Problems In

CEREBELLAR PHYSIOLOGY

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Written by a neurophysiologist for neurophysiologists, this monograph presents a critical examination of the results of recent investigations on cerebellar physiology which have been devoted to the anterior lobe. First of all the author summarizes the points on which all cerebellar physiologists agree and then he goes on to a discussion of new facts which have been observed in the last few years and on which experimental investigation is still being done.

124 pages   27 illustrations

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CHARLES C THOMAS · PUBLISHER
Springfield · Illinois · U.S.A.

CHARLES C THOMAS · PUBLISHER
BANNERSTONE HOUSE
301-327 EAST LAWRENCE AVENUE, SPRINGFIELD, ILLINOIS

Published simultaneously in the British Commonwealth of Nations by
BLACKWELL SCIENTIFIC PUBLICATIONS, LTD., OXFORD, ENGLAND

Published simultaneously in Canada by
THE RYERSON PRESS, TORONTO

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Printed in the United States of America

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INTRODUCTION

MANY of the recent investigations on cerebellar physiology have been devoted to the anterior lobe. This monograph was written with the aim of giving a critical survey of the results thereby obtained.

Probably only technical considerations determined the choice of earlier investigators. The surface of the anterior lobe is just behind the bone tentorium and it is easily exposed in a decerebrate cat; its stimulation gives rise to striking postural responses, which have been thoroughly analyzed. In the last years, however, evidence has been accumulated showing the peculiar physiological significance of this comparatively small part of the cerebellar surface.

Spinal, olivary and cortico-pontine impulses have been found to converge on the anterior lobe. The efferent discharges from the Purkinje cells of this area have been shown to reach, through fastigial relays, the bulbar reticular formation, whose far-reaching influence on central activities has been successfully investigated in recent times. Finally, the stimulation of the anterior lobe has been found to influence not only postural tonus, but also spinal, diencephalic and cortical activities.

Of course, other cerebellar areas might have functions no less important than those of the anterior lobe. Cerebellar physiology is now in rapid evolution, and it is impossible to foresee the future development of the discovery of visual and acoustic areas in *Lobulus medius medianus* (76) and of the finding of interrelations between *Lobulus ansiformis* and autonomic cortical areas (23). In fact, the only justification for devoting a monograph mainly to the anterior lobe is that our knowledge of this area is now more advanced and, therefore, an attempt can be made to understand its functional role.

The word paleocerebellum has sometimes been used in the text as a synonym for anterior lobe. In Larsell's sense paleocerebellum corresponds to the spinal "story" of the cerebellum, and there is no doubt that there are paleocerebellar areas outside the anterior lobe, as well as very small archi- and neocerebellar areas in the anterior lobe itself (see Moruzzi [58] for references and a critical survey). It is also true that the word paleocerebellum is sometimes misleading since it might imply that the anterior lobe has nothing to do with cortical or neopallial activities. However, since the areas of the anterior lobe which have been explored belong undoubtedly to the spinal level of the cerebellum and receive spinal somatic impulses, we have been unwilling to drop an expression which is certainly appropriate in the anatomical sense and which has been widely used by cerebellar physiologists.

I

CEREBELLAR INHIBITION OF POSTURAL TONUS*

THE INHIBITION of decerebrate rigidity produced by faradizing the anterior vermis is now a classic experiment, which is routinely made by any lecturer in neurophysiology. I think that anyone who has once seen the sudden disappearance of rigidity produced by a weak paleocerebellar faradization and the powerful extensor rebound following the end of the stimulation, will never forget the discovery which was independently made by Löwenthal and Horsley and by Sherrington about 50 years ago.

Few people, however, have fully realized the tremendous importance of this experiment in the history of cerebellar physiology. Only after the recent findings on somatotopic localizations in the anterior lobe and on relationships between cerebellar inhibitory area and bulbar reticular centers, would most of us consent that the discovery of Löwenthal and Horsley and of Sherrington was

* Lecture delivered at Northwestern University Medical School on December 6, 1948.

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probably of no less significance for cerebellar physiology than was the famous Hitzig and Fritsch experiment for the physiology of the cerebral cortex.

It is indeed most surprising to see that the discovery of a cerebellar inhibitory area did not apparently greatly impress contemporary investigators, and this cool reception appears still more striking if it is compared with the tremendous growth in cerebral physiology which followed the discovery of Hitzig and Frisch, when for some years cerebral physiology was investigated by such outstanding men as Ferrier, Albertoni, Luciani and Tamburini in the seventies and, in the earlier eighties, Exner, Bubnoff and Heidenhain, and François-Franck.

It would be stimulating to speculate about the possible reasons behind this fact, but it would be beyond the scope of this lecture. Our discussion would also be too lengthy if we attempted only to give an account of the experimental work which has been done during this half century on the paleocerebellar influence on postural tonus.[1] A much smaller field will be covered by us. We shall first of all summarize the points on which we think all cerebellar physiologists agree and then

[1] For critical survey and references, see (58).

we shall devote almost all our time to discussing some new facts which have been observed within the last years and on which experimental investigation is still being done.

Everyone would consent, I believe:

1. That paleocerebellar inhibition of postural tonus is merely the consequence of a discharge of impulses from the Purkinje cells of the stimulated area, i.e., that the effects we observe are not due to spread of current;

2. That the "excitable" area is chiefly correlated to the spinal division of the cerebellum and, above all, to the vermian part of the anterior lobe;

3. That there is a tonic activity of the paleocerebellar inhibitory area, at least in birds and lower mammals, since a strong extensor hypertonia appears when the anterior lobe is destroyed or its surface is cooled;

4. That a peculiar feature of paleocerebellar responses to electric stimulation is their diphasic character, i.e., that at the end of the stimulation there is a reversal of the effect, instead of an after-discharge which merely prolongs the original response, such as we have from the motor cortex or from the suppressor areas of the cerebral cortex.

The following problems of paleocerebellar physiology have been investigated in the last years and will be discussed here.

1. Site of inhibition, i.e., localization of neurons which are inhibited by the paleocerebellar cortex.
2. Efferent paths and relays for the impulses coming down from the Purkinje cells of the inhibitory area.
3. Somatotopic localizations in the inhibitory area.
4. Mechanism of reflex activation of Purkinje cells and nature of the tonic paleocerebellar inhibition.

As you will realize, our program is to go antidromically from the centers which are inhibited by the cerebellum to the very source of paleocerebellar inhibition. But our discussion would be incomplete if we should disregard a new aspect of paleocerebellar physiology which is now attracting to itself the attention of the investigators. I mean the facilitating influence of paleocerebellar cortex on postural tonus. We shall discuss this problem in the next lecture.

1. The Site of Inhibition

Both inhibition of bulbar facilitating centers and of spinal extensor motoneurons could account for the cerebellar suppression of decerebrate

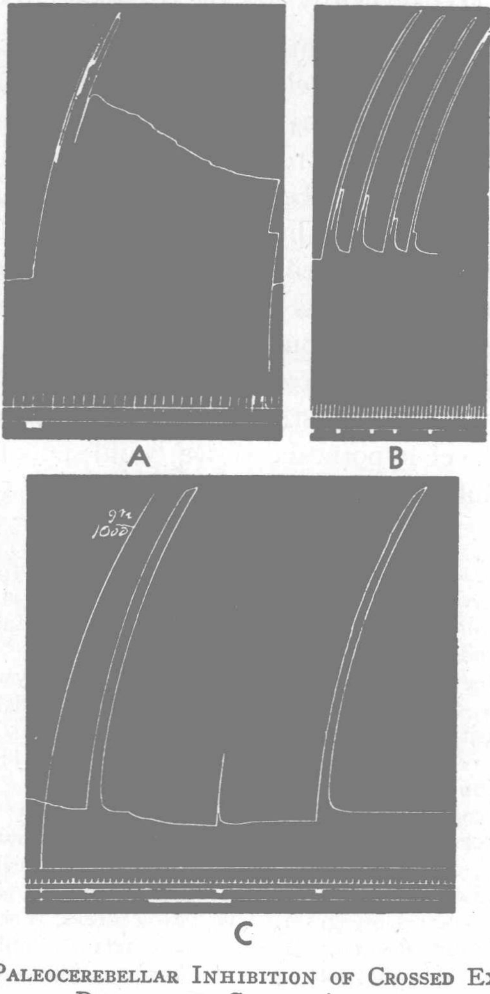

FIG. 1. PALEOCEREBELLAR INHIBITION OF CROSSED EXTENSOR REFLEXES IN CURARE ATONIA

(Legend continued on facing page.)

rigidity. The problem we face now is the determination of the level of the inhibition: bulbar versus spinal level hypothesis.

Crossed extensor reflexes are undoubtedly inhibited by paleocerebellar stimulations. This observation was made by Bremer (8) in 1922, and it has been confirmed by many investigators. It could be regarded as an evidence that Purkinje impulses arrive, through inhibitory relays, to the extensor spinal motoneurons. This assumption would, of course, strengthen the case for the spinal level hypothesis, if we could demonstrate that inhibition of these reflexes is really a direct

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←

A. Crossed extensor reflex after anaemic decerebration. From above downwards: isometric myogram of *m. vastocrureus,* time in seconds, signal of faradic stimulation of the central end of contralateral sciatic nerve.

B. After an intravenous injection of a subparalysing dose of curare, the long postural afterdischarge is abolished, but the intensity of the phasic component of the extensor reflex is not decreased (curare atonia of Bremer *et al.,* [11]). Same preparation (from Moruzzi [39]—Arch. di fisiol.).

C. Precollicular cat during curare atonia. Rigidity is abolished. Crossed extensor reflexes, showing no postural afterdischarge, are strongly inhibited by faradizing ipsilaterally the vermian part of the anterior lobe. From above downwards: isometric myogram of *m. vastocrureus,* time in seconds, stimulation of contralateral sciatic nerve, stimulation of ipsilateral anterior lobe (from Moruzzi [40]—Arch. di fisiol.).

one and not merely a consequence of inhibition of postural tonus.

In order to test this hypothesis, the effects of paleocerebellar stimulations on crossed extensor reflexes were investigated during curare atonia (40). It had been shown by Bremer, Titeca and van der Meiren (11) that subparalyzing doses of curare selectively abolish postural extensor tonus and the myotatic appendage or pseudo-afterdischarge of the crossed extensor reflex, without impairing the pure spinal phasic response (Fig. 1, A, B). During curare atonia, crossed extensor reflexes, reduced to their pure phasic component, were so strongly inhibited by paleocerebellar stimulations that an influence on spinal cord could not be denied (Fig. 1, C, [40]).

However, it was later pointed out (48) that these experiments do not give a convincing evidence for a direct paleocerebellar inhibition of spinal extensor motoneurons. We know that the crossed extensor reflex is severely depressed in the acute decapitate or spinal preparation, and it was recently shown by Bach and Magoun (3) that destruction of vestibular nuclei or sectioning the vestibulo-spinal tracts in decerebrate cats reduces phasic reflexes on the injured side. Inhibition of spinal extensor reflexes could then be regarded

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