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BRAIN RESEARCH

Peripheral and Spinal Mechanisms in the Neural Control of Movement

EDITED BY
M.D. BINDER

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Preface

This volume of *Progress in Brain Research* is dedicated to Professor Douglas G. Stuart, whose exemplary career has had a profound influence on both motor control neurobiology and on the scientific lives of his many students and colleagues throughout the world. The chapters in this volume are largely derived from presentations made at a Society for Neuroscience Satellite Symposium held in Doug's honor from November 4–6, 1998 at the University of Arizona in Tucson. The meeting was attended by more than 200 scientists, representing 18 different countries.

Douglas Gordon Stuart was born in Casino, New South Wales, Australia on October 5, 1931. He was educated at Sydney Teachers' College, Michigan State University, and UCLA, where he earned a Ph.D in physiology and neuroscience in 1961. His professional career includes appointments at the Long Beach Veterans' Administration Hospital (1961–65), UCLA (1961–65), UC Davis (1965–67), the University of Arizona (1967–), where he presently holds a Regents' Professorship.

Doug has made important contributions to several different areas in motor control research and has published more than 100 experimental papers in peer-reviewed journals. His papers are distinguished by their rigor and exceptional scholarship. Doug was among the first physiologists to question the notion that sensory input from muscle spindles alone controls the frequency of rhythmic movements. Using shivering and other forms of tremor in cats and humans, he and his colleagues showed that these rhythmic movements are dependent on interactions between rhythm-generating CNS mechanisms and the visco-elastic properties of the limb, in addition to sensory feedback.

Later, Doug and his colleagues made quantitative comparisons of the responsiveness of muscle spindles and Golgi tendon organs to sinusoidal muscle stretches and were the first to describe the contractile effects of fast- and slow-twitch motor units on the firing patterns of the tendon organs. They subsequently analyzed the relationship between the forces generated by single motor units and muscle receptor discharge patterns. Doug and his colleagues also used spike-triggered averaging to uncover the excitatory, mono-synaptic connections between muscle spindle group II afferents and their homonymous and synergist motoneurons. This surprising finding led to an extensive re-evaluation of the roles of muscle spindles and other proprioceptors in the reflex control of muscle activity.

Among Doug's most important and lasting contributions to motor control was the cinematographic analysis of cat hindlimb joint angles and muscle lengths during locomotion that he and his colleagues made in the early 1970s. This work was motivated by his interest in simulating natural-movement conditions for his studies of muscle receptor and motor unit mechanical properties. However, in addition to providing the data he needed, Doug also gave the field its definitive analysis of the step cycle, which

turned out to be crucial for testing a number of key hypotheses on reflexes, pattern generation, and muscle receptor function.

Another of Doug's long-standing interests is muscle fatigue. Again, he has made important contributions to this area by demonstrating that the association between the electromyogram and force during fatiguing contractions varies both in different muscles and with different types of muscle activation. He and his colleagues also revealed how subtle alterations in the pattern of motor unit activation can reduce and delay fatigue.

Most recently, Doug's laboratory has focused its attention on the electrical properties of motoneurons and interneurons in the turtle spinal cord. The goal of these studies is to describe how the intrinsic properties of identified neurons in the cord shape the input-output functions of spinal circuits. There is every reason to expect that this new avenue will again yield exciting new data and insights.

Despite the importance of Doug's original experimental work, his more than 70 book chapters, reviews and contributions to symposia volumes have had an even greater impact on the field. In these papers, he has provided critical reviews and elaborated new, synthetic hypotheses. Further, Doug has boldly directed challenges to his colleagues, even outlining the experimental projects they should undertake to resolve differences in their findings.

Outside of his laboratory, Doug's efforts as a champion for the field of motor control are legend. He has organized numerous national and international meetings and worked tirelessly to build interdisciplinary ties between biologists, clinicians, engineers, exercise physiologists and physical therapists. Moreover, he has been an exceptional mentor and role model, effectively 'raising' an entire generation of motor control scientists.

Marc D. Binder

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SECTION I

Perspectives

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CHAPTER 1

The segmental motor system – advances, issues, and possibilities

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DEDICATION

This article is dedicated to members of the post-WWII Moscow Motor Control School: the late Nicolai Bernstein, Israel Gelfand and Michael Tsetlin; Bernstein's student, Victor Gurfinkel; Ludmila Kudina and Raisa Person; Yuri Arshavsky, Michael Berkinblit, Tatiana Deliagina, Anatole Feldman, Olga Fookson, Sergei Kashin, Yakov Kots, Andrey Kulagin, Mark Lipshits, Micha Mirsky, Grigori Orlovsky, Yuri Panchin, Galina Pavolva, Konstantin Popov, Lyubov' Popova, Ivan Rodionov, the late Fyodor Severin, and Mark Shik; and, their many colleagues and trainees, including Yuri Levik and Mark Latash. Working under far-from-optimal circumstances, this group's accomplishments and emphasis on interactions between invertebrate and vertebrate neuroscientists, life- and physical scientists, and basic and clinical scientists, have been an inspiration to those of us who have attempted to emulate their interdisciplinary efforts in our own institutions' research and training programs in motor control neurobiology.

Introduction

The majority of topics addressed in this volume, and its preceding international conference (Binder et al., 1998), can be considered under the rubric of the segmental motor system. This term has proven to be useful in both invertebrate and vertebrate motor control neuroscience for summarizing work

on: (1) the properties and central actions of posture- and movement-related sensory feedback from the body's somatic structures; (2) interneuron (IN) and motoneuron (MN) discharge properties, MN recruitment properties, and the associations between MN, muscle fiber (MF), and motor unit (MU) properties for the graded development of muscle force; and (3) segmental pattern generation for the elaboration of intrinsic/rhythmic and learned/skillful movements. Each of these areas is being addressed currently from the molecular/

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cellular to the behavioral level of analysis in a wide variety of invertebrate and vertebrate species. Each has a particular attraction for life- and physical scientists, including roboticists, and each, in time, can provide a seamless integration between fundamental and applied clinical science. In all of the above instances, and irrespective of the level of analysis, the functional outcome is the elaboration of a posture and/or a movement. It is possible for all these reasons that the field of segmental motor research is so alive and well at the close of the 20th century. With this in mind, it is exciting to contemplate what the next generation of segmental motor neuroscientists might discover in the 21st century.

In what follows, I have attempted to capture the spirit of this field, as exemplified in this volume and its preceding symposium, by extolling recent advances, raising current issues, and pointing out future possibilities, at least for the immediate future. These topics are considered in a manner similar to the tripartite division above, even though their operation is highly integrated (chapter by Loeb [36], this volume). My strategy is useful in an historical sense, however, because, in any single decade or two, the areas of particular emphasis wax and wane as dependent on advances in techniques and technologies. For example, in this volume there is less emphasis on the first area, and more on the latter two, the reverse of the segmental motor field of the 1950s–1970s (Stuart and McDonagh, 1998). Some brief remarks are made about suprasegmental, descending command signals, because this area, which is currently profiting from new technical developments, was addressed, in part, in the 1998 conference, and in some of the chapters that follow in this volume.

I have shown how the chapters of the present volume, and some posters at its preceding conference, relate to the current state-of-the-play. What was presented and discussed in Tucson on November 4–6, 1998 also illustrates this timeliness. In my opinion, the present monograph is in the best traditions of the field of segmental motor neuroscience. It has continued to make optimal use of the contents of several post-1960s' international symposium volumes and journal compilations (from Barker [1962] to Stein et al. [1997], Binder and

Mendell [1990], Kiehn et al. [1998], Jabre and Binder [1999], and the present volume). This is particularly true for interdisciplinary training programs in motor control (see also chapter by P. Stein [23]).

Finally, I make no apologies for using this chapter as a bully pulpit for expounding on selected issues that are dear to me because they are relevant to the operation of an interdisciplinary training program in movement neuroscience. One primary goal of such programs should be to emphasize a broad perspective and interest in movement neuroscience, from the molecular/cellular to the behavioral level of analysis (Bunge, 1989). Another guiding principle, which is often underemphasized at international conferences, is to truly *mentor* trainees, network them with senior scientists, and extol their work. They are, after all, the next generation of segmental motor neuroscientists!

Properties and central actions of muscle and other limb receptors

Sensory receptors

Advances in the understanding of the properties of the muscle spindle, the Golgi tendon organ, and other mammalian muscle receptors (Stuart and McDonagh, 1997a) are best appreciated by first considering Matthew's (1972) timeless monograph, and then following subsequent advances by reference to Taylor and Prochazka (1981), Taylor et al. (1995), and Proske (1999). This progress has included work on both freely moving animals (Prochazka, 1996) and, for more limited movements, humans (Gandevia and Burke, 1992; Proske, 1999). In retrospect, it is remarkable how much post-WWII effort was directed to unraveling the structure-function relationships of the muscle spindle, but it must be remembered that this structure has an anatomical complexity that approaches that of the eye (Hasan and Stuart, 1984).

It is sobering to reflect that much is still to be learned about the functional significance of the muscle spindle's complex structure (Taylor et al., 1995) and their axons and other sensory receptors' axons (chapter by D. Burke and Gandevia [39]).

For example, what is the association between the consistent gamma innervation of the spindles of birds and mammals, and the beta innervation possessed by some but not all of these receptors? There is still no model that can accommodate the receptor's afferent discharge during a full array of muscle-length perturbations. Furthermore, no current model can predict the nature of fusimotor innervation on the basis of changes in muscle length and afferent discharge, particularly during natural movements (cf. however, Prochazka and Gorassini, 1998). For the latter, it is still not clear why both spindles (length detectors) and tendon organs (force detectors) are necessary. Perhaps the presence of both enables the CNS to distinguish between internal changes (e.g. as brought on by fatigue) and external impediments, like inertia (Hasan and Stuart, 1984). Further experimentation (chapters by Prochazka [11], Proske et al. [12], 1999) and discussion along these lines is both important and necessary as a prelude to further experimentation. Nonetheless, our current understanding of the transducing properties of muscle spindles and tendon organs is relatively more advanced than it is for the higher-threshold mechanoreceptors. These, too, play an important role in segmental motor control (e.g. Cleland and Rymer, 1990), particularly during bouts of exercise when muscle fatigue becomes a factor (Stuart and Callister, 1993; Garland and Kaufman, 1995; Windhorst, 1995). More work on relatively high-threshold mechanoreceptive and ergoreceptive muscle, joint and ligamentous receptors would be helpful at this stage. Such progress is apparent in the allied field of the properties of somatosensory receptors, including nociceptors, and their central involvement in autonomic functions (Sato et al., 1997), and in the perception of pain (Mense, 1993; Schmidt, 1996).

The above effort has been largely on mammalian mechanoreceptors. An all-encompassing monograph equivalent to that of Matthews (1972) on mammalian muscle receptors has not been forthcoming for non-mammalian and invertebrate receptors, so a fruitful field for future enquiry is the extent to which proprioceptors have been subject to evolutionary conservation in both invertebrates and vertebrates, along the lines already discussed for

motor control mechanisms in general (e.g. Fetcho, 1992; Pearson, 1993; Callister et al., 1995). For further recent reading on this intriguing topic, the reader is directed, in order, to: Clarac, 1982; Blackshaw, 1993; Gillespie, 1996; Dickinson et al., 1997; Keil, 1997; Watson and Mire, 1999.

There are relatively few technical impediments for advancing understanding of high-threshold mechanoreceptors in surgically reduced animals and in *in vitro* preparations. For the low-threshold spindles and tendon organs, however, the technology has been at a standstill for almost two decades for further work on freely moving animals. Similarly, for work on conscious humans, the possibility is still remote that a technical advance will shortly enable unitary recordings to be made during learned and unexpected movements of relative freedom and forcefulness. The current emphasis in human studies on behavioral psychophysics (e.g. Kakuda et al., 1997) is well warranted, however, particularly if it can advance along the lines already being applied to the study of precision grip (Flanagan et al., 1999).

Segmental actions of mechanosensory input

In my view, it would be helpful if modern textbooks began their discourse on the central segmental actions of peripheral sensory input onto mammalian MNs and INs by emphasizing the functional significance of Lundberg's (1969) focus on the critical role of segmental ventral-horn INs (Stuart et al., 1999). His work has continually emphasized that interneurons are the primary site of integration (convergence) of descending command signals and sensory feedback. He has also provided us with a major conceptual leap, the concept of alternative reflex pathways: i.e. the pathway chosen by the CNS depending on the phase and intent of a movement (Jankowska and Lundberg, 1981; chapter by Jankowska and Gladden [13]). The mammalian textbook focus is still heavily weighted toward results obtained in anesthetized cat preparations: e.g. the inhibitory action of Ib input from tendon organs onto homonymous MNs. For extensor MNs, however, this pathway is an excitatory one during locomotion (Prochazka, 1996), and it has been studied in detail in

unanesthetized decerebrate cats that were spinalized and chemo-stimulated with nialamide and L-DOPA (Conway et al., 1987; see also McCrea, 1998). This problem is exacerbated by textbooks' initial discourse on such central actions being presented prior to introducing the topic of spinal pattern generation and central pattern generators (CPGs; see below). For over 25 years, CPGs have been particularly revealing about phase-dependent reflex reversals during the elaboration of stepping (Grillner, 1975), this being the predominant principle to emerge from consideration of the segmental actions of mechanosensory input.

Since Lundberg's 1969 article, there has been: (1) a progressive elaboration of his (and Jankowska's) ideas and experimental strategies for unraveling spinal cord circuitry in the adult cat (Baldissera et al., 1981; Burke, 1985; McCrea, 1992, 1998); (2) virtuoso work on the identification and functional morphology of segmental INs in cats (Jankowska, 1992; Jordan, 1998; Matsuyama and Mori, 1998; chapter by Jankowska and Gladden [13]) and, now, even the firing patterns of INs during the voluntary movement of non-human primates (chapter by Fetzi et al. [28]); and (3) the testing of the applicability of Lundberg's (1969) ideas to human spinal cord circuitry (e.g. Katz and Pierrot-Deseilligny, 1999; chapter by Schieppati and Nardonne [43]). The summary message from this intense effort must become more widely promulgated by textbooks: "... During ... movements ... the brain can selectively open appropriate afferent pathways to MNs such that the MN command signals to the active muscles are appropriate for the task at hand." (Stuart and McDonagh, 1997b).

Despite the exceptional progress in this unusually demanding field, which is certainly not for the faint-at-heart, a host of problems await the next generation of segmental motor neuroscientists. Subtle, and sometimes-marked differences exist between the spinal circuitry controlling different muscle systems (e.g. limb, respiratory, head-neck; chapter by Richmond et al. [37]). This dictates that students of motor control keep abreast of findings on segmental control circuitry in both invertebrates and vertebrates ('interphyletic awareness'; Stuart, 1985; see also chapter by P. Stein [23]), in order to

recognize when a finding illustrates a species and/or particular-system specialization versus a conserved mechanism that can be considered to be a principle (e.g. phase-dependent reflex reversal).

Work on spinal connectivity patterns would also be facilitated if we had a better understanding of how sensory afferent input is actually used during movement. For example, evidence across and within invertebrate and vertebrate species, and involving a wide variety of tasks, now suggests several roles for proprioceptive input (Hasan and Stuart, 1988). Three roles arise from the mechanics of the musculoskeletal system and the need to smooth and stabilize internally generated motor programs: (1) linearization (correction for) non-linear muscle properties; (2) compensation for lever-arm variations; and (3) correction of interjoint interaction effects. Three additional roles arise from interactions between the mechanics of the musculoskeletal system and the physical environment; (4) selection of appropriate responses to unexpected perturbations; (5) selection of appropriate synergies of response; and (6) assistance to external forces for movements requiring maneuverability rather than stability. To date, the near-exclusive focus has been on the spinal connectivity patterns associated with two (1, 4) of the above six functions. The key problems about the other four areas are both technical and the lack of a sufficiently widespread appreciation for the continual need to strengthen the interface between cellular neurophysiology and biomechanics (Hasan et al., 1985). This situation is now changing rapidly, however (e.g. Nichols, 1994; chapters by Nichols et al. [32], and Hasan and Thomas [33]).

Since the early 1970s, a problem that has often been voiced by the most sympathetic of supporters of those who toil on the segmental motor system, is that the information on connectivity is becoming so detailed and complex that its ultimate meaning is lost. For example, while the monosynaptic spindle Ia excitation of MNs is derived largely from the homonymous muscle and its synergists, the remainder of the alternative-pathway, oligo- and polysynaptic excitation and inhibition of MNs is derived from afferents supplying virtually the entire limb. How can sense be made of this ever-increasing wealth of spinal circuitry (McCrea,

1992)? In my opinion, the answer to this important problem will require a new generation of interdisciplinary segmental motor scientists. From the 1950s to the mid-1980s, much accrued from the application to spinal reflexology of the proportional feedback control used in engineering control systems. Now, the focus is shifting to the application of more complex control system theories: finite state (conditional)-, adaptive (self-organizing)- and predictive networks; and, fuzzy logic. In a particularly readable and widely cited review, Prochazka (1996; chapter by Prochazka [11]) has emphasized that all of these control systems are being used in modern prosthetics research. He has proposed that each may play one or more roles, usually in combination with each other, in the control of multi-jointed movement during the elaboration of varied motor tasks. The marriage of these concepts to Lundberg/Jankowska-inspired alternative spinal cord circuitry (e.g. chapter by Jankowska and Gladden [13]) is a daunting but realizable interdisciplinary challenge for the immediate future.

Interneurons, motoneurons, motor units, and the size principle

INs have been added deliberately to this subdivision because, at the segmental level of CNS motor control mechanisms, their properties have generally received far too little attention (i.e. in contrast to their segmental connectivity patterns; viz., Jankowska, 1992; chapter by Jankowska and Gladden [13]). This situation is on the verge of changing, however, because, as reviewed elsewhere (McDonagh et al., 1999b) technical advances are now providing the requisite tools (Jordan, 1998; chapter by Fetzi et al. [28])

Most of what follows in this section is focussed on mammals. The properties of single INs and MNs in non-mammalian vertebrates and invertebrates have been studied and discussed intensively, especially with regard to the operation of segmental pattern-generating circuits (see below). Such properties have not generally been considered, however, in relation to the graded development of muscle force (cf., however, the lamprey work of Buchanan, 1993, 1996; chapter by Buchanan [27]). This then is both an issue and a possibility that is readily accomplishable with present-day techniques.

The passive and transitional properties of INs and MNs

Passive

These properties refer to those biophysical parameters measured when the cell is in its quiescent (not discharging, resting) state, and devoid of most (if not all) synaptic and neuromodulatory influences. These parameters include the resting potential (V_r), input resistance (R_N), and membrane time constant (τ_m). For MNs, a large database now exists on the association between these parameters and the cell's morphological properties, as exemplified in Rall et al. (1992) and Binder et al. (1996). For now, the main issues and possibilities to be tested with existing technology include further: (1) delineation of the relative efficacy of the expanding number of ion-channels contributing to V_r ; (2) measurements on (and wider appreciation of) the effect on V_r of the ever-present leak conductance produced by an imperfect seal of the membrane with the IC microelectrode (Binder et al., 1996), particularly those with an impedance $< 10 \text{ M}\Omega$) consideration of a long-standing issue, the unusually low R_N of very-high-threshold cat MNs (Kernell and Zwaagstra, 1981), despite which the differences in R_N across the MN pool gives a reasonably accurate indication of the efficacy of synaptic and IC-injected currents at the MN soma, their functional threshold, and their order of recruitment; and (3) quantification in *a representative numbers of neurons* of the effect of neuromodulators on all of the above passive properties.

Another key issue that seems now resolvable is that study of the fundamental features of V_r , R_N , and τ_m is still in its infancy for mammalian INs, the problem being even more obvious for repetitive-discharge parameters (see below).

It is important that irrespective of the level at which they undertake their research (i.e. molecular/cellular to animal behavior) our current and future movement-neuroscience trainees understand the *functional significance* of cellular properties within the segmental motor system. For example, in regard to τ_m , it is my experience that trainees learn and retain from their cellular neuroscience courses that due to a larger R_N (attributable more to differences in specific membrane resistance rather than the

cells' total surface area), its value is greater in the smaller type S MNs vs. the larger FR/FF MNs of the cat. Few trainees seem to realize, however, that a synaptic potential in a cell with a longer τ_m has a longer time to impress its effect upon that cell, and that this possibility is highly relevant to the functional operation of the size principle. It behooves the training faculty to emphasize routinely the functional significance of their didactic presentations on molecular/cellular properties for the next generation of movement neuroscientists.

Transitional

The transitional state refers to neuron behavior as it converts from the passive (resting) state to the threshold state for initiation of a single AP. Transitional properties include the rheobase current (I_{Rh}), and the spike and afterhyperpolarization (AHP) components to the rheobase action potential (AP). Fundamental parameters associated with the AHP include the amplitude of both its fast (AHP_{amp-f}) and slow (AHP_{amp-s}) component, and its duration which is usually characterized by either $AHP_{duration}$ (time from V_{Rh} to the termination of the AHP) or $AHP_{half-decay\ time}$ (voltage trajectory from the maximum hyperpolarized potential to the membrane potential $[V_m]$ at 1/2 amplitude from V_{Rh} to this negative potential).

The various issues about transitional properties, including their neuromodulation, and the possibilities to resolve them with existing technology have been well covered in several recent reviews (e.g. Binder et al., 1996) and also by one of our own laboratory group (Hornby, 1997). For this reason, it seems sufficient here to point out four areas of potentially fruitful future experimentation.

INs vs. MNs. Again, it must be emphasized that except for the lamprey (Buchanan, 1993), and some of our own recent work on the turtle (McDonagh et al., 1998a, b, 1999a, b) the vertebrate database is far too sparse on the fundamental properties of INs, and their comparison to those of MNs.

I_{Rh} . Rheobase is defined operationally as the current necessary to displace (reduce) the V_r to the firing level (threshold) for initiation of a single AP, as measured with an IC microelectrode passing

depolarizing current. Its values exhibit a 10-fold range across MNs within a single cat SC motor nucleus supplying a single muscle (Zengel et al., 1985), thereby indicating its association with R_N , and systematic variation with MN type. A practical issue about which there is doctrinaire thought is that this parameter captures aspects of cell excitability that are in addition to those accommodated in R_N (Fleshman et al., 1981; Binder et al., 1996). Our group has used this argument in the selection of cluster analysis parameters for the provisional classification of MNs, and MNs vs. INs, on the basis of electrophysiology alone (cf. Zengel et al., 1985; McDonagh et al., 1998a). The evidence supporting this generalization is relatively sparse, however. This issue invites rapid resolution with existing techniques.

AP spike. In our group, Hornby (1997) has argued that at the *coarse-grain* level, the ionic mechanisms of AP spike generation for turtle MNs (Hounsgaard et al., 1988b) are sufficiently similar to those reported for lamprey (Buchanan, 1993) and cat MNs (e.g. Schwindt and Crill, 1984) that the participating conductances can be assembled for a generic vertebrate MN (his Fig. 1; i.e. an extension of the generic mammalian MN summary of Binder et al., 1996; their Table 1.1.) Many would argue, however, that insufficient measurements are available on this issue: e.g. compare published records of the MN's AP-spike for lamprey vs. turtle vs. cat; i.e. Fig. 6 in Buchanan (1993) vs. Fig. 2 in McDonagh et al. (1999a) vs. Fig. 1 in Schwindt and Crill (1984). Interestingly, this issue has not been addressed for the well-known cat S vs. FR vs. FF MNs (Burke, 1981), even though the value of such a comparison has been well established for other cell groups (e.g. Koeber et al., 1988). A comparison of AP-spike characteristics across segmental ventral-horn neuron types and vertebrate species would be helpful at this time.

AHP. Mechanisms for a fast (duration, 2–10 ms) and slow (10–1000 ms) component of the AHP have been described in cat MNs (Gustafsson and Pinter, 1985), and also observed in turtle MNs (Hounsgaard et al., 1988b). 'Slow' here refers to a component of the AHP sometimes termed 'medium' by others (e.g. Binder et al., 1996) in