

THE EVOLUTION OF BEHAVIOR

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Evolutionary theorists not only point to the survival value of the present structure and function of an organism, they try to reconstruct earlier stages which should also have had survival value. An example of current interest is the flight of birds. Feathers may have evolved first as thermal insulation, but what about wings? Were they adaptations of forelimbs which first helped animals run faster or that helped tree animals leap from branch to branch or from branch to ground? (Even when a feature first evolved because of consequences quite different from those which explain its current survival value, a plausible early history is still needed.) Among the features to be explained in this way is behavior. The current survival value of reflexes and the released patterns of behavior studied by ethologists may be clear, but can we construct plausible sequences through which they could have evolved, with survival value at every stage?

The first behavior was presumably simple movement—like that of the amoeba reaching out into new territory and hence increasing its chances of finding materials necessary for its survival. A plausible second step was sensing, as the result of which movement could take the organism away from harmful stimuli and closer to useful materials. The assignment of different organs to sensing and moving should have led to the evolution of connecting structures, and eventually to tropisms and reflexes.

The released behavior patterns studied by ethologists also presumably evolved through increasingly complex stages. It is unlikely that many current instances occurred first in their present state as variations which were then selected by survival. In my paper "The Shaping of Phylogenetic Behavior" (Skinner, 1975),

I suggested that well established geological changes could have supplied some of the necessary sequences of contingencies. It would not be hard to teach a fish to jump from a lower level to a higher one. One could reinforce swimming across an underwater barrier, slowly raise the barrier until it reached the surface, and then raise it so that it became the wall of a second tank. As the levels of water slowly separated, the fish would jump with greater and greater force. Something of the same sort, over a very different time span, may have happened if the shallow, graveled bottom of a river in which salmon breed moved upstream as the river changed and as rapids and falls intervened between the graveled bottom and the ocean.

A different geological change has been suggested (Carr, 1967) to explain the behavior of the turtles that feed along the coast of Brazil but swim more than a thousand miles to Ascension Island where they breed. Apparently they once swam to nearer islands which have disappeared. As a third example, I cited the behavior of the Atlantic eel, which travels from either American or European rivers to a breeding ground near the Sargasso Sea. These long journeys are taken only once, and it is quite unlikely that they could have occurred first in their present form as variations. Before North America and Europe separated, however, the distances must have been very short. The present behavior could have evolved as each generation went at most a few centimeters farther than the preceding.

Like most evolutionary theories, these are speculations, but they appeal to known geological changes that could have provided the conditions under which complex innate behavior was shaped. So far as I know, ethologists have not given much attention to plausible histories of this sort. Some, indeed, have questioned whether reproduction with variation can explain complex behavior without appeal to mental processes. There is a heron, for ex-

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ample, that fishes by touching the surface of the water with a feather and seizing the fish that rises to this simulation of an insect. Does the heron not show some of the thought processes of the human angler? But the journey of the eel from the Nile River to the Sargasso Sea, a quarter of the way around the earth, is a much more complex example of innate behavior and is much harder to explain in "cognitive" terms. Anyone who has seen a slip of a plant grow into a complete plant with flowers and fruit, an achievement also hard to attribute to mental life, will have no difficulty in accepting the role of natural selection in the origin of behavior, no matter how complex.

Social behavior raises a special problem, as two interrelated but different kinds of behavior appear to evolve together. If bees returning to the hive dance in ways used by other bees in finding sources of food, what could have been the survival value of the dance before the response of the other bees had evolved, and how could it have evolved before returning bees danced? We must assume that returning bees behaved in ways related to the location of food for other reasons. A bee that had come a long way might show fatigue, a bee coming in a particular direction might make circular phototropic movements, and so on. Once the responses of other bees to these stimuli had evolved, further refinements could occur.

BEHAVIORAL PROCESSES: IMITATION AND MODELING

The evolution of the processes through which behavior changes also needs to be explained. An early example must have been imitation. A structural definition (behaving as another organism is behaving) will not suffice; the dog chasing the rabbit is not imitating the rabbit. Phylogenetic imitation could be defined as behaving as another organism is behaving for no alternative environmental reason. But some other reason may first have been necessary. Consider a group of grazing animals subject to frequent predation. They all exhibit a strong tendency to run, in response not only to predation but to stimuli correlated with predators. An example of the latter should have been the sudden running of one or more other members of the group,

already responding to the predator. At that stage the behavior would not be imitation; it would be released by either of two stimuli—the sight of a predator or the sight of another animal suddenly running. But a variation as a result of which one organism imitated another would then have had survival value as redundant support. As the process developed, the imitative model could take full control, and the imitator would then simply do what another animal was doing and for no other reason.

Once imitation has evolved, contingencies of selection exist which should produce *modeling*. A young bird will eventually fly by itself, but if it flies sooner when parent birds fly, and if early flying has survival value, then parental modeling should evolve, the parent birds flying often and in particularly conspicuous ways that are easily imitated.

RESPONDENT CONDITIONING

As evolved processes through which behavior changes during the lifetime of the individual, imitation and modeling prepare the individual only for behavior that has already been acquired by the organisms that model it. Other processes have evolved which bring the individual under the control of environments to which the individual alone is exposed. One is respondent (Pavlovian or classical) conditioning. Under what conditions could it have evolved?

Let us consider Pavlov's classical example: A bell frequently followed by the delivery of food eventually begins to elicit salivation. The unconditioned salivation is an evolved reflex. The commonest stimuli are substances in the mouth, but in a stable environment salivation to the mere appearance of a particular food should also have evolved, as seizing and eating the food evolved to the same stimuli. The contingencies would favor a stronger response to taste, however. Respondent conditioning could have begun as a variation which made the visible features of food *slightly more likely* to elicit salivation. Saliva would then have been secreted in response to the sight of food both as a weak reflex arising from natural selection and as a conditioned reflex. The conditioned version could take over in response to a stimulus (e.g., a bell) which had no effect due to natural selection.

Salivation does not suggest strong survival value, and the argument is more convincing for sweating and the acceleration in pulse rate associated with vigorous action. An evolved tendency to fight or run away at the sight of a predator could be accompanied by an evolved tendency to sweat and increase the pulse rate, but there would be more sweating and a more rapid pulse during the actual flight or attack. If early sweating and an increased pulse rate helped in preparing for effective flight or attack, variations leading to the process of respondent conditioning would have had survival value.

In these examples, respondent conditioning is explained as a supplementary increase in the strength of reflexes which have not fully evolved. The explanation is supported by certain features of respondent conditioning that are often overlooked. The Pavlovian conditioned reflex has no survival value unless it is followed by the unconditioned. Although one can demonstrate that salivation is eventually elicited by a bell, there is no advantage to the organism unless food follows. Similarly, an inclination to sweat or increase heart rate in response to the appearance of a predator also has no value unless vigorous action follows.

The scope of respondent conditioning is much broader than its role in the conditioned reflex. Releasers, studied by ethologists, are conditioned in more or less the same way, and imprinting is at least similar. There is obvious survival value in the behavior of a young duckling as it follows its mother. The features of the releasing object could have been sharply defined, but a lesser demand is placed on the genes if following is released by any large moving object. In the world of the duckling that object is almost always the mother. The looser specification suffices, because the mother duck is a consistent feature of the duckling's natural environment. The imprinting is a kind of statistical confirmation of a less than specific genetic instruction.

OPERANT CONDITIONING

A different explanation is needed for operant conditioning. Under what conditions could the smallest possible variation contribute to the evolution of the process? Innate behavior has consequences which are ultimately related to survival. The hand is withdrawn from a

painful stimulus, presumably because the painful stimulus is potentially damaging; the response promotes survival by preventing damage. Any slight change as the result of which subsequent damage would be more quickly terminated should have had survival value, and operant conditioning through negative reinforcement would be such a change. The operant response would be an exact duplicate of the phylogenic response, and the strengthening consequences would be the same, contributing to the survival of the individual and hence of the species through both natural selection and an evolved susceptibility to reinforcement by a reduction in painful stimuli.

A similar argument can be made for positive reinforcement. If eating a particular kind of food has had survival value (such as that which explains the behavior of eating the food), an increased tendency to eat because the taste of the food has become a reinforcer should have had survival value. Both the topography of the behavior and the immediate consequence (ingestion of a particular food) would be the same, but the consequence would have two effects—one related to natural selection and the other to an evolved susceptibility to operant reinforcement by a particular taste. Once the process of operant conditioning had evolved, topographies of behavior with less and less resemblance to phylogenic behavior could have been affected, and eventually behavior could have emerged in novel environments which were not stable enough to support it through natural selection.

Two other stages in the evolution of operant behavior need to be considered. Once the process existed, a susceptibility to reinforcement by new forms of stimulation could have evolved. It would have been supplemented by a new role for respondent conditioning—the conditioning of reinforcers. Stimuli which frequently precede unconditioned reinforcers could begin to have reinforcing effects in both respondent and operant conditioning.

A second stage may have been the evolution of unconditioned behavior having no survival value of its own but available for selection through operant reinforcement. It would enable the individual to develop a much wider repertoire of behavior appropriate to novel environments. The human infant shows a large repertoire of uncommitted behavior.

Many current contingencies of reinforce-

ment resemble contingencies of survival. We behave in a given way both because we are members of a given species and because we live in a world in which certain contingencies of reinforcement prevail. Thus, we avoid going over a cliff, we dodge objects, we imitate others, we struggle against restraint, we turn toward a movement seen out of the corner of an eye—and all for two kinds of reasons: contingencies of survival and contingencies of reinforcement. It would be hard to say how much of the strength of the behavior is due to each. Only a first instance can be said to be necessarily innate, and first instances are hard to spot. An example of current interest is aggression. We may have an innate repertoire of aggressive behavior, but similar behavior is generated by many contingencies of reinforcement. It does not matter whether a given instance is phylogenetic or ontogenic unless we are concerned with doing something about it. When we are, the variables to be changed must be identified.

In the human species, operant conditioning has very largely replaced natural selection. A long infancy gives the ontogenic process greater scope, and its role in adapting to very unstable environments is a great advantage. Nevertheless, the process is not untouched by environmental changes. As I have pointed out (1966), the human susceptibilities to reinforcement by sweet and salt, sexual contact, and signs of aggressive damage may once have had much greater survival values than they have now. Technological advances in the production, storage, and distribution of foodstuffs, in the control of famine and pestilence, and in the improvement of weapons may have made these susceptibilities more likely to be lethal.

Just as very complex innate behavior has led to an appeal to cognitive processes, so it is often argued that operant conditioning cannot account for complex learned behavior. Animals as well as people are said to transcend the shaping and maintenance of behavior by contingencies of reinforcement and to show insight, the development of concepts, and other cognitive processes. Such claims are vulnerable to demonstrations that operant conditioning will suffice. Robert Epstein, Robert Lanza, and I (1980, 1981), Epstein and I (1981), and Lanza, Starr, and I (1982) have recently simulated a variety of complex cognitive processes in pigeons. Not only can such behavior be ex-

plained by pointing to fortuitous contingencies of reinforcement, it can be produced by arranging the necessary contingencies.

It has also been said (by Thorndike, for example) that things reinforce because of the way they feel, but certainly the reinforcing effect must have evolved first. Only when that had happened would things have been felt as, and called, pleasing and satisfying. Perhaps we should speak of feelings only when what is felt is reinforcing. If we pull our hand away from a hot plate simply as a reflex, the reduction in painful stimulation plays no current role. Perhaps it is only because the behavior is reinforced by the same reduction that we say that the stimulation hurts. The same may be true of positive reinforcers. Insects copulating simply as phylogenetic behavior may not be “enjoying themselves.”

The conditions under which operant conditioning evolved are helpful in understanding its nature. Selection did not need to respect how a bit of behavior produced a consequence; any immediate consequence would have sufficed. Immediacy was essential for other reasons. Deferred reinforcers have a more powerful effect upon intervening behavior, and behavior must be in progress if it is to be changed by a consequence. The claim that behavior is affected by a general melioration, optimization, or maximization of a reinforcing condition conflicts with these principles, and the evidence should be reexamined—to make sure, for example, that gaps between behavior and deferred consequences are not bridged by conditioned reinforcers.

A concept of optimization is like the concept of health. The healing of a wound restores a normal condition of the body and the normal condition favors survival. But healing does not occur because it promotes survival; it occurs because certain structures in the individual have evolved because they have promoted survival. Similarly, in a hungry organism an operant is reinforced by the receipt of food. The food reduces a state of hunger and contributes to the survival of the individual and species. But the operant does not occur because it reduces hunger; it occurs because certain behavioral processes have evolved when a reduction in hunger has contributed to the survival of the species. Behavior is not reinforced by the melioration, optimization, or

maximization of anything. It is reinforced through evolved processes, to the ultimate effects of which those terms refer.

THE EVOLUTION OF CULTURAL PRACTICES

Operant imitation requires no new evolved process. When organisms are behaving because of prevailing contingencies of reinforcement, similar behavior in another organism is likely to be reinforced by the same contingencies. A general conditioned tendency to behave as others behave supplements phylogenetic imitation. Operant modeling then follows: When the behavior of another person is important, modeling is reinforced when the other person imitates.

Imitation and modeling play important roles in transmitting the results of exceptional contingencies of reinforcement. Some of the great human achievements were due to extraordinarily lucky accidents, when other people came under the control of the same fortuitous contingencies through imitation. The behavior was even more rapidly transmitted by modeling. The human species made further progress in the transmission of what had already been learned when its vocal apparatus came under operant control.

A culture may be defined as the contingencies of social reinforcement maintained by a group. As such it evolves in its own way, as new cultural practices, however they arise, contribute to the survival of the group and are perpetuated because they do so. The evolution of cultures is of no further relevance here because no new behavioral processes are involved.

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