

Ragnar Grant

# Mechanisms Regulating the Discharge of Motoneurons

## The Sherrington Lectures

In 1948, on the occasion of the ninetieth birthday of Sir Charles Scott Sherrington, O.M., G.B.E., M.D., F.R.S., the Council of the University resolved to institute a Lectureship in recognition of his distinguished contributions to Physiology and Medicine and of his association with the University of Liverpool as George Holt Professor of Physiology from 1895 to 1913.

The appointment to the Sherrington Lectureship is made biennially by the Council of the University on the joint recommendation of the Faculties of Medicine and Science.

The following lectures have been delivered and are published by Liverpool University Press:

- I *Sensory Integration*, by E. D. Adrian, O.M., M.D., F.R.C.P., F.R.S., Professor of Physiology in the University of Cambridge.
- II *The Frontal Lobes and Human Behaviour*, by John F. Fulton, O.B.E., M.D., D.Sc., LL.D., Sterling Professor of the History of Medicine, Yale University.
- III *The Invasive Adenomas of the Anterior Pituitary*, by Sir Geoffrey Jefferson, M.S.(LOND.), F.R.C.S., F.R.S., Emeritus Professor of Neurosurgery, University of Manchester.
- IV *Sherrington: Physiologist, Philosopher and Poet*, by the Right Honourable Lord Cohen of Birkenhead, M.D., D.Sc., LL.D., F.R.C.P., F.A.C.P., F.F.R., F.S.A., J.P., Professor of Medicine in the University of Liverpool.
- V *The Excitable Cortex in Conscious Man*, by Wilder Penfield, O.M., C.M.G., LITT.B., M.D., D.Sc., F.R.C.S., HON.F.R.C.P., F.R.S., Director, Montreal Neurological Institute, McGill University, Montreal, Canada.
- VI *Visual Pigments in Man*, by W. A. H. Rushton, SC.D., F.R.S., Reader in Physiology in the University of Cambridge.
- VII *The Conduction of the Nervous Impulse*, by A. L. Hodgkin, SC.D., F.R.S., Foulerton Research Professor of the Royal Society, University of Cambridge.
- VIII *The Cerebral Control of Movement*, by Derek Denny-Brown, O.B.E., M.D., D.PHIL., LL.D.(HON.), James Jackson Putnam Professor of Neurology, Harvard University.
- IX *The Inhibitory Pathways of the Central Nervous System*, by John C. Eccles, F.R.S., M.B., B.S., N.A., D.PHIL., F.R.A.C.P., F.R.F.N.Z., F.A.A., Faculty of Health Services, State University of New York at Buffalo.
- X *The Release of Neural Transmitter Substances*, by Bernard Katz, M.D., D.Sc., F.R.S., Professor of Biophysics, University College London.
- XI *Mechanisms Regulating the Discharge of Motoneurons*, by Ragnar Granit, PHIL.MAG., M.D., D.Sc., FOR.MEM.R.S., Professor Emeritus of Neurophysiology, The Royal Caroline Institute, Stockholm, Sweden.

The Sherrington Lectures XI

# Mechanisms Regulating the Discharge of Motoneurons

---

Ragnar Granit

Phil.Mag., M.D., D.Sc., For.Mem.R.S.

Professor Emeritus of Neurophysiology

The Royal Caroline Institute

Stockholm, Sweden

LIVERPOOL UNIVERSITY PRESS 1972

*Published by*

**LIVERPOOL UNIVERSITY PRESS**

*123 Grove Street, Liverpool L7 7AF*

*Copyright © Ragnar Granit 1972*

*All rights reserved. No part of this book  
may be reproduced in any form  
without permission in writing from  
the publishers, except by a reviewer who  
wishes to quote brief passages in connection  
with a review written for inclusion in  
a magazine or newspaper*

*ISBN 0 85323 340 3*

*First published 1972*

*Printed in England by Hazell Watson & Viney Ltd., Aylesbury, Bucks*

# Preface

My grateful thanks are offered to the Medical and Science Faculties of the University of Liverpool for the honour conferred by their appointment of me as Sherrington Lecturer. Their kind invitation arrived when I was in the midst of writing a book on *The Basis of Motor Control*, now published by the Academic Press.

The Sherrington Lectures have given me a much-appreciated opportunity of expanding Chapter VI of that book and presenting it in a manner suitable for the medical curriculum.

The emphasis is on the biological adaptations by which the motoneuron has responded to the challenge of serving as main executive for all commands leading to motor action, phasic or tonic, as the case may be.

The care devoted by the staff of Liverpool University Press to the editing and publication of these Lectures is gratefully acknowledged.

For permission to reproduce text-figures from a number of publications I wish to express my gratitude to the American Association for the Advancement of Science, Washington, D.C.; the American Physiological Society; the Australian and New Zealand Association for the Advancement of Science; *Journal of Anatomy*; *Journal of Neurology*, *Neurosurgery*, and *Psychiatry*; *Journal of Physiology*; *Nature*.

RAGNAR GRANIT

# Contents

I Basic concepts: Tonic and phasic motoneurons	1
Introduction	1
Synaptic action	3
Tonic and phasic motoneurons	8
'Gain' and after-hyperpolarization in small and large motoneurons	13
Motoneurons matching motor units	18
Slow and fast firing rates	24
II Artificial and natural firing of motoneurons	27
Antidromic and trans-membrane stimulation compared	27
The primary and secondary range of firing	29
The functional role of the secondary range	33
Algebraical addition within the primary range	35
Synaptic stimuli superposed within the secondary range	42
III Recurrent collaterals of motoneurons	47
Anatomy	47
The Renshaw cells	47
Distribution of recurrent inhibition	51
Interpretation of distributive factors	53
Quantitative aspects of recurrent inhibition	54
Recurrent inhibition at work. Surplus excitation	57
Recurrent excitation	61
Concluding remarks	61
 Bibliography	 63
 Author index	 73
 Subject index	 77

# Figures

1	Graph of dendritic pattern in motoneuron	2
2	Miniature monosynaptic postsynaptic potentials	4
3	Activation noise caused by stretching a muscle	5
4	Size of monosynaptic EPSPs related to membrane potential as influenced by stretch	7
5	Stretch reflex spikes in axons of phasic and tonic cells	9
6	Tonic motoneurons activated by crossed reflex	11
7	Diagram of neural organization supporting tonic firing	11
8	Records illustrating trans-membrane stimulation of rat motoneuron	14
9	Spike frequencies from Figure 8 plotted against current strength	14
10	Input resistance of cell membrane related to firing threshold and gain	16
11	Duration of after-hyperpolarization as a function of axonal conduction time	17
12	Threshold for repetitive firing to trans-membrane stimulation related to inverse value of duration of after-hyperpolarization	18
13	Histochemical identification of muscle fibres belonging to individual motor units	20
14	Distribution of twitch time-to-peak values in gastrocnemius motor units	21
15	Graphic reconstruction of the fastest and slowest types of twitches in gastrocnemius motor units	22
16	Relation between the maximum amplitudes of gastrocnemius monosynaptic EPSPs and cell input resistance	23
17	Axonal conduction velocity related to cell input resistance in the cells of Figure 16	23
18	Antidromic and trans-membrane stimulation of motoneuron compared	27
19	Intracellular records of firing in response to muscle stretch	28
20	Trans-membrane stimulation. Firing rate plotted as a function of current strength in cat motoneuron	29
21	As Figure 20, but to illustrate exceptionally wide primary range	30
22	Graph illustrating adaptation of the discharge rate to maintained trans-membrane stimulation	31
23	Records to illustrate moment of 'inactivation' to trans-membrane stimulation, graphically analysed	32
24	Plot of isometric tension produced by gastrocnemius motor unit against discharge frequency of its motoneuron	34



## FIGURES

25	Records illustrating reflex synaptic effect superposed on discharge set up by trans-membrane stimulation	35
26	Plot of constant increase or decrease in impulse frequency against the amount of postsynaptic potential required for it	37
27	Trans-membrane stimulation within primary range. Firing rates with excitatory or inhibitory reflex superposed plotted against response to current by itself	38
28	Illustrating for twenty-eight motoneurons additivity of discharge rates within primary range	39
29	Trans-membrane stimulation. Superposed inhibition	40
30	Illustrating for seventeen motoneurons algebraical additivity of reflex inhibitions within primary range	41
31	Trans-membrane stimulation carried into secondary range. Reflex facilitation superposed	42
32	As Figure 31, but illustrating that synaptic excitation more prone than injected current to induce firing within secondary range	43
33	Synaptic inhibition counteracting firing in secondary range	44
34	Diagram illustrating distribution of primary afferent depolarization from muscular afferents	45
35	Staining of Renshaw cells by passing current from tip of microelectrode	48
36	Diagram of recurrent circuit and records illustrating recurrent inhibition and firing Renshaw cells	49
37	Excitation of Renshaw cell by cerebellar stimulation	50
38	Diagram illustrating Renshaw cell with accessory circuits and interneurons	51
39	Effect of antidromic stimulus rate on amount of recurrent inhibition	55
40	Algebraical summation of recurrent inhibition	56
41	Effect of locking stretch reflex spike from root filament to antidromic shock from rest of the root	58
42	Brief antidromic tetanus inserted at constant intervals into tonic spike discharge maintained by stretch	60