Lessons from the Lab

Peter Marler describes bird song learning to colleagues at a meeting in Berlin.

Can laboratory experiments help scientists explain how animals learn in their natural environments?

Second of two articles on memory and learning.

By JULIE ANN MILLER

A bee leaves its hive and flies directly to the patch of flowers where it had found ample nectar on the previous day. A songbird listens to the singing of its neighbors and begins to warble a song in the appropriate local dialect. A child puts a puzzle together more quickly each time he tries.

A rat sits in a closed box and presses a bar; a pellet of food appears. A pigeon faces a panel of keys marked with colored lights and pecks them in a particular sequence. A sea snail stops withdrawing its siphon after no harm comes of repeated taps it receives.

These varied examples of learning intrigue scientists of different disciplines, who approach the phenomenon from their various perspectives. Some, in the branch of biology called ethology, find evidence of learning as they observe the behavior of animals in natural settings, as the animals search for food, feed their young, defend their territories. Other scientists describe learning by taking animals into laboratories and measuring their responses in strictly controlled, artificial situations. From this work comes learning theory.

These two major approaches to the biology of learning have developed with quite separate histories, ideas and terminologies. Recently in Berlin, at a meeting called the Dahlem Conference, representatives of the approaches tried to reconcile their differences in hope of achieving a combined understanding of learning. The question facing the group at the conference was, according to one scientist, "What can we do to get from animals inside little boxes to animals outside, doing real things?" Or as another scientist succinctly phrased it, "Do rats bar-press in the woods?"

Meeting participants were particularly excited by recent discoveries in the physiology and chemistry of learning at the level of individual cells (SN: 1/22/83, p. 58). Many believe those and similar findings will ultimately provide common ground for combining the views on learning that have arisen in the different disciplines.

"A change in an animal's behavioral propensities must reflect physical or chemical changes in its brain," says William G. Quinn of Princeton University. What is the character of the change? Recent work in invertebrates (especially sea snails and fruit flies) has begun to crack this problem. "I would not say we have all the building blocks of learning, but we have some and we will get more," Quinn says.

The most detailed description of learning behavior, however, comes from scientists in the discipline known as learning theory. Their goal has been to discover through laboratory experiments the immediate causes of learning common to all animals, or at least all vertebrates.

While the scientists in the field of learning theory argue among themselves over how successful they have been, a few concepts about learning have clearly emerged from their laboratory experiments. For example, the learning theorists agree that two phenomena—Pavlovian conditioning and operant conditioning — are basic to learning. The first of these was originally based on experiments in which dogs salivate when they hear a bell that they have learned signals the arrival of food. This and similar experimental set-ups arrange a relation between two events independent of the animal's behavior. The second basic phenomenon, operant conditioning, is based on rewards and punishments for certain behaviors.

The theorists have also developed rules for more complex experimental situations, for example how an animal reacts to different numbers, types and schedules of events. "The study of learning in conditioning experiments is not an end in itself. Its purpose is to further understanding of behavior at large, and to increase effectiveness in bringing about desired changes in behavior by design," says Herbert M. Jenkins of McMaster University in Ontario, Canada.

One salient difference in approach between the learning theorists and the ethologists is their outlook on the importance of differences between animal types. The ethologists delight in describing behaviors characteristic of different species. But learning theory is based on the belief that all animals, or at least all vertebrates, are likely to employ the same general processes for learning.

"Nervous systems at all phylogenetic levels of complexity are confronted with the same basic problem: How can the causal structure of the outer world be extracted from the experienced events and used to predict the occurrence of future events?" says Randolf Menzel of the Free University of Berlin. "Learning is the neural mechanism which solves these questions by applying a simple rule: Temporal relationships among events are interpreted as causal."

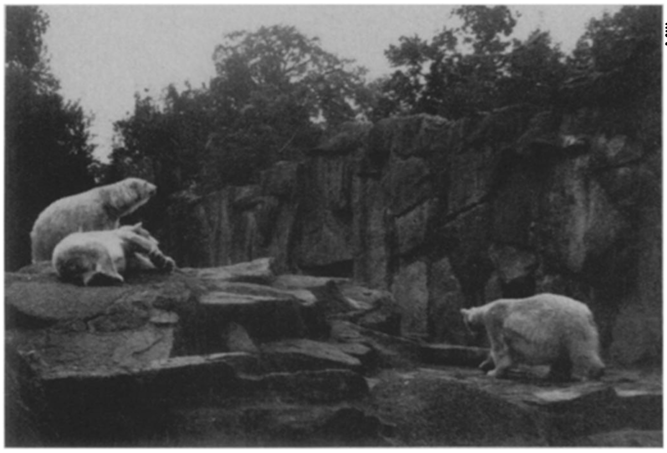
Some scientists suggest that learning processes evolved in many different branches of the animal kingdom because all animals face the same need to extract predictive information from their environments. Others believe learning processes evolved once and have been retained. Sam Revuskey of Memorial University of Newfoundland in Canada argues this view. He suggests that the conservatism of learning processes is similar to that of such basic physiological processes as digestion, which evolved just once, rather than being flexible among species, like body size or coloration.

Although the learning theorists focus on similarities in learning processes, now in part responding to the work of ethologists they are beginning to think more about differences between animals. When at the meeting one participant objected to another's use of the term pigeon, because there are different species of pigeon with different characteristics, Jenkins responded, "At least we don't talk about 'the organism' anymore."

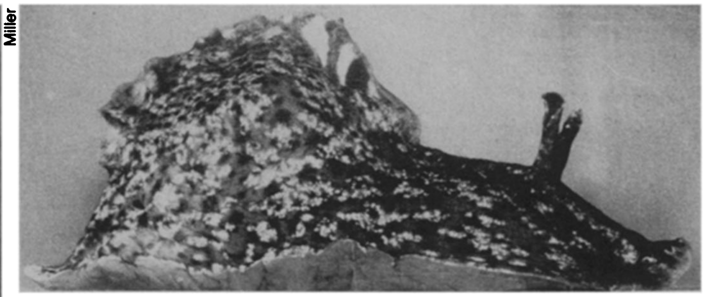
One new aspect of learning theory is experimentation with a wider variety of animals, going well beyond the rat and the pigeon. So far these experiments tend to vindicate the assumption of shared mechanisms, which the scientists call general processes. "Learning looks remarkably similar in different creatures," says Karen L. Hollis of Mount Holyoke College in South Hadley, Mass.

Bees, fruit flies and a slug called *Limax*

The motivation behind learning —in children as well as in animals —often remains a mystery.



Miller



Paul Kandel

Laboratory analysis of the slug Aplysia's *(above) somewhat limited learning repertoire gives clues to learning in higher animals.*

What is natural? Polar bears (left) are more sociable in zoos than they are in the wild.

are among the organisms that have been recently subjected to "classical" learning experiments. The work on these animals may help to bridge the chasms between different approaches to learning. Bees are a favorite subject of ethologists because of their impressive array of natural behaviors. Honeybees, for example, quickly learn where food sources are and communicate that information to their peers. Menzel now reports that in laboratory experiments honeybees demonstrate "surprising similarities" with the well-studied laboratory mammals.

In learning the association between two stimuli — that is Pavlovian conditioning — a honeybee, like a rat, depends on the timing of the stimuli and the reliability with which one stimulus predicts the other, Menzel says. He also finds similarities between bee and mammal in formation of memories. For example, there is short-term memory, which is converted to long-term memory.

Another invertebrate recently examined for learning processes is the garden slug *Limax maximus* (SN: 1/29/83, p. 74). Christie L. Sahley of Yale University now reports that this slug can master what learning theorists call "higher-order relations." For example, she trains a slug to associate the smell of carrots, which it likes, with a bitter-tasting chemical. Then the animals are trained to associate the smell of carrots with that of potato. The slugs consequently reduced their preference for the potato (and the carrot) smell. Thus they associated the smell of potatoes with the chemical they hoped to avoid. *Limax* might be an appropriate animal to use in biochemical and physiological experiments like those already performed on the sea snail, *Aplysia*.

Ethologists tend to ask of laboratory experiments, is the behavior under study ever observed in the wild? Other investigators turn the question around and ask, is any behavior observed in the laboratory irrelevant to the natural activity of the animal?

Klaus Immelmann of Bielefeld University in West Germany gives an example of how some captive animal studies may have implications for some behaviors in the wild: Polar bears generally live a solitary life in the wild. However, housed together in the zoo, the bears show characteristics of social life. They groom each other and develop a rank order. But recently, as the natural environment changes and the bears gather around garbage dumps, such social behavior is being observed in a "natural" environment.

Using the framework of laboratory experiments to explore behaviors observed in the field, Hollis argues that Pavlovian conditioning functions to optimize an animal's interaction with biologically important events. "The performance of a conditioned response allows the animal better to deal with food, rivals, predators and mates," she proposes.

She has explored this idea in experiments with male fish called blue gouramies. One group of fish was trained with Pavlovian conditioning — paired presentations of red light and a rival male. Another group, the control, was presented with red light and with rival males, but the stimuli were independent of each other. After 24 days of training, Hollis observed encounters between two fish, one from each group, preceded by the red light stimulus. The males that had the Pavlovian conditioning delivered significantly more bites and tailbeatings and won more of the territorial contests than did their control group opponents.

Hollis proposes, "These results suggest that Pavlovian conditioning could play an important role in the natural habitat of these fish: By means of the conditional aggressive response, rivals could be confronted at the territory boundary by an already aggressively displaying owner, strategically ready for battle."

While scientists are impressed with the learning-process similarities among species, ethologists still pursue species differences. They ask why some species of animals, even within a group such as insects, appear to rely on learning more heavily than do others. "A bee compared to a fly looks brilliant," says Quinn. Recent experiments on bees even indicate a very sophisticated type of learning — instructive learning — James L. Gould of Princeton University reports. Bees watching a dancing bee can learn the location of a food source without any physical contact.

Brain size was once considered to be the limiting factor for learning. But that is no longer believed. "Just consider what a bee learns with its 1-cubic-millimeter ... brain, and you may ask yourself what you are doing with the rest of your 999.999 cubic millimeters," says Menzel.

Why do some animals rely on learning more than others do? Some ethologists now take an economics approach, especially to questions about foraging. "The caloric cost of learning to manipulate the difficult flowers can be estimated from the improvement in handling accuracy and rate of flower visitation," says Bernd Heinrich of the University of Vermont in Burlington. He has calculated this cost for the bee *Bombus vagan* visiting the jewelweed, a rich flower but one which half the workers on first encounter probe in the wrong place for nectar. He concludes, "This cost [of learning] is well worth it."

While the processes behind learning cross species lines, animals in nature certainly learn different things. Sahley says, "Bees are equipped to learn certain things, slugs others and rats others." Even in laboratory experiments some tasks are more easily taught than others. "Animals seem to have some expectations," says Gould.

Pigeons, for instance, learn more readily to peck than to bar-press for food, whereas rats quickly learn to bar-press for food. On the other hand, pigeons can be trained to bar-press more readily than to peck to avoid electrical shock, whereas rats can most easily be taught to avoid danger by running away. Bees also preferentially learn to associate shapes, odors and colors with different aspects of their foraging behaviors.

While in many cases a species' perceptual and motor characteristics, or perhaps a predisposition to certain types of learning, can explain apparently different learning abilities, there still remains the question of whether any type of specific learning is substantially different from the general processes. The three most likely candidates for special learning are imprinting and song learning in birds and language acquisition in human babies.

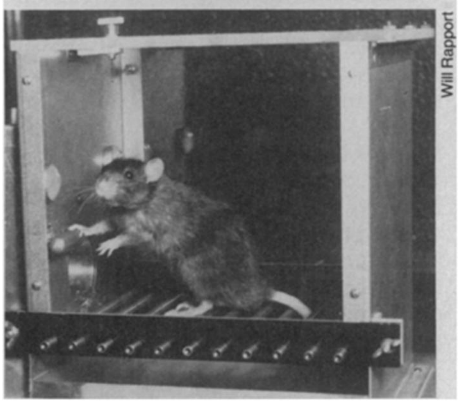
Imprinting, also called selective learning, tells a naive animal surrounded by a world full of potentially learnable stimuli *what* it should remember, and what to do with the information subsequently, say Gould and Peter Marler of Rockefeller University in New York. For example, filial imprinting, which teaches a young bird to follow its parent, enables an animal to learn about its species. "However, it is becoming apparent that imprinting may serve a more subtle but equally important function, enabling the young to recognize one or both of their parents as individuals," says Patrick Bateson of Cambridge University in England. The young bird must stay near a parent, but if it approaches another adult of its own species, it may be attacked or even killed.

What appears to make imprinting different from other processes is that it occurs during a sensitive period. This period ends when a suitable parent model is learned, and the period can be lengthened somewhat if no suitable object is available.

Whether imprinting involves the standard association learning processes has been a topic of lively debate. Recently Bateson and colleagues have identified a structure in the brain required for imprinting. "If you remove it, the animal can't imprint, but it can still learn other things perfectly well," Bateson says. The involvement of this structure, called the intermediate region of the medial hyperstriatum ventrale, dissociates imprinting from most other learning skills. Bateson says it appears that a particular part of the bird nervous system is dedicated to the recognition of close kin.

Bird song learning is another process that appears different from general learning. In about 4,000 bird species, birds learn socially to sing, in the sense that a bird reared in isolation will vocalize abnormally, says Marler. The song typically defends a male bird's territory and attracts and stimulates females. The songs are species specific, but are flexible enough to include local dialects and differences between individual birds. Imitation, improvisation and invention all participate in production of song, which has a discrete pathway in

Will Rapport



Will Rapport

Scientists are trying to reconcile natural learned behavior such as the warbling of songbirds with the results of laboratory experiments on pigeons and rats.

the brain. There is even recent evidence for specific nerve cells that respond only to bird's own song.

Marler sees bird song learning as the best-studied example of a broader set of behaviors, perhaps including such motor coordinations as nut-opening by squirrels, copulation in monkeys and such learned communicative systems as human facial expressions and human speech. He says, "[Bird song] promises to tell us more not just about how bird brains sustain complex behavior, but how any brain handles the problem of creating behavior that is permeated by the multiple consequences of learning and yet [is] sufficiently law abiding that [the behavior] is easy for others to understand."

The learning of language by children is certainly difficult to explain in terms of general learning processes. It takes place in a fixed sequence during a critical period, about ages one to five, and is acquired quickly from the child hearing an incomplete and often faulty set of examples. The child is also limited by his memory of speech previously heard. Explanations based on associations and rewards are generally unsatisfactory. The problem is confounded by the ease with which a child learns a second language during the critical period without any impairment of the first.

While the Dahlem Conference fell short of its stated goal to reconcile learning theory and natural behavior, the outcome was some agreement on the similarities in the findings of the fields and some new ideas for experiments.

In a sense, the promise that physiological and biochemical explanations of learning — such as neurochemical changes at brain synapses (SN: 1/22/83, p. 58) — are waiting in the wings reduces the urgency of conceptual reconciliations between those studying learning theory and natural behavior. Menzel, as spokesperson for the group that discussed invertebrate learning, says, "Many controversies and battles over meanings disappear when we have the [brain mechanisms] in our hands. We then can focus our efforts on the really important questions. So far we have not reached this firm ground, but we already sense an improvement."

Some areas where a combined biological approach might approach such important questions of human learning were suggested by William K. Estes of Harvard University. These questions include: What is the motivation for human learning? How do learning capacities develop as a child matures? How do people learn by thinking, rather than by doing? And are there biological constraints on human learning potential?

But others of the scientists do not see the biochemical and physiological work as the common denominator that will explain the varied observations on learning. Some believe that in mammals, especially in primates and humans, the complexity of the brain demands explanations above and beyond what happens in individual cells. Others reject all physical explanations. "For me, the brain could as well be porridge," one learning theorist at the conference says.

"The relationship between learning theory and natural behavior is only to be determined through functional representations of what the organism's nervous system does, not what it is," John C. Marshall of the Radcliffe Infirmary in Oxford, England, and John Morton of the Medical Research Council in London conclude from the discussion on human learning. "With humans it can at best only be done abstractly ... [Suppose] we had all the human neuro-biological information there was to have. We might then have an account of natural human behavior...but we would not have an explanation in terms of the questions we really wanted to ask."

Quinn consoles them. "People who recoil at the prospect of a humanistically interesting problem turning into squalid chemistry should remember that Penelope's steadfastness [the ideal of Homer described in the *Odyssey*], for example, depended on long-term memory, still experimentally untouched, and on network properties of the human cortex," he says, "a tangle unlikely to be completely unravelled, ever." □