially anaesthetized with ether or trilene and decerebration performed either by transection at a collicular level and removal of the entire cerebrum or by subpial aspiration of the left occipital pole, which exposed the mesencephalon, followed by division of the brain stem by aspiration from the superior colliculus down to a point just behind the mammillary bodies.

For both stimulation and recording chlorided silver electrodes were used. When recording from the cerebral and cerebellar cortices as well as from the dorsum of the spinal cord the exploring electrode was on the surface of the structures with the second electrode resting on adjacent non-neuronal tissue. The recording electrodes were so arranged that a positive potential was recorded as a downward deflection of the cathode beam.

The left splanchnic nerve was exposed through a retroperitoneal approach and severed at its point of junction with the coeliac ganglion. In most experiments the nerve was dissected free only to the point where it enters the diaphragm. For recording the afferent volley in the sympathetic trunk several of the lowest ribs were resected and the animal was then maintained by artificial respiration after the administration of curare. All the exposed cord and nerves as well as the exposed cerebellar cortex were covered with liquid paraffin except in the case of the splanchnic nerve when recording from the sympathetic trunk. The liquid paraffin and the rectal temperature of the animal were maintained at a constant temperature of 37—38° C by radiant heat. When recording from the sympathetic trunk only a small stretch of the trunk was dissected free and divided at the proximal end. The sympathetic trunk and the splanchnic nerve were immersed in a pool of warm Ringer's solution (cotton wool saturated with the solution). The proximal stimulating electrode (cathode) on the splanchnic nerve, connected to earth, and one of the recording electrodes on the sympathetic trunk were in the pool of Ringer's solution, while the second of each pair of electrodes was in the air. Essentially the same technique was employed when stimulating and recording from the superficial radial nerve.

The stimuli consisted of single rectangular pulses, mostly of 0.1 to 0.5 msec. duration. The action potentials were fed to an RC-coupled amplifier and recorded on a cathode ray tube. The cathode ray trace was photographed on to bromide paper.

A. CEREBELLAR REPRESENTATION OF HIGH THRESHOLD AFFERENTS IN THE SPLANCHNIC NERVE

Earlier Investigations of Splanchnic Afferent Fibres and Their Central Connections

It has long been known (Langley, 1896; Ranson and Billingsley, 1918) that visceral afferent fibres have their cell bodies in the posterior spinal root ganglia. At the thoracolumbar level of the spinal cord they travel with the sympathetic nerves from the viscera in the sympathetic trunk and via the white rami communicantes to the posterior roots. Recent experimental electrophysiological investigations (Amassian, 1951 b; Aidar, Geohegan and Ungewitter, 1952) have shown that afferent impulses from the splanchnic nerve of cat are conveyed *partly* via the ipsilateral fasciculus gracilis and nucleus gracilis, the internal arcuate fibres and the contralateral medial lemniscus to reach the contralateral nucleus ventralis posterolateralis of the thalamus and *partly* via the anterolateral funiculus in the region of the lateral spinothalamic tract on both sides.

The investigations of Amassian (1950, 1951 a, b) and Downman (1951) have shown that there is a cerebral cortical representation for afferent fibres in the splanchnic nerve of rabbit, cat, dog and monkey and that the impulses are mediated by the A beta group of afferent fibres.

It is known that the coarse afferent fibres in the splanchnic nerve—the A beta group—are at least partly derived from the Pacinian corpuscles in the mesentery (Edgeworth, 1892; Sheehan, 1932). Gernandt and Zotterman (1946) found that the Pacinian corpuscles in the cat mesentery were extremely sensitive to the gentlest pressure. They recorded afferent impulses from the corpuscles in the mesentery and the splanchnic nerve. The impulses were conducted at a fast speed and originated in large myelinated fibres which, in the splanchnic nerve, had a diameter of 6—10 μ and numbered about 300. Further, they found that the splanchnic nerve contained, in addition to the coarse fibres,