

to white non-Catholics. Although the extent of use may be lower among Catholics than non-Catholics, the proportion of Catholics who report use is substantial indeed in view of the persisting theological controversy.

The prospects for increased use of oral contraception seem very good at present, but they may be limited by further developments in the technology of fertility regulation. Meanwhile the birth rate has declined substantially. Although much sophisticated analysis of

other data from the survey will be required to determine the extent of the contribution of oral contraception to this decline, the findings presented here suggest that the contribution is substantial for young married couples.

The major effect on the couple's eventual number of children may be less than the effect on the time pattern of childbearing; in any event, both lower eventual parity and delayed fertility contribute to a decline in the numbers of births from year to year. Whatever

the intent may be, it is apparent that young American couples have adopted a new means for achieving their reproductive goals.

References and Notes

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2. P. K. Whelpton, A. A. Campbell, J. E. Patterson, *Fertility and Family Planning in the United States* (Princeton Univ. Press, Princeton, N.J., 1966).
3. The National Fertility Study is being directed jointly by the authors under a contract from the National Institute of Child Health and Human Development, Bethesda, Md.

The Phylogeny and Ontogeny of Behavior

Contingencies of reinforcement throw light on contingencies of survival in the evolution of behavior.

B. F. Skinner

Parts of the behavior of an organism concerned with the internal economy, as in respiration or digestion, have always been accepted as "inherited," and there is no reason why some responses to the external environment should not also come ready-made in the same sense. It is widely believed that many students of behavior disagree. The classical reference is to John B. Watson (1):

I should like to go one step further now and say, "Give me a dozen healthy infants, well-formed, and my own specified world to bring them up in and I'll guarantee to take any one at random and train him to become any type of specialist I might select—doctor, lawyer, artist, merchant-chief and, yes, even beggarman and thief, regardless of his talents, penchants, tendencies, abilities, vocations, and race of his ancestors." I am going beyond my facts and I admit it, but so have the advocates of the contrary and they have been doing it for many thousands of years.

Watson was not denying that a substantial part of behavior is inherited. His challenge appears in the first of four chapters describing "how man is equipped to behave at birth." As an

enthusiastic specialist in the psychology of learning he went beyond his facts to emphasize what could be done in spite of genetic limitations. He was actually, as Gray (2) has pointed out, "one of the earliest and one of the most careful workers in the area of animal ethology." Yet he is probably responsible for the persistent myth of what has been called "behaviorism's counterfactual dogma" (3). And it is a myth. No reputable student of animal behavior has ever taken the position "that the animal comes to the laboratory as a virtual *tabula rasa*, that species' differences are insignificant, and that all responses are about equally conditionable to all stimuli" (4).

But what does it mean to say that behavior is inherited? Lorenz (5) has noted that ethologists are not agreed on "the concept of 'what we formerly called innate.'" Insofar as the behavior of an organism is simply the physiology of an anatomy, the inheritance of behavior is the inheritance of certain bodily features, and there should be no problem concerning the meaning of "innate" that is not

raised by any genetic trait. Perhaps we must qualify the statement that an organism inherits a visual reflex, but we must also qualify the statement that it inherits its eye color.

If the anatomical features underlying behavior were as conspicuous as the wings of *Drosophila*, we should describe them directly and deal with their inheritance in the same way, but at the moment we must be content with so-called behavioral manifestations. We describe the behaving organism in terms of its gross anatomy, and we shall no doubt eventually describe the behavior of its finer structures in much the same way, but until then we analyze behavior without referring to fine structures and are constrained to do so even when we wish to make inferences about them.

What features of behavior will eventually yield a satisfactory genetic account? Some kind of inheritance is implied by such concepts as "racial memory" or "death instinct," but a sharper specification is obviously needed. The behavior observed in mazes and similar apparatuses may be "objective," but it is not described in dimensions which yield a meaningful genetic picture. Tropisms and taxes are somewhat more readily quantified, but not all behavior can be thus formulated, and organisms selected for breeding according to tropistic or taxic performances may still differ in other ways (6).

The experimental analysis of behavior has emphasized another property. The probability that an organism will behave in a given way is a more valuable datum than the mere fact that it does so behave. Probability may be

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inferred from frequency of emission. It is a basic datum, in a theoretical sense, because it is related to the question: Why does an organism behave in a given way at a given time? It is basic in a practical sense because frequency has been found to vary in an orderly way with many independent variables. Probability of response is important in examining the inheritance, not only of specific forms of behavior but of behavioral processes and characteristics often described as traits. Very little has been done in studying the genetics of behavior in this sense. Modes of inheritance are not, however, the only issue. Recent advances in the formulation of learned behavior throw considerable light on other genetic and evolutionary problems.

The Provenance of Behavior

Upon a given occasion we observe that an animal displays a certain kind of behavior—learned or unlearned. We describe its topography and evaluate its probability. We discover variables, genetic or environmental, of which the probability is a function. We then undertake to predict or control the behavior. All this concerns a current state of the organism. We have still to ask where the behavior (or the structures which thus behave) came from.

The provenance of learned behavior has been thoroughly analyzed. Certain kinds of events function as “reinforcers,” and, when such an event follows a response, similar responses are more likely to occur. This is operant conditioning. By manipulating the ways in which reinforcing consequences are contingent upon behavior, we generate complex forms of response and bring them under the control of subtle features of the environment. What we may call the ontogeny of behavior is thus traced to contingencies of reinforcement.

In a famous passage Pascal (7) suggested that ontogeny and phylogeny have something in common. “Habit,” he said, “is a second nature which destroys the first. But what is this nature? Why is habit not natural? I am very much afraid that nature is itself only first habit as habit is second nature.” The provenance of “first habit” has an important place in theories of the evolution of behavior. A given response is in a sense strengthened by

consequences which have to do with the survival of the individual and species. A given form of behavior leads not to reinforcement but to procreation. (Sheer reproductive activity does not, of course, always contribute to the survival of a species, as the problems of overpopulation remind us. A few well-fed breeders presumably enjoy an advantage over a larger but impoverished population. The advantage may also be selective. It has recently been suggested (8) that some forms of behavior such as the defense of a territory have an important effect in restricting breeding.) Several practical problems raised by what may be called contingencies of selection are remarkably similar to problems which have already been approached experimentally with respect to contingencies of reinforcement.

An identifiable unit. A behavioral process, as a change in frequency of response, can be followed only if it is possible to count responses. The topography of an operant need not be completely fixed, but some defining property must be available to identify instances. An emphasis upon the occurrence of a repeatable unit distinguishes an experimental analysis of behavior from historical or anecdotal accounts. A similar requirement is recognized in ethology. As Julian Huxley has said, “This concept . . . of unit releasers which act as specific key stimuli unlocking genetically determined unit behavior patterns . . . is probably the most important single contribution of Lorenzian ethology to the science of behavior” (9).

The action of stimuli. Operant reinforcement not only strengthens a given response; it brings the response under the control of a stimulus. But the stimulus does not elicit the response as in a reflex; it merely sets the occasion upon which the response is more likely to occur. The ethologists’ “releaser” also simply sets an occasion. Like the discriminative stimulus, it increases the probability of occurrence of a unit of behavior but does not force it. The principal difference between a reflex and an instinct is not in the complexity of the response but in, respectively, the eliciting and releasing actions of the stimulus.

Origins of variations. Ontogenic contingencies remain ineffective until a response has occurred. In a familiar experimental arrangement, the rat must press the lever at least once “for

other reasons” before it presses it “for food.” There is a similar limitation in phylogenetic contingencies. An animal must emit a cry at least once for other reasons before the cry can be selected as a warning because of the advantage to the species. It follows that the entire repertoire of an individual or species must exist prior to ontogenic or phylogenetic selection, but only in the form of minimal units. Both phylogenetic and ontogenic contingencies “shape” complex forms of behavior from relatively undifferentiated material. Both processes are favored if the organism shows an extensive, undifferentiated repertoire.

Programmed contingencies. It is usually not practical to condition a complex operant by waiting for an instance to occur and then reinforcing it. A terminal performance must be reached through intermediate contingencies (perhaps best exemplified by programmed instruction). In a demonstration experiment a rat pulled a chain to obtain a marble from a rack, picked up the marble with its forepaws, carried it to a tube projecting two inches above the floor of its cage, lifted it to the top of the tube, and dropped it inside. “Every step in the process had to be worked out through a series of approximations since the component responses were not in the original repertoire of the rat” (10). The “program” was as follows. The rat was reinforced for any movement which caused a marble to roll over any edge of the floor of its cage, then only over the edge on one side of the cage, then over only a small section of the edge, then over only that section slightly raised, and so on. The raised edge became a tube of gradually diminishing diameter and increasing height. The earlier member of the chain, release of the marble from the rack, was added later. Other kinds of programming have been used to establish subtle stimulus control (11), to sustain behavior in spite of infrequent reinforcement (12), and so on.

A similar programming of complex phylogenetic contingencies is familiar in evolutionary theory. The environment may change, demanding that behavior which contributes to survival for a given reason become more complex. Quite different advantages may be responsible for different stages. To take a familiar example the electric organ of the eel could have become useful in stunning prey only after developing

something like its present power. Must we attribute the completed organ to a single complex mutation, or were intermediate stages developed because of other advantages? Much weaker currents, for example, may have permitted the eel to detect the nature of objects with which it was in contact. The same question may be asked about behavior. Pascal's "first habit" must often have been the product of "programmed instruction." Many of the complex phylogenetic contingencies which now seem to sustain behavior must have been reached through intermediate stages in which less complex forms had lesser but still effective consequences.

The need for programming is a special case of a more general principle. We do not explain any system of behavior simply by demonstrating that it works to the advantage of, or has "net utility" for, the individual or species. It is necessary to show that a given advantage is contingent upon behavior in such a way as to alter its probability.

Adventitious contingencies. It is not true, as Lorenz (5) has asserted, that "adaptiveness is always the irrefutable proof that this process [of adaptation] has taken place." Behavior may have advantages which have played no role in its selection. The converse is also true. Events which follow behavior but are not necessarily produced by it may have a selective effect. A hungry pigeon placed in an apparatus in which a food dispenser operates every 20 seconds regardless of what the pigeon is doing acquires a stereotyped response which is shaped and sustained by wholly coincidental reinforcement (13). The behavior is often "ritualistic;" we call it superstitious. There is presumably a phylogenetic parallel. All current characteristics of an organism do not necessarily contribute to its survival and procreation, yet they are all nevertheless "selected." Useless structures with associated useless functions are as inevitable as superstitious behavior. Both become more likely as organisms become more sensitive to contingencies. It should occasion no surprise that behavior has not perfectly adjusted to either ontogenic or phylogenetic contingencies.

Unstable and intermittent contingencies. Both phylogenetic and ontogenic contingencies are effective even though intermittent. Different schedules of reinforcement generate different patterns of changing probabilities. If there is a phylogenetic parallel, it is obscure. A

form of behavior generated by intermittent selective contingencies is presumably likely to survive a protracted period in which the contingencies are not in force, because it has already proved powerful enough to survive briefer periods, but this is only roughly parallel with the explanation of the greater resistance to extinction of intermittently reinforced operants.

Contingencies also change, and the behaviors for which they are responsible then change too. When ontogenic contingencies specifying topography of response are relaxed, the topography usually deteriorates, and when reinforcements are no longer forthcoming the operant undergoes extinction. Darwin discussed phylogenetic parallels in *The Expression of Emotions in Man and Animals*. His "serviceable associated habits" were apparently both learned and unlearned, and he seems to have assumed that ontogenic contingencies contribute to the inheritance of behavior, at least in generating responses which may then have phylogenetic consequences. The behavior of the domestic dog in turning around before lying down on a smooth surface may have been selected by contingencies under which the behavior made a useful bed in grass or brush. If dogs now show this behavior less frequently, it is presumably because a sort of phylogenetic extinction has set in. The domestic cat shows a complex response of covering feces which must once have had survival value with respect to predation or disease. The dog has been more responsive to the relaxed contingencies arising from domestication or some other change in predation or disease, and shows the behavior in vestigial form.

Multiple contingencies. An operant may be affected by more than one kind of reinforcement, and a given form of behavior may be traced to more than one advantage to the individual or the species. Two phylogenetic or ontogenic consequences may work together or oppose each other in the development of a given response and presumably show "algebraic summation" when opposed.

Social contingencies. The contingencies responsible for social behavior raise special problems in both phylogeny and ontogeny. In the development of a language the behavior of a speaker can become more elaborate only as listeners become sensitive to elaborated speech. A similarly coordi-

nated development must be assumed in the phylogeny of social behavior. The dance of the bee returning from a successful foray can have advantageous effects for the species only when other bees behave appropriately with respect to it, but they cannot develop the behavior until the dance appears. The terminal system must have required a kind of subtle programming in which the behaviors of both "speaker" and "listener" passed through increasingly complex stages. A bee returning from a successful foray may behave in a special way because it is excited or fatigued, and it may show phototropic responses related to recent visual stimulation. If the strength of the behavior varies with the quantity or quality of food the bee has discovered and with the distance and direction it has flown, then the behavior may serve as an important stimulus to other bees, even though its characteristics have not yet been affected by such consequences. If different bees behave in different ways, then more effective versions should be selected. If the behavior of a successful bee evokes behavior on the part of "listeners" which is reinforcing to the "speaker," then the "speaker's" behavior should be ontogenically intensified. The phylogenetic development of responsive behavior in the "listener" should contribute to the final system by providing for immediate reinforcement of conspicuous forms of the dance.

The speaker's behavior may become less elaborate if the listener continues to respond to less elaborate forms. We stop someone who is approaching us by pressing our palm against his chest, but he eventually learns to stop upon seeing our outstretched palm. The practical response becomes a gesture. A similar shift in phylogenetic contingencies may account for the "intentional movements" of the ethologists.

Behavior may be intensified or elaborated under differential reinforcement involving the stimulation either of the behaving organism or of others. The more conspicuous a superstitious response, for example, the more effective the adventitious contingencies. Behavior is especially likely to become more conspicuous when reinforcement is contingent on the response of another organism. Some ontogenic instances, called "ritualization," are easily demonstrated. Many elaborate rituals of primarily phylogenetic origin have been described by ethologists.

Some Problems Raised by Phylogenic Contingencies

Lorenz has recently argued that "our absolute ignorance of the physiological mechanisms underlying learning makes our knowledge of the causation of phyletic adaptation seem quite considerable by comparison" (5). But genetic and behavioral processes are studied and formulated in a rigorous way without reference to the underlying biochemistry. With respect to the provenance of behavior we know much more about ontogenic contingencies than phylogenic. Moreover, phylogenic contingencies raise some very difficult problems which have no ontogenic parallels.

The contingencies responsible for unlearned behavior acted a very long time ago. The natural selection of a given form of behavior, no matter how plausibly argued, remains an inference. We can set up phylogenic contingencies under which a given property of behavior arbitrarily selects individuals for breeding, and thus demonstrate modes of behavioral inheritance, but the experimenter who makes the selection is performing a function of the natural environment which also needs to be studied. Just as the reinforcements arranged in an experimental analysis must be shown to have parallels in "real life" if the results of the analysis are to be significant or useful, so the contingencies which select a given behavioral trait in a genetic experiment must be shown to play a plausible role in natural selection.

Although ontogenic contingencies are easily subjected to an experimental analysis, phylogenic contingencies are not. When the experimenter has shaped a complex response, such as dropping a marble into a tube, the provenance of the behavior raises no problem. The performance may puzzle anyone seeing it for the first time, but it is easily traced to recent, possibly recorded, events. No comparable history can be invoked when a spider is observed to spin a web. We have not seen the phylogenic contingencies at work. All we know is that spiders of a given kind build more or less the same kind of web. Our ignorance often adds a touch of mystery. We are likely to view inherited behavior with a kind of awe not inspired by acquired behavior of similar complexity.

The remoteness of phylogenic contingencies affects our scientific methods, both experimental and conceptual. Until we have identified the variables

of which an event is a function, we tend to invent causes. Learned behavior was once commonly attributed to "habit," but an analysis of contingencies of reinforcement has made the term unnecessary. "Instinct," as a hypothetical cause of phylogenic behavior, has had a longer life. We no longer say that our rat possesses a marble-dropping habit, but we are still likely to say that our spider has a web-spinning instinct. The concept of instinct has been severely criticized and is now used with caution or altogether avoided, but explanatory entities serving a similar function still survive in the writings of many ethologists.

A "mental apparatus," for example, no longer finds a useful place in the experimental analysis of behavior, but it survives in discussions of phylogenic contingencies. Here are a few sentences from the writings of prominent ethologists which refer to consciousness or awareness: "The young gosling . . . gets imprinted upon its mind the image of the first moving object it sees" (W. H. Thorpe, 14); "the infant expresses the inner state of contentment by smiling" (Julian Huxley, 9); "[herring gulls show a] lack of insight into the ends served by their activities" (Tinbergen, 15); "[chimpanzees were unable] to communicate to others the unseen things in their minds" (Kortlandt, 16).

In some mental activities awareness may not be critical, but other cognitive activities are invoked. Thorpe (14) speaks of a disposition "which leads the animal to pay particular attention to objects of a certain kind." What we observe is simply that objects of a certain kind are especially effective stimuli. We know how ontogenic contingencies work to produce such an effect. The ontogenic contingencies which generate the behavior called "paying attention" also presumably have phylogenic parallels. Other mental activities frequently mentioned by ethologists include "organizing experience" and "discovering relations." Expressions of all these sorts show that we have not yet accounted for behavior in terms of contingencies, phylogenic or ontogenic. Unable to show how the organism can behave effectively under complex circumstances, we endow it with a special cognitive ability which permits it to do so. Once the contingencies are understood, we no longer need to appeal to mentalistic explanations.

Other concepts replaced by a more effective analysis include "need" or "drive" and "emotion." In ontogenic

behavior we no longer say that a given set of environmental conditions first gives rise to an inner state which the organism then expresses or resolves by behaving in a given way. We no longer represent relations among emotional and motivational variables as relations among such states, as in saying that hunger overcomes fear. We no longer use dynamic analogies or metaphors, as in explaining sudden action as the overflow or bursting out of dammed-up needs or drives. If these are common practices in ethology, it is evidently because the functional relations they attempt to formulate are not clearly understood.

Another kind of innate endowment, particularly likely to appear in explanations of human behavior, takes the form of "traits" or "abilities." Though often measured quantitatively, their dimensions are meaningful only in placing the individual with respect to a population. The behavior measured is almost always obviously learned. To say that intelligence is inherited is not to say that specific forms of behavior are inherited. Phylogenic contingencies conceivably responsible for "the selection of intelligence" do not specify responses. What has been selected appears to be a susceptibility to ontogenic contingencies, leading particularly to a greater speed of conditioning and the capacity to maintain a larger repertoire without confusion.

It is often said that an analysis of behavior in terms of ontogenic contingencies "leaves something out of account," and this is true. It leaves out of account habits, ideas, cognitive processes, needs, drives, traits, and so on. But it does not neglect the facts upon which these concepts are based. It seeks a more effective formulation of the very contingencies to which those who use such concepts must eventually turn to explain their explanations. The strategy has been highly successful at the ontogenic level, where the contingencies are relatively clear. As the nature and mode of operation of phylogenic contingencies come to be better understood, a similar strategy should yield comparable advantages.

Identifying Phylogenic and Ontogenic Variables

The significance of ontogenic variables may be assessed by holding genetic conditions as constant as possible—for example, by studying "pure"

strains or identical twins. The technique has a long history. According to Plutarch (*De Puerorum Educatione*) Licurgus, a Spartan, demonstrated the importance of environment by raising two puppies from the same litter so that one became a good hunter while the other preferred food from a plate. On the other hand, genetic variables may be assessed either by studying organisms upon which the environment has had little opportunity to act (because they are newborn or have been reared in a controlled environment) or by comparing groups subject to extensive, but on the average probably similar, environmental histories. The technique also has a long history. In his journal for the 24th of January 1805, Stendahl refers to an experiment in which two birds taken from the nest after hatching and raised by hand exhibited their genetic endowment by eventually mating and building a nest two weeks before the female laid eggs. Behavior exhibited by most of the members of a species is often accepted as inherited if it is unlikely that all the members could have been exposed to relevant ontogenic contingencies.

When contingencies are not obvious, it is perhaps unwise to call any behavior either inherited or acquired. Field observations, in particular, will often not permit a distinction. Friedmann (17) has described the behavior of the African honey guide as follows:

When the bird is ready to begin guiding, it either comes to a person and starts a repetitive series of churring notes or it stays where it is and begins calling. . . .

As the person comes to within 15 or 20 feet, . . . the bird flies off with an initial conspicuous downward dip, and then goes off to another tree, not necessarily in sight of the follower, in fact more often out of sight than not. Then it waits there, churring loudly until the follower again nears it, when the action is repeated. This goes on until the vicinity of the bees' nest is reached. Here the bird suddenly ceases calling and perches quietly in a tree nearby. It waits there for the follower to open the hive, and it usually remains there until the person has departed with his loot of honey-comb, when it comes down to the plundered bees' nest and begins to feed on the bits of comb left strewn about.

The author is quoted as saying that the behavior is "purely instinctive," but it is possible to explain almost all of it in other ways. If we assume that honey guides eat broken bees' nests and cannot eat unbroken nests, that men (not to mention baboons and rats) break bees' nests, and that birds more easily discover unbroken nests, then only one other assumption is

needed to explain the behavior in ontogenic terms. We must assume that the response which produces the churring note is elicited either (i) by any stimulus which frequently precedes the receipt of food (comparable behavior is shown by a hungry dog jumping about when food is being prepared for it) or (ii) when food, ordinarily available, is missing (the dog jumps about when food is not being prepared for it on schedule). An unconditioned honey guide occasionally sees men breaking nests. It waits until they have gone, and then eats the remaining scraps. Later it sees men near but not breaking nests, either because they have not yet found the nests or have not yet reached them. The sight of a man near a nest, or the sight of man when the buzzing of bees around a nest can be heard, begins to function in either of the ways just noted to elicit the churring response. The first step in the construction of the final pattern is thus taken by the honey guide. The second step is taken by the man (or baboon or ratel, as the case may be). The churring sound becomes a conditioned stimulus in the presence of which a search for bees' nests is frequently successful. The buzzing of bees would have the same effect if the man could hear it.

The next change occurs in the honey guide. When a man approaches and breaks up a nest, his behavior begins to function as a conditioned reinforcer which, together with the fragments which he leaves behind, reinforces churring, which then becomes more probable under the circumstances and emerges primarily as an operant rather than as an emotional response. When this has happened, the geographical arrangements work themselves out naturally. Men learn to move toward the churring sound, and they break nests more often after walking toward nests than after walking in other directions. The honey guide is therefore differentially reinforced when it takes a position which induces men to walk toward a nest. The contingencies may be subtle, but the final topography is often far from perfect.

As we have seen, contingencies which involve two or more organisms raise special problems. The churring of the honey guide is useless until men respond to it, but men will not respond in an appropriate way until the churring is related to the location of bees' nests. The conditions just described compose a sort of program

which could lead to the terminal performance. It may be that the conditions will not often arise, but another characteristic of social contingencies quickly takes over. When one honey guide and one man have entered into this symbiotic arrangement, conditions prevail under which other honey guides and other men will be much more rapidly conditioned. A second man will more quickly learn to go in the direction of the churring sound because the sound is already spatially related to bees' nests. A second honey guide will more readily learn to churr in the right places because men respond in a way which reinforces that behavior. When a large number of birds have learned to guide and a large number of men have learned to be guided, conditions are highly favorable for maintaining the system. (It is said that, where men no longer bother to break bees' nests, they no longer comprise an occasion for churring, and the honey guide turns to the ratel or baboon. The change in contingencies has occurred too rapidly to work through natural selection. Possibly an instinctive response has been unlearned, but the effect is more plausibly interpreted as the extinction of an operant.)

Imprinting is another phenomenon which shows how hard it is to detect the nature and effect of phylogenetic contingencies. In Thomas More's *Utopia*, eggs were incubated. The chicks "are no sooner out of the shell, and able to stir about, but they seem to consider those that feed them as their mothers, and follow them as other chickens do the hen that hatched them." Later accounts of imprinting have been reviewed by Gray (2). Various facts suggest phylogenetic origins: the response of following an imprinted object appears at a certain age; if it cannot appear then, it may not appear at all; and so on. Some experiments by Peterson (18), however, suggest that what is inherited is not necessarily the behavior of following but a susceptibility to reinforcement by proximity to the mother or mother surrogate. A distress call reduces the distance between mother and chick when the mother responds appropriately, and walking toward the mother has the same effect. Both behaviors may therefore be reinforced (19), but they appear before these ontogenic contingencies come into play and are, therefore, in part at least phylogenetic. In the laboratory, however, other behaviors can be made effective which phy-

logenic contingencies are unlikely to have strengthened. A chick can be conditioned to peck a key, for example, by moving an imprinted object toward it when it pecks or to walk away from the object if, through a mechanical arrangement, this behavior actually brings the object closer. To the extent that chicks follow an imprinted object simply because they thus bring the object closer or prevent it from becoming more distant, the behavior could be said to be "species-specific" in the unusual sense that it is the product of *ontogenic* contingencies which prevail for most members of the species.

Ontogenic and phylogenic behaviors are not distinguished by any essence or character. Form of response seldom if ever yields useful classifications. The verbal response *Fire!* may be a command to a firing squad, a call for help, or an answer to the question, *What do you see?* The topography tells us little, but the controlling variables permit us to distinguish three very different verbal operants (20). The sheer forms of instinctive and learned behaviors also tell us little. Animals court, mate, fight, hunt, and rear their young, and they use the same effectors in much the same way in all sorts of learned behavior. Behavior is behavior whether learned or unlearned; it is only the controlling variables which make a difference. The difference is not always important. We might show that a honey guide is controlled by the buzzing of bees rather than by the sight of a nest, for example, without prejudice to the question of whether the behavior is innate or acquired.

Nevertheless the distinction is important if we are to undertake to predict or control the behavior. Implications for human affairs have often affected the design of research and the conclusions drawn from it. A classical example concerns the practice of exogamy. Popper (21) writes:

Mill and his psychologistic school of sociology . . . would try to explain [rules of exogamy] by an appeal to 'human nature,' for instance to some sort of instinctive aversion against incest (developed perhaps through natural selection . . .); and something like this would also be the naïve or popular explanation. [From Marx's] point of view . . . however, one could ask whether it is not the other way round, that is to say, whether the apparent instinct is not rather a product of education, the effect rather than the cause of the social rules and traditions demanding exogamy and forbidding incest. It is clear that these two approaches correspond ex-

actly to the very ancient problem whether social laws are 'natural' or 'conventions.' . . .

Much earlier, in his *Supplement to the Voyage of Bougainville*, Diderot (22) considered the question of whether there is a natural basis for sexual modesty or shame (*pudeur*). Though he was writing nearly a hundred years before Darwin, he pointed to a possible basis for natural selection. "The pleasures of love are followed by a weakness which puts one at the mercy of his enemies. That is the only natural thing about modesty; the rest is convention." Those who are preoccupied with sex are exposed to attack (indeed, may be stimulating attack); hence, those who engage in sexual behavior under cover are more likely to breed successfully. Here are phylogenic contingencies which either make sexual behavior under cover stronger than sexual behavior in the open or reinforce the taking of cover when sexual behavior is strong. Ontogenic contingencies through which organisms seek cover to avoid disturbances during sexual activity are also plausible.

The issue has little to do with the character of incestuous or sexual behavior, or with the way people "feel" about it. The basic distinction is between provenances. And provenance is important because it tells us something about how behavior can be supported or changed. Most of the controversy concerning heredity and environment has arisen in connection with the practical control of behavior through the manipulation of relevant variables.

Interrelations among Phylogenic and Ontogenic Variables

The ways in which animals behave compose a sort of taxonomy of behavior comparable to other taxonomic parts of biology. Only a very small percentage of existing species has as yet been investigated. (A taxonomy of behavior may indeed be losing ground as new species are discovered.) Moreover, only a small part of the repertoire of any species is ever studied. Nothing approaching a fair sampling of species-specific behavior is therefore ever likely to be made.

Specialists in phylogenic contingencies often complain that those who study learned behavior neglect the genetic limitations of their subjects, as the comparative anatomist might ob-

ject to conclusions drawn from the intensive study of a single species. Beach, for example, has written (23): "Many . . . appear to believe that in studying the rat they are studying all or nearly all that is important in behavior. . . . How else are we to interpret . . . [a] 457-page opus which is based exclusively upon the performance of rats in barpressing situations but is entitled simply *The Behavior of Organisms?*" There are many precedents for concentrating on one species (or at most a very few species) in biological investigations. Mendel discovered the basic laws of genetics—in the garden pea. Morgan worked out the theory of the gene—for the fruitfly. Sherrington investigated the integrative action of the nervous system—in the dog and cat. Pavlov studied the physiological activity of the cerebral cortex—in the dog.

In the experimental analysis of behavior many species differences are minimized. Stimuli are chosen to which the species under investigation can respond and which do not elicit or release disrupting responses: visual stimuli are not used if the organism is blind, nor very bright lights if they evoke evasive action. A response is chosen which may be emitted at a high rate without fatigue and which will operate recording and controlling equipment: we do not reinforce a monkey when it pecks a disk with its nose or a pigeon when it trips a toggle switch—though we might do so if we wished. Reinforcers are chosen which are indeed reinforcing, either positively or negatively. In this way species differences in sensory equipment, in effector systems, in susceptibility to reinforcement, and in possible disruptive repertoires are minimized. The data then show an extraordinary uniformity over a wide range of species. For example, the processes of extinction, discrimination, and generalization, and the performances generated by various schedules of reinforcement are reassuringly similar. (Those who are interested in fine structure may interpret these practices as minimizing the importance of sensory and motor areas in the cortex and emotional and motivational areas in the brain stem, leaving for study the processes associated with nerve tissue as such, rather than with gross anatomy.) Although species differences exist and should be studied, an exhaustive analysis of the behavior of a single species is as easily justified as the study of the chemistry or

microanatomy of nerve tissue in one species.

A rather similar objection has been lodged against the extensive use of domesticated animals in laboratory research (24). Domesticated animals offer many advantages. They are more easily handled, they thrive and breed in captivity, they are resistant to the infections encountered in association with men, and so on. Moreover, we are primarily interested in the most domesticated of all animals—man. Wild animals are, of course, different—possibly as different from domesticated varieties as some species are from others, but both kinds of differences may be treated in the same way in the study of basic processes.

The behavioral taxonomist may also argue that the contrived environment of the laboratory is defective since it does not evoke characteristic phylogenetic behavior. A pigeon in a small enclosed space pecking a disk which operates a mechanical food dispenser is behaving very differently from pigeons at large. But in what sense is this behavior not “natural”? If there is a natural phylogenetic environment, it must be the environment in which a given kind of behavior evolved. But the phylogenetic contingencies responsible for current behavior lie in the distant past. Within a few thousand years—a period much too short for genetic changes of any great magnitude—all current species have been subjected to drastic changes in climate, predation, food supply, shelter, and so on. Certainly no land mammal is now living in the environment which selected its principle genetic features, behavioral or otherwise. Current environments are almost as “unnatural” as a laboratory. In any case, behavior in a natural habitat would have no special claim to genuineness. What an organism does is a fact about that organism regardless of the conditions under which it does it. A behavioral process is none the less real for being exhibited in an arbitrary setting.

The relative importance of phylogenetic and ontogenic contingencies cannot be argued from instances in which unlearned or learned behavior intrudes or dominates. Breland and Breland (4) have used operant conditioning and programming to train performing animals. They conditioned a pig to deposit large wooden coins in a “piggy bank.” “The coins were placed several feet from the bank and the pig required to carry

them to the bank and deposit them. . . . At first the pig would eagerly pick up one dollar, carry it to the bank, run back, get another, carry it rapidly and neatly, and so on. . . . Thereafter, over a period of weeks the behavior would become slower and slower. He might run over eagerly for each dollar, but on the way back, instead of carrying the dollar and depositing it simply and cleanly, he would repeatedly drop it, root it, drop it again, root it along the way, pick it up, toss it up in the air, drop it, root it some more, and so on.” They also conditioned a chicken to deliver plastic capsules containing small toys by moving them toward the purchaser with one or two sharp straight pecks. The chickens began to grab at the capsules and “pound them up and down on the floor of the cage,” perhaps as if they were breaking seed pods or pieces of food too large to be swallowed. Since other reinforcers were not used, we cannot be sure that these phylogenetic forms of food-getting behavior appeared because the objects were manipulated under food-reinforcement. The conclusion is plausible, however, and not disturbing. A shift in controlling variables is often observed. Under reinforcement on a so-called “fixed-interval schedule,” competing behavior emerges at predictable points (25). The intruding behavior may be learned or unlearned. It may disrupt a performance or, as Kelleher (26) has shown, it may not. The facts do not show an inherently greater power of phylogenetic contingencies in general. Indeed, the intrusions may occur in the other direction. A hungry pigeon which was being trained to guide missiles (27) was reinforced with food on a schedule which generated a high rate of pecking at a target projected on a plastic disk. It began to peck at the food as rapidly as at the target. The rate was too high to permit it to take grains into its mouth, and it began to starve. A product of ontogenic contingencies had suppressed one of the most powerful phylogenetic activities. The behavior of civilized man shows the extent to which environmental variables may mask an inherited endowment.

Misleading Similarities

Since phylogenetic and ontogenic contingencies act at different times and shape and maintain behavior in different ways, it is dangerous to try to ar-

range their products on a single continuum or to describe them with a single set of terms.

An apparent resemblance concerns intention or purpose. Behavior which is influenced by its consequences seems to be directed toward the future. We say that spiders spin webs in order to catch flies and that men set nets in order to catch fish. The “order” is temporal. No account of either form of behavior would be complete if it did not make some reference to its effects. But flies or fish which have not yet been caught cannot affect behavior. Only past effects are relevant. Spiders which have built effective webs have been more likely to leave offspring, and a way of setting a net that has effectively caught fish has been reinforced. Both forms of behavior are therefore more likely to occur again, but for very different reasons.

The concept of purpose has had, of course, an important place in evolutionary theory. It is still sometimes said to be needed to explain the variations upon which natural selection operates. In human behavior a “felt intention” or “sense of purpose” which precedes action is sometimes proposed as a current surrogate for future events. Men who set nets “know why they are doing so,” and something of the same sort may have produced the spider’s web-spinning behavior which then became subject to natural selection. But men behave because of operant reinforcement even though they cannot “state their purpose”; and, when they can, they may simply be describing their behavior and the contingencies responsible for its strength. Self-knowledge is at best a by-product of contingencies, it is not a cause of the behavior generated by them. Even if we could discover a spider’s felt intention or sense of purpose, we could not offer it as a cause of the behavior.

Both phylogenetic and ontogenic contingencies may seem to “build purpose into” an organism. It has been said that one of the achievements of cybernetics has been to demonstrate that machines may show purpose. But we must look to the construction of the machine, as we look to the phylogeny and ontogeny of behavior, to account for the fact that an ongoing system acts as if it had a purpose.

Another apparent characteristic in common is “adaptation.” Both kinds of contingencies change the organism so that it adjusts to its environment

in the sense of behaving in it more effectively. With respect to phylogenetic contingencies, this is what is meant by natural selection. With respect to ontogeny, it is what is meant by operant conditioning. Successful responses are selected in both cases, and the result is adaptation. But the processes of selection are very different, and we cannot tell from the mere fact that behavior is adaptive which kind of process has been responsible for it.

More specific characteristics of behavior seem to be common products of phylogenetic and ontogenic contingencies. Imitation is an example. If we define imitation as behaving in a way which resembles the observed behavior of another organism, the term will describe both phylogenetic and ontogenic behavior. But important distinctions need to be made. Phylogenetic contingencies are presumably responsible for well-defined responses released by similar behavior (or its products) on the part of others. A warning cry is taken up and passed along by others; one bird in a flock flies off, and the others fly off; one member of a herd starts to run, and the others start to run. A stimulus acting upon only one member of a group thus quickly affects other members, with plausible phylogenetic advantages.

The parrot displays a different kind of imitative behavior. Its vocal repertoire is not composed of inherited responses, each of which, like a warning cry, is released by the sound of a similar response in others. It acquires its imitative behavior ontogenically, but only through an apparently inherited capacity to be reinforced by hearing itself produce familiar sounds. Its responses need not be released by immediately preceding stimuli (the parrot speaks when not spoken to); but an echoic stimulus is often effective, and the response is then a sort of imitation.

A third type of imitative contingency does not presuppose an inherited tendency to be reinforced by behaving as others behave. When other organisms are behaving in a given way, similar behavior is likely to be reinforced, since they would not be behaving in that way if it were not. Quite apart from any instinct of imitation, we learn to do what others are doing because we are then likely to receive the reinforcement they are receiving. We must not overlook distinctions of this sort if we are to use or cope

with imitation in a technology of behavior.

Aggression is another term which conceals differences in provenance. Inherited repertoires of aggressive responses are elicited or released by specific stimuli. Azrin, for example, has studied the stereotyped, mutually aggressive behavior evoked when two organisms receive brief electric shocks. But he and his associates have also demonstrated that the opportunity to engage in such behavior functions as a reinforcer and, as such, may be used to shape an indefinite number of "aggressive" operants of arbitrary topographies (28). Evidence of damage to others may be reinforcing for phylogenetic reasons because it is associated with competitive survival. Competition in the current environment may make it reinforcing for ontogenic reasons. To deal successfully with any specific aggressive act we must respect its provenance. (Emotional responses, the bodily changes we feel when we are aggressive, like sexual modesty or aversion to incest, may conceivably be the same whether of phylogenetic or ontogenic origin; the importance of the distinction is not thereby reduced.) Konrad Lorenz's recent book *On Aggression* (29) could be seriously misleading if it diverts our attention from relevant manipulable variables in the current environment to phylogenetic contingencies which, in their sheer remoteness, encourage a nothing-can-be-done-about-it attitude.

The concept of territoriality also often conceals basic differences. Relatively stereotyped behavior displayed in defending a territory, as a special case of phylogenetic aggression, has presumably been generated by contingencies involving food supplies, breeding, population density, and so on. But cleared territory, associated with these and other advantages, becomes a conditioned reinforcer and as such generates behavior much more specifically adapted to clearing a given territory. Territorial behavior may also be primarily ontogenic. Whether the territory defended is as small as a spot on a crowded beach or as large as a sphere of influence in international politics, we shall not get far in analyzing the behavior if we recognize nothing more than "a primary passion for a place of one's own" (30) or insist that "animal behavior provides prototypes of the lust for political power" (31).

Several other concepts involving so-

cial structure also neglect important distinctions. A hierarchical "pecking order" is inevitable if the members of a group differ with respect to aggressive behavior in any of the forms just mentioned. There are therefore several kinds of pecking orders, differing in their provenances. Some dominant and submissive behaviors are presumably phylogenetic stereotypes; the underdog turns on its back to escape further attack, but it does not follow that the vassal prostrating himself before king or priest is behaving for the same reasons. The ontogenic contingencies which shape the organization of a large company or governmental administration show little in common with the phylogenetic contingencies responsible for the hierarchy in the poultry yard. Some forms of human society may resemble the anthill or beehive, but not because they exemplify the same behavioral processes (32).

Basic differences between phylogenetic and ontogenic contingencies are particularly neglected in theories of communication. In the inherited signal systems of animals the behavior of a "speaker" furthers the survival of the species when it affects a "listener." The distress call of a chick evokes appropriate behavior in the hen; mating calls and displays evoke appropriate responses in the opposite sex; and so on. De Laguna (33) suggested that animal calls could be classified as declarations, commands, predictions, and so on, and Sebeok (34) has recently attempted a similar synthesis in modern linguistic terms, arguing for the importance of a science of zoosemantics.

The phylogenetic and ontogenic contingencies leading, respectively, to instinctive signal systems and to verbal behavior are quite different. One is not an early version of the other. Cries, displays, and other forms of communication arising from phylogenetic contingencies are particularly insensitive to operant reinforcement. Like phylogenetic repertoires in general, they are restricted to situations which elicit or release them and hence lack the variety and flexibility which favor operant conditioning. Vocal responses which at least closely resemble instinctive cries have been conditioned, but much less easily than responses using other parts of the skeletal nervous system. The vocal responses in the human child which are so easily shaped by operant reinforcement are not controlled by specific releasers. It was the development

of an undifferentiated vocal repertoire which brought a new and important system of behavior within range of operant reinforcement through the mediation of other organisms (20).

Many efforts have been made to represent the products of both sets of contingencies in a single formulation. An utterance, gesture, or display, whether phylogenetic or ontogenic, is said to have a referent which is its meaning, the referent or meaning being inferred by a listener. Information theory offers a more elaborate version: the communicating organism selects a message from the environment, reads out relevant information from storage, encodes the message, and emits it; the receiving organism decodes the message, relates it to other stored information, and acts upon it effectively. All these activities, together with the storage of material, may be either phylogenetic or ontogenic. The principal terms in such analyses (input, output, sign, referent, and so on) are objective enough, but they do not adequately describe the actual behavior of the speaker or the behavior of the listener as he responds to the speaker. The important differences between phylogenetic and ontogenic contingencies must be taken into account in an adequate analysis. It is not true, as Sebeok contends, that

"any viable hypothesis about the origin and nature of language will have to incorporate the findings of zoo-semiotics." Just as we can analyze and teach imitative behavior without analyzing the phylogenetic contingencies responsible for animal mimicry, or study and construct human social systems without analyzing the phylogenetic contingencies which lead to the social life of insects, so we can analyze the verbal behavior of man without taking into account the signal systems of other species.

Purpose, adaptation, imitation, aggression, territoriality, social structure, and communication—concepts of this sort have, at first sight, an engaging generality. They appear to be useful in describing both ontogenic and phylogenetic behavior and to identify important common properties. Their very generality limits their usefulness, however. A more specific analysis is needed if we are to deal effectively with the two kinds of contingencies and their products.

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35. This article was prepared with the help of the NIH grant K6-MH-21, 775 and the Aaron E. Norman Fund.

Luminous Phenomena in Nocturnal Tornadoes

The existence of unusual electrical discharges in the Toledo tornado is confirmed by a photograph and eyewitnesses.

B. Vonnegut and James R. Weyer

A primary and unsolved problem concerning the tornado is that of accounting for the extraordinary speed of its winds, which, according to recent evidence (1), may reach 200 meters per second. On the assumption that the winds of the tornado are the result of temperature contrasts between air masses in the atmosphere, one of us

(Vonnegut) has calculated (2) that a chimney of air extending to the stratosphere would have to be at least 100°C warmer than its surroundings in order to produce such speeds. Fulks (3) has considered the problem on the basis of the estimated decrease in pressure in the tornado funnel and has come to the similar conclusion that "there is

some means of creating large temperature differences." It is not difficult to account for the tornado-like whirlwinds that commonly accompany large fires (4) or volcano eruptions (5), for here there are unquestionably volumes of intensely heated air. It is much more difficult, however, to explain how such thermal contrasts could arise in a thunderstorm. The rate of energy production in a large thunderstorm is ample to power a tornado. The problem, as Abdullah has pointed out (6), is to explain the process by which a portion of the energy becomes concentrated in the tornado vortex.

A possible explanation that has been proposed (7) for the anomalous high-energy density in a tornado is that the tornado may derive some of its energy from the intense electrification of the tornado-producing thunderstorm, which has been estimated to be equivalent

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