Book Review

Brain, Behavior and Evolution

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## Arthropod Brains: Evolution, Functional Elegance and Historical Significance

Belknap Press, Cambridge 2012
848 pp.; GBP 48.95/USD 65.00
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This is a marvelous book, but readers – take a hard look at the title and beware. I reckon it is a subtle advertisement to attract a new generation of elite neuroanatomists and breathe life into that essential but difficult way of life.

Because modern molecular techniques for phylogenetic reconstruction are in their infancy, the 'evolution' of the arthropod brain is still mostly 19th century intuitive guesswork but excellent for armchair discussion. The 'functional elegance' of dozens of related but different brains, when stained, is a powerful stimulant for the human mind but not testable experimentally. The 'historical significance' mentioned in the title seems to consist mainly of exceptional experts who turned up irregularly over the decades in a wide range of countries and walks of life. Only about a dozen great neuroanatomists, well scattered geographically, contributed 90% of the work. With one-track minds, against the odds, they persisted in difficult techniques as their life's work. However, they were relatively isolated in their own time and country. Strausfeld clearly enjoyed searching out their archives and publications, and he opened up some interesting dusty cupboards.

The scientific significance of the book and of their research, on the other hand, is enormous. Surely, our understanding of brains will be accelerated by careful attention to relatively simple nervous systems. Arthropods are the place to look for a stream of advances because a large number of the individual neurons can be named and recognized again in other specimens, even in different species, so that experiments on neuron differentiation and exact function can be repeated precisely.

As the author admitted to me, however, it is really an art book. The theme, single but broad, reminds me of Kenneth Clark's *The Nude,* being 'not the subject of art but a form of art', and also of the Pitt Rivers Museum in Oxford, where every conceivable object to catch one's interest was stashed with scant regard to explanation. Page after page of detailed, elegant, colorful illustrations of sections of arthropod brains appeal simultaneously to our sense of symmetry, beauty, and curiosity. Like other profuse artistic forms, it is intended primarily to capture the mind and enlist the whole life's work of an unusual few who might take up and extend the tradition. The author says that 'labels are avoided unless absolutely necessary, so as not to clutter the beauty of structures'. This was not really a problem because the labels of brain regions are beside the point; the illustrations are promotions with the intention to enthuse. As with any magnum opus of the first water, everyone, specialist and student alike, can now browse through the best that was published, together with a lot of new work. The subject's baseline has been reset.

Many who are now professors have told me that when 'Bullock and Horridge' was published in 1965, they scanned the pages for illustrations of large nerve cells, accessible unique synapses, and simple eyes or brains to get a head start. Right now a new generation of bright young hopefuls will be scanning these beautiful illustrations with the expectation of finding a new preparation to record from, to localize activity by fluorescence, to track activated iRNA molecules or released calcium ions, to probe with soft X-rays for molecular structures, or to find the best simple brain for their new molecular biology or electrophysiological techniques. Of course, they would also require a new idea. The value of the book lies in its guidance of aspiring neurobiologists who, in this regard, face an uphill task.

There are two consolations. The kind of anatomy described in Strausfeld's book is relatively cheap, as shown by the variety of experts who had negligible funding. Secondly, the published knowledge is enduring. There is something about anatomy, especially of nervous systems with identified neurons, that is solid. The details are fixed in metal and the significance can be discussed for a century. An anatomist can say 'I describe, therefore I am'. The author traces the history of arthropod neuroanatomy back to the early 19th century, to Cuvier, Leydig, and Muller's Archiv, to the roots of what is still useful. He did not miss much, but I found one omitted monograph, on the *Triops* nervous system by E.G. Zaddach (1841), written entirely in Latin.

Who would not wish to run off and study these astonishing brains, to work out how they function. Ah, there's the rub! What to do next, and how to succeed, even with a common species? Arthropods are supposed to be simple but there are problems at every turn. Mass staining may look pretty, but the unit of the nervous system, the neuron, is the place to start. The first aim is to find the right nerve cell and recognize it again, to fulfill one requirement of science, repeatability. This is rarely achieved! Moreover, the illustrations are two-dimensional and mostly of flat sections, while brains are solid objects. To find the right place in such a solid, you must make your own sections of the brain and build up a three-dimensional understanding of the arrangement of the areas and tracts. A major challenge in this task is that some brains are difficult to stain. I remember when Strausfeld visited Canberra, I found about 1,000 specimens of one species of millipede, which were marinated in strong liquor with no successful staining. Small species or young specimens are best for the neuron anatomy, but physiology requires the large ones.

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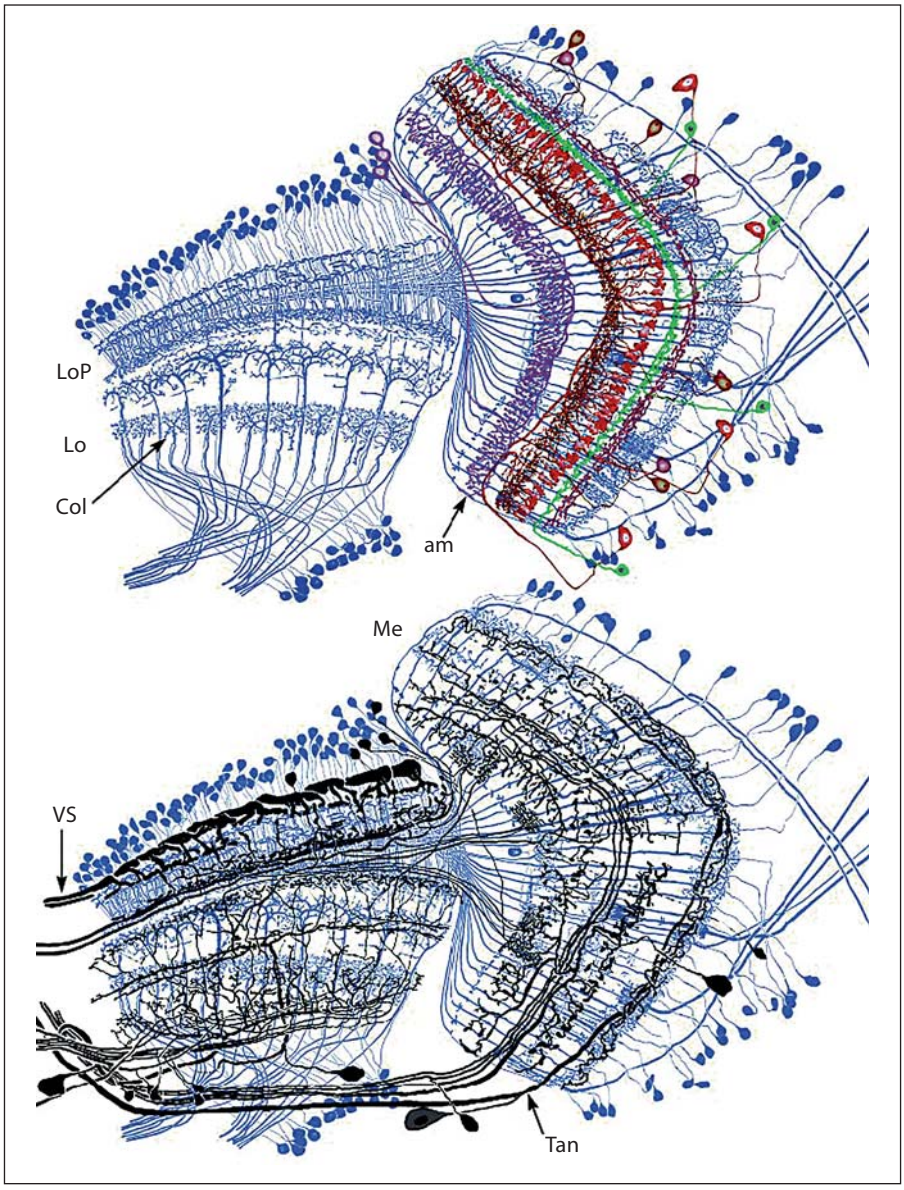


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**Fig. 1.** Optic lobes of the house fly. Two of the many examples in Strausfeld's book of sections through arthropod brains, stained by reduced silver to reveal some of the neurons. Reprinted with kind permission of The Belknap Press of Harvard University Press, ©2012 by the President and Fellows of Harvard College.

Only when you know where and when to find the same individual cell may you follow the process of differentiation or stick in an electrode and record the responses to a wide range of stimuli, inject a dye, and identify it later, slowly building up a collection. This requires long training, great patience, and a well-equipped laboratory with long-term funding. The old techniques to visualize neurons with methylene blue or reduced silver are few and tricky. The anatomy is the product of one expert; the functional analysis requires a battery of different difficult techniques by others. The small size of the nerve fibers, the electrical silence of many cell bodies, and the dense tangle of fine branched terminals and synapses, called neuropile, all hinder progress. In the second half of the 20th century, a few experts recorded diligently from neurons in the arthropod brain and ventral ganglia, but the successes came where the behavior was very well known. Even then, the behavior explained the neuron anatomy and the nerve cell activity, not the other way round. Beyond the superficial sensory inputs, efforts to explain behavior by recording from neurons with artificial stimuli in pinned down preparations were interesting but not sufficient to explain the behavior of freely moving animals.

The detailed neuron anatomy reveals that unlike vertebrate neurons, arthropod nerve cells are remarkably constant from animal to animal, so neuron maps are feasible. Most of the illustrations in this volume, however, show gross neuron topography (fig. 1) and not sensible circuits, and the chemical identification of the nerve cells reveals the cell bodies but not the connections. The anatomy tells nothing about excitation or inhibition, time constants, or other data that must come from careful electrophysiology, which at present is possible only in large animals with large neurons. *Drosophila* is really below the limit for available elec-

trodes and the nitty-gritty interactions are concealed in the tangles of fine fibers in the neuropile, not in the pattern of axons. We do not even know the alphabet or the language of active choice, learning, or recognition.

One cannot fail to notice the emphasis on works using methylene blue or reduced silver versus more recent methods. From 1974 onwards, however, there was a large effort to identify the functions of the neurons with their anatomy, as revealed in different colors by filling with cobalt or nickel ions, Lucifer dye, or peroxidase, through the electrode. The neurons could be visualized in whole cleared ganglia, and there was some hope of slowly building up a pantheon of known cells. By the end of the century, the progress was swamped by a shift of interest to molecular techniques and by loss of funding.

Also one cannot fail to notice the different treatments of deceased and living exponents of the art. Each dead anatomist gets an extensive account of tribulations and triumphs with a long list of index entries: living ones are mentioned once or twice by name in the text and get two or three indexed items, though their advances are accurately reported. Perhaps this was a wise result of careful strategy, considering that the living are still with us.

My wish list for improvement is small. The subject matter as a whole is a discussion of brain regions and their homologies, except in the olfactory and optic regions of a few type species. We scarcely reach the activity within the tracts, while the synaptic connections are still largely unknown. The significant mechanisms of recognition, organized motor action and learning have yet to be discovered. Only a few animals have been analyzed in detail; a huge diversity remains. It would be very desirable to have the 184 pages of profuse and informative notes digitized on a disc to allow for computer searches of topics. There is almost room for a third column of print on each page, but a lens is needed to read the page numbers and the print in the notes does not suit old eyes. However, every neuroscience department and dedicated professional should have a copy of this beautiful volume for browsing. It is a steal at the subsidized price.

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