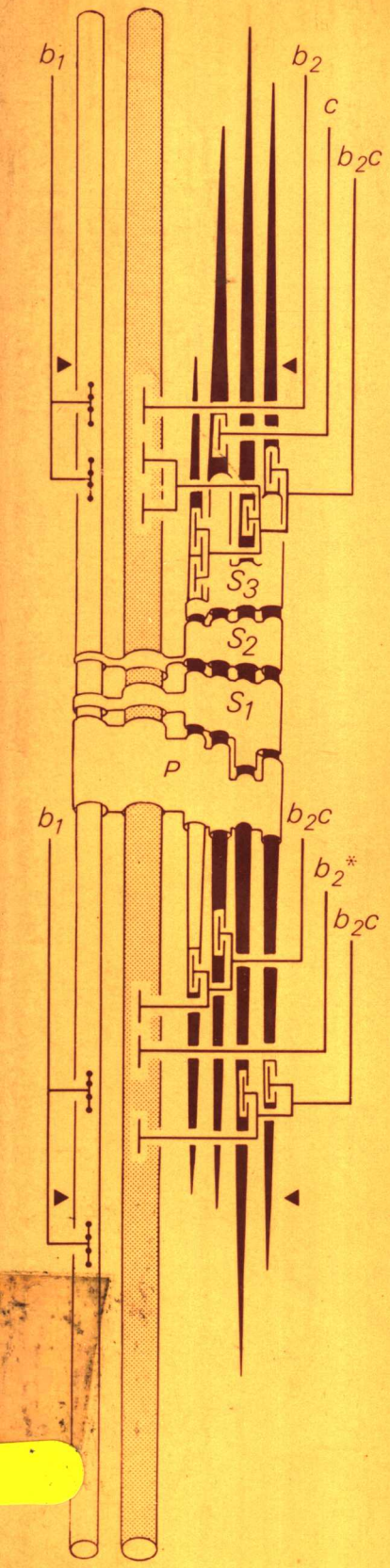

Muscle Receptors and Movement

EDITED BY

A. Taylor and A. Prochazka

MUSCLE RECEPTORS AND MOVEMENT

Proceedings of a Symposium held at the Sherrington School of Physiology, St Thomas's Hospital Medical School, London, on July 8th and 9th, 1980

Edited by

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and
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Foreword

For many decades of scientific endeavour the physiology of sensory receptors has been a major field of enquiry and one in which complexity of receptor structure is matched by a corresponding diversity in the experimental approaches used in its investigation. At one time it might have been thought that such complexity was the reserve of the special senses. However, that could hardly be accepted now, in the face of the continuous and increasing challenge to experimental skill, which questions concerning the structure and properties of muscle receptors and the role of these receptors in the control of muscular contraction pose for the investigator.

Accurately positioned within the three-dimensional space of the body image, the precise voluntary movements of the extremities occur on a postural stage, itself continuously and largely 'automatically' set through appropriately fine adjustment of the activities of the proximal and axial musculature. It is usually taken as axiomatic that the smooth precision of such movements is learnt and executed through mechanisms of muscular control which are highly dependent on the information supplied by the muscle receptors; only within the last decade however, has direct evidence become available as to the nature of the information transferred during voluntary movement, albeit, thus far, for a limited number of muscles and movements of the extremities. In 1965, on the occasion of the first symposium supported by the Nobel Foundation, which happened also to be on the topic of 'muscle afferents and motor control', the inaugural address was given by Adrian who thought that the subject was '. . . ripe for discussion . . . but still with some details to be filled in of the main outlines of the peripheral and spinal apparatus for controlling movement'. Although many symposia on the subject of motor control have been held since then, few have dealt so specifically with muscle receptors and their role in such control. Why then, it may be asked, is the time once again ripe for assembling a symposium of experts to discuss this subject; which key issues need to be debated and what extra details are still missing from the overall picture?

Each of us, according to age, training and experience, carries a very personal perspective of a given scientific topic, and with it, a highly individual view of what currently is important or at least interesting. With this in mind

and by way of introduction, I outline my own perspective as I contemplated attending the symposium whose subject matter comprises this book. This converges to that First Nobel Symposium, a memorable and exciting occasion which I was fortunate enough to attend. A year beforehand, I had begun my research on the human intercostal muscle stretch reflexes. The experiments took into account the coactivation of alpha and gamma intercostal motoneurons which occurs in response to the natural, spontaneous and centrally initiated command for respiratory movements as had been recently discovered independently by von Euler and myself. With these human experiments, done in collaboration with J. Newsom Davis and one of the organisers of this symposium—A. Taylor—we were already confronted with the fundamental problem of distinguishing between reflex and voluntary behaviour in the conscious human subject. Not surprisingly, therefore, the topic which perhaps interested me most was Oscarsson's account of his work with Rosen (1963), which had convincingly demonstrated the projection of Group I muscle afferents to the cerebral cortex, a projection whose existence had previously been denied save for a preliminary, brief report of one by Amassian and Berlin (1959), that had been overlooked by many investigators. The belief that such a projection did not exist, reinforced the idea, based on behavioural and psychophysical experiments, that the information signalled by Group I muscle afferents (muscle spindles and Golgi tendon organs) does not project into consciousness. This idea occupied a central place in Merton's servo theory of muscular control for which he proposed that the spinal servo loop, subserved by the stretch reflex, has an insentient mode of operation, both when driven through fusimotor activity as conceived for the 'length follow-up' servo-mechanism, or, when simply responding to muscle stretch.

The absence of behavioural responses to stimulation of Group I afferents in animal experiments (by other authors) had led Oscarsson to conclude 'that the Group I projection represents a cortical mechanism as unrelated to conscious perception as the motor regulating mechanisms in the cerebellum.' Since the cerebral cortex, like the cerebellum, is concerned with the execution and co-ordination of movement, and was now also similar with regard to the afferent information it received from muscular and cutaneous afferents through the fastest paths available, Oscarsson suggested that 'these supraspinal pathways to the sensorimotor cortex constitute feedback channels used in the integration of motor activity'. Interestingly, Hammond had previously suggested that the long latency of the stretch reflex of the human biceps muscle might be due to a cerebellar loop. Thus by 1965 the anatomical and physiological basis for such a loop through the cerebral cortex was known to exist and knowledge of this pervaded our own thoughts as, like Hammond had done, we wrestled with the problem of the long latency of the intercostal muscle stretch reflex.

A few years later, Phillips (1969) in The Ferrier Lecture, linked the results from studying the strength and distribution of the monosynaptic connections

of Group Ia muscle afferents to motoneurons of the primate hand to those revealing their projections to the cerebral cortex, to form his idea of a 'transcortical loop' in the conscious human subject, with a loop time for the stretch reflex shorter than the earliest voluntary response to a brief mechanical stimulation of a moving limb, i.e. shorter than a kinaesthetic reaction time. It will be seen that this proposal retains the idea of the insentient automatic compensation for unexpected variations in mechanical load inherent in the servo theory, but now the 'error' signal in the jargon of servo-mechanisms ultimately exerts its effects on the cells of origin of the cortico-motoneuronal tract. In effect, Sherrington's stretch reflex had been 'encephalised'. I emphasise this here because many authors use the term 'stretch reflex' with scant regard for its true meaning as originally embodied in Merton's theory, translated to Phillips's hypothesis, and having firm epistemological roots in Sherrington's stretch reflex, which is the sustained contraction of muscle (or motoneuron firing) in response to muscle stretch and dependent on the excitation of muscle receptors. During the last decade these key papers, particularly that of Phillips, have stimulated a great deal of human-based research on the 'long loop' reflexes. Furthermore, this effort has been paralleled by combined behavioural and electrophysiological studies aimed at deciphering the kind of information received by the primate cerebral cortex from muscle receptors during the course of normal and impeded 'voluntary' movements of the primate limb.

Equally importantly, the last decade has seen the full exploitation of microelectroneuronography, first introduced by Hagbarth and Vallbo in 1968. This allows direct recording from human muscle afferents during voluntary movement and so has allowed important inferences also to be drawn about alpha–gamma coactivation. Paralleling this remarkable achievement the convenors of our symposium—A. Taylor and A. Prochazka—have independently pioneered the recording of receptor nerve discharge for jaw and limb movements, respectively, in the awake animal.

Through the work of Smith, The First Nobel Symposium also saw the beginning of the exploration of living muscle spindle structure and function through direct visualisation, a method which Boyd and his collaborators have subsequently developed to a high degree of refinement.

These are only some of the topics critically discussed in this symposium. I have singled them out only for the purpose of illustrating the perspective we need to have on the continuously evolving nature of the concepts which we manipulate and the difficulties which thus arise in deciding, as Matthews asked in discussion, 'How much is new?', 'How much is true?' and 'How much is general?' While one might expect disagreement over the answers to such questions, which I encourage others to provide by reading this book, I am sure we can all agree how appropriate it is that this symposium on muscle receptors and movement should be held at the school where almost a century ago Sherrington not only received his medical training, but also as a lecturer

embarked on a scientific career that was to lay the foundations of the subject debated in the following pages.

August, 1980

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Preface and Acknowledgements

This book contains the Proceedings of the Symposium entitled *Changing Views of the Function of Muscle Receptors in Movement Control* held at the Sherrington School of Physiology, St Thomas's Hospital Medical School, London, UK on July 8th and 9th, 1980. The symposium was attended by 105 leading international scientists engaged in research into the control of movement in mammals.

An innovative feature of the symposium was the inclusion of short, formal critiques of presentations by recognised experts in the topics concerned. Each 'critic' had been sent copies of the relevant presentations two to three weeks prior to the meeting. Critiques varied from the very mild to the downright scurrilous, but were taken in good part by all concerned. Judging by the favourable (indeed almost gleeful) audience reaction, this formula might well reappear in symposia in the future.

We should like to make mention of the efforts of our publishers—Dr S. Sharrock and Mr R. M. Powell of Macmillan Publishers Ltd—in ensuring the availability of this book within nine months of the meeting. Finally, we wish to thank all of the contributors to the book for their enthusiasm and their willingness to act as subjects in this peer-review experiment.

The illustration on the front of the dust jacket is taken from the paper by R. W. Banks, D. Barker and M. J. Stacey, and we thank Professor Barker and his co-authors for permission to use it.

September, 1980

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