Functional Neuroanatomy

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Nicholas J. Strausfeld

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Preface

The "functional" in the title of this book not only reflects my personal bias about neuroanatomy in brain research, it is also the gist of many chapters which describe sophisticated ways to resolve structures and interpret them as dynamic entities. Examples are: the visualization of functionally identified brain areas or neurons by activity staining or intracellular dye-iontophoresis; the resolution of synaptic connections between physiologically identified nerve cells; and the biochemical identification of specific neurons (their peptides and transmitters) by histo- and immunocytochemistry.

I personally view the nervous system as an organ whose parts, continuously exchanging messages, arrive at their decisions by the cooperative phenomenon of consensus and debate. This view is, admittedly, based on my own experience of looking at myriads of nerve cells and their connections rather than studying animal behaviour or theorizing. Numerous structural studies have demonstrated that interneurons in the brain must receive hundreds of thousands of synapses. Many neurons receive inputs from several different sensory areas: each input conveys a message about the external world and possibly also about past events which are stored within the central nervous system. Whether an interneuron responds to a certain combination of inputs may be, literally, a matter of debate whose outcome is decided at the postsynaptic membrane. A nerve cell responding to an overriding command is possibly a rare event.

To understand how the nervous system works we must be able to observe its parts. How can we visualize the integrative activity of the nervous system? Only a few cells can be simultaneously recorded by intracellular electrodes and filled with dyes. Can the data obtained be sufficient for us to understand how neurons interact to generate behaviour? How are we to recognize the identity, or even the existence, of all the other neurons involved in generating even a small subroutine of a behavioural pattern? This is the substance of this book and its predecessor.

Why *insect* neuroanatomy? Why do certain neurobiologists eschew mice, cats and monkeys? Insects are indisputably more convenient experimental

animals. It matters not a whit that they have exoskeletons and compound eyes. What interests the neurobiologist is that insects have hundreds of thousands of nerve cells, synapses, axons and dendrites, organized in much the same way as those of vertebrates, and that insects have predictable patterns of behaviour. It is also mighty handy to put all the sections of a cricket or fly central nervous system on one slide and to tour through all its sensory and motor projections to and from recognizable regions of neuropil.

Alongside nematodes, gastropods, annelids and crustaceans, insects offer unique opportunities in neurobiology. One is the study of genetic control of CNS development and structure where neurological defects can be related to the chromosomal map and, eventually, to molecular genetics. Another is the study of cell lineage in early development of the nervous system (although arguably the leech is a length ahead): segmentation, neuronal differentiation and pathfinding by identified neurons at the cellular and molecular level. Yet another is the study of integration by uniquely identified neurons that are involved in specific behaviour patterns. I refer particularly to identified neurons in multimodal sensory pathways controlling locomotion – ranging from "simple" jump responses, through control of flight or walking, to the courtship of fruit flies or grasshoppers where we may expect to find a high level of pattern recognition by single neurons. Despite the use of the word, none of these behaviours is "simple" in terms of the sheer number and variety of neurons involved.

Many behaviours, sophisticated or otherwise, may also be modulated by peptidergic systems. To understand the role of these vertebrate-like neuropeptides it is necessary to identify the neurons that contain them and to see these in the context of sensory-motor pathways. Again, insects provide compact but behaviourally sophisticated nervous systems for this line of research.

The purpose of this volume is to describe strategies that hopefully will encourage more substantial descriptions of neuronal control mechanisms. This book is the promised follow-up of *Neuroanatomical Techniques: Insect Nervous System* edited by Thomas A. Miller and myself which is hereafter referred to as Vol. 1. That volume (published in 1980) dealt mainly with the application of more classical techniques to insect central nervous systems. It also included electron microscopy and intracellular dye injection methods as well as several chapters on cobalt techniques – one of the most powerful neuroanatomical methods for structural studies of invertebrate and amphibian nervous systems.

As in Vol. 1, certain subjects in this one are covered by several chapters, e.g. multiple cell marking. Many of us recognize the need to expand our tunnel vision, particularly when we look into the electron microscope. Thin sections restrict our view severely, unless we can distinguish landmarks belonging to something familiarly three-dimensional. Methods that allow us to recognize as many as three differently marked neurons that were selected earlier in

thick sections in the light microscope are a logical development from electron microscopy of the classical Golgi method (see Chaps. 1, 3 and 6).

As in Vol. 1, chapters are grouped together to cover specific fields. Chapters 1–5 include electron microscopy of marked neurons (Golgi, cobalt, nickel, heme proteins) followed by a chapter about combined techniques (Chap. 6). Chapter 7 describes the histology for Lucifer yellow marked neurons, and Chaps. 8 and 9 outline computer reconstructions for displaying structural data obtained by this and other methods. Direct anatomical-functional correlates are the subject of Chaps. 10 and 11 (both of which truly represent functional anatomy). The next six chapters deal with the biochemical (peptide and transmitter) identity of neurons both in the light and electron microscope. The last two chapters focus on the detailed aspects of cell contacts and synapses using freeze fracture and high-voltage electron microscopy.

I would like to thank all the authors for their contributions and some for their patience while later manuscripts came in. My thanks also go to Springer-Verlag for their civilized custom of waiting almost sublimely, without too frequent breathing down my neck. I am also grateful to Wendy Moses and Heide Beschorner for typing some of the manuscripts, to Renate Weisskirchen for printing many of the photographs and to Susan Mottram for researching incomplete references. Eduardo Macagno and Corey Goodman kindly donated data and figures for Chap. 6 (Figs. 8, 9) and Chap. 16 (Fig. 8), respectively.

Special and personal thanks go to Sir John Kendrew, F.R.S. to whom this book is dedicated. As founding Director-General of the European Molecular Biology Laboratory (which was conceived as an institute for fundamental biological research), he encouraged the individual scientist and provided the wherewithal for a small group of insect neurobiologists, all of whom benefited greatly from his sponsorship. He in no small way contributed to the achievement of this and the preceding volume.

Finally, I thank Camilla, my wife, for the effort she put into this book – language editing and condensing many of its chapters – and for her help and love.

Heidelberg, August 1983 NICHOLAS J. STRAUSFELD

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