

ing physical constraints placed on stimulus detection, are examined. Examples for vision and hearing are most numerous, but all major sensory systems are discussed. (This appears to be the only major reference to the tactile modality in the book.) The author makes clear the need to examine sensory systems within a framework of the natural environment in which they are utilized. The biases inherent in various experimental methods used to determine sensory capabilities are also discussed.

In chapter 7, Hopkins discusses social communication in aquatic environments. The first part of the paper defines communication and reviews biological systems specialized for communication under different conditions, e.g. air versus water or fresh versus saltwater. The remainder concerns social communication in weakly electric fish. Studies on acoustic and electric signaling are considered in some depth. The latter demonstrate the usefulness of integrated behavioral-physiological-ecological studies in animal sensory biology.

Using examples in electroreception as well as other modalities, Bullock (chapter 10) covers an area that has received little attention by comparative neurobiologists. He points out many examples where the central nervous system has built-in (innate and learned) systems that 'expect' certain stimuli by controlling perceptual processes as well as certain overt behavior patterns that increase the probability of such stimulation. Information from diverse disciplines of neuroscience is synthesized using a comparative evolutionary approach. The analysis leads to the definition of what may be a fundamental property of complex nervous systems. The chapter is provocative and should be of great interest to both sensory biologists and neuroethologists.

Northcutt (chapter 34) discusses the process of adaptation, especially as it relates to sensory and neural traits. He points out that most arguments for the evolutionary adaptation of a character trait are based on correlational information which, by itself, is insufficient to support such statements. Several strategies for defining adaptive characters (traits that have originated and been maintained by the same selective process) are considered. The author spells out the 'rules of the game' using examples familiar to neurosensory biologists. The book editors justifiably state that the chapter is a fitting capstone to the volume because it deals with fundamental principles that apply throughout. This is a seminal paper which should be read and comprehended by all who wish to use the term 'adaptive significance'.

Summary

This large volume should be a useful reference to workers and students in the areas of sensory biology, comparative neurobiology and behavioral ecology. Excellent coverage of the physical nature of stimuli in aquatic environments is provided (part I). Most sensory systems in fishes (more teleosts than others) and, to a lesser degree, certain invertebrates (mostly decapods) are reviewed in detail with respect to detection, information processing and control of behavior. An exception is somatic sensation which is generally not covered. The book is an outstanding reference for fish neurosensory biologists. The lack of detailed coverage of tetrapod vertebrates and many invertebrate taxa limits its usefulness to more general audiences as well as specialists working on these groups. This is especially disappointing considering the broadness of its title. Thus, the stated goal of demonstrating general principles of sensory adaptation to specific environments is only partially reached. These criticisms notwithstanding, a wealth of useful information in

timely review articles marks the book as an important contribution to both neurosensory and aquatic biology.

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Neural Control of Rhythmic Movements in Vertebrates

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Of the great diversity of behaviors exhibited by vertebrates, rhythmic movements are the best studied by far. Rhythmic activity is critical for vital vertebrate functions such as feeding, locomotion, and respiration, allows repeated observations of the same behavior, and greatly facilitates measurement of complex movements. Rather than attempt to study single, isolated behaviors, neurobiologists have rightly focused their attention on patterns of movement that are rhythmic in character and have attempted to study the regulation and genesis of rhythmic patterns. This volume provides an update on the analysis of rhythmic movements in vertebrates with a focus on the control of such movements via central pattern generators (CPG's) and the processing of information from the periphery.

This volume is unusual in that nearly all the papers are of very high quality. With only a few exceptions, the papers present excellent, succinct, and informative overviews of some specific aspect of the control of rhythmic movements. In my experience it is rare for a multiauthored book to exhibit such consistency in contribution quality, and the editors have clearly done an outstanding job. My two complaints concern the choice of topics and the order of presentation of the subjects in the book.

The book begins with three chapters on each of the major vertebrate systems involved in rhythmic movements: locomotor (by Grillner et al.), masticatory (by Lund and Enomoto), and respiratory (by Feldman et al.). The next chapter by Getting (on invertebrate CPG's) and a later chapter by Harris-Warwick (on chemical modulation of CPG's) are both first-rate but seem out of place in this book with its focus on vertebrates. The goal of the editors to use these two chapters to (p. ix) 'highlight some of the principles that are useful to better understand vertebrate systems' would have been better served if the authors had been asked to focus explicitly on general concepts applicable to vertebrate and invertebrate CPG's and if the chapters had been placed at the start of the book. As it is, Harris-Warwick's enlightening review comes too late to be appreciated in the light of other contributions.

Rhythmic movement during locomotion receives further attention in the chapters by Cohen, Gelfand et al., and Rossignol et al. Cohen presents an interesting hypothesis on the evolution of vertebrate CPG's which states (p. 153) that 'throughout vertebrate evolution homologues of the oscillators which drive the dorsal and ventral muscles of lampreys have continued to drive the muscles of the respective dorsal and ventral muscle masses'. This hypothesis suggests that the neural control of the limbs has been conserved during vertebrate evolution and that CPG mechanisms are less evolutionarily plastic than peripheral morphology. Data supporting this general concept have recently been reported by several workers [Goslow et al., 1989; Lauder and Shaffer, 1988], and the data of Edwards [1989] and Peterson [1984] provide additional information useful

for understanding terrestrial locomotor patterns. I found the article by Rossignol et al. on sensory input and CPG regulation in locomotion, respiration, and mastication to be a very useful, logically organized review due particularly to the comparisons presented among the three different rhythmic behaviors.

The final four chapters deal with models of CPG output (Rand et al., Kopell, and Mulloney) and with the analysis of CPG patterns (Patla). These chapters contribute importantly to the book by providing an overview of techniques and concepts used in model building and by emphasizing the utility of close interactions between experimental and theoretical investigations of rhythmic movements.

Two additions would have enhanced the coverage of the book: (1) a paper on the study of fictive systems: methods, conclusions, and cautions from the study of such preparations; (2) a final concluding chapter attempting a synthesis of general issues and questions that pervade the book. My own attempt to generate such a synthesis focused on four points that seemed to join threads present in many of the papers.

First, when we consider how to explain rhythmic patterns special attention needs to be given to the role of peripheral structures. As noted specifically by Patla (pp. 458, 479) but implied by several other authors, the topology and structure of the periphery may have a profound effect on how the motor output from a CPG is translated into kinematic and behavioral patterns. Motor unit size, muscle fiber types, force-velocity relationships, lever arms, connective tissue linkages, and joint articulations act as a 'filter' through which CPG output acts. Species which possess identical CPG output may exhibit very different behaviors due solely to differences between the species in the design of peripheral morphology [Lauder, 1985; Lauder and Shaffer, 1988]. Thus, I feel that increased attention needs to be given to how CPG output interacts with peripheral structures. Such studies would be a complementary research program to investigations using fictive preparations and isolated spinal cords to investigate the CPG in detail. Such complementary research programs are necessary because preparations that involve removal of all peripheral structures severely limit our ability to predict how alterations in CPG output change behavioral kinematics in the intact animal.

Secondly, there is a real need, as emphasized by Cohen, for documentation of motor patterns actually used by animals during the execution of behavior. For some extremely well-studied taxa (e.g., lampreys), motor patterns have been well worked out. But for most taxa we have little idea of the nature of motor output and its variability. This lack of data makes generalizations about the evolution of motor patterns and muscle function extremely difficult and hinders the development of general concepts and hypotheses on the evolution of motor systems.

Thirdly, motor patterns, once they have been measured, need to be quantitatively analyzed. This is the theme of Patla's contribution, but I feel that even more is needed. Analysis of CPG output is

often surprisingly qualitative and anecdotal. Patla is correct that the analysis of CPG output would benefit from the use of pattern recognition techniques, but in addition the use of univariate and multivariate statistical procedures is essential if reproducible conclusions are to be drawn from CPG output. When output in as few as four or five motor neurons is simultaneously obtained and then manipulated by experimental modifications to the preparation, it is impossible to visually analyze all the possible changes in phase relationships and durations: a quantitative statistical approach is essential.

Fourthly, a marriage of workers in evolution and phylogenetic analysis with investigators of CPG output and the regulation of rhythmic movements should prove to be extremely fruitful. A consideration of historical patterns and transformations of motor output are essential to understanding the neural bases for the evolution of behavior. However, not even a mild courtship has yet taken place. As this is an area of my own interest, it is disturbing to see both extremely naive phylogenetic arguments made by workers interested in speculating on the evolution of CPG output, and unsophisticated comments on the neural bases of behavioral change made by morphologists and phylogeneticists. My hope is that a union of concepts and analytical techniques between these two research avenues (similar to that which took place in neuroethology) will occur and provide the basis for broad advances in our understanding of the evolution of motor systems.

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