Life Sciences Research Report 29

The Biology of Learning

P. Marler and H. S. Terrace,
Editors

Dahlem Konferenzen

Springer-Verlag
Berlin Heidelberg New York Tokyo

The Biology of Learning

P. Marler and H. S. Terrace, Editors

Report of the Dahlem Workshop on
The Biology of Learning
Berlin 1983, October 23-28

Rapporteurs:
P. C. Holland · D. E. Kroodsma · J. C. Marshall
R. Menzel · J. Morton

Program Advisory Committee:
P. Marler and H. S. Terrace, Chairpersons
T. Bever · L. L. Cavalli-Sforza · J. L. Gould
K. Immelmann · R. F. Thompson · A. R. Wagner

Springer-Verlag
Berlin Heidelberg New York Tokyo 1984

The Dahlem Konferenzen

Founders

Recognizing the need for more effective communication between scientists, especially in the natural sciences, the Stifterverband für die Deutsche Wissenschaft*, in cooperation with the Deutsche Forschungsgemeinschaft**, founded Dahlem Konferenzen in 1974. The project is financed by the founders and the Senate of the City of Berlin.

Name

Dahlem Konferenzen was named after the district of Berlin called "Dahlem", which has a long-standing tradition and reputation in the arts and sciences.

Aim

The task of Dahlem Konferenzen is to promote international, interdisciplinary exchange of scientific information and ideas, to stimulate international cooperation in research, and to develop and test new models conducive to more effective communication between scientists.

Dahlem Workshop Model

Dahlem Konferenzen organizes four workshops per year, each with a limited number of participants. Since no type of scientific meeting proved effective enough, Dahlem Konferenzen had to create its own concept. This concept has been tested and varied over the years, and has evolved into its present form which is known as the *Dahlem Workshop Model.* This model provides the framework for the utmost possible interdisciplinary communication and cooperation between scientists in a given time period.

**The Donors Association for the Promotion of Sciences and Humanities*

***German Science Foundation*

The main work of the Dahlem Workshops is done in four interdisciplinary discussion groups. Lectures are not given. Instead, selected participants write background papers providing a review of the field rather than a report on individual work. These are circulated to all participants before the meeting to provide a basis for discussion. During the workshop, the members of the four groups prepare reports reflecting their discussions and providing suggestions for future research needs.

Topics
The topics are chosen from the fields of the Life Sciences and the Physical, Chemical, and Earth Sciences. They are of contemporary international interest, interdisciplinary in nature, and problem-oriented. Once a year, topic suggestions are submitted to a scientific board for approval.

Participants
For each workshop participants are selected exclusively by special Program Advisory Committees. Selection is based on international scientific reputation alone, although a balance between European and American scientists is attempted. Exception is made for younger German scientists.

Publication
The results of the workshops are the Dahlem Workshop Reports, reviewed by selected participants and carefully edited by the editor of each volume. The reports are multidisciplinary surveys by the most internationally distinguished scientists and are based on discussions of new data, experiments, advanced new concepts, techniques, and models. Each report also reviews areas of priority interest and indicates directions for future research on a given topic.

The Dahlem Workshop Reports are published in two series:
1) Life Sciences Research Reports (LS), and
2) Physical, Chemical, and Earth Sciences Research Reports (PC).

Director
Silke Bernhard, M.D.

Address
Dahlem Konferenzen
Wallotstrasse 19
1000 Berlin (West) 33

Table of Contents

The Dahlem Konferenzen
S. Bernhard ix

Introduction
P. Marler and H.S. Terrace 1

GENERAL ISSUES IN THE BIOLOGY OF LEARNING

Animal Learning, Ethology, and Biological Constraints
H.S. Terrace 15

Ethology and the Natural History of Learning
J.L. Gould and P. Marler 47

Genes, Evolution, and Learning
P.P.G. Bateson 75

The Study of Animal Learning in the Tradition of Pavlov and Thorndike
H.M. Jenkins 89

Learning by Selection
J.-P. Changeux, T. Heidmann, and P. Patte 115

BIOLOGY OF INVERTEBRATE LEARNING

Learning in Invertebrates
B. Heinrich 135

Natural History of Honey Bee Learning
J.L. Gould 149

Behavior Theory and Invertebrate Learning
C.L. Sahley 181

Work in Invertebrates on the Mechanisms Underlying Learning
W.G. Quinn 197

Biology of Invertebrate Learning
Group Report
R. Menzel, Rapporteur
G. Bicker, T.J. Carew, K.-F. Fischbach, J.L. Gould, B. Heinrich, M.A. Heisenberg, M. Lindauer, H.S. Markl, W.G. Quinn, C.L. Sahley, A.R. Wagner 249

BIOLOGY OF LEARNING IN NONMAMMALIAN VERTEBRATES

The Natural History of Bird Learning
K. Immelmann 271

Song Learning: Innate Species Differences in the Learning Process
P. Marler 289

A Logical Basis for Single-neuron Study of Learning in Complex Neural Systems
M. Konishi 311

The Neural Basis of Imprinting
P.P.G. Bateson 325

Signals, Conditioned Directed Movements, and Species-typical Response Predispositions in Nonmammalian Vertebrates
E. Hearst 341

Cause and Function of Animal Learning Processes
K.L. Hollis 357

Complex General Process Learning in Nonmammalian Vertebrates
S.E.G. Lea 373

Biology of Learning in Nonmammalian Vertebrates
Group Report
D.E. Kroodsma, Rapporteur
P.P.G. Bateson, H.-J. Bischof, J.D. Delius, E. Hearst, K.L. Hollis, K. Immelmann, H.M. Jenkins, M. Konishi, S.E.G. Lea, P. Marler, J.E.R. Staddon 399

BIOLOGY OF LEARNING IN NONHUMAN MAMMALS

Natural History and Evolution of Learning in Nonhuman Mammals
S.J. Shettleworth 419

Species-typical Response Predispositions
R.C. Bolles 435

Associative Predispositions
S. Revusky 447

Learning to See: Mechanisms in Experience-dependent Development
W. Singer 461

Physiological and Anatomical Mechanisms: Neural Bases of Learning
R.F. Thompson and T.W. Berger 479

Spatial Cognition and Memory in Captive Chimpanzees
E.W. Menzel, Jr. 509

Biology of Learning in Nonhuman Mammals
Group Report
P.C. Holland, Rapporteur
R.C. Bolles, J.-P. Changeux, J. Gibbon, E.W. Menzel, Jr., M. Mishkin, J.P. Rauschecker, S. Revusky, S.J. Shettleworth, W. Singer, H.S. Terrace, T.F. Werka, K. Zielinski 533

BIOLOGY OF LEARNING IN HUMANS

Biological Predispositions to Learn Language
L.R. Gleitman 553

On Perceptual Predispositions for Human Speech and Monkey Vocalizations
M.R. Peterson and P.W. Jusczyk 585

Human Learning and Memory
W.K. Estes 617

Models of Language Acquisition
D.N. Osherson and S. Weinstein 629

Brain Mechanisms of Language
J.W. Brown 643

The Neuropsychology of Memory
L.R. Squire 667

Biology of Learning in Humans
Group Report
J.C. Marshall and J. Morton, Rapporteurs
T.G. Bever, J.W. Brown, W.K. Estes, K.E. Grossmann, W.G.H. Huber, M.R. Petersen, L.R. Squire, S. Weinstein 687

List of Participants with Fields of Research 706

Subject Index 711

Author Index 739

1984. Berlin, Heidelberg, New York, Tokyo: Springer-Verlag.

Introduction

P. Marler* and H.S. Terrace**
*The Rockefeller University Field Research Center
Millbrook, NY 12545
**Dept. of Psychology, Columbia University
New York, NY 10027, USA

For the first half of this century, theories of animal conditioning were regarded as the most promising approach to the study of learning - both animal and human. For a variety of reasons, disillusionment with this point of view has become widespread during recent years.

One prominent source of disenchantment with conditioning theory is a large body of ethological observations of both learned and unlearned natural behavior. These challenge the generality of principles of animal learning as derived from the intensive study of a few species in specialized laboratory situations. From another direction, the complexities of human language acquisition, surely the most impressive of learned achievements, have prompted developmental psychologists to doubt the relevance of principles of animal learning.

Even within the realm of traditional studies of animal learning, it has become apparent that no single set of currently available principles can cope with the myriad of new empirical findings. These are emerging at an accelerating rate from studies of such phenomena as selective attention and learning, conditioned food aversion, complex problem-solving behavior, and the nature of reinforcement. Not very surprisingly, as a reaction against the long-held but essentially unrealized promise of general theories of learning, many psychologists have asked an obvious question: does learning theory have a future?

THE FUNDAMENTAL IMPORTANCE OF LEARNING

We believe that the proper answer to the above question is affirmative. It is an inescapable fact that organisms learn about their environments and that the remarkable abilities involved cry out for scientific explanation. The current disarray of learning theory should not detract from the fundamental goal of understanding the general principles of learning, even though the form of a fully viable theory of learning remains to be determined.

Numerous discoveries have given added impetus to efforts to reformulate and supplement traditional theories of learning in order to encompass findings they cannot presently explain. Learning theory has also retrenched from its original, perhaps overambitious, aims. In so doing, it has developed new and sophisticated models of a variety of compelling phenomena.

Contemporary studies of Pavlovian conditioning provide numerous examples of the kind of approach currently followed by students of animal learning (see Hearst, Jenkins, and Terrace, all this volume). Empirical findings concerning contingency learning, overshadowing and blocking, and sophisticated theoretical analyses of these phenomena (cf. (2, 6, 11)) have made clear the scope and complexity of Pavlovian conditioning. This research has also revealed the inadequacy of traditional approaches when they have focused exclusively on preparations in which mere temporal contiguity between conditioned and unconditioned stimuli was regarded as sufficient for learning to occur and in which the conditioned response was regarded as a form of the unconditioned response.

For the first time, students of animal learning have undertaken a systematic study of cognition in animals. This line of inquiry, which would have been unthinkable a decade ago, promises to provide a basis for comparing cognitive processes in animals and man (Lea and Menzel, both this volume; also see (12, 13)). New insights are also flowing into learning theory from both ethology and physiology. These areas in turn derive inspiration from burgeoning psychological research on such topics as autoshaping and the conditioning of food aversions.

Recent advances in the study of animal learning would undoubtedly be seen in a more positive light were it not for a strong and widespread disappointment over the failure of general learning theory to make good on its all-embracing promissory notes. While it is probably premature to anticipate a new generation of general theories of learning in the near future, students of animal learning can derive some comfort from the opportunities currently available for investigating associative principles of learning with unprecedented rigor. At the same time it is important to recognize that principles of association, which provide the basis for the only model of animal learning that currently enjoys a significant following, are by themselves an insufficient basis for a truly general theory.

BIOLOGICAL "CONSTRAINTS"

Some of the findings not readily accommodated by classical principles of association are referred to widely under the rubric of "biological constraints on learning." Several examples are reviewed by Bolles, Revusky, and Shettleworth (all this volume). They fall into two general categories. One group comes from demonstrations of how readily specific stimuli can be associated with one another, how selective attention determines the effectiveness of a stimulus in particular situations, and how an animal behaves as a result of forming a particular association.

One of the most robust and widely cited examples of this type of biological constraint is food aversion learning. Indeed, thanks to the ease of establishing conditioned food aversion, a variety of empirical findings have stimulated learning theorists to conceptualize the relevant variables as "parameters" of associative learning. It should, however, be noted that this point of view begs the question of why, on a priori grounds, particular organisms attend to and associate specific stimuli and why they are then disposed to take particular patterns of action. While it is heartening to discover that several features of food aversion learning are consistent with other instances of associative learning (Revusky, this volume), one must not lose sight of the fact that we still lack any general means of predicting, even in this instance, whether a particular stimulus will be an effective signal.

A second category of so-called "biological constraints" is exemplified by instances of "specialized" learning. Primary illustrations of such learning are imprinting and song learning (Bateson ("The Neural Basis of Imprinting"), Immelmann, Konishi, and Marler, all this volume). Examples of specialized learning pose different and perhaps more fundamental problems for association theory than does food aversion learning. As yet there is virtually no evidence that these phenomena are instances of associative learning. If they are not, new principles of learning must be formulated to account for them. Indeed, instances of specialized learning suggest that the very term biological constraints is a misnomer. There are many indications of brain mechanisms that have positively and explicitly evolved for particular learning tasks. Such findings are hardly consistent with the view that specialized learning is simply a constrained version of a more generalized, and thus by implication, more significant form of learning.

PSYCHOLOGICAL VS. BIOLOGICAL APPROACHES TO LEARNING

One aim of this Dahlem Workshop on "The Biology of Learning" was to reach beyond the traditional boundaries of learning theory and search for common ground with those engaged in formulating novel biological approaches to behavioral plasticity. Thus, aside from recognizing specialized instances of learning as phenomena that warrant study without preconceptions as to their nature, we also sought to bring to bear on the study of learning a wide range of issues, for example, the neurophysiological and cellular bases of learning, behavioral ecology, and the general natural history of learning.

A major dichotomy is evident between psychologists concerned with learning theory and biologists studying behavioral plasticity. Learning theorists tend to favor preparations in which learning can be studied at a particular plateau of growth and development. In their view, the essence of learning can be found in the ability of organisms to adapt to any problem that might be thrust on them by changing and unpredictable environments, whether natural or synthetic ones of the experimenter's choosing. Typically, the learning theorist's choice of problem is guided more by theory-based logic than by a knowledge of the organism's natural history.

Biologists, on the other hand, have tended to think of behavioral plasticity in the larger context of the organism's daily round of activities for survival and reproduction. These activities are conducted in environments that are unique for each species and that often vary drastically from one phase of the life cycle to another. In satisfying its requirements, an animal must actively seek out microenvironments, the optima for which change with the time of day and the season, and even more radically as the organism proceeds from birth to maturity.

The life cycle approach of the ethologist focusses especially on the plasticity of natural behavior and the relationship between learning and the dynamics of natural patterns of development. A parallel can be drawn in human infant studies. Learning theorists may study conditioning simply to verify that certain effects can be obtained at a particular stage. Developmental psychologists and psycholinguists, on the other hand, are likely to relate an infant's behavior and learning abilities to particular phases of emotional or cognitive development. Such concerns have led those who favor a naturalistic approach to learning to be especially sensitive to the functional necessity for behavioral plasticity to vary with age and with stages of neuropsychological development. It is no accident that research on imprinting, song learning, and infant development in particular, has illuminated the underlying mechanisms and the functional significance of sensitive phases in behavioral development.

ORGANISMAL STATE AND SPECIES

Observations of many kinds, originating in the field and subsequently transposed to the laboratory for experimentation, leave little doubt that comparative studies of natural learning processes call for a stronger emphasis upon species differences than appears relevant when organisms are learning to cope with more arbitrary paradigms.

The mechanisms that underlie imprinting and song learning cannot be understood without first acknowledging the pervasive role of unlearned, functionally adaptive predispositions to associate particular classes of stimuli. These are often species-specific and state-dependent. Such predispositions influence motor aspects of behavior and bias the formation of certain stimulus-response associations over others. As the state of the organism changes, so rates of associative learning vary accordingly, in harmony with the organism's adaptive needs at the time. It should also be recognized that state dependence extends beyond passive receptivity. It influences recall processes in functionally relevant ways and drives organisms to seek out situations that, on the basis of previously learned expectations, have the potential to satisfy current needs.

Changing states also prime the organism for responsiveness to stimuli specific to certain requirements. Thus, ducklings typically imprint while following an object that they have sought out. Following is initiated most effectively by an object that, while it may or may not satisfy specific visual requirements, also emits the maternal call of the species. Such learning has later impact on the choice of partners and not, for example, on the choice of food objects. Similarly, song-learning birds are innately predisposed to favor sounds that incorporate species-specific elements. In turn, such elements trigger memorization of associated stimuli. These stimuli are remembered in a particular context and linked by state-dependent recall with specific and predetermined behaviors in future life. Thus, memorized songs are applied to the task of song development and not, as memorized predator sounds might be, to the recognition of danger.

The intrusion of genetic influences into behavioral development and learning became one of the workshop's most controversial themes. The inevitable question arose, to what extent do imprinting and song learning represent phenomena that are fundamentally different from the more typical paradigms of the animal learning theorist? To biologists at least, it seemed reasonable to ask whether such special learning has less in common with phenomena such as maze running or keypecking than with the learning that occurs in the course of human development, especially during language acquisition. One must also consider the prospect that some aspects of behavioral plasticity in human infancy may be allied more closely with processes of growth and differentiation than with learning in the traditional sense.

SPECIALIZED LEARNING, VISUAL DEVELOPMENT, AND CORTICAL PLASTICITY

Striking commonalities were uncovered in the course of the workshop between song learning and imprinting in birds, development of the mammalian visual system, and the emergence of human speech in infancy. All display clearly defined critical periods or sensitive phases in which early experience has its maximal impact on subsequent behavior. The sensitive phases have a self-terminating quality, as though organisms wait for appropriate stimulation before closing one phase of development and progressing to another. Depriving a cat of certain kinds of visual stimulation postpones termination of the sensitive phase of visual plasticity. In both imprinting and song learning, the sensitive phase can be extended beyond its normal limits by witholding fully optimal stimuli.

Especially intriguing are apparent parallels between the stimulus requirements of experimentally-sensitive single units in the developing visual cortex and the stimulus requirements of auditory mechanisms underlying song learning. Evidence was presented to suggest that songbird brains come equipped with circuitry specifically responsive to song components but held back from guiding vocal development by auditory feedback until activated by specific stimuli. Lacking appropriate stimulation, such mechanisms, although innate, remain latent and the bird must develop its song abnormally, without their help. Similarly, in visual development, preferred orientations of cortical neurons can be changed by visual experience only within certain limits. Neurons that are already highly selective for orientation cannot change their orientation preference as a result of visual experience but will maintain their original response properties if exposed to corresponding visual stimuli. If not, they become unresponsive ((10); see also Singer, this volume).

The possible extent of cortical plasticity during visual development is thus quite limited. It is surely inappropriate to view these limitations as reflecting a fundamental deficiency in cortical plasticity. Rather than invoking constraints, it seems more productive to think in terms of a functionally optimal balance between neural plasticity and genetically preordained neurological connectivity. It is presumably to this end that the response properties of neurons can only be changed within the limits set by genetic programs (9, 10).

THE NEUROPHYSIOLOGY OF LEARNING

For the first time in the history of research on learning, there exist some compelling opportunities for making a choice between psychological and physiological approaches on the basis of empirical developments rather than the bias of individual investigators. As attested to by many contributors to this volume, discoveries in a variety of rapidly growing subdisciplines provide a concrete basis for such now familiar neurophysiological metaphors as "analyzers," "detectors," "cell assemblies," and "centers of excitation" (see Bateson ("The Neural Basis of Imprinting"), Brown, Changeux, Konishi, Quinn, Sahley, Singer, Squire, and Thompson, all this volume).

Most dramatic are the pioneering investigations of Kandel and his associates into the cellular basis of learning in the invertebrate, Aplysia. Thanks to such efforts, Pavlov's goal of delineating the neurophysiological basis of classical conditioning seems within reach (at least of the type exemplified by alpha-conditioning). In Aplysia we now know that in a monosynaptic sensory-motor system, habituation and sensitization result from presynaptic changes in the transmission of sensory stimulation. Through the involvement of additional circuitry, classical conditioning and sensitization have both been shown to involve enhanced transmission of a sensory signal. It will be a major challenge to extend these findings to other preparations, in particular to the variety of phenomena now regarded as instances of classical conditioning (for examples see Hearst, Jenkins, and Terrace, all this volume).

The impressive progress we have witnessed in understanding the neurophysiology of basic behavioral phenomena in invertebrates provides a firm basis for anticipating the discovery of equivalent mechanisms underlying more complex phenomena in vertebrates. It is nevertheless important to strike a balance between recognizing the importance of behavioral, neurological, and physiological specializations for certain types of learning, while at the same time acknowledging that fundamentally similar processes may be involved at the cellular level.

In principle, one can begin to see how to assemble networks from simple "Aplysia-like" circuits that must sustain higher-order learning phenomena such as classical conditioning (4). It is now reasonable to extend such modelling to encompass special cases such as song learning (Konishi, this volume). As this exercise proceeds, there will be increasing demands for specialized "hard-wired" circuits.

One of the more lively and productive controversies in neurobiology in the next few years will focus on whether it is more appropriate to think of learning in terms of "instruction" or "selection." Changeux (this volume) clearly favors the latter. His concept of selective stabilization of innate "pre-representations" as a consequence of experience found a receptive audience, especially among students of learning in songbirds and honey bees (Marler and Gould, both this volume). The analogy between learning and immunological theory is a compelling one (1) and promises to have a far-reaching impact on future research on the mechanisms of plasticity. Such mechanisms are especially relevant to such phenomena as the development of perceptual categories and concepts that fall outside the domain of classical learning theory. Again there are close affinities with developmental neurobiology, especially in the field of visual development where neuroselectional processes appear to play an important role (Singer, this volume).

LOCALIZATION OF BRAIN FUNCTION

One factor contributing to renewed interest in special learning is the growing evidence of localization of brain function. Since Broca and Wernicke, we have been accustomed to the existence of centers for the control of speech. The symptoms of different kinds of aphasia are very much a function of the precise location of brain damage (Brown, this volume).

The issue of localization of function is arising more and more frequently with other kinds of learned behaviors. Both song learning and imprinting involve highly localized brain structures (Bateson ("The Neural Basis of Imprinting") and Konishi, both this volume; see also (8)). Knowledge of the neuroanatomical circuitry underlying a given learning paradigm is becoming increasingly important for its interpretation. Garcia interprets the selective association of experience of taste and of nausea as a direct consequence of the convergence of gustatory and visceral afferents in the brain stem, indicating an intimate relationship among taste, ingestion, and emesis (Revusky, this volume). As Thompson notes (this volume), lesioning studies appear to implicate the cerebellum in very specific ways in the control of eyelid conditioning.

Such research is important, not only for its obvious bearing on how the brain sustains learning, but also as a source of new distinctions between fundamentally different learning processes. Clinical studies of amnesic brain-damaged humans appear to indicate two distinct, anatomically separable memory systems, one "procedural," the other "declarative" (Squire, this volume). The latter appears to correspond roughly to perceptual and cognitive functions and the former to learned sequences of stimulus-response interactions. The distinction is especially notable because it is drawn along lines that differ from the traditional dimensions of learning theory (but see Holland et al., this volume).

Mishkin's discovery (7) of what appears to be an equivalent dichotomy in memory mechanisms in the monkey brain lends additional weight to a distinction between two systems of storing information, one a "habit" system, the other a system for storing stimulus representations. Lesion studies indicate that these two neuroanatomically distinct systems normally work in parallel and in such close harmony that it is only as a consequence of the artificial disruption of one that the other suddenly becomes apparent. Cognitively oriented theorists may find it easier to relate to these new neuroanatomical findings than theorists using learning taxonomies based on traditional classical and instrumental training paradigms.

COGNITION AND LEARNING

Given the uniqueness of human language, it is hardly surprising that