STUDIES IN PHYSIOLOGY

Presented to John C. Eccles

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Edited by

D. R. Curtis and A. K. McIntyre

With 80 Figures

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PREFACE

This collection of papers is presented to Sir JOHN ECCLES by his former and present collaborators to commemorate the award of the 1963 Nobel Prize in Medicine, which was shared with A. L. HODGKIN and A. F. HUXLEY. Sir JOHN'S interest in, and influence on, the study of physiology, particularly that of the nervous system, is reflected by the range of topics discussed, and by the distribution of the various authors in laboratories throughout the world. Those who have been privileged to work with him in Oxford, Sydney, Dunedin or Canberra have enjoyed a good discipline in scientific thought, as well as in the use of neurophysiological techniques. Basic knowledge is always transferable, and the inspiration which comes from association with a great scientist is not confined to any one field of physiology.

The contributors to this volume were requested to review briefly that aspect of physiology of current interest to them, and it is hoped that the resulting papers will serve as an up to date review of many physiological problems.

The editors are greatly indebted to the publishers, Springer-Verlag, particularly to Dr. H. GÖTZE for his advice and interest. It is also a pleasure to thank Mrs. H. WALSH for her unfailing assistance during the preparation of this book.

Canberra
Melbourne
1965.

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CONTENTS

RHYTHMIC THALAMIC ACTIVITY

by PER ANDERSEN

The ability to produce rhythmic activity is a fundamental property of the nervous system, especially of the higher levels of the central nervous system. Best known is the rhythmic activity of about 10/sec that can be recorded from the thalamus and the cortex. The rhythmic activity in the thalamus appears in two separate, but related, forms, both having a frequency around 10/sec. First, there is the rhythmic discharge in response to a synchronous afferent volley. This activity will be called the rhythmic burst discharges. Second, there is the spontaneously occuring rhythmic activity that appears in short periods. This activity will be called the thalamic spindle activity.

I. The evoked rhythmic burst discharges

In his pioneering study, ADRIAN (1941) reported that a single afferent volley in a cutaneous sensory nerve produced a series of rhythmical waves in the sensory cortex and that a related activity was found simultaneously in the white matter, signalling the discharges of thalamic neurones. BREMER found essentially the same types of responses in the auditory cortex and in the medial geniculate nucleus, respectively (BREMER 1937; BREMER and BONNET 1950). With newer neurophysiological techniques, it has been possible to throw further light upon the mechanism underlying the rhythmic thalamic activity, and to locate the neural substrate necessary for its production (ANDERSEN, BROOKS and ECCLES 1963; ANDERSEN, BROOKS, ECCLES and SEARS 1964; ANDERSEN and SEARS 1964).

Most of the information has been gathered from the posterolateral part of the ventral nucleus (VPL) which relays somaesthetic impulses to the sensory cortex. The possibility of orthodromic as well as antidromic activation of the VPL cells provides a necessary measure of control over the experimental situation.

A single shock to a foreleg cutaneous nerve elicits in the VPL a response (Fig. 1 A, B, D, E, F), consisting of a series of discharges of about 10/sec, confirming the earlier reports (ADRIAN 1941; BREMER 1953). The activity consists of a group of cell discharges followed by a large positive wave (the P-wave), subsequently a new group of discharges followed by another P-wave, and so

on, repeating itself from 4—20 times (Fig. 1 A, B, D). The P-waves last from 80—150 msec, being longer the deeper the anaesthesia (ANDERSEN et al. 1963; ANDERSEN et al. 1964). Concomitant with the burst discharges in the thalamus, an evoked slow wave appears in the postcruciate corticogram (Fig. 1 A, lower line). When the cortex was removed, and recording was made from the killed ends of the thalamocortical fibres in the white matter, a sharp positive wave

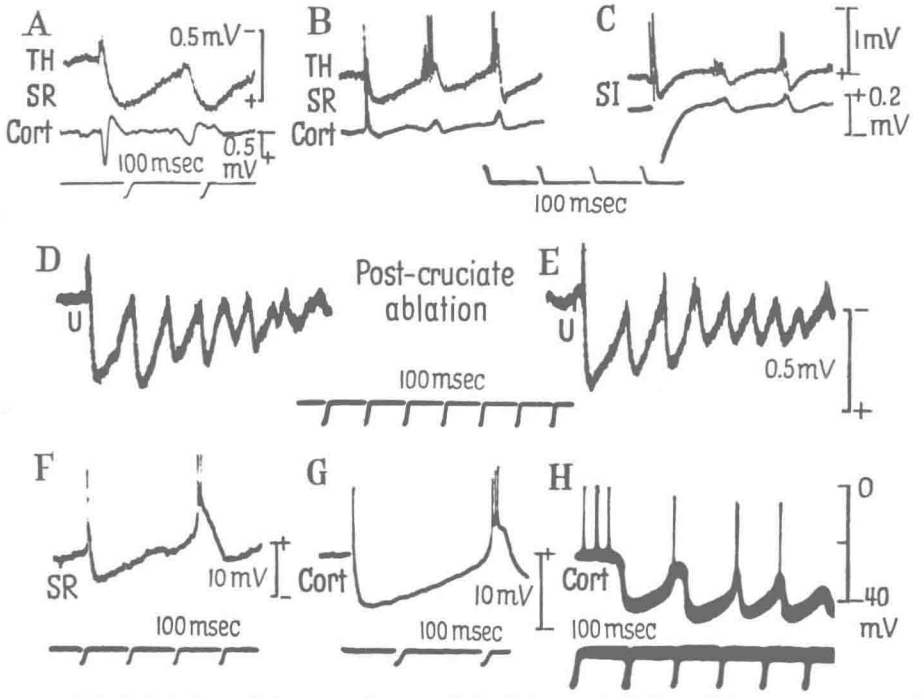

Fig. 1. Evoked rhythmic burst discharges in the VPL of the thalamus. *A—E.* Extracellular records. *A.* Records obtained from the VPL nucleus (TH) and pericruciate cortex (CORT) in response to a single shock to the superficial radial nerve (SR). Negativity upwards. *B.* As *A*, but lower line is recording from white matter, and has positivity upwards. *C.* Similar to *B*, but following stimulation of white matter underlying area SI. *D.* Rhythmic VPL response to a single ulnar (U) volley before, and after (E) removal of all pericruciate cortex. *F—H.* Intracellular records. *F.* Response of a VPL cell to a SR volley. *G.* Response of VPL cell to antidromic activation in a chronically decorticate preparation. *H.* Similar to *G*, but another preparation and slower sweep speed. Voltage and time calibrations as indicated

was obtained simultaneously with the thalamic burst discharges, signalling the rhythmic volleys along these fibres. Simultaneous recording from the dorsal column nuclei showed no repetitive activity of this kind. In conclusion, a single afferent volley entering the VPL is transformed to a rhythmic train of thalamocortical volleys at a frequency of about 10/sec.

Verifying the observations of ADRIAN (1941, 1951) and BREMER (1953), extensive ablation of the cortex does not change the rhythmic thalamic activity (Fig. 1 C, E) (ANDERSEN et al. 1963). Therefore, in the absence of any rhythmical input to the thalamus, the mechanism for the rhythmic activity probably resides within the thalamus itself.

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Intracellular records show that the initial discharge is due to an excitatory postsynaptic potential (EPSP) generated by the afferent volley. Subsequently, there appears a large and long-lasting hyperpolarization (Fig. 1 F), fulfilling all criteria for an inhibitory postsynaptic potential (IPSP) (ECCLES 1963). Following the IPSP, a depolarizing wave is often present, giving rise to a series of discharges of the cell (Fig. 1 F). Subsequently, a new IPSP develops — and the cycle repeats itself several times before the activity vanishes.

A possible explanation of the depolarization with a burst of spikes occurring after an IPSP is the phenomenon of post-anodal exaltation (PAE) (ECCLES 1963; ANDERSEN and ECCLES 1963; ANDERSEN et al. 1964). An additional possibility is a synaptic influence derived from excitatory interneurones.

As seen in Fig. 1 C, G and H, thalamic rhythmic activity, similar to that evoked by an orthodromic volley, can be produced by an antidromic volley (ANDERSEN et al. 1964). Since typical responses also can be obtained in chronically decorticate animals (ANDERSEN et al. 1964), the effect is evoked by an antidromic volley along the axons of the VPL neurones, and the inhibition is, therefore, due to a pathway employing recurrent collaterals of these axons.

There was invariably a latency difference of about 1.5 msec between the antidromic invasion of a VPL neurone and the onset of the IPSP (ANDERSEN et al. 1964). Thus, it is supposed that one inhibitory interneurone is intercalated in the recurrent inhibitory pathway (ANDERSEN and ECCLES 1963), its extensive axonal ramifications explaining the observed greater distribution of IPSPs than EPSPs in orthodromically activated cells.

Similar EPSP-IPSP sequences are seen in the anterior thalamic nucleus in response to midline thalamic stimulation at 7/sec (PURPURA and COHEN 1962; PURPURA and SHOFER 1963).

Mechanism of the rhythmic burst discharges

It is postulated that an orthodromic volley brings a restricted number of neurones to discharge. Through their axon collaterals, a set of inhibitory interneurones is activated, producing IPSPs in many neurones. In these cells, the IPSPs are followed by a post-anodal exaltation (PAE) that brings a proportion of the cells to discharge. The firing of these neurones will subsequently be followed by new IPSPs leading to a PAE with discharges, and so on. The activity will fade away because of slight asynchrony in the discharge of the different cells due to a varying duration of the IPSPs.

Histological evidence of interneurones in the thalamus is given by the survival of a large number of thalamic cells, mostly small, following decortication with subsequent retrograde degeneration of cells sending their axons to the cortex (SHEPS 1945; MCLARDY 1950; CLARK and POWELL 1953). Small neurones within VPL with extensive axon arborizations were described by CAJAL (1911).

II. Spontaneous rhythmic thalamic activity

In a lightly anaesthetized animal there appears periods of rhythmic activity whose basic components are the same as for the evoked rhythmic burst discharges (ANDERSEN and SEARS 1964). The spontaneous activity appears as a series of burst discharges each separated from the next by a P-wave (Fig. 2 A). Because of its shape, and its simultaneity with the barbiturate cortical spindles, each period of spontaneous rhythmic activity is called a thalamic spindle (ANDERSEN

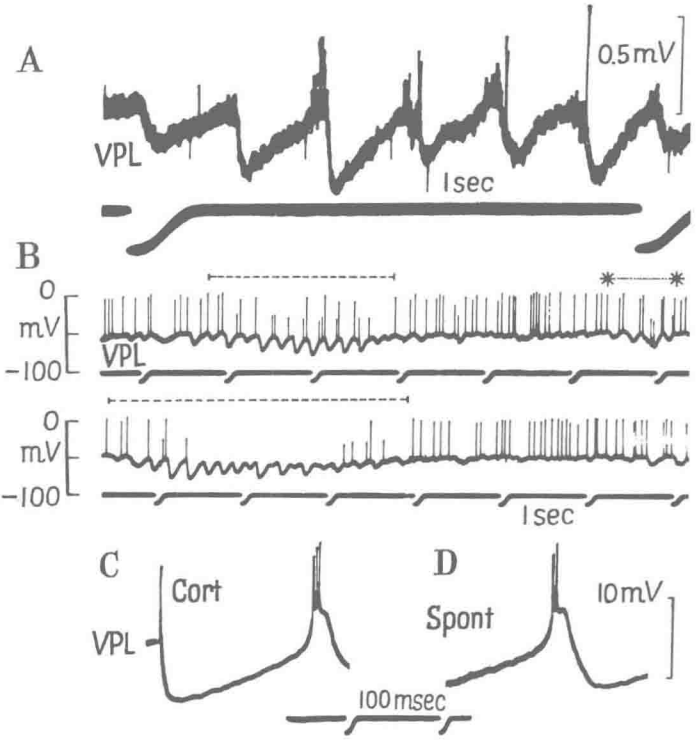

Fig. 2. Spontaneous rhythmical discharges in VPL. *A*. Extracellular record of the first half of a thalamic spindle. Negativity upwards. *B*. Intracellular DC-recording of a VPL cell, continuous recording. Two periods of spindle activity are marked with dotted lines above the record. An abortive spindle is marked with asterisks. *C*. Response of a VPL neurone to antidromic activation. *D*. Excerpt of a spontaneous spindle from the same cell as in *C*, showing the similar sequence of an IPSP followed by the post-anodal depolarization with spike discharges

and SEARS 1964). The P-waves of these spindles are most likely identical to the spontaneous series of slow waves recorded from the thalamus by MORISON, FINLEY and LOTHROP (1943).

Intracellular recording from neurones in various thalamic nuclei showed the spindle activity as a series of augmenting and summating IPSPs (Fig. 2 B). Since the cell only fired on the crest between two successive IPSPs, the interspindle irregular pattern of firing was changed to rhythmic discharges. Comparison between an IPSP-PAE sequence evoked by an antidromic volley (Fig. 2 C) and

an excerpt from a spindle (Fig. 2 D) shows that the same sequence was found in the two types of rhythmic activity. On the basis of these observations, an inhibitory phasing theory was advanced (ANDERSEN and SEARS 1964). It explains the mechanism of the thalamic spindle activity as due to the operation of a system of neurones, each having the possibility of influencing its neighbours through a recurrent inhibitory pathway. According to this theory, a spindle starts with the discharge of one or a few neurones. Through their axon collaterals, these cells activate some inhibitory interneurones that, in turn, produce IPSPs in a greater number of neighbouring neurones. The PAE that subsequently develops in these cells brings a certain proportion of them to discharge, which through their recurrent inhibitory pathway produces IPSPs in an even larger number of neurones. In this manner the rhythmic activity spreads until a majority of cells beat in unison. The duration of the IPSPs will act as the *timing device* for this rhythm. Through its elicitation of the PAE, the IPSP also acts as the *triggering device* for the neuronal discharges.

III. Simulation of the rhythmic activity in a model

A test of the whole assembly of thalamic neurones with their rhythmic interactions is made impossible by the requirement of simultaneous recording from a large number of relatively closely spaced cells. Therefore, a tentative test has been made by the simulation of a neuronal network in which the individual cells have been given characteristics according to the theory described above (ANDERSEN and RUDJORD 1964). Eighty cells were defined on an electronic computer, IBM 1620. The initial part of the thick line in Fig. 3 A indicates that the cells in the network discharged randomly, at a mean probability of firing (PF) of 20 per cent. Since the scanning time was equivalent to 10 msec in an animal preparation, this frequency corresponds to 20/sec. Following the discharge of any neurone, up to 10 other cells (Fig. 3 B) underwent a change in the PF indicated by the thick line: an immediate drop to zero (simulating an IPSP) for 10 units of time (equalling 100 msec) followed by a period of increased PF (simulating the post-anodal exaltation) before the cell again resumed its random firing at 20 per cent probability. The number of discharging cells in each unit of time was printed out and subsequently plotted (Fig. 3 C). Since for technical reasons the starting of the computer initiated the discharge of about half of the neurones (falling just to the left of the Y-axis) the first part of the diagram is comparable to an afferent volley exciting a certain proportion of thalamic cells. Each peak in the diagram indicates the near simultaneous firing of many neurones. Thus, the model behaves similarly to the evoked burst discharges.

Leaving the simulated neuronal network to operate by itself, there appeared short periods of rhythmic activity (arrows) composed of peaks in the diagram,

as in the initial part or the graph. Although varying in length and frequency of occurrence, the periods are all characterized by a gradual onset and offset, thus resembling the thalamic spindles. By varying the parameters of this model, two factors were found to be important for the occurrence of periodic rhythmic activity. First, more pronounced rhythmic activity was observed the greater the difference was between the random PF and the post-inhibitory period of enhanced PF. Second, the larger the number of neurones being inhibited following the discharges of one cell, the more pronounced was the rhythmic activity.

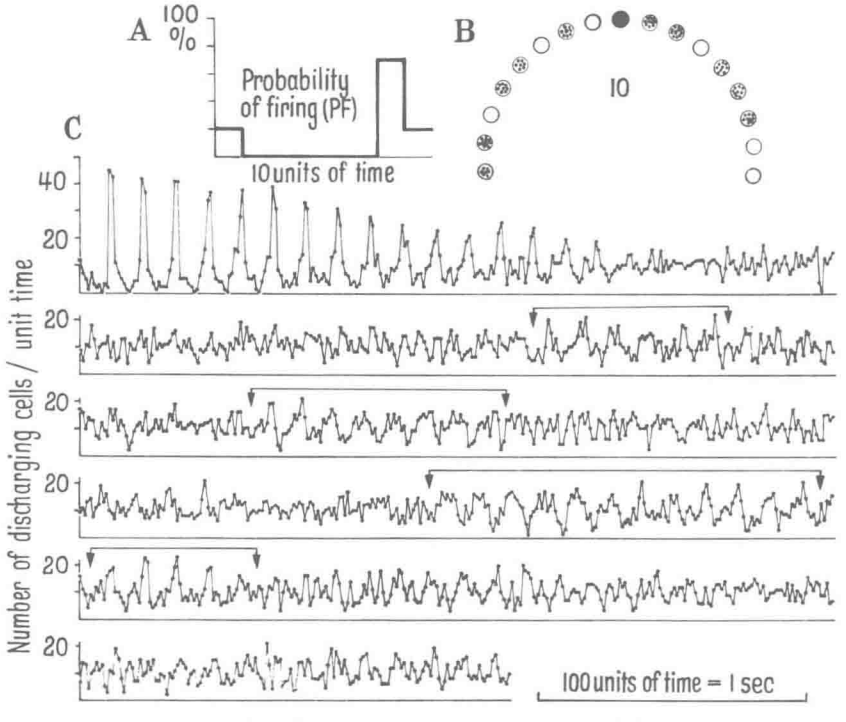

Fig. 3. Model simulation of a rhythmically active network. *A*. Change in probability of firing (PF) of a cell subsequent to the discharge of a neighbouring cell. Zero PF is maintained for 10 units of time, equalling 100 msec in animal experiments. *B*. The circles denote 17 of the 80 cells, the dotted circles marking the maximum number (10) of inhibited cells subsequent to the discharge of one neurone (black circle). *C*. Graph showing the total number of cells discharging within each unit of time. The initial period of rhythmic activity simulates the evoked burst discharges, whereas the periods marked with arrows are similar to the thalamic spindles

In conclusion, the computer model with a network having relatively simple characteristics gives rhythmical discharges, both evoked and "spontaneous". Furthermore, it has underlined the role that the post-inhibitory excitation and the distribution of the inhibition play in such a network. Although the simulation uses a highly simplified network, the results still suggest that future animal experiments on thalamic rhythms should be focussed upon the mechanism underlying the post-anodal exaltation and the connections and properties of the inhibitory interneurones.

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DIFFERENCES IN THE DIAMETER AND CONDUCTION VELOCITY OF MOTOR AND FUSIMOTOR FIBRES IN NERVES TO DIFFERENT MUSCLES IN THE HIND LIMB OF THE CAT

by I. A. BOYD

Two distinct types of motor nerve fibre supplying the muscle spindles of the cat were described by BOYD (1962). It was concluded from indirect evidence that the parent fibres of both types were contained within the gamma efferent group in the muscle nerves. A simultaneous study of the composition of the de-afferented nerves from the same cats showed that there were two distinct types of gamma efferent fibre in most nerves (BOYD and DAVEY 1962), fibres with myelin sheaths about 1 μ in thickness, and fibres of approximately the same axon diameter but with myelin sheaths about 0.1 μ in thickness. Compound action potentials were recorded from a number of normal nerves and in some it proved

possible to differentiate two groups of gamma efferent fibres in terms of conduction velocity and of threshold to stimulation (Boyd and Eccles 1962).

In further experiments compound motor action potentials were recorded from the de-afferented nerves to fourteen different muscles in two cats anaesthetised with pentobarbitone sodium, in response to stimulation of the ventral spinal roots. The nerve electrodes were placed proximal to the bifurcation of individual motor fibres. The nerves and spinal roots were immersed in paraffin pools at 37° C. To obtain monophasic recording each nerve was severed from its muscle and crushed between the electrodes, and 0.1 % procaine hydrochloride was applied over the distal electrode if necessary. Values of conduction velocity obtained orthodromically and antidromically were similar.

The nerves were fixed *in situ* by perfusing 12 % formalin through the abdominal aorta and the lumbar plexus and muscle nerves were removed intact. Each nerve was dissected back about 2 cm into its parent trunk and a portion which had not previously been in paraffin or handled in any way was stained with osmium tetroxide. Transverse sections of each nerve were prepared and fibre-size histograms constructed for all the myelinated motor fibres. All very small fibres were traced through serial transverse sections.

The histological results are summarised in Fig. 1. There was a range of 1 to 3 μ between the alpha and gamma groups containing no fibres in all the nerves to the tibialis posterior and flexor digitorum brevis muscles and also in some of the nerves to other muscles. The histogram of the alpha fibres in one extensor digitorum longus nerve had two peaks. The range and mean diameter of the alpha fibres in a particular nerve in different cats were fairly consistent. There was clearly a difference, however, in both the maximum and the mean diameter of the alpha fibres in different nerves in the lower leg measured at about the same level. The mean diameter in the soleus nerve was 75 % of that in the gastrocnemius nerve, comparable with the figure of 78 % given by Eccles and Sherrington (1930). The nerves to the small muscles of the foot contained small alpha fibres, probably because of their greater distance from the spinal cord.

The groups of thickly and thinly myelinated gamma fibres overlapped considerably in most nerves. Two distinct gamma peaks were present, however, in the histograms of nerves containing a large number of thinly myelinated gamma fibres, and in which the mean diameters of the two gamma groups were well separated, e. g. popliteus, tibialis posterior, flexor and extensor digitorum brevis.

The maximum and mean total diameters of the thickly myelinated gamma fibres differed from nerve to nerve in a manner similar to the alpha fibres. The nerves to the peroneal group of muscles, and to the small muscles of the foot, however, had thickly myelinated gamma fibres which were large relative to their alpha fibres. The mean diameter of the thinly myelinated gamma fibres varied from nerve to nerve, also. It was difficult, however, to obtain reliable mean values in nerves such as those to the plantaris, flexor digitorum longus and the

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