FUNCTIONAL ASPECTS
OF CEREBELLAR AFFERENT SYSTEMS
AND OF CORTICO-CEREBELLAR RELATIONSHIPS

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INTRODUCTION

Since the pioneer works of Dow (4 and 5), Adrian (1), Snyder (10 and 11), Grundfest and Campbell (6), the afferent projections to the cerebellum have been studied by several authors. The main trends of research at the present time are concerned with the organization and the physiological properties of the various afferent tracts, the inter-

ference of diverse afferent sources in the cerebellar cortex, the waveform
of the cerebellar evoked potential, the discharges of individual Purkinje
cells. On most of these aspects there is still considerable disagreement
and only further work will modify or solve the existing discrepancies.

In spite of the well known differences of structural organization
between cerebral and cerebellar cortices the response to afferent volleys is
practically identical for both cortices.

The cerebellar evoked potential is a diphasic (positive-negative)
wave which stands out very prominently on the low amplitude high
frequency activity of the cerebellum (7). A small positive deflection
which precedes the main diphasic wave has been interpreted as due to
afferent activity in the granular layer. The main diphasic wave is
identical to the cerebral evoked potential but the mechanism of its origin
has not been as extensively analyzed. If the mechanism proposed by
Bishop and Clare (2 and 3) for the sensory activation of the visual cortex
is also valid for the cerebellar evoked potential an initial depolarisation
close to the cell body of the Purkinje cells should occur. The great
density of the axons of the granules (parallel fibers) around the proximal
part of the dentrite would account for this. However, the role of the
basket cells and of their conspicuous axo-somatic synaptic fields, and of
the Golgi cells and their extensive axonal branching in the granular layer
remain to be established. At the present stage of our knowledge it
appears premature either to extend to the cerebellar cortex Bishop's
theory or to refute it on the basis of inadequate experimental evidence.

Our interest during the last few years was concerned primarily with
problems that can be better outlined by comparing the general features
of the afferent systems to the cerebral and to the cerebellar cortex.
From an anatomical point of view, one has only to consider the number
of afferent tracts for the cerebellum and the number of cells the axons
of which form those tracts. Compared to the cerebellar afferent systems
the medial lemniscus and the spinothalamic tract appear to be rather
simple and modest entites.

Medullary and cerebellar evoked potentials :

In view of the multiplicity of afferent cerebellar tracts and of the
medullary structures projecting to the cerebellum it appeared con-

venient to study the activation of these structures following afferent stimulation.

In a group of experiments (figure 1) (in cats) records were taken simultaneously from the inferior olive (spinal part) and the anterior lobe
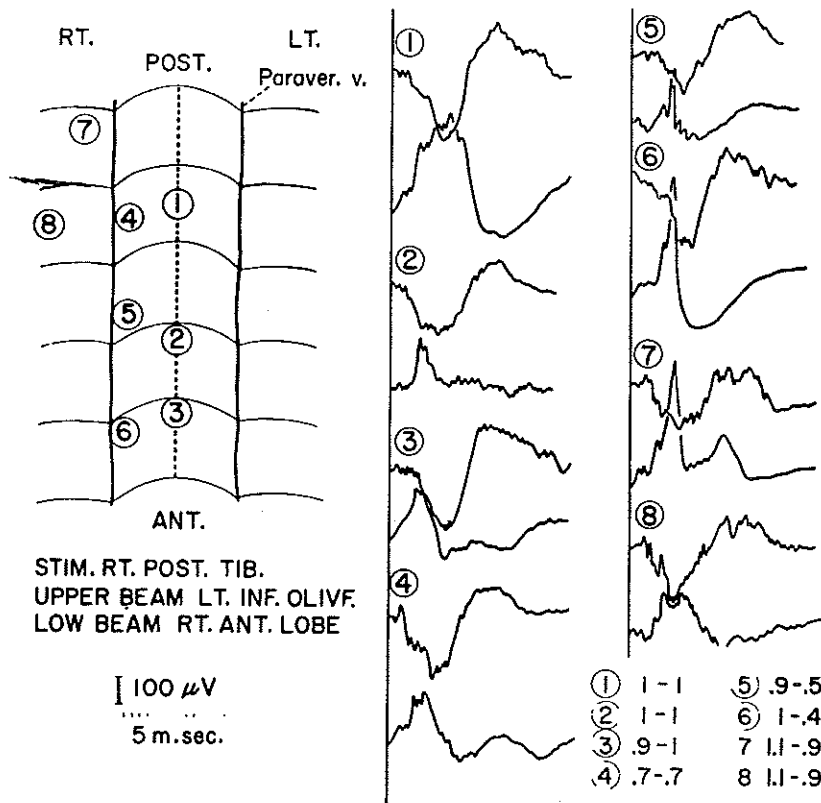

Figure 1. — Evoked potentials from left inf. olive and right ant. lobe elicited by stimulation of the right post. tibial nerve. In the right lower corner are the thresholds, in arbitrary units, of the olivary, upper beam, and the cerebellar potentials (lower beam). Notice that threshold for cerebellar potentials recorded from midline (1, 2, 3), is higher than for potentials record more laterally, 5, 6, close to paravermian vein (paraver. V.). In this and following figures negativity is downward ; experiments are on lightly anæsthetized cats.

following stimulation of various cutaneous and mixed nerves. It was found consistently that the evoked potentials in the paravermal zone had lower threshold than those present in the vermal midline zone of the anterior lobe. The midline potentials have almost constantly the same

treshold as those elicited in the inferior olive (opposite to the stimulated nerve). By recording the nerve action potentials simultaneously with either the midline or olivary potentials it was seen that the slower conducting fractions of the A group were almost constantly activated when the olivary or midline vermal potentials were present. The paravermal
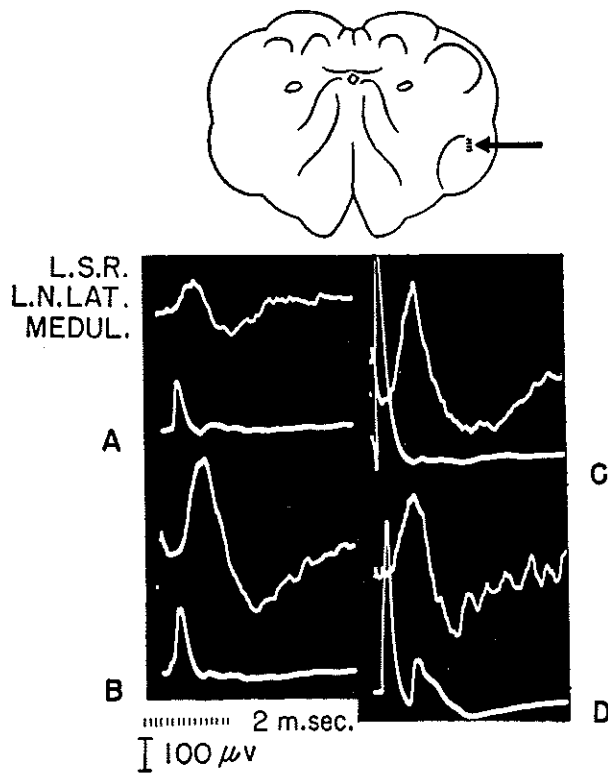

Figure 2. — Evoked potentials from left lateral nucleus of the medulla, upper beam, and action potential of left superficial radial nerve recorded from distal end (conduction dist. 10 cm.). A at threshold ; B C D at increasing stimulus strengths.

zone and the paramedian lobule receive axons from the lateral nucleus of the medulla. Both these cerebellar areas and the nucleus were found to be activated by the most excitable fibers of the A group, and the projections to the nucleus were prominently from the ipsilateral cutaneous nerves (figures 2 and 3). It seems therefore, that the longitudinal division

of the anterior lobe of the cat cerebellum established on the basis of the nuclear connections is also present to a certain degree for the afferent projections. The paramedian reticular nucleus also projects to the cerebellum and receives spinal afferents. We were unable to record
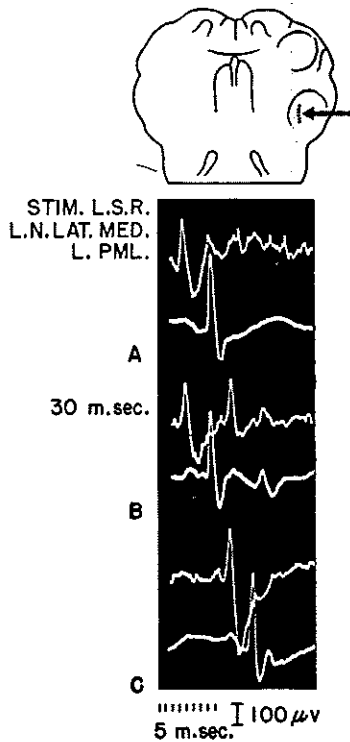

Figure 3. — Potentials from left lateral nucleus of the medulla, upper beam, and left paramedian lobule elicited by stimulation of left superf. radial nerve. In A first simulus alone, in B two stimuli 30 msec. apart, C. second stimulus alone.
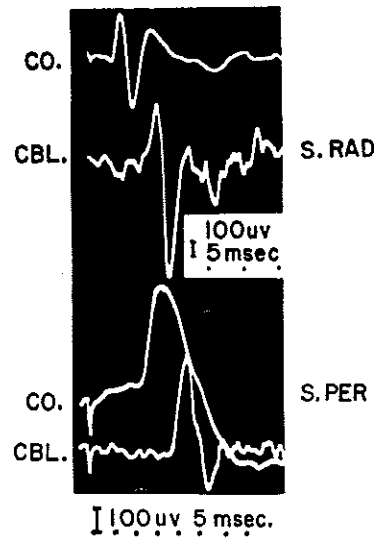
Figure 4. — Illustrates latency differences between cortical and cerebellar evoked potentials following stimulation of cutaneous nerves, superficial radial and superficial peroneal of right side to left sensory cortex and right anterior lobe.

evoked potentials from this nucleus and this might be due to inadequacy of technique and to the paucity of spinal afferents. The reticular formation lateral and slightly caudal to it was, however, found to respond constantly to afferent stimulation. In contrast with the lateral nucleus of the medulla these reticular responses were elicited by ipsi and contra-

lateral peripheral nerves, and, similarly to the inferior olive potentials, were dependent on activation of slower conducting fibers of the A group. This spino-reticular system is presumably extraneous to cerebellar afferent systems.

All of this structural wealth and complexity of the cerebellar sensory system does not have anything to do with sensation, its physiological significance is concerned with motor activity. The visual and the auditory representation in the cerebellum should also be included as visual and auditory stimuli arise in connection with motor performances.

Cerebello-cortical relationships :

The problems of cortico-cerebellar interrelationship and of the cerebellar regulation of postural tonus have been intensively investigated and recently reviewed by G. Moruzzi. An important difference between cerebellar and cerebral sensory systems is revealed by the evoked technique. Cerebellar evoked potentials produced by sensory stimulation have longer latencies than the corresponding potentials led from the sensory cortex. This fact has been observed consistently by several investigators but apparently did not attract any attention, (figure 4).

We thought that if sensory messages reach the two cortices, cerebral and cerebellar, at different time intervals, the efferent discharges from both cortices could depend on that temporal sequence.

In a series of acute experiments in cats the motor cortex of the left side and the anterior lobe of the right side were stimulated with single shocks in different sequence and intervals and the ventral root action potential recorded oscillographically.

Figures 5 and 6 show the results of one of these experiments. As can be seen, when the cerebellar shock follows the cortical shock the ventral root response is increased ; when the sequence is reversed the anterior lobe being stimulated before the motor cortex, the amplitude of the ventral roots response decreases. Because of this effect a series of alternating cortical and cerebellar shocks produces ventral root discharges of constant amplitude since the individual response from the motor cortex would be reduced by the cerebellar response preceeding it and augmented by the cerebellar response following it. This mechanism would account for the smoothness of normal muscular contraction and

its absence for the disorders occurring in cerebellar tremor. The modulatory or coordinating action of the cerebellum then presumably resides in the correct timing of its action with the motor cortex. Several new problems arise from this concept and are being investigated. First, where does the interference between cortical and cerebellar discharges
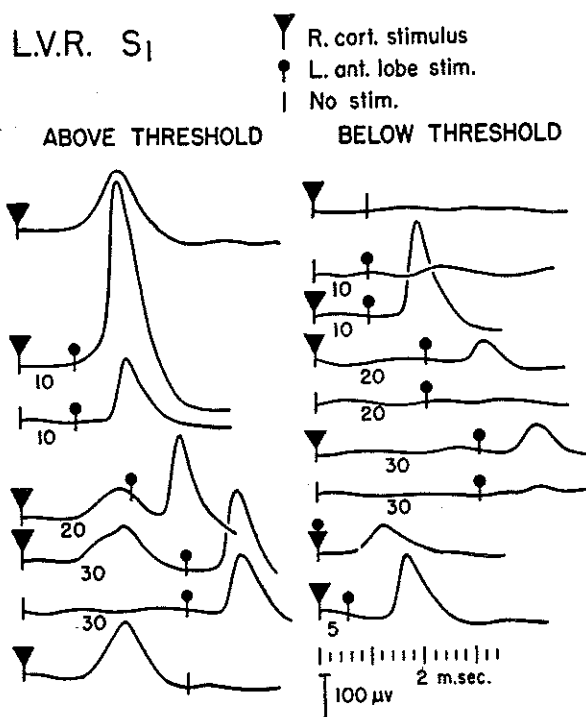

Figure 5. — Records are obtained from left ventral root, sacral 1, by stimulating the right motor cortex and the left anterior lobe. In this figure the motor cortex is stimulated first, the ant. lobe later at different intervals, from 10 to 30 msec. after the cortical shock.

occur and how is its structural substratum organized? The effect illustrated in figure 5 was observed in a few cases after acute section of the superior cerebellar peduncle at the intercollicular level, indicating that the spinal neuron pool was affected directly from the anterior lobe. The location and distribution of the fibers reaching the motor neuron pool from the anterior lobe, the synaptic arrangement of these fibers at

the spinal level and their relations with the termination of the cortico-spinal tract should be investigated.

Thus from a consideration of the time differences between afferent activation of cerebral and cerebellar cortices some clues can be gained on the mechanism of cerebellar function in motor performances. Other interesting information can be obtained by considering the links of the circuit between the periphery, the cerebellum and the cerebral cortex.

The connections between motor cortex and receiving areas of the anterior lobe or paramedian lobule are well known and it is known that
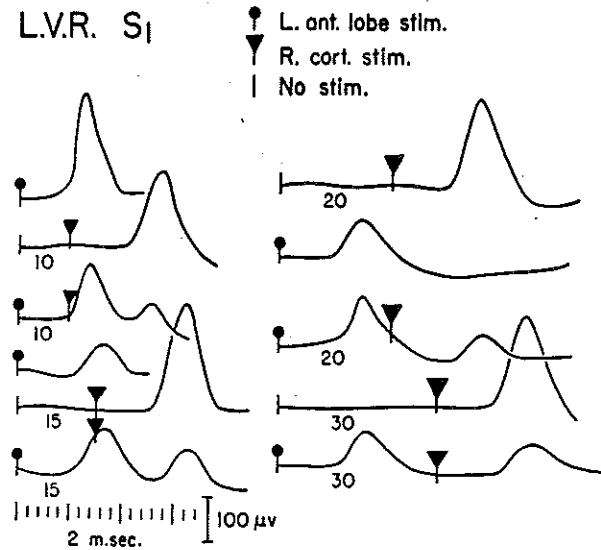

Figure 6. — As in figure 5 but the anterior lobe is stimulated first and the motor cortex later at different intervals from 10 to 30 msec.

the latency of evoked potentials elicited in those parts of the cerebellum by stimulation of the motor cortex is a long one, a few milliseconds less than the latency of the potential evoked in the same cerebellar area by stimulations of a peripheral nerve of the limbs. By the conventional method of double stimulation it can be easily seen that both sources of afferents (cortico-cerebellar and periphery to cerebellum) converge and share the same group of responsive elements in the cerebellar cortex (anterior lobe), (figure 7). In contrast the cerebellofugal projection to the motor cortex and toward the spinal cord are much faster. Because of its

afferent connections the anterior lobe is in a position of receiving signals
from the center initiating the movement and from the parts of the body
subjected to that movement, and because of its efferent connections it
can rapidly influence both the cortex and the spinal centers governing
that movement. When these anatomical and functional details are
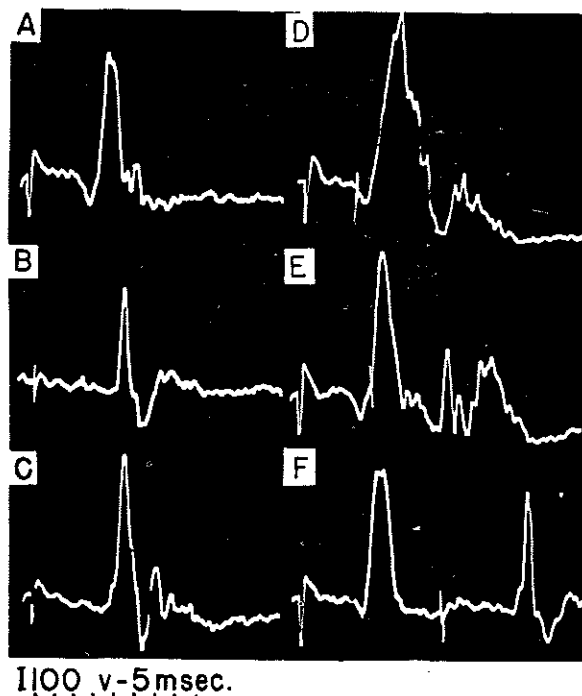explained to an expert in control engineering, he will not hesitate to

I|OO v.-5 msec.

Figure 7. — Records from the rt. anterior lobe following stimulation of left
motor cortex, and of right superficial paroneal. A. Motor cortex stimul.
B. Nerve stimul. C. Cortex and nerve simultaneously. D. Nerve 13 msec.
after cortex. E. 20 and F, 35 msec. after cortex.

classify the cerebellum as an error detecting device which compares the
intended performance (signals coming from the motor cortex, « input »)
with the obtained performance (signals coming from the periphery,
« output ») and can originate a correcting signal for both. And the
timing of the arrival of these two sets of information (the input from the
cortex and the output from the periphery) fits the necessary requirements

for such a device. In such a system the malfunctioning of the error detecting device either in excess (as in artificial stimulation of the cerebellum) or in defect (as in cerebellar ablations or disease) always results in the same type of disorder the most prominent manifestations of which are overshooting and oscillations of the moving parts. We are well aware of the fact that there are many possible objections and many limitations to this concept.' It appears to us, however, that it is helpful in explaining many anatomical and functional properties of the afferent and efferent connections of the anterior cerebellar lobe.*

Summary

Two aspects of the problem of cerebellar afferents are here considered. The first deals with the activation of the medullary structures (inferior olive, lateral nucleus of the medula), and of the cerebellar receiving areas by afferent stimulation. The findings indicate that the spinal-olivo-cerebellar system is mainly confined to the midline of the anterior lobe (vermal zone) and is involved in response to excitation of slower conducting peripheral fibers (of the A group). The spinal-lateral nucleus-cerebellar system is distributed more prominently to the lateral zone (paravermal) of the anterior lobe and to the paramedian lobule and transmits impulses from the fastest conducting fibers of peripheral nerves.

The second aspect deals with a comparison between the afferent system of the cerebellum and of the cerebral cortex. Considerations of the different latency of afferent peripheral excitation of the two centers suggested that final motor discharge could be dependent on timing and sequence of cortical and cerebellar activation. Some evidence to this effect is presented. Other features of the connections between cortex-cerebellum and periphery are considered and the suggestion is made that a basic function of the cerebellum is that of accomplishing a comparison between intended (by the cortex) and obtained (from the periphery) motor performance and of originating the necessary correcting signals.

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* The concept of the cerebellum as a « comparing organ » was put forward in the past by T. Ruch (1951) when discussing cortico-cerebellar circuits. Reference to Ruch's ideas was found in the recent review by P. Passouant « Étude synthétique de la physiologie du cervelet » *Revue neurol.*, **98** : 129-184 ; 1958.

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