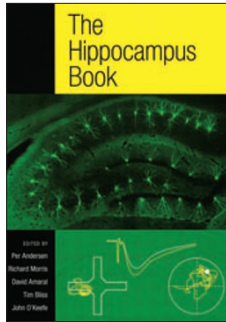


## The fame of the seahorse



### The Hippocampus Book

Edited by Per Andersen, Richard Morris,  
David Amaral, Tim Bliss and John O'Keefe

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Seahorses (genus *Hippocampus*, with about 35 species) are unique members of the class of ray-finned fishes. The male and female form a strong monogamous bond. The male stays within a territory of  $\sim 1 \text{ m}^2$ , pregnant with their eggs, while the female wanders freely around, greeting her mate warmly when she visits back home. This information raises the following questions for an ichthyologist: can we gain knowledge about fishes in general by studying seahorses as a model system, and what special features allow this creature to fulfill its ecological role? These are exactly the two questions posed by the editors of this most magnificent compilation ever written about the namesake of the hippocampus in the brain. What can we learn about the general principles of neuroscience from studying the hippocampus, and what does the hippocampus do?

Upon initially looking through the book, the answer to the first question is evidently “a lot.” The list of groundbreaking discoveries that derive from studies of the hippocampus is mind-boggling. Apparently, most branches of neuroscience have their foundation (or at least some milestones) in hippocampus research. No wonder we experienced a *Principles of Neuroscience déjà vu* while turning the pages of *The Hippocampus Book*. This volume serves as a precise guide to hippocampal discoveries, and hence we can forget about PubMed: here we have almost all of the important information about the hippocampus, in context.

Much more than just a source of elegant experimental results, the hippocampus was also instrumental in the development of new techniques and theories in neuroscience. To name just a few listed in the book, the hippocampus taught anatomists the basics of cortical microcircuits and interneuron diversity, whereas *in vitro* electrophysiologists learned—in addition to target-dependent transmitter release and the niceties of active dendrites—that synaptic weights are subject to modification. Their *in vivo* colleagues discovered the best-characterized behavior-dependent electroencephalogram pattern and the surprising representation of complex environmental stimuli (place), and developed multielectrode recording technology. Developmental neurobiologists ponder the whys and hows of adult neurogenesis, for which the hippocampus is presently

the only unquestionable example in the mammalian (including human) cortex. Neuropathology, somewhat underrepresented in the book, would be a different discipline without the hippocampal discoveries linked to epilepsy, ischemic brain damage and Alzheimer's disease. Finally, for neuropsychology, the concept of memory systems was born from the study of selective memory impairments following hippocampal damage. The hippocampus probably drew so many eminent minds—among them the editors and authors of this book—because of its almost crystal-like regular structure and central involvement in several diseases. Thus, in addition to being beautiful, the hippocampus is a perfect model system.

The far more difficult question is whether any specific features evolved to enable the hippocampal network to fulfill its role in memory. Are the operational principles required for coding complex memories similar to those involved in classical neocortical functions, such as vision, touch or motor control? Or does memory formation require a radically different cortical network, plasticity and coding strategy? Are there any features of pyramidal cells, interneurons, dendritic integration, firing properties, action potential timing, long-term potentiation and network architecture that are unique to the hippocampus, or are all of them shared by the rest of the cortical mantle? If some are exclusive to the hippocampus, are they causally related to its function? Although glimpses are allowed into these questions, the book does not focus extensively on the comparative aspects of hippocampal and neocortical circuits in its search for unique hippocampal features and their functional implications.

The reason may be that we lack the answers to several basic questions. Why does the hippocampus have a largely unidirectional information flow, whereas reciprocity in cortico-cortical connections is a general rule in all other parts of the brain? Why is there an apparent lack of recurrent connectivity among principal cells at two different stages of hippocampal information processing, whereas heavy interconnectivity is a typical characteristic of the entire cortical mantle? Why do distinct electroencephalogram patterns ‘electrically isolate’ the hippocampus from the rest of the cortex? In sum, why is the hippocampus, and only the hippocampus, able to form interference-free representations of complex environmental events (episodes)? After all, every cortical area is rich in recurrent, autoassociative networks with modifiable synapses, active dendrites and a plethora of interneuron classes, and yet, after hippocampal damage, the formation of new contextual memories is lost forever. No other cortical area, not even those having access to similar higher-order, multimodal information, can replace this simple, evolutionarily ancient structure.

Obviously, the lack of answers to these questions is not an imperfection of the book, but simply reflects the present state of our knowledge and theories of the hippocampus. The hippocampus has helped us a lot in understanding the rest of the brain, but we have not gained as much with regard to uncovering its own peculiarities. The elusive sea dragon of the brain is guarding its secrets tightly, leaving future researchers plenty to study and discover.

#### COMPETING INTERESTS STATEMENT

The authors declare no competing financial interests.

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