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Invertebrate neuroethology

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Introduction

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Neuroethology as a discipline traces its roots to two sources – field studies of animal behavior by ethologists such as Lorenz and Tinbergen, and network or cellular studies by neurobiologists such as Sherrington. Indeed, Lorenz's concept of the fixed action pattern, Tinbergen's ideas about sign stimuli, and Sherrington's concept of the reflex are among the neuroethologist's most useful organizational principles.

In line with its dual roots, neuroethology's principle aim is to understand the natural behavior of animals on the basis of their nervous systems. It is a discipline very much in its growth phase. It boasts a new society (The International Society for Neuroethology), and recent textbooks[1, 2] and symposia[3, 4]. Yet the very important contributions of this field may be partly obscured by other developments. The field of animal behavior has largely been drawn away from studies of proximate causes, and has zoomed ahead in studies of ultimate causes. And neurobiology is increasingly being drawn into the domains of clinical medicine and molecular biology. It is largely to help bring attention to the many outstanding contributions being made specifically within the neuroethological framework that I have agreed to organize this multi-author review.

The present review deals with invertebrates. The tendency to split the animal kingdom in two, using the backbone as a dividing line, is in fact not entirely reasonable. All animals face more or less the same life problems and solve them using nervous systems composed of more or less similar neurons. The decision to focus on invertebrates was partly practical, permitting a coherent treatment. But the decision also reflects a notion that invertebrate studies make a special type of contribution to neuroethology, in which basic mechanisms can be analyzed on the cellular level in a way rarely achievable in vertebrate animals.

As in any reductionist field of science, one can subdivide the major overall goal into several parts: 1) to define the phenomenon one wishes to explain; 2) to define the sub-components responsible for this larger phenomenon; 3) to determine the functional properties of each component; 4) to determine the functional interactions among the components; and 5) finally to try to account for the overall phenomenon on the basis of the components, their properties and their interactions.

Let us address each of these partial goals in turn, within the framework of invertebrate neuroethology, and with special reference to the articles that follow. First, what are the phenomena one wishes to explain? Probably most of the authors of this review undertook the study of invertebrates in the first place because they provide model systems for studying general principles. One way to indicate that the principles are general is to compare them in widely different animals. When a female white-throated sparrow, for instance, hears the voice of her potential mate and flies off to meet him, her nervous system faces problems very similar to those of a cockroach that is escaping from predatory attack. These problems include: signal detection, signal to noise discrimination, signal identification, signal localization, decision whether or not to act and choice among possible alternative acts, coordination of several body parts in space and time, generation of rhythmic locomotory activity, orientation, and sequencing from one behavior to the next. Note that I speak here of a bird and an insect, one moving towards and the other away from a stimulus, one about to engage in courtship behavior, the other about to be attacked – and yet there are abundant similarities in the momentary problem solving needs of their two nervous systems.

It is fair to say that each of the presentations in this review deals, directly or indirectly, with one or more of the above problems. Fullard's paper is concerned largely with signal detection and discrimination, Schildburger's and Jacobs and Miller's papers deal in part with directional localization, Kristan et al.'s with behavioral choice, Camhi's with coordination of body parts in space and time, Rowell's and Selverston's papers concern rhythmic behavior, and Reichert's sequencing among behavioral acts. Beyond this, the paper by Marcus et al. concerns the ontogenetic development of behavior, and that of Wu et al. describes techniques useful in studying various aspects of neural network functioning.

As to the second partial goal, defining sub-components, one can ask at what level these components should be sought. Most workers would probably answer that since the individual cell is the structural basis of the nervous system and of neural integration, it should therefore be the main point of attack. This approach has much merit, and probably the majority of the contributors to the present review would subscribe to it. These individuals are sometimes referred to colloquially as "circuit breakers". Their research strategy regards each cell as a circuit element, and a major milestone of their endeavors is working out the circuit diagram for a given behavior. Examples in the present review are seen in the work of Reichert, Kristan et al., Selverston and others. But there are other valid points of attack as well. One is sub-cellular; indeed, an important present need in understanding the processing of behaviorally relevant information is to decipher the flow of electrical signals in a neuron's dendritic tree, which determines what the cell's output response will be. Jacobs and Miller's paper describes such an analysis, using photic killing of specific parts of the dendritic tree. Alternatively, it is also possible to consider functional units of neural organization at the multicellular level. In fact, most behavioral functions appear to be relegated not to single cells but to groups[5]. Thus, regarding the group as a unit may have special merit. In this connection, Wu et al.'s paper describes methods for analyzing multicellular activity using voltage sensitive dyes; and Camhi describes a multicellular code for stimulus direction.

Concerning the third partial goal, determining the functional properties of the system's components, which properties does one want to analyze? Speaking of a single neuron, it has been learned in recent years that these come with a rich variety of properties. There are cells, probably the majority, that support all-or-none action potentials, and others that do not use action potentials at all. There are cells whose output directly reflects their synaptic input, and others whose membranes are capable of generating rhythmic oscillations or prolonged plateau potentials. Indeed, the number of known types of membrane channel, each producing a different variety of voltage signal across the neuronal plasma membrane, has grown enormously in recent years. A proper analysis of a cell as a circuit element is thus a deeply complex affair. Moreover, the physiological properties of the cell are subject to neuromodulatory variation, as the paper by Selverston points out.

As to the fourth partial goal, analyzing the interactions among components, again numerous complexities of synaptic interactions have been described in recent years. Aside from the classic distinctions; electrical vs chemical, excitatory vs inhibitory, functionally strong vs weak, facilitating vs nonfacilitating or antifacilitating synapses, we now have as well synapses with a variety of types of conductance change, those with short-term or long-term modifiability, and those using first and/or second chemical messengers. Again, the analysis at this level is highly complex.

The fifth partial goal, reconstructing a behavior on the basis of its known components and their interactions, has rarely been achieved. Partial attempts are seen in several of the papers of this collection.

It is fair to say that no single example of behavior has been fully analyzed with regard to all five of the partial goals mentioned above. But the fact is that there is yet a sixth partial goal that must be mentioned. For as ethologically oriented scientists, we must try to understand how the animal's nervous system solves the problems it encounters under real field conditions. And even beyond this, one would want to know how the solution to these problems has developed since the animal's a birth, and has evolved through time.

The papers in this collection provide, then, partial insights into the overall problem of understanding the neural basis of natural behavior. It is hoped that by 'connecting the dots' between these contributions, the reader will be able both to see the whole sweep of the field of neuroethology, and to recognize vast and exciting areas ripe for investigation.

The papers are sequenced in a 'bottom up' order, beginning with subcellular analysis, then on to network studies, and onward to the whole animal in the field. I am delighted that a true grand master of invertebrate neuroethology, Franz Huber, has provided us with an epilog that offers wise guidance for the future development of our discipline.

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Analysis of synaptic integration using the laser photoinactivation technique

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Summary. Crickets (and many other insects) have two antenna-like appendages at the rear of their abdomen, each of which is covered with hundreds of 'filiform' hairs resembling the bristles on a bottle brush. Deflection of these filiform hairs by wind currents activates mechanosensory neurons at the base of the hairs. The axons from these sensory neurons project into the terminal abdominal ganglion to form a topographic representation (or "map") containing information about the direction, velocity and acceleration of wind currents around the animal. Information is extracted from this map by primary sensory interneurons that are also located within the terminal abdominal ganglion. In this paper, we review the progress that has been made toward understanding the mechanisms underlying directional sensitivity of an identified sensory interneuron in the cricket, *Acheta domesticus*. The response properties of the cell have been found to depend to a large extent upon the structure of its dendritic branches, which determines its synaptic connectivity with the sensory afferents in the map of wind space and the relative efficacy of its different synaptic inputs.

Key words. Cricket; cercal sensory system; mechanosensory interneuron; photoinactivation.

Introduction

It has been a long-term goal of many neuroscientists to determine how information is processed in central nervous systems. A great many researchers have focused their attention upon information processing in sensory systems. One general principle that has emerged from studies of the structure and function of sensory systems is that the 'relevant properties' of sensory stimuli are often represented within computational maps. As defined in a recent review[13], a map is an array of neurons through which there is a systematic variation in the 'tuning' of neighboring neurons for a particular parameter. The representations of retinal coordinates on the tectum and higher visual areas are familiar examples of topographic sensory maps, in which the mapped parameter is the location of an object in visual space. A 'computational map'