Book Reviews

The Comparative Study of Learning

Invertebrate Learning. W. C. CORNING, J. A. DYAL, and A. O. D. WILLOWS, Eds. Plenum, New York. Three volumes. Vol. 1, Protozoans through Annelids. 1973. xviii, 296 pp., illus. $18.50. Vol. 2, Arthropods and Gastropod Mollusks. 1973. xiv, 284 pp., illus. $18.50. Vol. 3, Cephalopods and Echinoderms. 1975. xii, 220 pp., illus. $19.50.

Man is unique not because he does science, and he is unique not because he does art, but because science and art equally are expressions of his marvellous plasticity of mind.—J. BRONOWSKI (*1*)

These three volumes are in some sense a celebration of the uniqueness of man. The yardstick of vertebrate learning ability is applied and the invertebrates are found wanting. We come away from these volumes reassured that our position on the axis of behavioral plasticity still defines the limit. Thus reassured we can examine the general issues raised by the comparative study of learning.

The first such issue is what type of yardstick for learning ability will yield meaningful comparisons across the diversity of forms and lifestyles constituting the invertebrates, or, more generally, within the kingdom Animalia. Is the vertebrate yardstick the best metric? Is the search for categories of learning derived from psychological learning theory the most generally useful comparative strategy? Dyal and Corning examine the possibilities of an affirmative answer in chapter 1, where they present a "behavior taxonomy" based on such concepts as habituation, sensitization and pseudoconditioning, punishment, classical conditioning, and instrumental learning. The countervailing point of view is not well represented in these volumes. In this view learning is regarded as a specific adaptation to a particular problem. Animals can learn certain things very well and others not at all. In his recent book *Sociobiology* (*2*) E. O. Wilson states the matter as follows:

> How can learning evolve? . . . What evolves is the directedness of learning—the relative ease with which certain associations are made and acts are learned, and others bypassed even in the face of strong reinforcement.

This formulation suggests that evolutionary comparison be made by using a common adaptive challenge as the axis along which to array the behavioral solutions of various species. It questions the concept of general learning ability or the existence of "laws of learning." Which of the two viewpoints one takes has a dramatic bearing on how one interprets the entire literature, but the reader of *Invertebrate Learning* will have to depend on the proceedings of recent symposia (*3*) dealing with the biological constraints on learning to fully appreciate their impact.

A moment of high drama is provided in the present work by M. E. Bitterman's invited commentary, wherein he delivers a scathing attack on subjective and poorly controlled learning studies, which in his view account for the majority of the available data. Bitterman's attacks are so pointed that the editors felt constrained to include a countercommentary defending the value of the enterprise. Bitterman makes the valid point that the vertebrate learning tradition provides explicit guidance as to the proper controls for formal learning experiments and there can be no justification for publication of work lacking the requisite controls. His call for greater automation and his denigration of the ethological approach are less convincing but serve to sharpen an important issue. His Thorndike Centenary Address, which recently appeared in these pages (*4*), contains further elaboration of the psychological versus ethological conceptions of the comparative study of learning.

As several of the contributors to *Invertebrate Learning* note, one of the most attractive features of invertebrate nervous systems for physiological work is the opportunity they provide to work with individual nerve cells that can be reliably identified from animal to animal. Each identifiable neuron has a unique constellation of presynaptic inputs, postsynaptic outputs, membrane biophysics, and transmitter biochemistry. In spite of this emphasis on the individuality of nerve cells, which continues to be one of the dominant themes of modern integrative neurophysiology, several attempts have been made to dissect learning mechanisms by means of biochemical or pharmacological treatments of whole ganglia. It should be clear that such global manipulations of a heterogeneous population of interneurons and motoneurons are unlikely to yield unequivocal data, and indeed two recent studies have failed to confirm an earlier report of decreased cholinesterase activity with learning of leg position in cockroach ganglia. Real insight into the relationship between electrical and biosynthetic activity in neurons and its bearing on synaptic plasticity can be expected from several lines of work currently applying microtechniques of transmitter and protein determination to single identified nerve cells of known reflex function.

T. M. Alloway presents an analysis of learning in insects excluding Apoidea which effectively portrays the wide range of tasks and preparations available for study in this group. The survival of a learned position discrimination through metamorphosis in the grain beetle, which Alloway's own work has discovered, is one of the more interesting phenomena awaiting physiological study. The section on learning in fruit flies requires clarification. Murphy has not, as Alloway believes, trained fruit flies to turn left or right. The T-maze used by Murphy contains runways of circular cross section. Because the flies can walk on the floor, ceiling, or walls, they can arrive at the end of the maze having made a left turn, a right turn, or no turn at all. A recent paper by W. G. Quinn *et al.* (*5*) that convincingly demonstrates associative learning in *Drosophila* opens the way to a rigorous neurogenetic analysis of learning in this animal.

The treatment of learning in the honey bee (*Apis mellifera*) by P. H. Wells is generally disappointing in the uncritical acceptance of experiments on conditioning that lack controls for sensitization or pseudoconditioning. Alloway's discussion of classical conditioning in insects may be read to appreciate this point. The reader of Wells's account must resort to the original papers on honey bee conditioning to sort the wheat from the chaff. The experiments of Nuñez are incorrectly cited as an example of instrumental conditioning. In fact, the apparatus used by Nuñez was arranged so that explorations of the feeding tube, which always contained food, would inevitably lead to depression of a lever that delivered more food. Nuñez did not interpret the results in terms of instrumental conditioning, nor was the lever-pressing response dissociated from the act of exploring the feeding tube. Elegant and well-controlled conditioning experiments such as those of Menzel demonstrate the utility of sophisticated behavioral experiments as a device to sharpen the questions which ultimately must be attacked neurophysiologically.

Students of honey bee learning who have followed the micromaelstrom occasioned by Wenner's experiments on the role of odors in recruitment of foragers should be aware of J. L. Gould's recent work (*6*), which elegantly settles the matter.

Learning in Crustacea is reviewed by F. B. Krasne, who brings a noticeably biological and evolutionary perspective to his subject. Rather than simply catalog experiments showing that Crustacea can learn, Krasne raises questions concerning "the relationships among what an animal can learn, the organization of its nervous system, and the demands for learning made on it in life." A discussion of ecological constraints on learning is followed by a discussion of the kinds of learning shown by Crustacea. The latter discussion is particularly useful in that it breaks free of the traditional learning categories and considers types of learning representing solutions to general problems of adaptation. Plastic aspects of navigation, social behavior, and food selection provide axes along which one can make biologically meaningful comparisons between species. Krasne gives a particularly thorough treatment of the neural circuit mediating tactilely evoked tail-flip responses in the crayfish. This circuit has recently yielded insights into the way presynaptic inhibition can be used to protect afferent terminals from habituation during tail movement. The tail-flip circuit displays several forms of synaptic plasticity and is one of the most thoroughly and insightfully analyzed "simple systems" in all the invertebrates.

The octopus has been characterized as the closest thing to man outside the Vertebrata. The chapter on the cephalopods by G. D. Sanders supports this contention by being the longest and presenting an excellent summary of the massive and diverse body of information available, primarily on *Octopus vulgaris*. The experiments had their impetus both from formal learning theory (reversal learning, delayed reinforcement) and from ethological considerations of the types of adaptive challenges normally encountered (tactile discrimination, taste by touch). It will be interesting to see if taste aversion learning similar to that found in rats, slugs, and people also occurs in octopuses. The octopus work is now leading to detailed cellular analysis of the vertical lobe system, which has been found to be centrally involved in processes of learning and memory storage. This effort may prove to be a severe test of the ability to analyze function in a neural network on the basis of extensive behavioral and fine-structural information with only sparse underpinnings from direct neurophysiological recording.

It is interesting to consider why out of the more than a million species available the two that receive the most extensive treatment in these volumes, *Apis mellifera* and *Octopus vulgaris*, have been so attractive to researchers. The studies that have been done on these two animals have several features in common. In both cases visual discriminations have been involved and the visual stimuli have been used as signals for the presence of food. The learning shown by both creatures has been rapid and reliable. Certainly part of the explanation lies in the ease with which we, as visual animals, think of questions to ask other primarily visual animals. Moreover, the learning demonstrated in these species has direct relevance to their ecology. Particularly with the bee, ecological and ethological considerations have provided a wellspring of ideas for experiments to delineate the limits of learning ability. Food-related learning, whether concerned with location or safety, is a very general phenomenon that can be found in every major group of invertebrates, and the work that has been done on these two animals provides the most extensive and sophisticated sets of data within which to test general questions of the evolution of learning.

The demands for clean, rapid learning and few, large neurons are most likely to be met simultaneously among the gastropod mollusks. In this group more than any other, one is prone to have a tidy neural circuit analyzed at the cellular level that requires behavioral experiments to determine its reflex function and plastic capabilities. The more complex behavior modes seen in gastropods contain numerous suggestions of plastic components. A. O. D. Willows provides a thorough and informative summary of learning in this group. The identification of categories of learning that both have clear foundation in the animal's ethology and can be as rigorously analyzed as the habituation of gill withdrawal in *Aplysia* will be greatly aided by his treatment.

It should be clear that these volumes contain a large amount of useful information. The theoretical underpinning is incomplete, but the facts are there as grist for the reader's mill. Basic insights into the evolution of learning are yet to be generated, and the volumes are a progress report on the road to such insights. More detailed work, behavioral, anatomical, and physiological, is required on the most favorable organisms. This must be followed by sufficiently detailed work on closely related species that evolutionary trends are revealed.

The problem of making comparisons of learning ability is highlighted by the following passage from a recent review (*7*) of Leon Kamin's *The Science and Politics of I.Q.*

> Intelligence is a biological adaptation whose most distinctive characteristic is plasticity. Intelligence manifests itself in the ability to devise effective responses to new and unforeseen environmental challenges and to make creative use of relevant past experience. Criteria for assessing and comparing intelligent behavior must therefore necessarily vary from one culture or subculture to another. In seeking to devise "culture-free" tests of intelligence psychometricians are pursuing a chimera.

The parallels and problems are clear. Their resolution is one of the most interesting current themes in neurobiology.

ALAN GELPERIN

Department of Biology, Princeton University, Princeton, New Jersey

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Evolutionary Genetics

Molecular Population Genetics and Evolution. MASATOSHI NEI. North-Holland, Amsterdam, and Elsevier, New York, 1975. xiv, 288 pp., illus. $34. Frontiers of Biology, vol. 40.

The past ten years have witnessed an almost revolutionary change in population genetics. The doldrums of the previous academic period of this subject terminated, not with its death, but rather with its entrance into a second romantic phase. This revolution, or at least revitalization, can be attributed to the application of the techniques of biochemistry and molecular biology to problems of evolutionary genetics. These made it possible to estimate both the amount of genetic diversity in natural populations and the rates of gene evolution. Most fortunately for the persistence of population genetics, the empirical estimates of these fundamental parameters were far different from the values that had been expected on the basis of the existing theory.

The author of this book, Masatoshi Nei, has been a leader of one of the two major