Movement is arguably the most fundamental and important function of the nervous system, since the organism cannot exist without it. Purposive movement requires the coordination of actions within many areas of the cerebral cortex, cerebellum, basal ganglia, and spinal cord, as well as in peripheral nerves and sensory receptors—in other words, most of the nervous system. Together, these neural structures must control a highly complex and sometimes capricious biomechanical apparatus made up of the skeleton and muscles. It should not be surprising, therefore, that we are only beginning to understand how coordinated movement can take place.

Although the specific topics in movement control addressed in this volume are not exhaustive, they were chosen to provide a broad view of this area of neuroscience. The topics are presented in a hierarchical order, beginning at the level of biomechanics and spinal reflexes and proceeding to brain structures in the cerebellum, brainstem, and cerebral cortex. Each chapter highlights important issues that need to be addressed by researchers to further our understanding of movement and how it is produced by the nervous system.

One unique feature is the critical treatment of each chapter by 10–20 commentaries. The authors of the commentaries were selected to provide a balanced treatment of the chapters by experts in a variety of areas related to movement, including behavior, physiology, robotics, and mathematics. This interactive format is used in the scientific journal Behavioral and Brain Sciences, and the contents of this volume are reproduced in their entirety from an issue of that journal dedicated specifically to the conference "Controversies in Neuroscience."
Movement control
Movement control

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Contents

Preface ix

1 E. Bizzi, N. Hogan, F. A. Mussa-Ivaldi, and S. Giszter
Does the nervous system use equilibrium-point control to guide single and multiple joint movements? 1

2 S. C. Gandevia and D. Burke
Does the nervous system depend on kinesthetic information to control natural limb movements? 12

3 D. A. McCrea
Can sense be made of spinal interneuron circuits? 31

4 D. A. Robinson
Implications of neural networks for how we think about brain function 42

5 G. E. Alexander, M. R. DeLong, and M. D. Crutcher
Do cortical and basal ganglionic motor areas use "motor programs" to control movement? 54

6 J. R. Bloedel
Functional heterogeneity with structural homogeneity: How does the cerebellum operate? 64

7 E. E. Fetz
Are movement parameters recognizably coded in the activity of single neurons? 77

8 J. F. Stein
The representation of egocentric space in the posterior parietal cortex 89

Open Peer Commentary and Authors’ Responses 100

Table of Commentators

Open Peer Commentary

Adamovich, S. V. – How does the nervous system control the equilibrium trajectory? 102

Agarwal, G. C. – Movement control hypotheses: A lesson from history 103

Alexander, G. E. – Neurophysiology of motor systems: Coming to grips with connectionism 104

Andersen, R. A. and Brodchie, P. R. – Spatial maps versus distributed representations 105

Barmack, N. H., Errico, P. and Fagerson, M. – Microzones, topographic maps and cerebellar "operations" 107

Berkholtz, M. B., Sidorova, V. Y., Smetanin, B. N. and Tkach, T. V. – Affenter influence on central generators and the integration of proprioceptive input with afferent input from other modalities 107

Beuter, A. – Modulation of kinesthetic information can be explored with nonlinear dynamics 109

Bischof, H. and Finz, A. J. – Artificial versus real neural networks 110


Bosuut, D. F. – Implication of neural networks for how we think about brain function 112

Bower, J. M. – Is the cerebellum a motor control device? 112

Braitenberg, V. and Freid, H. – Why is the output of the cerebellum inhibitory? 113

Bridgeham, R. – Taking distributed coding seriously 115

Bullock, D. and Contraszas-Vidal, J. L. – Adaptive behavioral phenotypes enabled by spinal interneuron circuits: Making sense the Darwinian way 115

Burgess, P. R. – Equilibrium points and sensory templates 118

Burke, D. – Movement programs in the spinal cord 120

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Contents

Carey, D. P. and Servos, P. – Is “attention” necessary for visuomotor transformations? 121
Cavallari, P. – From neuron to hypothesis 121
Cavanaugh, P. R., Simoneau, G. G. and Ulbrecht, J. S. – Posture and gait in diabetic distal symmetrical polyneuropathy 122
Clark, F. J. – How accurately can we perceive the positions of our limbs? 123
Clarke, T. L. – Mathematics is a useful guide to brain function 124
Colby, C. L., Duhamel, J-R. and Goldberg, M. E. – Posterior parietal cortex and retinocentric space 125
Connolly, C. L. – A robotics perspective on motor programs and path planning 126
Cordo, P. J. and Bevan, L. – Successive approximation in targeted movement: An alternative hypothesis 127
Dawson, M. R. W. – FINSTs, tag-assignment and the parietal gaze-detector 128
Dean, J. – Is equilibrium-point control all there is to coding movement and do insects do it, too? 129
Dietz, V. – Control of natural movements: Interaction of various neuronal mechanisms 130
Duyens, J. and Gielen, C. C. A. M. – Spinal integration: From reflexes to perception 131
Eagleson, R. and Carey, D. P. – Connectionist networks do not model brain function 132
Feldman, A. G. – Fundamentals of motor control, kinesthesia and spinal neurons: In search of a theory 133
Flanders, M. and Soechting, J. F. – Network magic 136
Frolov, A. A. and Biryukova, E. V. – Adaptive neural networks organize muscular activity to generate equilibrium trajectories 137
Fuchs, A. F., Ling, L., Kaneko, C. R. S. and Robinson, F. R. – Network simulations and single-neuron behavior: The case for keeping the bath water 138
Fuster, J. M. – Brain systems have a way of reconciling “opposite” views of neural processing; the motor system is no exception 139
Gandevia, S. C. – How complex is a simple arm movement? 141
Gilbert, P. F. C. and Yeo, C. H. – Cerebellar function: On-line control and learning 141
Giszer, S. – Spinal movement primitives and motor programs: A necessary concept for motor control 142
Gnadt, J. W. – Area LIP: Three-dimensional space and visual to oculomotor transformation 143
Goodale, M. A. and Jakobson, L. S. – Action systems in the posterior parietal cortex 145
Gordon, A. M. and Inhoff, A. W. – Intermittent use of feedback during movement phase transitions and during the updating of internal models 146
Gottlieb, G. L. – Kinematics is only a (good) start 147
Graziano, M. S. and Gross, C. G. – Somatotopically organized maps of near visual space exist 148
Grohstein, P. – Information processing styles and strategies: Directed movement, neural networks, space and individuality 148
Gutman, S. R. and Gottlieb, G. L. – Virtual trajectory as a solution of the inverse dynamic problem 150
Hallett, M. – Operations of the motor system 152
Hamm, T. M. and McCurdy, M. L. – Making sense of recurrent inhibition: Comparisons of circuit organization with function 154
Hasan, Z. – Is stiffness the mainspring of posture and movement? 154
Heuer, H. – Computations, neural networks and the limits of human understanding 156
Horak, F. B., Shupert, C. and Burleigh, A. – Implications for human motor control 156
Iansek, R. – Converging approaches to the problem of single-cell recording 158
Ingle, D. – Spatial short-term memory: Evolutionary perspectives and discoveries from split-brain studies 158
Joffe, M. E. – The necessity of a complex approach in studying brain mechanisms of movement 160
Itu, M. – Function versus synapse: Still a missing link? 161
Jaeger, D. – Toward an integration of neurophysiology, performance analysis, connectionism and compartmental modeling 161
Kalaska, J. F. and Crommond, D. J. – Neurophysiological mechanisms for the planning of movement and for spatial representations 162
Kirkwood, P. A. – The identification of corticomotoneuronal connections 164
Kuo, A. D. and Zajac, F. E. – What is the nature of the feedforward component in motor control? 165
Kupfermann, I. – Neural networks: They do not have to be complex to be complex 165
Lacquaniti, F. – Bellex control of mechanical interaction in man 166
Lan, N. and Cracco, P. E. – Equilibrium-point hypothesis, minimum effort control strategy and the triphasic muscle activation pattern 167
Lataf, M. L. – Are we able to preserve a motor command in the changing environment? 169
Lemmon, R. – The meaning for movement of activity in single cortical output neurons 171
Levine, D. S. – Toward a genuine theoretical neuroscience of motor control 172
Loeb, G. E. – Past the equilibrium point 172
Lundberg, A. – To what extent are brain commands for movements mediated by spinal interneurons? 173
Contents

MacKay, W. A. and Riehle, A. – The single neuron is not for hiding 174
Masson, G. and Pullous, J. – Locomotion, oscillating dynamic systems and stiffness regulation by the basal ganglia 176
McCollum, G. – Global organizations: Movement and spinal 177
Morasso, P. and Sauguet, V. – Equilibrium point and self-organization 179
Neilson, P. D. and Neilson, M.D. – Adaptive model theory 180
Nichols, T. B. – Stiffness regulation revisited 181
Ostry, D. J. and Flanagan, J. R. – Aspects of the equilibrium-point hypothesis (a model) for multijoint movements 182
Paillard, J. – Between perception and reflex: A role for contextual kinaesthetic information 184
Phillips, J. G., Jones, D. L., Bradshaw, J. L. and Inase, R. – Levels of explanation and other available clinical models for motor theory 185
Pouget, A. & Sejnowski, T. J. – A distributed common reference frame for egocentric space in the posterior parietal cortex 185
Pratt, C. A. and Macpherson, J. M. – The many disguises of “sense”: The need for multitask studies of multiarticular movements 186
Prochazka, A. – A vital clue: Kinaesthetic input is greatly enhanced in sensorimotor “vigilance” 187
Proctor, R. W. and Franz, E. A. – Is the posterior parietal cortex the site for sensorimotor transformation? Cross-validation from studies of stimulus-response compatibility 188
Quinlan, P. – Real space in the head? 189
Rager, J. E. – There is much information in neural network unit activations 190
Ross, H. E. – Command signals and the perception of force, weight and mass 191
Rudomin, P. – Presynaptic inhibition and information transmission in neuronal populations 191
Schieppati, M. – Selection of task-related motor output through spinal interneurons 192
Schwarz, G. and Pouget, A. – Signals, brains and explanation 193
Seltzer, B. – An anatomy of parallel distributed processing 194
Smeets, J. B. J. – What do fast goal-directed movements teach us about equilibrium-point control? 194
Smith, A. M. – Can the inferior olive both excite and inhibit Purkinje cells? 195
Stein, J. F. – The role of the cerebellum in calibrating feedforward control 196
Stein, R. B. – Varying the invariants of movement 197
Summers, J. J. – The demise of the motor program 198
Tanji, J. – Cortical area-specific activity not yet found? 198
Thompson, R. F. – The cerebellum and memory 199
Tsuda, I. – Nonlinear dynamical systems theory and engineering neural network: Can each afford a plausible interpretation of “how” and “what”? 200
Van Gisbergen, J. A.M. and Duyfens, J. – Coordinate transformations in sensorimotor control: Persisting issues 201
Van Ingen Sefnau, G. J., Beek, P. J. and Bootma, R. J. – Is position information alone sufficient for the control of external forces? 202
Winters, J. M. and Mullin, P. – Synthesized neural/biochemical models used for realistic 3-D tasks are more likely to provide answers 203

Authors’ Responses

Gandevia, S. C. and Burke, D. – Afferent feedback, central programming and motor commands 213
McCrea, D. A. – Spinal interneuronal connections: Out of the dark comes a ray of hope 217
Robinson, D. A. – How far into brain function can neural networks take us? 221
Bloedel, J. R. – Concepts of cerebellar integration: Still more questions than answers 231
Fetz, E. E. – Saving the baby: Toward a meaningful reincarnation of single-unit data 236
Stein, J. F. – Real spatial maps? 240

References

243

Index

275
Preface

Producing purposive movement is one of the most fundamental functions of the nervous system, yet it is arguably one of the most complex. Other functions of the brain, such as memory, vision, and the automatic control of homeostatic systems, have close analogues in engineering and computer science, but the production of robots that move "naturally" continues to elude us. This lack of success in replicating animal-like movement is surely due to the complexity of the motor apparatus: skeletal, muscular, and neural. The human skeleton consists of 206 bones, roughly 100 articulations, and more than 600 muscles. This mechanical system is far more complex than any current robotic device. A large proportion of the nervous system — including the peripheral nerves, much of the spinal grey and white matter, and large portions of the brainstem, cerebellum, basal ganglia, and cerebral cortex — is involved in the production of coordinated movements. And yet we move almost effortlessly and without having to "think" about it.

Given this complexity, it should not be surprising that there exist in neuroscience research a large number of controversies concerning how the nervous system actually controls purposive movement. The articles and commentaries in this volume originated at the first of a series of conferences entitled "Controversies in Neuroscience." The purpose of these conferences is to address the most controversial areas in neuroscience, bringing together diverse groups of investigators who work in the same area but focus on different levels of the nervous system and adopt different approaches in their research. These conferences are sponsored by the Robert S. Dow Neurological Sciences Institute, Portland, Oregon, U.S.A., which is affiliated with Good Samaritan Hospital and that North Portland, a private community hospital with a strong commitment to scientific research. Robert S. Dow is a neurologist and well-known researcher in the area of cerebellar neuroanatomy and neuropathology. The institute grew out of his research program in the 1960s and currently consists of about 20 independent research laboratories focusing on a wide range of neuroscience, from molecular biology to human psychophysics. This institute is an ideal environment for the Controversies conferences. The diversity of its research programs allows us to draw from a wide range of expertise to organize each conference in the series. Since the first of these conferences, on movement control (1990), we have held others on neural transplantation (1991), G protein receptors (1992), and synaptic plasticity in the cerebellum (1993), and we are currently planning conferences on persistent pain (1994) and the vestibular system (1995).

The papers and commentaries contained in this volume were originally published as a special issue of the interdisciplinary journal Behavioral and Brain Sciences (BBS) and appear here with virtually no changes. BBS's "open peer commentary" format was a natural one for recapturing the interactive flavor of the presentations and discussions, each accorded equal time. In the conference, BBS also made it possible to include many investigators who were not present at the conference and to have all contributions refereed and revised for publication. We plan to publish the papers from each of the conferences in BBS and, when appropriate, as a book.

It is clearly impossible to address all of the controversial issues in any area of neuroscience in one conference, but we try to cover a wide range of topics. Thus the topics addressed in this volume ran the gamut of movement control, from biomechanics to behavior. Chapter 1, by Bizz, Hogan, Mussa-Ivaldi, and Gitter, addresses a topic related directly to biomechanics and indirectly to the structure of motor commands. In a reassessment of the so-called equilibrium point hypothesis, the authors evaluate the extent to which the biomechanics of muscles and their attachments to the skeleton constrain (or simplify) the organization of motor commands. Chapter 2, by Gaedevia and Burke, explores the evidence linking kinesthetic input from sensory receptors in muscles, tendons, skin, and joint capsules to the control of movement. Whereas the question of whether kinesthetic information influences movement has become somewhat academic, the question of how this influence comes about remains controversial. Moving to the topic of the spinal cord in Chapter 3, McCrea attempts to make sense of the myriad interconnectedness of spinal cord circuitry with peripheral, spinal, and descending input. He uses the "wiring diagram" approach to understand this circuitry, arguing that the functions of different connections can be understood, not as rigid reflexes, but as a flexible, state-dependent substrate for processing multimodal information. In Chapter 4, Robinson uses eye movements, which are controlled principally by the brainstem, to attack the idea that the nervous system can be understood on a neuron-by-neuron basis. He argues that we must instead try to understand the processing of movement information at higher levels, such as that of entire networks.

Chapter 5, by Alexander, DeLong, and Crutch, focuses on the basal ganglia-motor cortex loop as a substrate for motor processing. In contrast to more traditional views of serial processing of information by localized neural networks, the authors' position is that much of the processing through the basal ganglia occurs in parallel loops through distributed networks. In Chapter 6, Bloc del examines the long-debated question of what function is served by the cerebellum. Based on anatomical and physiological evidence, he hypothesizes that climbing fiber input to the cerebellum...
Preface

modulates the influence of mossy fiber input on Purkinje cells to integrate spatial features of external and internal space in targeted movements. In Chapter 7, Feizi reexamines the rationale of a chronic unit recording study in which the discharge of single motor cortical neurons has been used to infer coding of movement parameters. He argues that functional interpretations of discharge properties may be misleading, and that understanding the processing of motor output will require the examination of whole networks of neurons. In Chapter 8, Stein revises the posterior parietal cortex (PPC) to understand better how this structure participates in the control of movement. He argues that attention plays an important role in the sensory transformations occurring in the PPC, which involve visual, auditory, somesthetic, and vestibular sensory input.

Following these eight chapters are roughly 100 commentaries by leading researchers in neuroscience and related fields, who critically evaluate the position papers in the preceding chapters.

Most of the position papers from the Controversies conference present models of various operations or structures to illustrate the authors’ positions on controversial issues. The purpose of these models differs from article to article, so it will be worthwhile to conclude this preface by addressing the proper use of modeling.

Nicolai Bernstein wrote about the modeling of motor function and organization in 1958. He pointed out that it is difficult to compare different models of the same system – to determine which model is “correct.” The mere fact that one model can predict the behavior of a system under more conditions than another does not mean it is correct. Bernstein reasoned that the only strong inference one can draw from modeling is that it is wrong. Modeling involves the use of a construct, often mathematical, to describe a highly complex system. It must be kept in mind that a model is not a realistic description of the actual system being modeled but a way to help us think about it and develop hypotheses to test our ideas. If a particular system were already understood, modeling it would serve little practical purpose. The very presentation of a model is therefore evidence that the operation or structure being modeled is not understood.

The value of modeling is in provoking new lines of thinking about a particular problem, not in explaining how things actually work. As modelers of the nervous system and movement, we sometimes find it difficult to accept Bernstein’s observations. We want our models to be right, yet it seems inevitable that most will be wrong, at least in their specifics. Nevertheless, modeling is a necessary step to understanding. Models should not produce stress; that is, they should conform to the system they are attempting to describe. Humans and other animals cannot be described by the same rules as robots. The nervous system, in particular that of humans, has been built up through evolution into a multilayered and redundant structure. A complete description of how the nervous system produces coordinated movement will have to include not one nor even a few but many different models for different types of movements, using different parts of the motor apparatus, in different environments. Attempts to stretch models beyond reasonable limits to order the behavior of a system accurately can be costly and counterproductive. We must learn to accept the limits of our models.

This volume provides useful information for all students of movement, including neuroscientists (physiologists, anatomists, and behaviorists), neurologists, physical therapists, and physical educators, as well as those who have yet to determine the ultimate direction of their research careers. Its interactive format can also provide a useful new kind of text for graduate level courses in movement. The uniqueness of this volume is in the critical evaluation of existing research, in both the questions being asked and the techniques brought to bear on these questions. Whereas most textbooks provide a somewhat fixed and perhaps complacent view of a topic such as movement control, this volume was designed to point out what we do not know and, by inference, what we need to know about this area of neuroscience. We hope the chapters and discussion contained herein will provoke novice and experienced researchers alike to explore certain areas in movement control that need a more critical scientific evaluation. From a historic perspective, the volume also provides a snapshot of what we know and do not know about movement at the beginning of the last decade of the millennium.

In closing, we wish to acknowledge the contributions of the many individuals who contributed either directly or indirectly to this volume. First and foremost, we are grateful to the organizers of the first Controversies conference: Neal Barnack, Curt Bell, Fay Horak, Jane Margherio, Carol Pratt, and all scientists at the R.S. Dow Neurological Sciences Institute (RSD-NSI). Also important in making the conference possible were Dr. Robert S. Dow, Scientist Emeritus, and Dr. Tom Morris, founding member of Biocet Inc. and Chairman of the RSD-NSI Development Committee. Funding for the conference was generously contributed by the National Science Foundation and the Good Samaritan Foundation. Of course, the biggest contribution came from the authors of the eight chapters in this volume and the many individuals who contributed commentaries. We also acknowledge the efforts of Jim Alexander, Julia Hough, and Robin Smith of Cambridge University Press, who made possible the publication of the BBS issue and this book.

We look forward to collaborating on future volumes on controversies in other areas of neuroscience.

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