Learning and Memory, the Ecology of

Introductory article

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CONTENTS

Specialized learning and memory mechanisms have sometimes evolved in response to the particular demands of the ecological niches occupied by different species.

INTRODUCTION

For most of the hundred or so years that scientists have studied how animals learn and remember, investigations of these topics have been carried out without attention to differences in the environments in which different species evolved. For example, one of the twentieth century's foremost investigators of animal learning, B. F. Skinner, when discussing the behavior of animals given food rewards, expressed unambiguously the prevailing view of how learning should be studied: 'Pigeon, rat, monkey, which is which? It doesn't matter.'

Skinner, of course, realized that different animals behave in different ways. However, for half a century and more behavioral scientists focused on the many features of animal learning in laboratory situations (for example, in mazes or in boxes where levers had to be pressed to obtain food) that were similar in all species. Such an approach to the study of animal learning, emphasizing similarities across species, is often referred to as a 'general process' approach, because it is based on the assumption that there are one or two basic learning mechanisms (or general processes) that are responsible for all learning by all animals.

A different view of animal learning and memory proposes that specialized learning and memory processes have evolved in response to differences in the selective pressures acting on different species; after all, differences in the physical characteristics and sensory systems of animals are known to be products of natural selection acting in different ecological situations. There is no reason why learning and memory mechanisms should not also have

evolved to respond to the different environmental demands faced by members of different species. According to this view, animals would not only learn and remember in general, but also learn and remember particularly well things that are especially important to their survival and reproduction in the natural world.

TASTE-AVERSION LEARNING

In 1966, John Garcia discovered that learning not to eat substances that are associated with illness might be very different from learning in other situations. Garcia was looking at the effects of radiation on feeding behavior, an issue of potential importance both for patients receiving radiation therapy and to the military whose members might have to survive in radioactive areas in the event of war.

Garcia was studying the feeding behavior of rats exposed to X-irradiation while eating a type of food that they had never before eaten. He discovered, quite unexpectedly, that even though the illness resulting from X-irradiation did not start until some time after the rats had finished eating, the rats later refused to eat that type of food a second time. In most situations, in order for an animal to learn to associate two stimuli (in this case the taste of the unfamiliar food and the illness resulting from exposure to radiation), the stimuli have to occur within tenths of a second of one another. Many pairings of stimuli are often needed before learning is observed. Garcia had discovered a situation in which learning of an association between two stimuli occurred in a single trial, and despite the fact that the stimuli to be associated were separated by many minutes. Indeed, later experiments were to show that learning of an aversion to an unfamiliar taste followed by illness could occur in one trial even when taste and illness were separated by several hours.

In a now-classic second experiment, Garcia demonstrated that, although rats would learn to avoid the taste of a food associated with illness, they would not learn to avoid either visual or auditory properties of a food that had been associated with illness. In this second experiment, rats drank a sweetened solution from drinking tubes wired so that each time the rat's tongue contacted the sweet solution (and the rat experienced a sweet taste) a bell rang and a light flashed. Members of one group of rats received X-irradiation whenever they drank this 'sweet, bright, noisy' water; members of a second group received a mild electric shock to their feet whenever they drank it. A day later, half of each group of rats (one that had been X-irradiated and the other with shocked feet) were tested to determine whether they had learned to avoid drinking a sweet solution. The other halves of each group were tested to determine if they had learned to avoid drinking plain water when licking caused a bell to ring and a light to flash.

Garcia found that rats that had been exposed to X-irradiation after drinking 'sweet, bright, noisy' water avoided ingesting sweet water, but did not avoid 'bright, noisy' water. On the other hand, rats that had received foot shock after drinking 'sweet, bright, noisy' water drank sweet water, but avoided 'bright, noisy' water.

These results were a surprise, because in most other situations learning proceeds equally well regardless of what stimuli are paired with one another. Garcia's rats, on the contrary, associated only taste with illness and only audiovisual cues with shock. Even worse, from the general process point of view, it was soon discovered that birds such as quail more readily learned to avoid the visual properties than the tastes of foods associated with illness.

The general process view of animal learning was faced with a serious challenge because learning about the consequences of eating foods seemed to be different from other kinds of learning: it occurred faster, it occurred with longer delays between the stimuli to be associated, and different species seemed to learn to use different cues to avoid potentially dangerous foods. Pigeon, rat, monkey, which is which? It did seem to make a difference.

It was soon pointed out that there was some biological sense to animals being able both to learn to avoid a potentially dangerous new food after a single pairing of that food with illness and to tolerate long delays between eating a food and becoming ill. After all, eating spoiled food or poisonous substances can result in illness delayed by many hours, and repeated ingestion of toxic substances can have fatal consequences. So, if animals are to be able to learn to avoid ingesting poisons in nature, they would have to be able to learn rapidly to associate properties of substances they ate with consequences of ingesting those substances, even if the consequences of ingestion were long delayed.

It also seemed to make some biological sense for rats to depend on taste cues and birds to depend on visual cues to identify potential poisons. Birds select foods largely on the basis of the food's visual properties, whereas rats tend to eat at night, and use their senses of taste and smell to select things to eat. So, if animals preferentially learn to associate with illness only stimuli in the sensory modality that they use when choosing foods (taste for rats and sight for birds), one might expect the differences among species found in learning associations to illness.

The results of studies of taste-aversion learning clearly suggested that all animal learning might not reflect one or two basic processes. Rather, learning might be in some way modular, with evolution producing a variety of specialized learning and memory systems each of which facilitated learning about biologically important relationships in the natural environment. If so, there should be special processes for learning things other than poison avoidance.

LANDMARK LEARNING

Bee-hunting Wasps

Early students of animal behavior had already shown that some animals whose general ability to learn did not seem particularly impressive could learn surprisingly well those few things most important to the animals' survival and reproduction. Niko Tinbergen, who was later to win a Nobel prize for his work on animal behavior, conducted extensive studies of bee-hunting wasps of the genus *Philanthus*, which lived in Tinbergen's native Holland.

Philanthus is a solitary wasp that lives in small burrows excavated in sandy soil. After stinging and paralyzing a honeybee, a female *Philanthus* returns with her paralyzed prey to her burrow where she stores the bee along with her maturing larvae. The paralyzed honeybees serve as food for the developing young wasps.

The problem that a *Philanthus* female faces after capturing prey, often thousands of meters from home, is how to find her nest entrance, a hole less

than a centimeter in diameter. Tinbergen, in his best-known experiment, waited until rainy weather kept wasps in their nests for a couple of days, and early in the morning of the first fair day, just before a wasp emerged from her nest to go hunting, placed a ring of pine cones around her burrow entrance. When the wasp first emerged from her burrow, she circled above her nest entrance for 6–12 s before flying off to hunt for honeybees. While the wasp was gone, Tinbergen moved the circle of pine cones, which the female had seen only once in her life, a few tens of centimeters from its original position around the nest entrance. He then waited for the wasp to return with a paralyzed bee for her young.

If, during the brief flight she made near the nest entrance before leaving to hunt honeybees, the wasp learned the location of the nest entrance with respect to the pine cones, then she should have landed inside the displaced circle of pine cones when she returned with a honeybee to provision her young. In fact, wasps were four times as likely to land in the ring of pine cones (and at a distance from the true nest entrance) than at the nest entrance itself. Clearly, the wasps had learned about the pine cones in the few seconds between coming to the surface and flying off to hunt for bees.

Of course, it is just possible that wasps are more intelligent than is generally suspected. That turns out not to be the case. This same wasp, *Philanthus*, hunts bees by first approaching any bee-sized moving object, and then flying downwind of it. If the wasp detects honeybee scent while hovering downwind of the object it is inspecting, the wasp lands on the object. If the object feels like a honeybee, the wasp stings it and takes it back to its burrow.

Tinbergen conducted another experiment in which he tethered both a dead honeybee and a honeybee-sized piece of wood on separate threads suspended from a clothes line. The piece of wood was hung a few centimeters downwind of the bee. A wasp would, as usual, approach the objects and then fly downwind of them. Because the smell of the scent of a honeybee was on the wind, the wasp then landed. However, it landed on the piece of wood downwind from the suspended, dead honeybee, not on the honeybee itself. Because the piece of wood did not feel like a bee, the wasp then ended its attack without stinging. The wasps never learned to recognize wooden dummies by sight and avoid attacking them. Instead, the wasps repeatedly attacked the piece of wood, rather than the honeybee just a few centimeters upwind of the

wooden decoy, and would land on the decoy dozens of times. So here, in a single animal, one sees both a striking ability to learn about landmarks around a nest and a striking inability to learn to use visual cues to distinguish bees from sticks.

Of course, in the natural world, there are rarely if ever inanimate objects hovering in midair between a bee and a hunting wasp. On the other hand, all bee-hunting wasps have to learn the location of their burrow entrances, if they are to raise their young successfully. *Philanthus* wasps appear to be specialized to learn just those things that they need to learn in the natural environment.

Clark's Nutcracker

Many species of bird and mammal create hoards of food to eat during times of food shortage. Some, like chipmunks or dormice, create a single large cache of food. Others, like squirrels or chickadees, called 'scatter hoarders', create a number of food caches in different locations.

Clark's nutcracker (a middle-sized bird about the size of a blue jay but without a crest, and colored gray and black with white wing and tail patches), is probably the champion among scatter-hoarding birds. In late summer, a single Clark's nutcracker will place twenty to thirty thousand pine seeds in six to eight thousand separate caches. During the next winter and early spring, when relatively little food is available on the mountainsides, each nutcracker recovers the seeds it has cached. The cached seeds, rich in protein and fat, enable nutcrackers to breed far earlier in the spring than other birds that live in the same area but either do not cache seeds or cache far fewer seeds than do the nutcrackers. Nutcrackers are also different in having special pouches that open under their tongues (sublingual pouches) where they can place ninety seeds or more, thus easing transport of seeds to caching sites.

The scrub jay is phylogenetically closely related to and lives in the same area as Clark's nutcracker. However, scrub jays are considerably less dependent than nutcrackers on cached food, and do not have specialized pouches for carrying seeds.

The fact that nutcrackers must remember the locations of thousands of seed caches for weeks or even months suggests that, along with a physical structure for transporting food to caches, nutcrackers might have evolved a specialized system of learning and memory to keep track of the cache sites they have created. Indeed, in natural circumstances, after a nutcracker lands and begins to dig in the ground, more than 70 percent of the time it

recovers pine seeds cached there. This level of accuracy is truly remarkable considering that a nutcracker spends only about 30 s hiding each cache, has to remember thousands of caches, returns to harvest its caches months after creating them, and recovers caches from areas which may have changed considerably in appearance since caching took place: nutcrackers cache seeds in the late summer, when the ground is free of snow, but retrieve them in winter and early spring, when the ground is often snow-covered.

It is, of course, possible that nutcrackers do not really remember where they have cached seeds at all. Perhaps they simply locate caches by their smell, or make marks near caches that they use to guide them to hidden pine seeds. In the laboratory, smells can be removed, as can any marks made by the birds. Laboratory studies, in which cache recovery depends entirely on learning and remembering landmarks that identify cache sites, have shown repeatedly that both nutcrackers and scrub jays can use memories of landmarks to recover cached seeds. However, nutcrackers, the caching specialists, are significantly better than are scrub jays at recovering seed caches a week after creating them. Such findings, and there are a number of them, suggest a specialization of learning and memory for caches in birds that cache extensively in nature.

If there is indeed specialization in nutcrackers for learning and remembering landmarks associated with caches, you might expect to find areas of the brain involved in learning and remembering landmarks better developed in nutcrackers than in scrub jays. Further, one might predict that, in caching bird species in general, brain areas involved in landmark learning would be larger than the same brain areas in noncaching bird species.

The hippocampus, a part of the cortex of the brain, is extensively involved in memory for cache sites. We know that the hippocampus is involved in cache recovery because, although caching birds with lesions in this structure show normal feeding and caching behavior, they are unable to remember where they have cached seeds when they later look for them.

In comparison with noncaching birds, caching birds have large hippocampi for their body size. It is important to be sure that the different body size of caching and noncaching birds is taken into account, because otherwise if caching species were just generally larger than noncaching species and bigger birds tended to have bigger brains, it would look as if the hippocampus of food-storing birds was especially large, even though that was not true.

Homing Pigeons

Caching birds are not the only birds with especially large hippocampi. Lesions of the hippocampus disrupt the ability of homing pigeons to use local landmarks to return to their lofts, and the hippocampi of homing pigeons are larger than those of breeds of pigeon that do not home.

Meadow and Pine Voles

Meaningful relationships have also been found between the need for navigational skill and hippocampus size in mammals, although the best-studied relationship between spatial learning and brain size in a mammal involves differences between the sexes, as well as differences between species.

Various species of vole (small, plump, short-tailed rodents) are to be found in grasslands throughout North America, and different vole species differ markedly in their mating patterns. For example, male meadow voles mate with several different females, and during the breeding season each male meadow vole moves about an area that overlaps the territories of several female meadow voles. Male pine voles, on the other hand, are relatively faithful to a single female, and the territories of male and female pine voles are of roughly the same size throughout the year.

Because male meadow voles travel greater distances than do female meadow voles, whereas male and female pine voles travel equal distances, male meadow voles (but not male pine voles) would seem to need greater proficiency in navigation than would females of their respective species. Indeed, in the laboratory, male meadow voles (but not male pine voles) perform better than do females of their species on tests of spatial learning. As you might expect, male meadow voles (but not male pine voles) have larger hippocampi than do females of their species.

BIRDSONG LEARNING AND IMPRINTING

Learning

Males of many bird species produce a series of notes, trills and pauses (a song) that is used during the mating season both to attract females and to defend territory against intrusion by other males. Males of each species sing a different song, and in some species birds from different geographical areas sing local 'dialects', not unlike the different

dialects of native English speakers coming from different parts of the world.

It has long been known that birds learn to sing the song typical of their species. However, the special properties of birdsong learning were clearly demonstrated only in the 1960s by Peter Marler and his associates, who studied song learning in a common North American species, the white-crowned sparrow.

Marler took young sparrows from the nest and reared them by hand in the laboratory under conditions where they could not hear other sparrows sing. When hand-reared sparrows that had never heard a sparrow song grew to adulthood and began to sing, they sang abnormal, simplified songs. Marler reared other white-crowned sparrows in the laboratory and allowed them to listen to tape recordings of adult male white-crowned sparrows. When adult, these sparrows sang not just normal song but also the same dialect as the male whose song was recorded on the tape. Clearly, learning was important for development of song in this bird species.

Marler also found that, although hand-reared white-crowned sparrows would learn white-crowned sparrow song from tape recordings, they would not learn the songs of other species of birds from such tutor tapes. Indeed, white-crowned sparrows reared listening to the songs of other bird species sang simplified songs, just like white-crowned sparrows reared in total auditory isolation. Further, tapes of white-crowned sparrow song played to sparrows when they were between 10 days and 50 days old saved them from singing simplified song as adults, while the same tapes played to the sparrows later in life had little or no effect. So, song learning in white-crowned sparrows was restricted both to certain songs and to certain times of life. The fact that sparrows learn song when young, but do not use this information until they are adult, also differentiated song learning from other types of learning.

Song learning is obviously very different from learning to traverse a maze or to press a lever for food, and like landmark learning has its own special physical basis in the brain. Nottebohm and his colleagues removed various areas from the brains of canaries and recorded their songs both before and after these operations. As a result, the researchers were able to describe a series of clusters of nervous tissue and their connections that control both song learning and song production. The more songs a male sang, the larger were his brain areas concerned with song. Males (which sing) had larger structures than did females (which do not

sing). The relevant brain areas, but not others, also grew in the spring and summer, when males sing, and shrank in the fall and winter, when singing ceases.

Imprinting

Imprinting is a term used to describe two kinds of effects of early social experience on later social behaviour. Filial imprinting refers to the learned tendency of young precocial birds to become attracted to and follow their parents (precocial birds are those that hatch in a relatively mature state, like ducks and chickens). Sexual imprinting refers to the effects of early social experience on adult mate preference.

Similar features distinguish imprinting and birdsong learning from the usual types of learning:

- there is restriction on the stimuli which a young bird will learn to follow or to respond to sexually
- there is a restricted period during life when imprinting will occur
- there is (in sexual imprinting) a long interval between the time of imprinting and expression of the imprinted behavior
- there are identifiable neural structures that support imprinting.

CONCLUSION

Immediately following discovery of the special properties of taste-aversion learning, there was a reasonable expectation that many similar cases of adaptively specialized or domain-specific learning and memory processes would soon be discovered, and that a new era would dawn in the study of animal learning and memory. It was an expectation that was to prove difficult to fulfill. Although a few apparently novel learning and memory systems have been discovered, particularly those concerned with landmark learning, progress has been slow.

Nevertheless, the search for adaptively specialized learning processes has led both biologists and psychologists to look to the behavior of animals in their natural environments to identify instances in which animals in nature appear to need to learn. Such instances are not hard to find. Animals have to learn to recognize predators and prey; they have to learn to recognize both kin and other members of their social groups; they have to learn their way around their home ranges; they often have to learn mate preferences or vocalizations appropriate to their species. As we have seen, members of some species have to remember where they have stored caches of food.

However, field data pointing to instances in which animals need to learn provide little information on how learning occurs. Is the learning of biologically important relationships similar to learning in artificial situations, or is such learning special? Such questions can be answered only under the controlled conditions of the laboratory.

Although the search for adapatively specialized learning mechanisms in the laboratory has been in progress since the 1970s, it is not yet clear just how common such domain-specific cognitive processes are. In some cases, such as those described above and a very few others, learning does seem to reflect information-processing systems evolved to respond to particular environmental demands. However, more frequently than was anticipated, general process learning seems to be all that is needed to get the job done.

Further Reading

Balda RP, Kamil AC and Bednekoff PA (1996) Predicting cognitive capacity from natural history. *Current Ornithology* 13: 33–66.

Balda RP, Pepperberg IM and Kamil AC (1998) *Animal Cognition in Nature: The Convergence of Psychology and Biology in Laboratory and Field*. San Diego, CA: Academic Press.

Bateson PPG, Rose EP and Horn G (1973) Imprinting: lasting effects on uracil incorporation into chicken brain. *Science* 181: 576–578.

Immelmann K (1972) Sexual and other long-term aspects of imprinting in birds and other species. *Advances in the Study of Behavior* 4: 147–174.

Jacobs LF, Gaulin SJ, Sherry DF and Hoffman GE (1990) Evolution of spatial cognition. *Proceedings of the National Academy of Sciences of the USA* 87: 6349–6352.

Konishi M (1965) The role of auditory feedback in the control of vocalization in the white-crowned sparrow. *Zeitschrift für Tierpsychologie* 22: 770–783.

Marler P (1970) A comparative approach to vocal learning: song development in white-crowned sparrows. *Journal of Comparative and Physiological Psychology* 71: 1–25.

Marler P (1991) Song-learning behavior: the interface with neuroethology. *Trends in Neurosciences* 14: 199–206.

Marler P and Terrace HS (1984) *The Biology of Learning*. Berlin, Germany: Springer-Verlag.

Nottebohm F (1991) Redressing the mechanisms and origins of vocal learning in birds. *Trends in Neurosciences* 14: 206–211.

Rozin P and Kalat J (1971) Specific hunger and poison avoidance as adaptive specializations of learning. *Psychological Review* 78: 459–486.

Sherry DF and Schacter DL (1987) The evolution of multiple memory systems. *Psychological Review* 94: 439–454.

Sherry DF, Jacobs LF and Gaulin SJ (1992) Spatial memory and adaptive specialization of the hippocampus. *Trends in Neurosciences* 15: 298–303.

Shettleworth SJ (1998) *Cognition, Evolution and Behaviour*. Oxford, UK: Oxford University Press.

Skinner BF (1956) A case history in scientific method. *American Psychologist* 11: 221–233.