

Neurophysiology

A conceptual approach

Fifth edition

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Dark mysteries are here – old pathways, secret places
Under the tangled cortex, grown snugly thick now:
Intricately synapsed: electrode-proof



Gratefully dedicated to Christine and Mary

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PREFACE TO THE FIFTH EDITION

Since the last edition, the internet has arrived in earnest. Does this mean the death of the textbook? Are students no longer to read? No; but a very positive consequence of all this is that reading becomes less of a reflex activity. No longer will heads be bowed over turgid texts as line after line is dutifully enhanced with fluorescent highlighter; it is now permissible to *think* a little before deciding whether, and what, to read. Time is precious: one should never pick up a book without asking a preliminary, and rather fundamental, question: Why am I doing this? Is it to look up a specific fact? Is it to understand an elusive concept? Or is it to gain an overall perspective of a topic on a more expansive canvas? So much of the mind-numbing cramming that medical students in particular have to endure is, quite literally, meaningless. But it need not be like that.

To be sure, from the point of view of not killing people, nothing could be more important than memorizing the proprietary names of pharmaceutical substances. But from the point of view of developing one's intelligence and nurturing one's imaginative powers – of learning how to be a *producer* rather than a consumer of knowledge – nothing could matter less. The internet is only a threat to the kinds of books that merely list facts. *Neurophysiology*

has never been a conventional book; its special qualities mean that it is needed more than ever as an adjunct to what is so easily available online. But the facts are still of course there, complemented now by new sections that explicitly relate science and clinical practice; these are supplemented by a comprehensive set of practice MCQs.

We believe passionately that – like scientists – some doctors at least should be permitted to *think*, and it is this prejudice that permeates the pages of this book. Since thinking is also quite fun, once you get used to it, we hope that you will enjoy the experience of reading it.

It is a pleasure to acknowledge our indebtedness to the students who have provided valuable feedback about previous editions of the book as well as identifying those particularly sticky areas that they needed us to address; to Dr Deborah Field and Dr Danielle Reddi for clinical comment; to Dr Joanna Koster, Stephen Clausard and Amina Dudhia at Hodder; to Dr Sanjay Manohar; to Lotika Singha; and to the various authors and publishers where mentioned for permission to reproduce material.

Roger Carpenter and Benjamin Reddi
Cambridge and Adelaide, 2012



PREFACE TO THE FOURTH EDITION

The rapid march of technology means a CD-ROM rather than diskette, and therefore very much more in the way of goodies. NeuroLab is still there, in an improved form that – thanks to it having been translated into Java – no longer insists on being run on a PC: Macs welcome! But in addition we have full-colour illustrations, short video clips of neurological interest, a complete brain atlas of histological sections and scans, with interactive labels and the ability to do self-tests, a selection of audio material relating to sound perception and disorders of speech, a somewhat experimental three-dimensional interactive brain, and of course a complete version of the text, with the advantage that you can search it for individual words. Meanwhile the book itself has had a spring-clean, with much rewriting and additional material and redrawing of the illustrations, a new Appendix on methods of studying the brain, and a large number of completely new figures.

Much of this has been due to the hard work of a number of present and former students: I would like to thank Robin Marlow, Oliver Sanders and especially Sanjay Manohar for their brilliant translation of NeuroLab into Java, Dr Dunecan Massey and Dr Chris Allen for the video material, Alice Miller for her work on the brain atlas, and Ruaraidh Martin, Atman Desai and Atanu Pal for their contributions to the rotatable brain. Lastly, I must acknowledge a huge debt to Ben Reddi, whose trenchant criticisms and suggestions have immeasurably strengthened both text and figures.

R. H. S. Carpenter
Montalcino, 2001

PREFACE TO THE THIRD EDITION

Most of neurophysiology is concerned with dynamics, with sensory coding, with feedback, with plasticity and stability. These are easy concepts to teach to a few students round a table, with a plentiful supply of paper to scribble on, less easy to convey in a book. But the coming of age of the personal computer has changed all that, and with NeuroLab you have the opportunity – the first of its kind – to experiment with model systems and see for yourself how they respond, as well as having the chance to try out experiments and demonstrations on yourself. It has been fun to develop, and I am certain that you will find it fun to use. Meanwhile, the text has been thoroughly revised and updated, with some changes of emphasis, and a more extensive use of supplementary notes, that are indicated

with the following symbol in the text: . The increasingly molecular approach to much of neurophysiology is an unwelcome trend in many ways, not least for the medical student who faces the 'anatomization' of yet another area of study – how soon will it be before they are required to memorize stretches of DNA? But it has also brought with it some unifying simplifications which have helped to bring a little more tidiness to certain areas.

Once again, to my students huge thanks for their stimulation and support, particularly in fine-tuning NeuroLab to meet their needs.

R. H. S. Carpenter
Studland, 1995

PREFACE TO THE SECOND EDITION

A second edition has provided an opportunity to remedy some defects in the first. One of which I was particularly conscious was that in trying to achieve a connected and coherent narrative, I had sometimes neglected to be sufficiently exhaustive in enumerating the factual detail that is so greatly enjoyed by both students and examiners. This has now been rectified by the use of boxes containing tables and other systematic information outside the text itself. In addition, a number of topics receive a wider coverage; these include: pain, subcortical visual mechanisms, eye movements, central auditory mechanisms and the hypothalamus. Finally, an attempt has been made in the

last chapters to distil from the preceding ones some kind of answer to that troublesome question that students so frequently ask: what principles govern the processes that convert patterns of sensory information into patterns of behaviour? What, in short, does the brain do?

As always, I owe a special debt to my long-suffering students for acting as guinea pigs for certain lines of approach, and for their encouragement and criticism.

R. H. S. Carpenter
Talloires, August 1989

PREFACE TO THE FIRST EDITION

The supervision system practised at Cambridge and elsewhere brings many benefits both to teacher and taught: not least, that lecturers are brought face to face with the results of deficiencies in their own teaching in a peculiarly immediate and painful way. What has seemed to many supervisors a most worrying trend over the last 10 years or so is the extent to which a student may come away from a series of lectures on (let us say) the circulation, with an impressive amount of detailed information, including perhaps the minutiae of experiments published only a month or two previously, yet with little sense of what might be called function: of what the circulation really does, of how it responds to actual examples of

changed external conditions, and how it relates to other major systems. And in the case of the central nervous system things seem even worse: a student may acquire an immensely detailed knowledge of the anatomical intricacies of the motor system, yet not be able to tell you even in the broadest terms what the cerebellum actually does, or have the slightest feel for what kinds of processes must be involved in such an act as throwing a cricket ball. The result is much knowledge, but little understanding, and very little sense of ignorance.

I believe this to be the result of two factors. The first is, paradoxically, that over the last decade or so, Universities and Teaching Hospitals have quite rightly begun to take

teaching much more seriously than once was the case, and consequently a perfectly laudable sense of competition has developed amongst lecturers to gain the approval of their audiences. But students – at least in the short term – tend to form judgements rather on the basis of the number of ‘facts’ that they have succeeded in copying down in the course of a lecture: the more recent these facts are, the better they are pleased. Lecturers naturally respond to this by filling their lectures with increasing amounts of detail, at the expense of fundamental principles. The students’ notebooks swell with quantities of undigested information, but they are bewildered – even resentful – when asked simple but basic questions like ‘how does a man stand upright?’. This change in emphasis has made physiology less enjoyable either to study or teach than it used to be, as well as less educational in the broadest sense: there is no time and little motivation to ask questions of oneself, and all is reduced, in the end, to rote-learning.

The second factor that has debased the intellectual quality of much of our teaching is the increasing emphasis that is put on mechanism instead of function. More time is often spent in talking about the detailed physics of nerve conduction than in discussing exactly what information is being carried by nerves, how it is coded, and how the nervous system is actually used. Again, lecturers’ fear of instant student opinion is perhaps partly the cause: most students get immediate and easy satisfaction (of a limited kind) by seeing the detailed steps that cause a particular phenomenon; and if all can be reduced to a series of biochemical reactions, then so much the better. To understand whole systems and their interactions requires rather more effort of thought, and one can never be sure one is right. But in the long run, and most particularly for medical students, it is precisely the large-scale functioning of physiological systems that is important. A doctor needs to have a feel for what is likely to be the consequence of chronic heart failure in terms of problems

of fluid balance, or for what may happen if his asthmatic patient decides on a holiday in the Andes. Whether the cardiac action potential is due mainly to calcium or to sodium, and whether or not the substantia nigra projects to the red nucleus, are for him matters of singularly little interest or significance.

This book is an attempt to go counter to this trend by starting from the premise that a more satisfactory way to teach physiology is to build a scaffold of general principles on which factual details may later be hung as the need arises, and to prefer to consider what systems do rather than how they do it. However, this is largely a matter of emphasis and organization rather than of content, and the reader will find details of mechanism if they are required. Above all, the aim has been to recreate something of the intellectual excitement to the study of physiology that has been lost sight of in recent years, and to encourage the student to think and to question. If it is at all successful in this, the thanks should go not to me but rather to those past and present students of mine for whose intellectual stimulation I am – as all teachers must surely be – deeply indebted.

Cambridge, 1984
R. H. S. Carpenter

It is a pleasure to acknowledge my indebtedness to Dr Susan Aufgaerdem, Professor George L. Engel, Mr Austin Hockaday, Dr J. Keast-Butler, Dr Richard Kessel, Dr Peter Lewis, Dr J. Purdon Martin, Dr N. R. C. Robertson, Dr T. D. M. Roberts and Mr Peter Starling for their help in providing illustrations; to the editors and to the staff of Hodder Arnold for their criticisms and support; to various authors and publishers where mentioned for permission to reproduce material; and above all to the late Dr R. N. Hardy, who died so tragically while the book was in its final stages: his friendly encouragement, and his qualities of wisdom and humanity are sadly missed by all who knew him.

NEUROLAB AND OTHER WEB RESOURCES

Play is a serious matter. It is the way in which the developing brain learns the correlations that define our conceptual models of how the world functions. And what is science if not the construction of such models? One of the sadder aspects of how the teaching of science in schools has declined is the near-elimination of play, partly because of lack of time, and to a large extent through overzealous application of Health and Safety. Fortunately we still have the playgrounds provided by the great science museums: the Exploratorium in San Francisco, the Deutsches Museum in Munich, the pioneering Exploratory in Bristol, the Dutch Continium, the Science Museum in London. Their interactive exhibits enable the visitor to probe the world in focused and challenging ways, the pleasure that this affords the receptive mind demonstrated by the excited hubbub they provoke – and not just from children.

NeuroLab is a series of ‘exhibits’ of this kind. They enable the reader to try out some of the concepts presented in this book in an interactive way, supplementing the relatively superficial learning that comes through reading with the more profound knowledge that comes through *doing*. Full instructions about how to use each

exhibit are listed by chapter under the NeuroLab section of the website; they are also provided at the end of the relevant chapters of the print book (flagged in the text with a computer symbol), to enable their use alongside the text.

In addition to NeuroLab itself, we provide some other resources that we hope will be useful:

NeuroScan and **NeuroSlice** – brain sections as scans and histological images, with facilities for self-testing, an indispensable aid to learning neuroanatomy

NeuroSound – sound clips illustrating the chapter on the auditory system (flagged in the text with a headphone symbol)

NeuroVid – a comprehensive set of movie clips showing the components of a standard clinical neurological examination (flagged in the text with a clipboard symbol)

NeuroQuestions – sixteen sets of interactive MCQs

In order to access these resources – as well as the VitalSource e-book, complete with downloadable images – please refer to the instructions on the inside front cover of this book.

