

PROGRESS IN BRAIN RESEARCH

VOLUME I

BRAIN MECHANISMS

INTERNATIONAL COLLOQUIUM SPONSORED BY
THE INTERNATIONAL BRAIN RESEARCH ORGANIZATION (IBRO)
ON SPECIFIC AND UNSPECIFIC MECHANISMS
OF SENSORY MOTOR INTEGRATION, PISA, 1961

EDITED BY

G. MORUZZI

A. FESSARD AND H. H. JASPER

ELSEVIER

PROGRESS IN BRAIN RESEARCH

VOLUME 1

BRAIN MECHANISMS

This Page Intentionally Left Blank

PROGRESS IN BRAIN RESEARCH

VOLUME 1

BRAIN MECHANISMS

*INTERNATIONAL COLLOQUIUM SPONSORED BY
THE INTERNATIONAL BRAIN RESEARCH ORGANISATION (IBRO)
ON SPECIFIC AND UNSPECIFIC MECHANISMS OF
SENSORY MOTOR INTEGRATION; PISA, 1961*

EDITED BY

GIUSEPPE MORUZZI

Istituto di Fisiologia, Università di Pisa, Pisa, Italia

ALFRED FESSARD

Laboratoire de Neurophysiologie Générale, Collège de France, Paris, France

HERBERT H. JASPER

Montreal Neurological Institute, Montreal, Canada



ELSEVIER PUBLISHING COMPANY

AMSTERDAM - LONDON - NEW YORK

1963

SOLE DISTRIBUTORS FOR THE UNITED STATES AND CANADA
AMERICAN ELSEVIER PUBLISHING COMPANY, INC.
52 VANDERBILT AVENUE, NEW YORK 17, N.Y.

SOLE DISTRIBUTORS FOR GREAT BRITAIN
ELSEVIER PUBLISHING COMPANY LIMITED
12B, RIPPLESIDE COMMERCIAL ESTATE
RIPPLE ROAD, BARKING, ESSEX

LIBRARY OF CONGRESS CATALOG CARD NUMBER 62-19695

WITH 246 ILLUSTRATIONS AND 1 TABLE

ALL RIGHTS RESERVED
THIS BOOK OR ANY PART THEREOF MAY NOT BE REPRODUCED IN ANY FORM,
INCLUDING PHOTOSTATIC OR MICROFILM FORM,
WITHOUT WRITTEN PERMISSION FROM THE PUBLISHERS

This Page Intentionally Left Blank



The participants in the Pisa Colloquium. Front row: O'Leary, Eccles, Moruzzi, Albe-Fessard, Bremer, Anokhin, Fessard, Granit, Lissák, Adey. Second row: Jung, Grey Walter, Jasper, Brookhart, Magoun, Rossi, Carreras, Pompeiano. Third row: Jovet, Hagbarth, Dumont, Hugelin, Buser, Dell, Arduini, Zanchetti, Naquet, Ricci.

Participants to Pisa Colloquium

W. R. ADEY, Department of Anatomy and Brain Research Institute, University of California Medical Center, Los Angeles, Calif., U.S.A.

C. AJMONE MARSAN, Branch of EEG and Clin. Neurophysiology, National Institutes of Health, Bethesda, Md., U.S.A.

D. ALBE-FESSARD, Centre d'Études de Physiologie Nerveuse et d'Électrophysiologie du C.N.R.S., Paris, France

P. ANOKHIN, Academy of Medical Sciences, Moscow, U.S.S.R.

A. ARDUINI, Istituto di Fisiologia dell'Università di Pisa, Italy

I. BERITASHVILI, Institute of Physiology, Academy of Science of the Georgian SSR, Tbilisi, U.S.S.R.

M. A. B. BRAZIER, Brain Research Institute, University of California Medical Center, Los Angeles, California, U.S.A.

F. BREMER, Laboratoire de Pathologie Générale, Université Libre de Bruxelles, Belgium

J. M. BROOKHART, Department of Physiology, University of Oregon Medical School, Portland, Oregon, U.S.A.

P. BUSER, Laboratoire de Neurophysiologie Comparée, Faculté des Sciences, Université de Paris, France

M. CARRERAS, Clinica delle Malattie Nervose dell'Università di Parma, Italy

P. DELL, Laboratoire de Neurophysiologie, Hôpital Henri Rousselle, Paris, France

J. C. ECCLES, Department of Physiology, The Australian National University, Canberra, Australia

E. FADIGA, Istituto di Fisiologia Umana, Università di Bologna, Italy

A. FESSARD, Laboratoire de Neurophysiologie Générale, Collège de France, Paris, France

H. GASTAUT, Unité de Recherches Neurobiologiques de l'Institut National d'Hygiène, Marseille, France

R. GRANIT, The Nobel Institute for Neurophysiology, Karolinska Institutet, Stockholm, Sweden

K.-E. HAGBARTH, Department of Clinical Neurophysiology, Akademiska Sjukhuset, Uppsala, Sweden

A. HUGELIN, Laboratoire de Neurophysiologie, Hôpital Henri Rousselle, Paris, France

H. H. JASPER, Montreal Neurological Institute, McGill University, Montreal, Canada

M. JOUVET, Laboratoire de Physiologie, Faculté de Médecine, Université de Lyon, France

R. JUNG, Abteilung für klinische Neurophysiologie der Universität, Freiburg i/Br., Germany

K. LISSÁK, Physiological Institute of the University of Pécs, Hungary

H. W. MAGOUN, Graduate Division, University of California, Los Angeles, 24, Calif., U.S.A.

G. MORUZZI, Istituto di Fisiologia dell'Università di Pisa, Italy

R. NAQUET, Laboratoire EEG, Hôpital la Timone, Marseille, France

S. NARIKASHVILI, Institute of Physiology, Academy of Sciences of the Georgian SSR, Tbilisi, U.S.S.R.

J. L. O'LEARY, Departments of Neurology and Neurosurgery, Washington University School of Medicine, Saint Louis, Mo., U.S.A.

O. POMPEIANO, Istituto di Fisiologia dell'Università di Pisa, Italy

G. F. RICCI, Istituto di Farmacologia dell'Università di Pisa, Italy

G. F. ROSSI, Clinica Neurochirurgica dell'Università di Genova, Italy

S. TYC-DUMONT, Laboratoire de Neurophysiologie, Hôpital Henri Rousselle, Paris, France

W. GREY WALTER, Burden Neurological Institute, Bristol, Great Britain

A. ZANCHETTI, Istituto di Patologia Speciale Medica dell'Università di Siena, Italy

Introductory Remarks on Behalf of IBRO and UNESCO

HERBERT H. JASPER

It is with great pleasure that I have accepted the invitation of Professor Moruzzi to speak on behalf of the International Brain Research Organization at the inaugural ceremonies of this Colloquium. In so doing, I am merely the spokesman for the many scientists from varied disciplines and special training in many countries who have formed a world community of colleagues with common interests in the brain sciences. We have been working together and communicating more frequently with each other during recent years.

The formation of the International Brain Research Organization in October 1960, less than one year ago, is only the formalization of a growing body of scientific workers determined to promote and improve the quality of basic research on the brain independent of political barriers which separate us, often by chance, into different countries. We are also determined to do what we can to improve the working relations between our various countries by our demonstration of cordial and effective collaboration in spite of political situations which would seem to place us in conflict one with another. But in keeping with the traditions of the first international scientific colloquium held in Pisa in October of 1839, 122 years ago, we will abide by the wishes of the Grand Duke of Tuscany and try to refrain from political discussions during our formal meetings — though we cannot make any promises for many informal sessions which are often the best part of such colloquia.

I take pleasure also in bringing greetings and salutations from UNESCO to this first colloquium sponsored by their very young offspring, IBRO, which is actually less than a year old. I must say that Unesco is somewhat astounded by the vigor of their young child, and perhaps fearful at times that we are trying to run before we have learned to walk, but the splendid manner in which Prof. Moruzzi and his co-workers have organized this colloquium with the generous assistance of the Valentino Baldacci Foundation — and the eminent scientists gathered here from near and far — should reassure them that we can not only walk, but we can run and even fly.

We are particularly grateful to Prof. Ugo Baldacci who has made this conference possible — even before IBRO was formally organized, and certainly before we have become sufficiently well established financially to undertake such a meeting. We are pleased to be able to pay tribute in this manner to his distinguished father, Dr. Valentino Baldacci of Pisa.

This is one of a series of colloquia started by the Laurentian symposium on *Brain*

mechanisms and consciousness held in 1953 (Blackwell, Oxford, 1954). This was followed by the Detroit symposium *Reticular formation of the brain* (Little, Brown and Co., Boston, 1958), the CIBA conference on *Neurological basis of behaviour* (Churchill, London, 1958), and the Moscow colloquium on *Electroencephalography of higher nervous activity* (*Electroenceph. clin. Neurophysiol.*, 1960, *Suppl. 13*). Several additional symposia were held along the same lines, as for example the Montevideo symposium on *Brain mechanisms of learning* (Blackwell, Oxford, 1961).

I would like to take this occasion to pay tribute to one of our members who has provided much of the initiative and inspiration for many of these symposia, including the first held in 1953 in Canada, that is Professor Henri Gastaut. He has worked in the background for many of these important meetings, and he deserves more credit than is usually given him in the publication of their proceedings.

The proceedings of this colloquium are to be published *in extenso* for the benefit of our many colleagues who are unable to be with us. The Baldacci Foundation is to publish the French edition, while IBRO will publish the English edition, in keeping with our policy to publish in the two working languages of UNESCO.

Introductory Remarks by the Honorary President

PROFESSOR FREDERIC BREMER

My dear Colleagues,

I owe to the date of my birthday the privilege and pleasure of expressing on your behalf our gratitude to all who have made this Colloquium such a pleasant reality.

We are all especially grateful to the University of Pisa for the hospitality it has offered us at the Istituto di Fisiologia, and for the interest expressed in our work by the presence at this inaugural session of Professor Faedo, Rector of the University, and Professor Puccinelli, Dean of its Medical Faculty. You will all wish me, I am sure, to ask them to accept our sincere thanks for their kind attendance.

Our thanks are due also to the International Brain Research Organization, who are the sponsors of the Colloquium, and to our colleague Herbert Jasper, the energetic Executive Secretary of this Organization, who has played a major role in the preliminary stages of the excellent arrangements made for this meeting. Equally grateful are we to our dear colleague Giuseppe Moruzzi and to Mrs. Moruzzi, who have devoted so much time and ingenuity to ensure that the Colloquium will be the success that it already promises to be.

Further, I should like to thank on your behalf, the Fondazione Valentino Baldacci, whose generous financial aid has been so valuable. The director of this Foundation, our colleague Professor Ugo Baldacci, and its secretary, Doctor F. Suma, have once more shown the meticulous solicitude and cordiality which have been, in the past, characteristic of the contributions made by the Fondazione to the success of scientific enterprises.

The Pisa meeting follows, after three years, the memorable Moscow Colloquium. The support given to us by the International Brain Research Organization is an indication that this Organization approves of the idea that the understanding of cerebral integration requires the spatial and spiritual cooperation of those who are studying this supreme problem in neurophysiology. In this era of political unrest in which we are condemned to live, our meeting here will be a vivid symbol of what can be done by friendly cooperation in a domain of science which is so intimately associated with the problems of human destiny and progress.

We shall work in the shadow of the great monuments of a glorious city. They are the comforting testimony that great things can be accomplished in the midst of struggle and warfare, though the warfare to which I allude was certainly, I must

admit, a warfare performed with the “conventional” weapons of the 12th century!

To me it is particularly moving that our session will be held in the Institute of my old friend Giuseppe Moruzzi, an Institute which has made, as you know, outstanding contributions to the themes that we shall discuss.

Our only regret is that Professors Beritashvili, Narikashvili and Smirnov, and Doctor Terzian are unable to share in our meetings.

As a compensation for this, however, we shall enjoy the full attendance of Professor Richard Jung, who has happily recovered so quickly from the accident which recently, as a result of his passionate interest in Romanesque architecture, he had the misfortune to suffer.

This Page Intentionally Left Blank



Frédéric Bremer

Dedication to Professor Bremer

This volume is dedicated to a friend whose work has greatly advanced our understanding of the nervous system, whose presence can enliven the dullest meeting and whose 70th birthday gives us the excuse for expressing our feelings.

Fortunately Frédéric Bremer's age has no relation to his present activity. Forty years in the laboratory have not lessened his keen interest in new investigations and his critical appreciation of the problems they bring. Though he can look back to the string galvanometer, he has retained his mastery of experimental technique.

The use of some new technique has often led to a rapid advance in the physiology of the nervous system. Few nowadays can appreciate the difficulties of experiments on the brain before the barbiturates were available: indeed the introduction of Dial as a suitable anaesthetic in 1930 can count as a major advance in technique and the short note on it by Fulton, Liddell and Rioch deserves to rank as a turning point in the history of cerebral physiology. But the brain depressed by drugs is not the normal brain and another turning point came when Bremer introduced the "Cerveau isolé" and "Encéphale isolé" preparations in 1935-36. His preparation solved the problem of anaesthesia by providing for the division of the pathways for pain below the cerebral level leaving intact much of the regulating mechanism for cortical activity. He found, after mid-brain transection, that the pattern characteristic of sleep would be shown both in the EEG record and in oculomotor behaviour: the pattern changed from time to time to that characteristic of arousal and he found that the change could be brought by appropriate sensory stimuli. Thus his "Cerveau isolé" and "Encéphale isolé" preparations made it possible to start a new chapter in the analysis of the brain stem regulating centre. They have given a fresh impetus to research on the problems of sleep and attention and have opened up fields which are still the centre of interest.

This work on the brain stem in relation to cerebral activity has been a major contribution to the physiology of the central nervous system but it is far from being the only important contribution he has made. His early study of the cerebellum in Sherrington's laboratory and his more recent work on the auditory and visual pathways and cortical responses have established valuable results, and Bremer has always been attracted by the general problems which have been left unsolved because there is so much detail to be filled in. He has been concerned with the waves as well as the spikes, with the factors which can lead to synchronised rhythms in the cord and in the brain and with the general problem of auto-rhythmicity.

It is indeed his concern for the whole advance and his knowledge of the way it has gone which gives him a special claim to our good wishes. Research on the central

nervous system offers an immense variety of topics, from the anatomy of the cell to the psychology of the individual: very few of us can hope to follow all the developments recorded in so many fresh publications, but Bremer has never lost touch with the major issues. In any discussion he can refer to the details and make us see them as part of the whole picture: and we can enjoy his own papers for their light on our immediate problems as well as for the lucid writing which commands our interest.

Throughout his career Bremer has influenced the development of research on the central nervous system. We have profited by the methods he has introduced and the ideas he has given us. It is a pleasure to express our thanks to such a colleague and to send our congratulations on his seventieth birthday.

ADRIAN

Contents

Participants in the Pisa Colloquium	vii
Introductory remarks on behalf of IBRO and UNESCO by H. H. JASPER	ix
Introductory remarks by the Honorary President by F. BREMER	xi
Dedication to Professor Bremer by Lord ADRIAN	xv
Contents	xvii
Postsynaptic and presynaptic inhibitory actions in the spinal cord by J. C. ECCLES (Canberra, Australia)	1
Recurrent inhibition as a mechanism of control by R. GRANIT (Stockholm)	23
Studies of the integrative function of the motor neurone by J. M. BROOKHART and K. KUBOTA (Portland, Oreg.)	38
The plasticity of human withdrawal reflexes to noxious skin stimuli in lower limbs by K.-E. HAGBARTH and B. L. FINER (Uppsala, Sweden)	65
Reticular homeostasis and critical reactivity by P. DELL (Paris)	82
Thalamic integrations and their consequences at the telencephalic level by D. ALBE-FESSARD and A. FESSARD (Paris)	115
Influence of unspecific impulses on the responses of sensory cortex by S. P. NARIKASHVILI (Tbilisi, U.S.S.R.)	155
The tonic discharge of the retina and its central effects by A. ARDUINI (Pisa, Italy)	184

Multisensory convergence on cortical neurons: Neuronal effects of visual, acoustic and vestibular stimuli in the superior convolutions of the cat's cortex by R. JUNG, H. H. KORNUBER and J. S. DA FONSECA (Freiburg/Br., Germany)	207
The direct cortical response (DCR). Associated events in pyramid and muscle during development of movement and after-discharge by S. MINGRINO, W. S. COXE, R. KATZ, S. GOLDRING and J. L. O'LEARY (St. Louis, Missouri)	241
Brief survey of direct current potentials of the cortex by J. L. O'LEARY (St. Louis, Missouri)	258
Studies of non-specific effects upon electrical responses in sensory systems by H. H. JASPER (Montreal, Canada)	272
Aspects of sensorimotor reverberation to acoustic and visual stimuli. The role of primary specific cortical areas by P. BUSER, P. ASCHER, J. BRUNER, D. JASSIK-GERSCHENFELD and R. SINDBERG (Paris)	294
New data on the specific character of ascending activations by P. K. ANOKHIN (Moscow)	325
The characteristics and origin of voluntary movements in higher vertebrates by I. S. BERITASHVILI (Moscow).	340
Responses in non-specific systems as studied by averaging techniques by MARY A. B. BRAZIER (Cambridge, Mass.)	349
A transcranial chronographic and topographic study of cerebral potentials evoked by photic stimulation in man by H. GASTAUT, E. BEEK, J. FAIDHERBE, G. FRANCK, J. FRESSY, A. RÉMOND, C. SMITH and P. WERRE (Marseille, France)	374
Specific and non-specific responses and autonomic mechanisms in human subjects during conditioning by W. GREY WALTER (Bristol, Great Britain).	395
Sleep mechanisms. Chairman: J. M. BROOKHART	404

General discussion on inhibition.	
Chairman: F. BREMER	444
Final discussion	453
Author index	475
Subject index	481