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Volume 508

SENSORIMOTOR CONTROL OF MOVEMENT AND POSTURE

Edited by Simon C. Gandevia, Uwe Proske, and Douglas G. Stuart

SENSORIMOTOR CONTROL of Movement and Posture

Edited by

Simon C. Gandevia
Prince of Wales Medical Research Institute
Sydney, New South Wales, Australia

Uwe Proske
Monash University
Melbourne, Victoria, Australia

and

Douglas G. Stuart
University of Arizona
Tempe, Arizona, USA

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AUTHORS

A

C. M. Adreani
University of California
Davis, CA 95616-8636 USA

J-M. Aimonetti
Centre National de la Recherche Scientifique (CNRS)
DPM-CNRS 31 chemin Joseph Aiguier
13402 Marseille cedex 20, France

A. Alaburda
MFI 12.5.9. The Panum Institute
University of Copenhagen
Blegdamsvej 3DK-2200N, Denmark

B. Alstermark
Department of Integrative Medical Biology
University of Umeå
S 901 87 Umeå, Sweden
Email: bror.alstermark@physiol.umu.se

J. Armand
Centre National de la Recherche Scientifique (CNRS)
Université de la Mediterranée
Faculté des Sciences du Sport
Marseille, France

B

R. W. Banks
University of Durham
Durham DH1 3LE
United Kingdom
Email: r.w.banks@durham.ac.uk

D. Bennett
University Centre for Neuroscience
University of Alberta
Edmonton ABTG6 2H9 Canada
Email: david.bennett@ualberta.ca

E. N. Benz
Rehabilitation Institute of Chicago & Department of Physical Medicine and Rehabilitation
Northwestern University Medical School
Chicago, IL 60611-3015 USA

G. S. Bewick
University of Aberdeen
Aberdeen AB25 2ZD UK
Email: g.s.bewick@abdn.ac.uk

M. D. Binder
Department of Physiology and Biophysics
University of Washington School of Medicine
Seattle, WA 98195 USA
Email: mdbinder@u.washington.edu

J. A. Brock
Prince of Wales Medical Research Institute
Randwick NSW 2031 Australia
Email: j.brock@unsw.edu.au

C. L. Brockett
Department of Physiology
Monash University VIC 3800 Australia
Email: camilla.brockett@med.monash.edu.au

I. E. Brown
A.E. Mann Institute for Biomedical Engineering
University of Southern California
Los Angeles, California 90089-1112 USA

J. Buchanan
Texas A&M University
College Station, Texas 77843 USA

D. Burke
Spinal Injuries Research Centre
Prince of Wales Medical Research Institute
Randwick NSW2031 Australia
Email: d.burke@unsw.edu.au

R. E. Burke
Laboratory of Neural Control
National Institute of Neurological Disorders and Stroke
National Institutes of Health
Bethesda, MD 20092-4455 USA
Email: reburke@helix.nih.gov

J. E. Butler
The Miami Project to Cure Paralysis
Department of Neurological Surgery
University of Miami School of Medicine
Miami, FL 33101 USA
Email: jbutler@miami.edu

C

M. B. Calford
School of Biomedical Sciences
University of Newcastle
Newcastle NSW 2308 Australia
Email: mike.calford@newcastle.edu.au

R. W. Carr
Prince of Wales Medical Research Institute
Randwick NSW2031 Australia
Email: rcarr@unsw.edu.au

O. Carter
Vision Touch and Hearing Research Centre
School of Biomedical Sciences
University of Queensland
St Lucia QLD 4072 Australia
Email: o.carter@vthrc.uq.edu.au

R. Chua
University of British Columbia
School of Human Kinetics
University of British Columbia
Vancouver BC V6T 1Z1 Canada
Email: rchua@interchange.ubc.ca

J. Cole
University of Southampton
Department of Clinical Neurosciences
University of Southampton and Poole Hospital
UK

J. G. Colebatch
Department of Neurology and Clinical School
Prince of Wales Hospital
Randwick NSW 2031 Australia
Email: j.colebatch@unsw.edu.au

D. F. Collins
Faculty of Physical Education and Recreation
University of Alberta
Edmonton, AB T6G 2H0 Canada
Email: dave.collins@ualberta.ca

R. Creath
Department of Kinesiology
University of Maryland
College Park, MD 20742 USA

D

B. L. Day
MRC Human Movement and Balance Unit
Institute of Neurology, Queen Square
London WC1N 3BG UK
Email: bday@ion.ucl.ac.uk

R. Davoodi
A.E. Mann Institute for Biomedical Engineering
University of Southern California
Los Angeles, California 90089-1112 USA

A. De Troyer
Brussels School of Medicine and Chest Service
Erasme University Hospital
Brussels 1070 Belgium
Email: a_detroyer@yahoo.fr

P. DiZio
Ashton Graybiel Spatial Orientation Laboratory & Center for Complex Systems
Brandeis University
Waltham, MA 02454 USA
Email: dizio@brandeis.edu

R. Durbaba
Division of Neuroscience
Imperial College School of Medicine
London W6 8RF UK
Email: r.durbaba@ic.ac.uk

M. Duxson
Department of Physiology
Otago School of Medical Sciences
University of Otago
PO Box 913
Dunedin, New Zealand
Email: marilyn.duxson@stonebow.otago.ac.nz

P. Dyhre-Poulsen
Institute of Medical Physiology and Institute of Anatomy
Panum Institute, University of Copenhagen
DK 2200 Copenhagen N Denmark
Email: dyhre@mfi.ku.dk

E

P. Ellaway
Division of Neuroscience
Imperial College School of Medicine
London W6 8RF UK
Email: p.ellaway@ic.ac.uk

F

J. B. Fallon
Department of Electrical Engineering and Computer Systems Engineering
Monash University
Clayton VIC 3800 Australia
Email: fallonj@mail.medoto.unimelb.edu.au

E. E. Fetz
Department of Physiology and Biophysics
University of Washington
Seattle, WA 98195-7290 USA
Email: fetz@u.washington.edu

R. C. Fitzpatrick
Prince of Wales Medical Research Institute
Randwick NSW 2031 Australia
Email: r.fitzpatrick@unsw.edu.au

H-J. Freund
Department of Neurology
Heinrich Heine University Duesseldorf
Duesseldorf 40225 Germany
Email: freund@rz.uni-duesseldorf.de

T. Fukunaga
Department of Life Sciences (Sports Sciences)
University of Tokyo
Komaba 3-8-9 Meguro Tokyo, Japan
Email: fukunaga@idaten.c.u-tokyo.ac.jp

G

S. C. Gandevia
Prince of Wales Medical Research Institute
Randwick NSW 2031 Australia
Email: s.gandevia@unsw.edu.au

M. Gorassini
University Centre for Neuroscience
University of Alberta
Edmonton AB TG6 2H9 Canada
Email: monica.gorassini@ualberta.ca

J. E. Gregory
Department of Physiology
Monash University VIC 3800 Australia
Email: ed.gregory@med.monash.edu.au

V. Gritsenko
Centre for Neuroscience
University of Alberta
Edmonton, Alberta T6G 2S2 Canada
Email: valeriya@ualberta.ca

M. Guerraz
Laboratoire "Sport, Performance
Santé" UFR STAPS, Montpellier, France

H

S. G. Hayes
University of California
Davis, CA 95616-8636 USA
Email: sghayes@ucdavis.edu

C. J. Heckman
Department of Physiology and Biophysics
University of Washington School of Medicine
Seattle, WA 98195 USA
Email: cjheckman@u.washington.edu

F. B. Horak
Neurological Sciences Institute
Oregon Health Sciences University
Beaverton, OR 97006 USA
Email: horakf@ohsu.edu

J. Hounsgaard
MFI 12.5.9. The Panum Institute
University of Copenhagen
Blegdamsvej 3DK-2200N Denmark
Email: j.hounsgaard@mfi.ku.dk

H. Hultborn
Department of Medical Physiology
Faculty of Health Sciences
University of Copenhagen
Blegdamsvej 3
Copenhagen DK-2200 Denmark
Email: h.hultborn@mfi.ku.dk

I

J. T. Inglis
School of Human Kinetics
University of British Columbia
Vancouver BC V6T 1Z1 Canada
Email: tinglis@interchange.ubc.ca

T. Isa
Department of Integrative Physiology
National Institute for Physiological Sciences
Myodaiji Okazaki 444-8585 Japan
Email: tisa@nips.ac.jp

J

J. Jeka
Department of Kinesiology
University of Maryland
College Park, MD 20742 USA
Email: jj96@umail.umd.edu

R. S. Johansson
Department of Integrative Medical Biology
Umeå University
SE 901 87 Umeå, Sweden
Email: roland.s.johansson@physiol.umu.se

K

H. Kanehisa
Department of Life Sciences (Sports Sciences)
University of Tokyo
Komaba 3-8-9 Meguro, Tokyo, Japan

R. Katz
Laboratoire de Neurophysiologie Clinique
Hôpital de la Salpêtrière
75651 Paris Cedex 13, France
Email: rose.katz@psl.ap-hop-paris.fr

M. P. Kaufman
Departments of Internal Medicine and Human Physiology
Division of Cardiovascular Medicine
University of California
Davis, CA 95616 8636 USA
Email: mpkaufman@ucdavis.edu

Y. Kawakami
Department of Life Sciences (Sports Sciences)
University of Tokyo
Komaba 3-8-9 Meguro, Tokyo, Japan
Email: kawakami@idaten.c.u-tokyo.ac.jp

P. M. Kennedy
School of Human Kinetics
University of British Columbia
Vancouver BC V6T 1Z1 Canada

D. Kernell
Department of Medical Physiology
University of Groningen
PO Box 196
9700 AD Groningen, The Netherlands
Email: dhkernell@hotmail.com

G. K. Kerr
School of Human Movement Studies
Queensland University of Technology
Brisbane QLD 4059 Australia
Email: g.kerr@qut.edu.au

P. A. Kirkwood
Sobell Department for Motor Neuroscience and Movement Disorders
Institute of Neurology
University College London
Queen Square, London WC1N 3BG UK
Email: pkirkwoo@ion.ucl.ac.uk

L

J. R. Lackner
Ashton Graybiel Spatial Orientation Laboratory & Center for Complex Systems
Brandeis University
Waltham, MA 02454 USA
Email: lackner@brandeis.edu

T. Lam
Centre for Neuroscience & Department of Physiology
University of Alberta
Edmonton AB T6G 2S2 Canada
Email: tlamb@ualberta.ca

N. Lan
A.E. Mann Institute for Biomedical Engineering
University of Southern California
Los Angeles, California 90089-1112 USA

R. N. Lemon
Sobell Department for Motor Neuroscience and Movement Disorders
Institute of Neurology
University College London
Queen Square, London WC1N 3BG UK
Email: rlemon@ion.ucl.ac.uk

G. E. Loeb
A.E. Mann Institute for Biomedical Engineering
University of Southern California
Los Angeles, California 90089-1112 USA
Email: gloeb@usc.edu

M

V. Macefield
Prince of Wales Medical Research Institute
Randwick NSW 2031 Australia
Email: vg.macefield@unsw.edu.au

M. A. Maier
INSERM U483
Université Pierre et Marie Curie
75005 Paris, France

V. Marchand-Pauvert
Service de Rééducation Neurophysiologie
Hôpital de la Salpêtrière
756551 Paris Cedex 13, France

Y. Matsuzaka
Department of Physiology
Tohoku University School of Medicine
Sendai 980-8575 Japan

P. B. C. Matthews
University Laboratory of Physiology
Parks Road, Oxford OX1 3PT UK
Email: peter.matthews@physiol.ox.ac.uk

C. Maurer
Neurological University Clinic
University of Freiburg
D 79106 Freiburg, Germany
Email: maurer@uni-freiburg.de

P. McNulty
Prince of Wales Medical Research Institute
Randwick NSW 2031 Australia
Email: p.mcnulty@unsw.edu.au

T. Mergner
Department of Neurology
University of Freiburg
D 79106 Freiburg, Germany
Email: mergner@uni-freiburg.de

S. Meunier
Laboratoire de Neurophysiologie Clinique
Hôpital de la Salpêtrière
75651 Paris Cedex 13, France
Email: meunier@chups.jussieu.fr

T. S. Miles
Department of Physiology
University of Adelaide
Adelaide SA 5005 Australia
Email: timothy.miles@adelaide.edu.au

D. L. Morgan
Department of Electrical and Computer Systems Engineering
Monash University VIC 3800 Australia
Email: david.morgan@eng.monash.edu.au

T. Muraoka
Department of Life Sciences (Sports Sciences)
University of Tokyo
Komaba 3-8-9 Meguro, Tokyo, Japan
Email: muraoka@idaten.c.u-tokyo.ac.jp

N

T. R. Nichols
Department of Physiology
Emory University
Atlanta, GA 30322 USA
Email: trn@physio.emory.edu

J. B. Nielsen
Department of Medical Physiology
University of Copenhagen
2200 Copenhagen N Denmark
Email: j.b.nielsen@mfi.ku.dk

M. A. Nordstrom
Department of Physiology
University of Adelaide
Adelaide SA 5005 Australia
Email: michael.nordstrom@adelaide.edu.au

P

A. Paul
Dept. of Anatomy and Structural Biology
Otago School of Medical Sciences
University of Otago
PO Box 913
Dunedin, New Zealand
Email: angelika.paul@stonebow.otago.ac.nz

K. G. Pearson
Centre for Neuroscience & Department of Physiology
University of Alberta
Edmonton, AB T6G 2S2 Canada
Email: kpearson@ualberta.ca

S. I. Perlmutter
Department of Physiology and Biophysics
University of Washington
Seattle, WA 98195 7290 USA

J-F. Perrier
MFI 12.5.9. The Panum Institute
University of Copenhagen
Blegdamsvej 3DK-2200N Denmark

R. J. Peterka
Neurological Sciences Institute
Oregon Health and Science University
Portland, Oregon USA

N. T. Petersen
Prince of Wales Medical Research Institute
Randwick NSW 2031 Australia
Email: nicolas@unsw.edu.au

J. D. Pettigrew
Vision Touch and Hearing Research Centre
School of Biomedical Sciences
University of Queensland
St Lucia QLD 4072 Australia
Email: j.pettigrew@vthrc.uq.edu.au

J. G. Pickar
University of California
Davis, CA 95616-8636 USA
Email: jgpickar@ucdavis.edu

E. Pierrot-Deseilligny
Service de Rééducation Neurophysiologie
Hôpital de la Salpêtrière
756551 Paris Cedex 13 France
Email: emmanuel.pierrot-deseilligny@chups.jussieu.fr

R. K. Powers
Department of Physiology and Biophysics
University of Washington School of Medicine
Seattle, WA 98195 USA
Email: rkpowers@u.washington.edu

A. Prochazka
Centre for Neuroscience
University of Alberta
Edmonton, Alberta T6G 2S2 Canada
Email: arthur.prochazka@ualberta.ca

U. Proske
Department of Physiology
Monash University VIC 3800 Australia
Email: uwe.proske@med.monash.edu.au

Y. Prut
Department of Physiology and Biophysics
University of Washington
Seattle, WA 98195 7290 USA

R

S. Rawlinson
Division of Neuroscience
Imperial College School of Medicine
London W6 8RF UK
Email: s.rawlinson@ic.ac.uk

K. Refshauge
School of Physiotherapy
Cumberland College of Health Sciences
University of Sydney
PO Box 170
Lidcombe NSW 2141 Australia
Email: k.refshauge@cchs.usyd.edu.au

B. Reid
University of Aberdeen
Aberdeen AB25 2ZD UK
Email: brian.reid@abdn.ac.uk

C. Richardson
University of Durham
Durham DH1 3LE UK
Email: a.c.richardson@durham.ac.uk

J. C. Rothwell
Sobell Department of Neurophysiology
Institute of Neurology
Queen Square, London WC1N 3BG UK
Email: j.rothwell@ion.ucl.ac.uk

M. J. Rowe
Department of Physiology and Pharmacology
University of New South Wales
Sydney NSW 2052 Australia
Email: m.rowe@unsw.edu.au

P. Rudomin
Department of Physiology, Biophysics and Neurosciences
Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional
México DF 07000 Mexico
Email: rudomin@fisio.cinvestav.mx

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W. Z. Rymer
Rehabilitation Institute of Chicago &
Department of Physical Medicine and Rehabilitation
Northwestern University Medical School
Chicago, IL 60611-3015 USA
Email: zevric@casbah.acns.nwu.edu

S

M. H. Schieber
Departments of Neurology & Neurobiology and Anatomy
University of Rochester School of Medicine and Dentistry
Rochester, New York 14642 USA
Email: mhs@cvs.rochester.edu

B. D. Schmit
Rehabilitation Institute of Chicago &
Department of Physical Medicine and Rehabilitation
Northwestern University Medical School
Chicago, IL 60611-3015 USA

A. Schmied
Centre National de la Recherche Scientifique (CNRS)
DPM-CNRS 31 chemin Joseph Aiguier
13402 Marseille cedex 20
France
Email: schmied@dpm.cnrs-mrs.fr

K. Seki
Department of Physiology and Biophysics
University of Washington
Seattle, WA 98195-7290 USA

P. Sheard
Department of Physiology
Otago School of Medical Sciences
University of Otago, PO Box 913
Dunedin, New Zealand
Email: phil.sheard@stonebow.otago.ac.nz

K. Shima
Department of Physiology
Tohoku University School of Medicine
Sendai 980-8575 Japan

M. Simonetta-Moreau
Institut National de la Santé et de la Recherche Médicale (INSERM)
455CHUPurpan, Toulouse, France

E. B. Simonsen
Institute of Medical Physiology and Institute of Anatomy
Panum Institute
University of Copenhagen
DK 2200 Copenhagen N Denmark

T. Sinkjaer
Center for Sensory-Motor Interaction
University of Aalborg
9220 Aalborg, Denmark

D. G. Stuart
Department of Physiology
The University of Arizona College of Medicine
Tucson, AZ 85724-5051 USA
Email: dgstuart@u.arizona.edu

T

J. Tanji
Department of Physiology
Tohoku University School of Medicine
Sendai 980-8575 Japan
Email: tanjij@mail.cc.tohoku.ac.jp

A. Taylor
Division of Neuroscience
Imperial College School of Medicine
London W6 8RF UK
Email: ataylor@ic.ac.uk

J. L. Taylor
Prince of Wales Medical Research Institute
Randwick NSW 2031 Australia
Email: jl.taylor@unsw.edu.au

C. K. Thomas
The Miami Project to Cure Paralysis
Department of Neurological Surgery
University of Miami School of Medicine
Miami, FL 33101 USA
Email: cthomas@miami.edu

K. S. Türker
Department of Physiology
University of Adelaide
Adelaide SA 5005 Australia
Email: kemal.turker@adelaide.edu.au

V

J-P. Vedel
Centre National de la Recherche Scientifique (CNRS)
DPM-CNRS 31 chemin Joseph Aiguier
13402 Marseille cedex 20 France
Email: vedel@dpm.cnrs-mrs.fr

W

D. L. Wardman
Prince of Wales Medical Research Institute
Randwick NSW 2031 Australia
Email: d.wardman@unsw.edu.au

C. Wells
School of Human Kinetics
University of British Columbia
Vancouver BC V6T 1Z1 Canada

A. K. Wise
Department of Physiology
Monash University
Clayton VIC 3800 Australia
Email: wisea@mail.medoto.unimelb.edu.au

C. J. Worringham
School of Human Movement Studies
Queensland University of Technology
Brisbane QLD 4059 Australia

Y

S. Yakovenko
Centre for Neuroscience
University of Alberta
Edmonton, Alberta T6G 2S2 Canada
Email: sergiy@ualberta.ca

H-W. Yang
Department of Life Sciences
Chung Shan Medical and Dental College
Taichung 402 Taiwan

Z

I. Zijdewind
Department of Medical Physiology
University of Groningen
Groningen
The Netherlands
Email: i.zijdewind@med.rug.nl

FOREWORD

This collection of contributions on the subject of the neural mechanisms of sensorimotor control resulted from a conference held in Cairns, Australia, September 3-6, 2001. While the three of us were attending the International Union of Physiological Sciences (IUPS) Congress in St Petersburg, Russia, in 1997, we discussed the implications of the next Congress being awarded to New Zealand. We agreed to organise a satellite to this congress in an area of mutual interest - the neuroscience of movement and sensation.

Australia has a long-standing and enviable reputation in the field of neural mechanisms of sensorimotor control. Arguably this reached its peak with the award of a Nobel Prize to Sir John Eccles in 1963 for his work on synaptic transmission in the central nervous system. Since that time, the subject of neuroscience has progressed considerably. One advance is the exploitation of knowledge acquired from animal experiments to studies on conscious human subjects. In this development, Australians have achieved international prominence, particularly in the areas of kinaesthesia and movement control. This bias is evident in the choice of subject matter for the conference and, subsequently, this book. It was also decided to assign a whole section to muscle mechanics, a subject that is often left out altogether from conferences on motor control.

Cairns is a lovely city and September is a good time to visit it. Since we wanted to offer our international colleagues something more than just a high-standard conference, we picked Cairns as the venue. It meant that we would be close to one of the wonders of the world, the Great Barrier Reef. The organisers took the unprecedented decision to completely interrupt the conference for one day, while all conference delegates visited and enjoyed the marvels of the Great Barrier Reef. It generated an atmosphere of informality and shared adventure that helped to break down even the most intractable communication barriers between conference delegates. The free exchange of ideas led in several instances to the formulation of new consensus views and to agreement over the way forward in future experiments. The conference was brought to a dramatic end with a gala dinner at which delegates were introduced to aspects of Australian aboriginal culture.

In assembling the book we have chosen to slightly alter the order of presentations from that used at the conference. This was done in an attempt to bring related topics as close together as possible. Each section is preceded by a Preface. In the preface we make reference to particular chapters and use the names of the presenting authors from the conference rather than first-named authors of the chapters. Each chapter underwent a formal review process by experts in the field so, hopefully, the standard maintained during the conference is reflected in the level of scholarship achieved in this book.

The volume includes contributions by two authors who were unable to attend the Symposium: a chapter on presynaptic inhibition by Pablo Rudomin and one on motoneurones by Peter Matthews, who also wrote a Preface for the whole volume.

Organising a conference with 180 delegates, most of whom were coming from overseas, proved to be a mammoth job. It would not have been possible without considerable help from various quarters. We would like to thank in particular the various helpers in Sydney and Melbourne in Australia, and Tucson in the USA. The bulk of the organisational burden fell on the Sydney group, in particular, Jane Butler, Robert Gorman and Nicolas Petersen. Communication between the organisers and delegates, attendance at the reception desk and overseeing many crucial details at the conference were all competently and efficiently carried out by Mary Sweet and Emily Mifsud. We would also like to thank Emily for her huge input to the task of formatting chapters and assembling the book. We gratefully acknowledge financial support from the Prince of Wales Medical Research Institute, Sydney and Monash University, Melbourne. Additional financial support for American delegates was provided by the National Institutes of Health, Bethesda, MD, USA (NS 41876). Finally, we would like to acknowledge support from the IUPS and thank its representatives for assigning to the meeting the status of an official satellite symposium.

Simon C. Gandevia **Uwe Proske** **Douglas G. Stuart**

PREFACE

Those from the Antipodes have contributed nobly to the advance of neurophysiological understanding of movement and sensation, the basis of all human activity. In the first half of the last century their talent was largely exported, especially to Britain and the USA, and this has continued with several such emigrants returning home for the present meeting. Notable examples in other fields of science include Rutherford, a New Zealander working in Cambridge, who laid the groundwork for "splitting the atom" and Florey, an Australian working in Oxford, who showed that Fleming's curiosity of penicillin could be used to such wondrous effect in man. In the second half of the 20th century the balance shifted and most remained at home, developing many distinguished laboratories. This was facilitated by the dramatic growth in the ease and speed of travel and most recently by electronic communication; speaking personally, in 1965 I took over a month to reach Sydney from the UK by ship. Jack Eccles, whose contribution and influence was spelt out in a Poster, marked the turning point; educated in Melbourne, he travelled to Oxford in 1925 to work with Sherrington and established himself there apparently for ever. But he then returned to Australia in 1937, subsequently moved to New Zealand where he discovered the IPSP in 1951, and then came back to Australia to make Canberra a Mecca for a generation of neurophysiologists; finally, approaching 65, he postponed retirement by moving to the USA in 1966. The present symposium, held in Australia with a wide-ranging international attendance, helped celebrate this maturation of home-grown neuroscience; its organisers have a long record of distinguished contribution, 17 of the speakers were Australian as would have been equally appropriate if the meeting had been held somewhere else, and 33 of the 84 posters were Australian.

The format of the meeting was standard, with 10 two hour sessions ranging from sensory receptors, motoneurones, and interneurones to the motor cortex with the emphasis on the lower level mechanisms. Each session started with an overview by the chairman followed by a single major paper; four "discussants" then each gave shorter descriptions of their own work within the same area. The present volume gathers these papers together, with each section now briefly introduced by the organisers. Thus the volume ranges from the general to the specific. It thereby provides a welcome up-dating on a variety of topics. This is all most helpful; although the topics may sound familiar the focus of interest has shifted very considerably, with new findings leading to new thinking.

Certain particular advances may be high-lighted by comparing this volume with a comparable symposium on "Muscle afferents and the spinal control of movement" held 10 years earlier in Paris to which 19 of the present speakers also contributed. The muscle spindle remains of central interest, especially its role in walking. The underlying fusimotor drive for the cat gastrocnemius has now apparently been definitively fractionated, both

temporally and into its functional components. The stretch reflex retains its importance in supporting extension during the stance phase, but tendon organ afferents are now thought to assist rather than antagonise the spindle afferents. Moreover, both types of afferent have been shown to take part in timing the switching from extension to flexion, and back again, in multi-sensory rule based operations instead of being simply responsible for "resistance reflexes". In addition, their signals are essential in enabling higher control centres to adaptively adjust their output to match the biomechanical properties of the limb, including the effect of changing gravitational fields and the effects of rotation (Coriolis forces). These Coriolis studies have also dealt a severe blow to servo type hypotheses of goal-directed movements in which the movement is specified by the balance of spindle or muscle activity required at the end point. Interest in proprioception continues unabated, but muscle receptors no longer reign in isolation; detailed information from cutaneous receptors has now been shown to contribute both to sensory awareness and to the up-dating of motor commands. Finally, the histology of the spindle continues to surprise with new evidence suggesting that the liberation of glutamate from synaptic type vesicles contributes to its firing.

The motoneurone has also moved on from ten years ago. Plateau potentials have come of age and are now seen as the outward sign of an extreme action of an omni-present mechanism for regulating MN responsiveness; there is intense investigation of the underlying metabotropic receptors which facilitate the voltage activated channels that generate the prolonged inward current. Human motor studies continue in health and disease, with modelling becoming inreasingly important for interpreting the findings. Synaptic noise has been recognised as crucial in triggering low-frequency firing, which occurs while the MN's mean membrane potential remains subthreshold, with firing continuing at the final equilibrium potential when the AHP is completed. The biomechanical properties of the motor unit remains of interest, with a new concentration on the effect of forcibly lengthening contracting muscle fibres (eccentric contraction). Interneurones have been successfully recorded from during voluntary hand movments in the monkey, but remain an enigma because of their great functional plasticity; moreover, violent debate continues on a largely anatomical matter, namely whether or not humans have a powerful C3\C4 propriospinal system mediating motor commands as in the cat. The "silent" vestibular system continues to be probed in man, and in particular how it interacts with other sensory inputs in controlling posture.

The classical study of the motor cortex continues with a mix of stimulation and recording, showing that simple ideas of a finely-grained topographical localisation of function become ever less tenable. Grossly separate motor areas are confirmed to differ in anatomical and functional organisation; but little emerges as to the precise parcellation of function between them, in the way things are known for many of the multiple cortical visual areas. The new light on the horizon is the recognition of a synchronisation of the firing of neurones in cortical motor areas that varies with the conditions; this occurs at 15-30 Hz and "paces" the motoneurones so that it can be detected in the EMG, giving a signal that is coherent with both electric and magnetic cortical recordings. The current challenge is to decide whether this of itself represents an important form of signal coding or is simply an epi-phenomenon arising from other mechanisms. This was approached from the standpoint of the human studies, without the related animal work being presented. It remains an important topic for the future, probably requiring the development of yet more detailed ways for the mathematical analysis of multiple recordings, accompanied by modelling.

In conclusion, contrasting this volume with its related predecessor of ten years ago shows a steady advance rather than dramatic breakthroughs. But the progress has been very

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