

THE SHAPING OF PHYLOGENIC BEHAVIOR

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An unusual topography of operant behavior can often be shaped by making the contingencies of reinforcement increasingly more complex. In a simple demonstration, a box is divided into two parts by a low wall, and a hungry rat is placed on one side and food on the other. The rat possesses an initial repertoire of responses (climbing and jumping), with which it crosses the wall and which are reinforced by the food. As a result, responses having the required topography are strengthened and soon occur on later occasions. If the wall is then made slightly higher, only some of these responses will be successful, but they will begin to occur more frequently, and as a result, new topographies of response will appear that will meet even more demanding contingencies when the height of the wall is again increased. If the height is not increased too rapidly (if some responses are always successful), a very energetic and skillful repertoire will result. The rat will eventually go over a wall that it would never cross if it had not been exposed to such a program.

A similar result could be obtained by genetic selection. Rats that most readily or successfully crossed a wall of a given height could be selected for breeding to produce a population among which some members would be more likely to cross a higher wall, and the

process could then be repeated. Two strains of hooded rats used in some early genetic experiments at the old Bussey Institute at Harvard University could be separated instantly by putting them one at a time in a shallow box; members of one strain quickly escaped, while members of the other strain remained in the box indefinitely. From the observed facts alone, it was impossible to tell whether the difference was due to operant conditioning, following some such procedure as just described, or whether it was genetic. When ontogenic shaping can be ruled out, it is standard practice to infer that genetic selection has been responsible for an observed difference of this sort.

The behavior of homing to a fixed site raises similar questions. An organism can be taught to home through operant conditioning by repeatedly placing it in positions from which returns to a fixed site are reinforced. The field may be progressively enlarged, subject only to the limits imposed by the available time and the locomotor capacities of the organism. A parallel process, in which contingencies of survival replace contingencies of reinforcement, is usually inferred in order to explain, for example, the behavior of bats in leaving and returning to a cave. As the size of the original group increased, those bats that went farther and farther afield to obtain food and returned successfully were presumably more likely to survive and breed and transmit the behavior.

Contingencies of reinforcement that shape ontogenic behavior can be arranged and studied in the laboratory. Most of the contingencies of survival responsible for phylogenetic behavior observed in the field are merely inferred. But some evidence of environmental conditions that probably changed in such a way as to shape complex phylogenetic behavior

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has emerged in connection with the theory of continental drift and the spreading of the sea floor.

An example that has recently attracted attention is the behavior of the green turtle (*Chelonia mydas*), which feeds in the water pastures along the coast of Brazil and swims more than a thousand miles to breed on Ascension Island. The journey takes several weeks and demonstrates remarkable navigational skills, since a five-mile target must be hit after about one thousand miles of travel in the open sea. As Carr (1966) argued, it is hard to imagine that behavior as complex as this could have evolved through natural selection under the present circumstances. In 1964, Fraser pointed out that 150 million years ago the turtles "would have only a narrow arm of the sea to negotiate; for since the ancient latitudes of Rio Doce and the projection of Ascension on the African coast are in precise agreement, the nesting ground was lying there just across the water, a mere hundred miles or so from its land-based home among the elephant grass of east Brazil".

The case is not quite that simple, however, as Carr and Coleman (1974) have recently pointed out. Ascension Island is a relatively late member of a chain of volcanic islands that have appeared as the sea floor spread. The turtles may first have gone to islands close to Brazil, but these slowly submerged. They presumably then went on to more distant islands in the same general direction, of which Ascension was the last to appear. The fact remains that the behavior of feeding along the shores of Brazil and swimming to a breeding ground relatively safe from predators met progressively more demanding conditions as the distances increased, either continuously or in a step-wise fashion.

Another program of contingencies of survival resulting from the spreading of the sea floor may explain the behavior of American and European freshwater eels, which appear to have a common spawning ground in the Sargasso Sea. It was Alfred Wegener, the father of the theory of continental drift, who noted the relevance of this fact to his theory, in the fourth edition of his *Origin of Continents and Oceans* (1966). The point was suggested to him, as early as 1922, by J. Schmidt. Schmidt's early research (1923) showed that the European eel (*Anguilla anguilla*) breeds

in an area northeast and north of the West Indies. The young eels in the larval stage (called *leptocephali*) are small and leaf-like in appearance. They rise to the surface and with the help of the Gulf Stream move toward Europe. Year-old larvae are to be found in the mid-Atlantic and as far east as the Azores; two-year-old larvae are found on the shores of Europe and in the Mediterranean; after three years, they undergo metamorphosis and appear as elvers in freshwater streams, where they mature. Years later, the mature eels return to the place in which they were hatched. As the sea floor spread, the spawning ground moved much farther from European rivers than from American, and Wegener credits H. Osterwald with realizing that "the gradual drift of this ocean basin plus America away from Europe" explains the fact that the larval stage of the European eel is three years while that of the American is only one.

In 1969, the present author pointed out the possible relevance of the spreading of the sea floor to the shaping of the phylogenetic behavior of the eel (Skinner, 1969). The behavior is truly remarkable. From the breeding ground to the mouth of the Nile, for example, a young eel in the larval stage travels, as Schmidt pointed out, about 6000 miles in a period of three years. Ocean currents will explain only part of this migration. The mature eel makes a return journey of the same distance against the currents. As with the green turtle, it is hard to believe that this extraordinary behavior could have arisen from natural selection under present environmental conditions. But if the distances were at first short, and if they increased *no more than a few inches each generation*, as the theory of continental drift implies, then some members of each generation could have satisfied the new contingencies and bred to transmit the behavior.

In 1948, Wolfson argued that "continental drift was the stimulus for the evolution of the more highly developed forms of migration [of birds]". He stated his hypothesis in four steps:

- (a) Before the advent of continental drift many birds were performing short flights between breeding and feeding areas.
- (b) With the onset of drift these areas diverged slowly.

- (c) The birds continued their use of these areas because of their well-developed homing instincts.
- (d) As the distances increased, only those individuals that had the necessary energy for the flight survived.

Wolfson pointed to the fact that, for example, the Arctic tern, which breeds in northern North America and migrates to the Antarctic, first flies *eastward* across the Atlantic to Europe and then southward along the African coast. The eastward journey may at first have been very short, but as the continents separated, successive generations would have flown slightly greater distances and what seems now like a nonadaptive flight pattern is thus explained.

North Atlantic salmon show a pattern that is the reverse of that of the eel; they breed in freshwater rivers but live most of their adult lives in the ocean. They also show a long east-west migration that could have been shaped by the separation of the continents. According to Orr (1970), "American Atlantic salmon have been taken on the West Coast of Greenland, and those from Sweden have also been recorded there, a distance of almost three thousand miles from the home streams of both." At one time, the distances were very much shorter, and navigation must have been scarcely more than a matter of moving along a coastline.

A different effect of the plate tectonics related to continental drift may have produced contingencies of survival that shaped certain features of the behavior of salmon on the West Coast. Columbia River salmon, for example, breed in shallow, relatively still fresh water, with a gravel base, but spend most of their lives in the Pacific Ocean, particularly in the Gulf of Alaska. At the present time, the mature salmon reach suitable breeding grounds only by fighting their way up through treacherous rapids and waterfalls. At an earlier stage in the development of the river, however, suitable breeding conditions may have been found close to shore. At that time, the salmon need not have possessed any of the extraordinarily skillful and powerful behavior with which they now conquer the hazardous flow of the river. As the river matured, suitable breeding grounds should have receded from the shore, setting up a program

of contingencies of survival that shaped the present behavior, each generation being required to meet contingencies only very slightly more difficult than the preceding.

Phylogenetic shaping of behavior is plausible, of course, only if the species, or at least some recognizable earlier form, was in existence when the geological change occurred. The green turtle, the eel, and migrating birds seem to meet this requirement, and Professor Coleman has pointed out that "the Western seaboard is a geologically young entity and a development of the west flowing rivers is certainly within the time span of the salmon group as it is recognized today." (P. J. Coleman, *personal communication*.)

A continuous shaping process, in both ontogenic and phylogenetic behavior, has been only slowly recognized. Wegener and Schmidt pointed to the breeding practices of the eel mainly to support the theory of continental drift. Wolfson emphasized the selection of birds capable of flying greater distances and pointed out that the *path* of flight was more significant than the *extent* in supporting an explanation in terms of continental drift, but he assumed that birds followed such a path because of a homing instinct. Fraser drew on conclusions from the lengthening voyage of the green turtle, but Carr (1966) emphasized the importance of evidence "bearing on probable paleolithic conditions at the time or origin, *or of refinement*, of each pattern [of island-finding behavior]" (*italics added*). Carr argued that:

any female with the urge and capacity to go out to the island will contribute more genes to reinforce the island breeding pattern in the race. Each generation, more turtles go out to the island simply because their genotype was made more prevalent by the island-seeking tendency of the preceding generation. The island-seeking migration is thus a successful evolutionary venture, and has become the established regimen for the population.

It is this genotype that changed under selection as the continents moved apart. Carr and Coleman speak of the repetitive extension of previous travel paths and suggest that "the process of racial learning is of the repetitive, stepping-stone type, which requires no radical change in behavior at any point".

It is possible to be a little more specific. The shaping of phylogenetic behavior, like the shaping of ontogenic behavior, involves at least three things:

1. Behavior comes under the control of new stimuli. In the phylogenetic case this could involve extensive changes in sense organs, but it also involves the development of particular forms of stimulus control which, as in the ontogenic case, do not require changes in sensitivity. Shaping usually involves a shift in the range of controlling stimuli. When a stimulus that is not central to an existing range acquires special controlling power (either through genetic selection or operant reinforcement), a new range emerges in which new stimuli are now for the first time effective and can be strengthened to produce a range differing still further from the original. Thus, if an unusual visual pattern becomes particularly effective, new patterns even more unusual begin to exert control and are subject to further selection as the contingencies change.

A distinction is often made in discussing homing behavior or migration between "knowing where to go" and "knowing how to find the way", but the concept of knowledge causes trouble. The organism begins to migrate or home by responding to current stimuli; some of its responses may produce other stimuli, which then take over. In following a long path, the organism may be under the control of a succession of discrete stimuli or such a sustained stimulus as that used in celestial navigation. (The present argument does not, unfortunately, identify the stimuli that actually exert control, although the search for such stimuli may be aided by a consideration of the probable requirements in earlier stages of the shaping process.)

2. The topography of behavior changes. In phylogenetic behavior this may involve elaborate changes in the strength and mode of operation of effectors, but it also involves changes in the effective topography of a stable system, as in the ontogenic case. Shaping usually involves a shift in the range of effective topographies. When an unusual form of response is strengthened by genetic selection or operant conditioning, new forms may appear for the first time, which can in turn be strengthened as the contingencies change.

3. Easily overlooked is a third effect of

shaping—a maintenance of, or an increase in, the probability that behavior having a given topography and under the control of given stimuli will actually occur. The effect on probability is due, in phylogenetic behavior, to the selection of genotypes and, in ontogenic behavior, to operant conditioning. The tendency to behave in a given way upon a given occasion has been attributed to instinct in the phylogenetic case and habit in the ontogenic case. In both, it has been associated with the concept of purpose, and in ontogenic behavior with expectation or intention. Concepts of this sort add nothing to the observed facts, and they cause trouble because, by appearing to refer to inner determiners of behavior, they often serve as substitutes for the further explanation that will eventually be provided by physiology.

It is not necessary to refer to underlying structures or functions in order to study the way in which an organism inherits a tendency to behave in a given way in the presence of given stimuli, but the physiology will, it is hoped, eventually be understood. What evolves is an organism as a physical system, and it is such an organism that is modified by operant conditioning. We do not know whether the physiological changes that occur in the shaping of phylogenetic behavior are similar to those that occur in operant conditioning. Certainly, there are vast differences in the basic conditions. It is not impossible, however, that operant conditioning, itself an evolved feature of an organism, should have utilized a physiological system that had already been developed in natural selection.

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