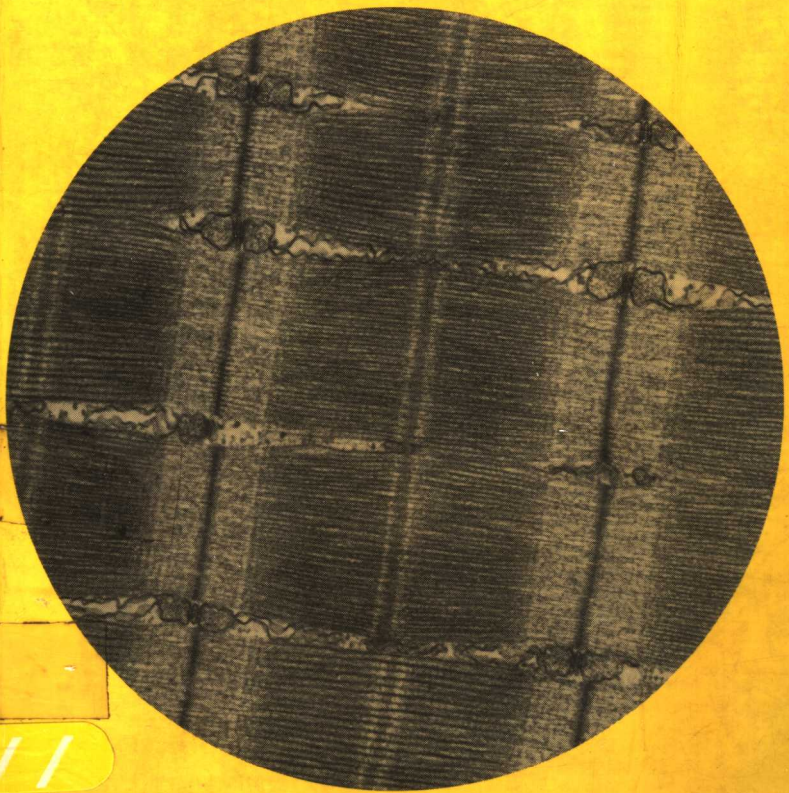
Comparative Neurobiology

P. J. Mill

CONTEMPORARY BIOLOGY



Comparative Neurobiology

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CONTEMPORARY BIOLOGY

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A series of student texts in

CONTEMPORARY BIOLOGY

Preface

The primary aim of this book is to serve as an introductory neurobiology text for undergraduates. As far as possible the approach is comparative, with examples chosen from both invertebrate and vertebrate work, since I feel that this will help to give the reader a greater feeling for, and depth of understanding of, neurobiology. The first chapter deals with the structure of nerve and muscle. Nerve and muscle cells share the ability not only to maintain a large potential difference across their surface membranes (Chapter 2), but also to restore this potential difference after a change in its level has been effected by an event external to the cell, such as an environmental stimulus or activity in another nerve cell. Information passes from one cell to the next via narrow discontinuities, called synapses, which in most cases only conduct the information in one direction. Two types of potential change occur, graded potentials and action potentials. Graded potentials are not propagated and are hence decremental and serve for integration at a local level, while action potentials have an 'all-or-none' property and are propagated and hence are used to code information for transport over long distances. The concept of excitability and the basic differences between the two types of potential change are dealt with in Chapter 3. Chapter 4 is concerned with the graded potentials, which occur both in sensory cells, as a result of the transduction of external stimuli, and postsynaptically in nerve and muscle cells. Chapter 5 considers synaptic transmission in more detail, while Chapter 6 deals with the action potential and Chapter 7 with muscle physiology. The next two chapters are concerned with the structure and physiology of the

various types of sense organs, Chapter 8 dealing with mechanoreceptors, Chapter 9 with photoreceptors, chemoreceptors, thermoreceptors and electroreceptors. Central nervous systems and the integration of sensory information are dealt with in Chapter 10, while the last chapter considers the neural control of behaviour, a rapidly expanding area of neurobiology. The figures have been carefully selected to supplement the text and to cover a wide range of literature. Further references, in the form of reviews, edited volumes and books are given at the end of the book. These methods of referencing should provide the reader with sufficient sources to enable him or her to follow up any area of neurobiology, and have the merit that the flow of the text is not interrupted by innumerable literature references.

I should like to thank Professor E. J. W. Barrington, F.R.S., who suggested to me that I should write this book, and who has since offered encouragement and much useful advice, and the staff of Edward Arnold for their help, particularly during the editorial stages. I should also like to thank my wife for her continued support and understanding throughout the preparation and writing of this book.

University of Leeds,
1982.

P.J.M.

Contents

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The Structure of Nerve and Muscle

NEURONS (NERVE CELLS)

Neurons which conduct information towards the central nervous system are classically called ***sensory*** or ***afferent neurons***; those which conduct information out from the central nervous system are called ***motor*** or ***efferent neurons***; while those which are contained completely within the central nervous system and whose function it is to distribute and integrate information within the latter are termed ***interneurons*** or, in vertebrates, ***internuncial neurons***. Implicit in this definition of interneurons is that they both receive information from, and transmit it to, other neurons. However, there are some neurons which do not fall neatly into one of the above three categories. These are the so-called dual-function neurons which have an output both on to other neurons and on to an effector organ such as a muscle. An example of this type of neuron is the Right Pedal Giant (RPG) of molluscs. Many mammalian motor neurons could also be ascribed to this category as they synapse with interneurons (the Renshaw cells) as well as with muscle fibres (see p. 204). In this case, however, the Renshaw cell is a controlling device for the same motor neuron which synapses with it and is thus functionally an integral part of the motor output.

All neurons have certain features in common, but there is no such thing as a typical neuron—Fig. 1.1 shows just a few of the many different forms which they take. There is always a cell body (***soma***) and, in many cases, a division of the peripheral processes into one or more which receive information (***dendrites***), and one which conducts information towards the next cell (***axon***).

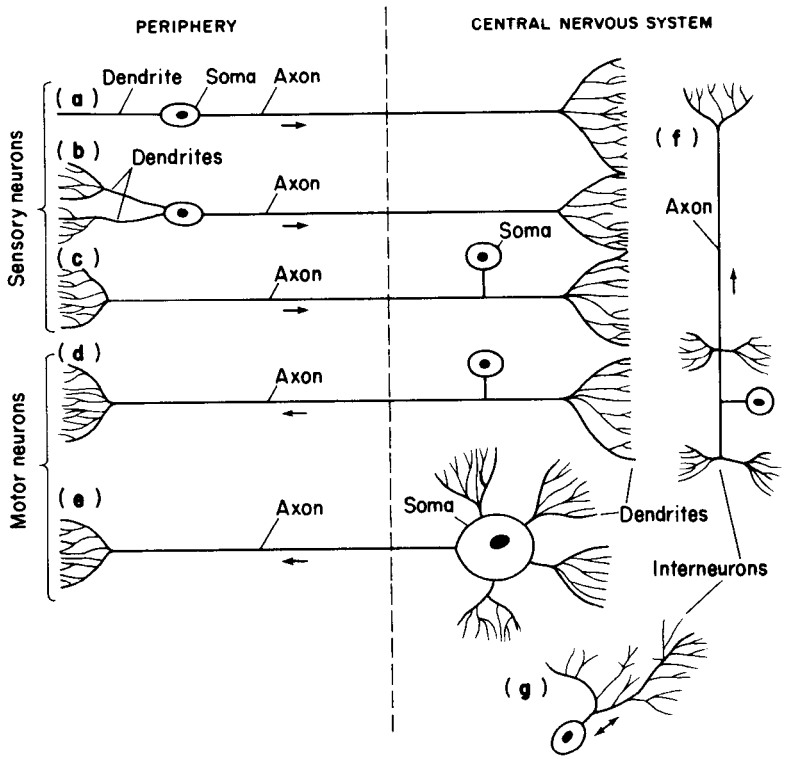

Fig. 1.1 Diagrammatic representation of a selection of neuron types. (**a**) Arthropod bipolar sensory neuron; (**b**) arthropod multipolar sensory neuron; (**c**) vertebrate sensory neuron; (**d**) arthropod motor neuron; (**e**) mammalian motor neuron; (**f**) arthropod intersegmental interneuron; (**g**) amacrine cell (local interneuron). Arrows indicate the direction of information flow.

Arthropod sensory neurons (Fig. 1.1a,b) nearly always have their cell body in the periphery and, in addition to a long axon, have either one dendrite (bipolar cells; Fig. 1.1a) or several dendrites (multipolar cells; Fig. 1.1b). The dendrite of a bipolar cell may be unbranched, as in some stretch receptors (p. 129) and in chordotonal organs (p. 140), or branched as in the majority of stretch receptors (p. 129). The dendrites of multipolar cells are typically branched. In contrast to these neurons the cell body of the vertebrate sensory neuron (Fig. 1.1c) lies in a ganglion adjacent to the nerve cord and is connected to its axon by a short process, an arrangement termed pseudo-unipolar. The relationship between the soma and its processes in the arthropod

motor neuron (Fig. 1.1d) is similar to that in the vertebrate sensory neuron, while the mammalian motor neuron (Fig. 1.1e) has several branched dendrites arising directly from its soma and is thus a multipolar neuron. The axon of all these cells is branched at one end and the terminations of the branches are often dilated into 'axon terminals'. Interneurons may also have a long axon (Fig. 1.1f).

If can be seen from the above examples that there is a functional paradox in the use of the term 'axon'. In the arthropod sensory neuron information in the form of action potentials (see Chapter 7) is transmitted along the axon away from the cell body, whereas in the vertebrate sensory neuron the axon transmits information towards the cell body over much of its length. Thus the term axon is applied to any long nerve cell process which is unbranched except at its end(s). However, it also applies to the long processes of interneurons which, in many instances, have side branches (Fig. 1.1f).

There are many interneurons in which an axon, as defined above, is not present. One example is the amacrine cell (microneuron), which has a single, branched process (Fig. 1.1g), some branches of which receive information whilst others distribute it; although it cannot be ruled out that some branches may do both. The branches are all of limited extent and, in arthropods for example, remain within the confines of the ganglion which contains the cell body.

When fixed and stained in what is currently the conventional manner for examination in the transmission electron microscope (i.e. fixation in glutaraldehyde with post-fixation in osmium, followed by staining the sections with lead citrate and uranyl acetate), sections of a neuron reveal the following structure.

The cell is surrounded by a membrane consisting of a light zone bordered by two electron dense zones, each zone being about 2.5 nm wide. It is not obviously different from other plasma membranes and, like them, is called a unit membrane. The appearance of this membrane has been explained as a double layer of phospholipid molecules sandwiched between two layers of protein molecules (Fig. 1.2). The phospholipid molecules each have a centrally directed hydrophobic (water-repellent) non-polar region and an outwardly directed hydrophilic (water-attracting) polar region; the protein molecules are attached to the latter. Ion channels (pores) in the membrane may well be lined with protein, and the passage of ions through them (pp. 33, 77) may be regulated by their diameter and/or by the charge on their walls.

The nucleus of a neuron often has a prominent nucleolus (or nucleoli). Rough endoplasmic reticulum is fairly abundant in the soma region and smooth endoplasmic reticulum associated with

vesicles (Golgi body) is often in evidence. Where the rough endoplasmic reticulum is juxtaposed to the Golgi body there tends to be a heavy concentration of ribosomes. This corresponds to the Nissl substance of light microscopy. Neurotubules (microtubules) occur in

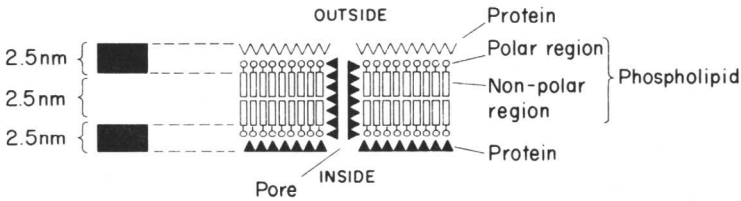

Fig. 1.2 Hypothetical structure of the unit membrane of a neuron. Its appearance in the electron microscope after osmium treatment is indicated on the left hand side. (After Usherwood, P.N.R. (1973). *Nervous Systems.* Studies in Biology, no. 36. Edward Arnold, London.)

both soma and axon, particularly the latter, where they are longitudinally oriented. With appropriate fixation techniques they have also been observed in the axon terminals. Details of the regions associated with connections between neurons or between neurons and muscles (synapses) will be deferred until the structure of muscles has been dealt with (see p. 22).

SHEATH CELLS

Associated with neurons are other cells which ensheath them. Within the central nervous system the ensheathing cells are called ***glial cells*** in invertebrates and ***oligodendrocytes*** in vertebrates; in the periphery they are usually referred to simply as ***sheath cells*** in invertebrates and ***Schwann cells*** in vertebrates. In receptors, other names are often used for sheath cells which have a particular functional or structural relationship with the receptor ending. Examples are the tormogen and trichogen cells of insect hairs (p. 117), and the enveloping, scolopale and canal cells of crustacean chordotonal organs (p. 143).

The sheath cells are generally small in volume in comparison with the neurons, although in the central nervous system they often have many ramifying processes. Several cells are required to ensheath a long axon, although at any one point along its length there is generally only a single sheath cell. Several small diameter axons may share a common sheath cell (Fig. 1.3a), but large diameter axons

generally have their own (Fig. 1.3b). The juxtaposition of the sheath cell against itself is called the ***mesaxon***. The most complex arrangement seen in invertebrates is when the sheath cell is wrapped several times around an axon (Fig. 1.3c), but in many vertebrate peripheral

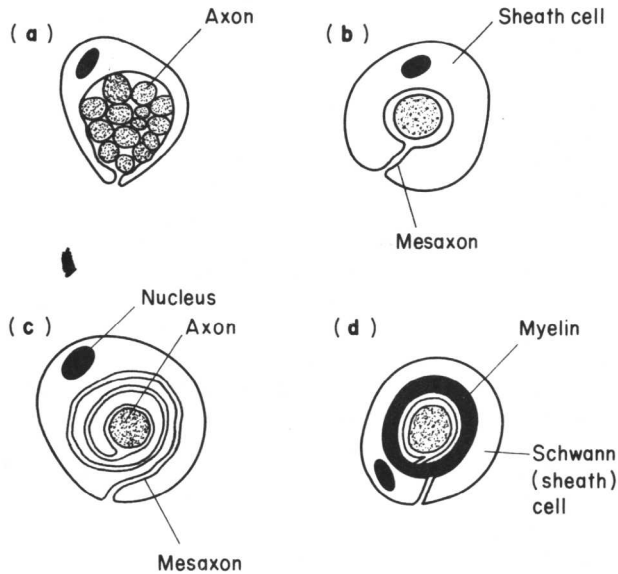

Fig. 1.3 Diagrams illustrating the types of axon sheath cells. (**a**) A group of several small axons surrounded by a single sheath cell; (**b**) an axon with a single sheath cell and a simple mesaxon; (**c**) an axon surrounded by a sheath cell which is wrapped several times around the axon; (**d**) an axon with a myelin sheath.

axons the enveloping layers of the Schwann cells become closely apposed to each other and fuse to form a myelin sheath (Fig. 1.3d). Such axons are said to be ***myelinated*** or ***medullated***. Since a number of Schwann cells are required to ensheath a whole vertebrate axon, discontinuities occur in the myelin sheath where adjacent Schwann cells meet. These discontinuities are called ***nodes of Ranvier.***

MUSCLE CELLS

Muscles consist of a number of cells or ***muscle fibres*** which may or may not have a striated appearance. In striated muscles the striations either run at right angles to the longitudinal axis of the muscle fibres

(***cross-striated muscle***), or are oriented at an oblique angle (***obliquely striated muscle***). Non-striated muscle is generally called ***smooth muscle***.

All muscle fibres contain protein filaments concerned with the contractile mechanism, as well as sarcoplasmic (endoplasmic) reticulum and mitochondria (sarcosomes). They may possess a single nucleus or be multinucleate.

Cross-striated muscle

All arthropod muscles and vertebrate skeletal and cardiac muscles are cross-striated. Each muscle fibre contains two types of longitudinally oriented protein filaments, generally referred to as ***actin*** and ***myosin***, but often called thin and thick filaments respectively. These filaments are organized to varying extents in different muscles into groups called ***myofibrils***. Within each myofibril, and to some extent between adjacent myofibrils, the actin and myosin filaments are each closely aligned. It is primarily this alignment which gives cross-striated muscle its characteristic appearance (Fig. 1.4a–c).

Under the light microscope the individual myofilaments are not visible, but the striations resulting from their alignments can be seen clearly. Thus zones of high birefringency (Anisotropic- or A-bands) alternate with zones of lower birefringency (Isotropic- or I-bands) along the length of the muscle fibre. Under the electron microscope the same basic appearance is seen, with the A-bands darker (i.e. more electron-dense) than the I-bands (Fig. 1.4a–c). Each I-band is bisected, at right angles to the fibre, by a dark narrow line, the Z-line; while the centre of the A-band is generally observed to have a lighter region (the H-zone). The H-zone often has a dark central M-line bounded on either side by a very narrow light zone; this is especially noticeable in vertebrate muscles.

The region between two successive Z-lines is called a ***sarcomere***. Its length varies in different muscles (also in the same muscle, depending on the degree of contraction; see Chapter 7). In relaxed vertebrate skeletal muscle the sarcomere is about 2.5 μm long. In insect flight and cardiac muscle it is of similar length (2–4 μm), but is longer in

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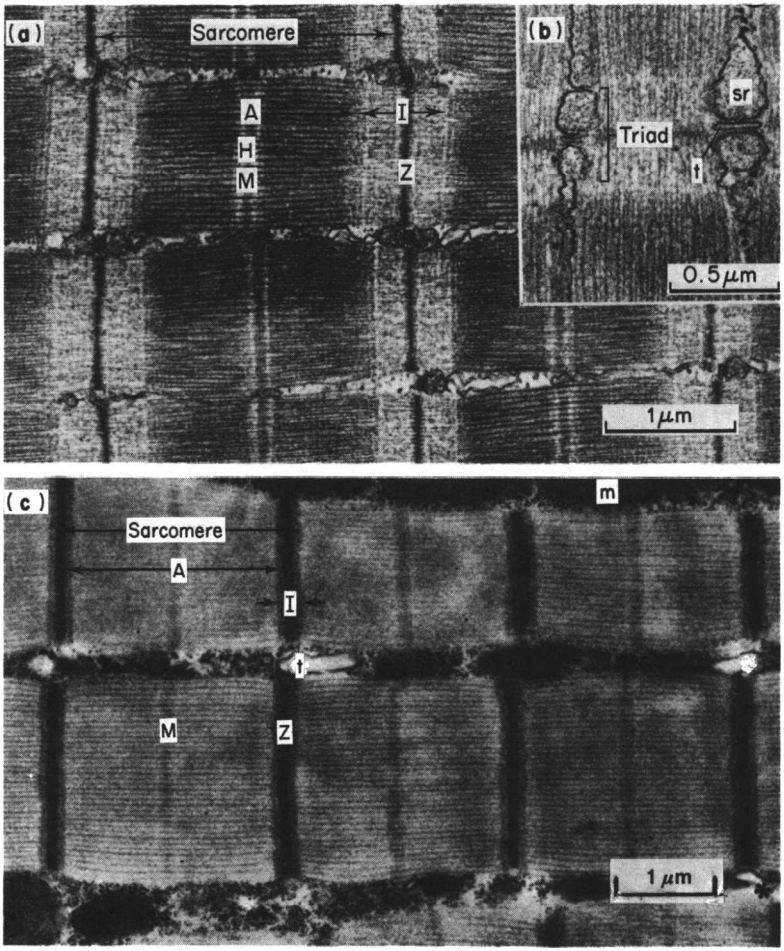
Fig. 1.4 Cross-striated muscle. (**a**), (**b**) Electron micrographs of longitudinal sections of frog skeletal muscle; (**c**) electron micrograph of longitudinal section of aphid flight muscle. (**d**) Diagram of a longitudinal section through a sarcomere to show the principal regions and to illustrate the relationship between the filaments and these regions. A, A-band; H, H-zone; I, I-band; M, M-line; m, mitochondrion; sr, sarcoplasmic reticulum: t. T-system tubule: Z. Z-line. ((**a**). (**b**) From Franzini-Armstrong, C. (1970). *Journal of Cell Biology*, **47**, 488–99; (**c**) from Smith, D. S. (1965). *Journal of Cell Biology*, **27**, 379–93.)


(a)
Sarcomere
A
H
M
I
Z
(b)
sr
Triad
t
0.5μm
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(c)
m
Sarcomere
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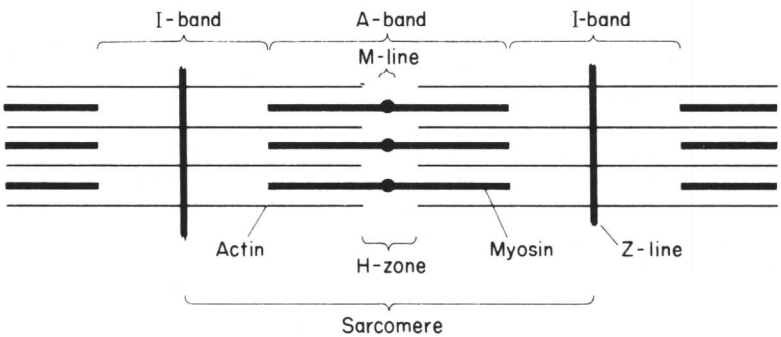
1μm

(d)


I-band
A-band
I-band
M-line
Actin
H-zone
Myosin
Z-line
Sarcomere

other insect skeletal (3–7 μm) and visceral and alary (7–8 μm) muscles.

Examination with the electron microscope has revealed the detailed structure responsible for the cross-striations. The actin and myosin filaments are arranged in overlapping bands. Thus the I-band contains only actin filaments, attached at one end to the Z-line, while the A-band contains myosin and the ends of the actin filaments (Fig. 1.4d). In relaxed muscle the actin filaments do not reach to the centre of the A-band and this central zone, where the myosin filaments are not overlapped by actin filaments, is the H-zone. The M-line results from a thickening of the myosin filaments in their central region.

In transverse sections, the actin and myosin filaments are seen to be arranged in a regular matrix within each fibril (Figs 1.5, 1.6).

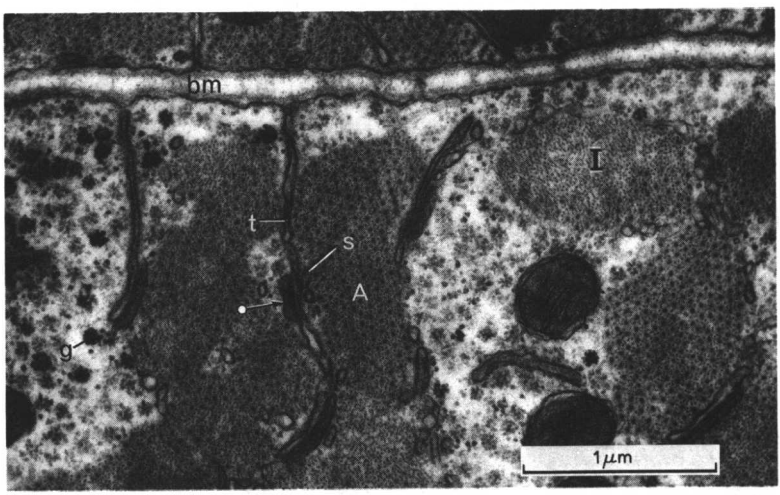


Fig. 1.5 Cross-striated muscle. An electron micrograph of a transverse section through a skeletal muscle of a dragonfly larva. Due to the slight stagger of adjacent sarcomeres in this muscle, sections through A- and I-bands can be seen. bm, basement membrane; g, glycogen; s, sarcoplasmic reticulum; t, T-system tubule; ○→, dyad. (From Mill, P. J. and Lowe, D. A. (1971). *Journal of Insect Physiology*, **17**, 1947–60.)

Figure 1.6 shows the patterns in various muscles in the region where the actin and myosin filaments overlap (i.e. in the A-band outside the H-zone). Obviously, sections through the I-band and the H-zone will show only actin and myosin filaments respectively (Fig. 1.5), but their matrices remain as in the zone where they overlap. In vertebrate skeletal muscle and insect fibrillar flight muscle, each myosin fila-