*FUNCTION, CAUSATION, EVOLUTION, AND
DEVELOPMENT OF BEHAVIOR: A REVIEW OF
THE ANIMAL IN ITS WORLD, BY N. TINBERGEN¹*

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Since psychology and ethology both include well-developed bodies of theory and data about the behavior of animals, it has sometimes been suggested that both might be encompassed within one general framework (e.g., Staddon and Simmelhag, 1971; Verplanck, 1955). Indications of a move in this direction have appeared frequently of late as an increasing number of phenomena such as auto-shaping, adjunctive behavior, and the findings of the Brelands have seemed to require something beyond traditional principles of operant conditioning for their explanation. It has seemed to some (e.g., Rozin and Kalat, 1971; Schwartz, 1974) that a broader and more biologically oriented approach, as exemplified by ethology, might provide the basis for a systematic account of such apparently anomalous phenomena. The appearance of a highly readable introduction to the original literature of ethology in the form of this collection of papers by one of its founders provides an occasion to examine whether a marriage of these two areas of psychobiology is either appropriate or likely to be fruitful.

In fact, the two volumes of Tinbergen's *The Animal in Its World* are apparently not intended as introductory reading but rather as a way of making accessible to students and workers in ethology a sample of nearly 40

years' work on an impressive variety of empirical problems and some recent more general papers. Many of these papers have been published before, although not all in English. Because the collection aims to illustrate as great a variety as possible of problems and techniques, some important papers are omitted, including the 1952 analysis of displacement activities (Tinbergen, 1952).

The core question of ethology is: why does the animal behave as it does? Tinbergen distinguishes four aspects of this question: what are the immediate causes, internal and external, of a particular behavior; how does the behavior develop in the individual; how does it evolve in the species; and how does it contribute to survival? The first three have to do with mechanism or, as Tinbergen puts it, "how is it done?"; and the last, with function or "what is its use?" One theme of these volumes is that behavior can be fully understood only through investigation that constantly turns from one to another of these two classes of questions. Thus, mechanisms of behavior are not studied for their own sake but out of concern for how the animal meets certain environmental pressures; conversely, recognition of certain environmental pressures leads to concern with mechanisms for meeting them. One of Tinbergen's great contributions has been to show how function, or the survival value of behavior, so easy to speculate about, may be subject to experiment. This is illustrated by several of the selections and is discussed extensively in one of the general papers, "Behavior and Natural Selection".

Because the concerns of most of the 18 selections range so widely, it would have been impossible to segregate them according to subject matter. Instead, they have been separated into four types: observational and interpretive studies, field experiments, laboratory ex-

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periments, and general papers. Each section is prefaced by a brief introduction touching on the main significance of most of the papers in it.

The first section contains a single observational study, the 70-page "Comparative Studies of the Behavior of Gulls (*Laridae*): a Progress Report". Tinbergen depicts such observational field studies as an essential starting point for ethology and for individual ethologists. The detailed descriptions of the gulls' displays will make clear to anyone unfamiliar with ethological literature that "behavior" in these volumes is defined largely topographically, in terms of the sort of motor units originally called fixed action patterns. One aim of the comparative studies of gulls was to identify and describe the distinctive motor patterns (displays) involved in courting and defending territory in several closely related species. Thus, it illustrates how species-specific forms of displays may be used as taxonomic characters, a notion originally developed by Lorenz. It also contains discussion and examples of how causation and function of displays are inferred from observation in field conditions.

The nine papers in the second section, "Field Experiments", include three on egg shell removal in the black-headed gull, which beautifully illustrate the way "why does the animal do that?" can be asked in several senses about the same piece of behavior. A few hours after a chick has hatched, the parent gull picks up the empty egg shell, flies or walks off, and drops it away from the nest. This behavior occurs very seldom in the life of an individual animal. Its function was initially obscure. Yet the fact that it occurs so consistently and predictably suggests that it has an important function: why else would a gull leave its vulnerable chick even for a few moments? Such a question about survival value motivates the studies of egg shell removal. Accordingly, the first demonstrates how egg shell removal functions to keep the nest camouflaged. It does this by showing that eggs in an artificial nest containing a broken egg shell are more likely to be found and taken by predators than are those in a nest without a broken egg shell. The second of the papers on egg shell removal deals with one aspect of its development: does the color of eggs a gull incubates influence the color of objects selected for carrying away? The influence

of experience here is far from overwhelming. The final paper on egg shell removal analyzes the stimuli by which a gull distinguishes empty from occupied egg shells by means of experiments with models differing along various dimensions from real egg shells.

A theoretically important finding about external stimulus control is contained in the paper on the behavior of the grayling butterfly. Feeding graylings are responsive to color, selectively approaching yellow and blue, while courting graylings approach a variety of models regardless of their color, but are greatly influenced by shape and movement. Such motivational dependence of selective responsiveness has been described more recently in the herring gull (Baerends and Kruijt, 1973). It is apparently not confined to untrained responses, as is shown by the recent demonstrations of "reversal of overshadowing" in appetitive as compared to aversive training with pigeons (Foree and LoLordo, 1973; cf. also Garcia and Koelling, 1966). In the case described by Foree and LoLordo, pigeons trained to press a treadle for food with a compound light-tone discriminative stimulus were strongly controlled by the light, but if they were treading to avoid shock in the presence of the same compound they were more strongly controlled by the tone than by the light. That this aspect of stimulus control may be shared by responses with apparently very different developmental histories suggests that a full account of such phenomena need not assign an important role to the origin of the stimulus control.

The group of field experiments also contains translations from the German of three papers on a rather well-known example of "learning in the wild", the homing of the digger wasp, *Philanthus triangulum*. The wasp's learning of landmarks around its nest is noteworthy because of its speed. In some cases, a few seconds' inspection of the nest when leaving is sufficient for the wasp to recognize it later. The selectivity of this learning is also noteworthy. How much of the selectivity in the cues about which a wasp will learn is due to differences in their perceptibility and how much to true specific predispositions for learning about them apparently remains to be fully analyzed. Tinbergen notes here that the wasp not only is able to learn the location of the nest very quickly, it also behaves so as to expose itself to the stimuli necessary for learn-

ing by flying around over the nest in a "locality study" before departing. This behavior would appear to have something in common with what studies of observing responses have tried to capture in the laboratory.

The "Field Experiments" conclude with selections on the food-searching behavior of two predators on the gull colonies, foxes and carrion crows. The latter is a splendid example of how the behaviors of predator and prey species can be closely adapted with respect to one another. A crow that has found one gull egg tends to walk about in the same area, as if searching for another. If it does not find one in a certain time it flies off. This pressure may be one reason why nests in the gull colony are no closer together.

Two selections comprise the "Laboratory Experiments". The first, the study of the control of the gaping response of young thrushes, is a classic demonstration that releasing and orienting stimuli for a given response can be distinguished. For example, in the youngest nestling thrushes, gaping for food is released by mechanical stimuli such as jiggling the nest, and is always directed upwards, *i.e.*, it is oriented by gravity. Soon after they open their eyes, gaping is released by certain visual stimuli but still oriented by gravity, so the young birds do not gape toward a parent arriving at the nest from the side. Only later is the response both released and oriented visually.

The second laboratory experiment investigates the function of a morphological adaptation, the spines of the three-spined and ten-spined sticklebacks. As might be suspected, predatory fish spit out the prickly sticklebacks when they catch one. They also learn not to bother catching sticklebacks: after experience with sticklebacks, the pike predators' prey-catching sequence of eye movement, turn toward prey, stalk, leap, snap, turn prey head-forward in the mouth, and swallow, begins to be broken off at various points before the last two stages. The comparison with heterogeneous chains in the laboratory is obvious. The effects of unreinforced experience on this usually rather rigid feeding sequence might also profitably be compared to the effects of negative autoshaping on feeding and drinking sequences in pigeons (Wessells, 1974; Morrison, 1974; Morgan, 1974, discusses other cases).

The final section, "General Papers", begins with three more systematic discussions of is-

suues raised here and there in the primarily empirical papers. These are "Behavior and Natural Selection", "On Appeasement Signals", and "Ethology". The last-mentioned is Tinbergen's summary of the development of the various aspects of modern ethology. Anyone unfamiliar with the arguments about why the innate-learned dichotomy is a sterile one could hardly find a better brief discussion of the issues involved than is included here in the discussion of behavioral ontogeny.

The concluding three selections deal in various ways with the relevance of ethology for the study of human behavior. A frequent claim, discussed here, is that while the results of ethological investigations may not be applicable in detail to man, methods and assumptions about what they reveal are applicable. "Early Childhood Autism" is a concrete example of this approach. Although others more familiar with the syndrome will have to judge this paper's general usefulness, it appears to be an illuminating analysis of the motivation and possible cure of autistic behavior. The Tinbergens (Mrs. Tinbergen collaborated on this work) point out how careful analysis of the facial expressions and gestures of autists and of their reactions to strangers suggest that they are not over- but under-responsive to social stimuli. Presenting this selection in company with such papers as "On Appeasement Signals" emphasizes that exactly the same methods are being applied in both. Two other sorts of application of ethology to human affairs are illustrated in discussions of functional and evolutionary considerations in the concluding selections.

On "Botanizing" in Ethology

Although most of the six General Papers review some data that are presented in more detail in the experimental and observational studies, they also draw on a breathtaking wealth of additional facts. Consider, for example, the relation between the relatively great age of oystercatchers at first breeding, the fact that they feed their young (unusual among precocial birds), and the lengthy specialized training the young need to be able to feed effectively on the species-typical diet of cockles and mussels ("Ethology and the Human Sciences"). Or the fact that the Godwit has a special way of lifting and folding its feet while walking through tall grass not

shared by long-legged birds that normally inhabit shorter grass ("Behavior and Natural Selection"). It will be clear to anyone who even skims these volumes that whatever the deeper relevance of ethology to the laboratory study of acquired behavior, ethology has a far wider data base in terms of species and situations studied. These two volumes, the General Papers in particular, provide a first-hand view of a science of behavior that would superficially appear to consist of the "botanizing of reflexes" (Herrnstein and Loveland, 1972; Skinner, 1938). But if "botanizing" is taken to mean detailed study of a wide variety of cases for their own sakes, it is not what Tinbergen is engaged in. None of the examples in these volumes, at least, is mentioned without reference to one of the core questions outlined at the beginning of this review. Moreover, as in the comparative studies of gulls, comparison of such things as the forms of homologous displays in different species is sometimes itself the object of inquiry. This selection illustrates some forms that generalizations about numerous separate behavior patterns may take. For example, a number of differences between the displays of kittiwakes and other gulls can be related to the kittiwakes' nesting not on dunes or other more open areas but on tiny ledges in cliffs, with their concomitant freedom from predators and danger of falling off. As an example from another selection, of the two sticklebacks the species that is better protected because its spines are sharper has the higher threshold for fleeing (*i.e.*, is less "shy") and the more conspicuous nuptial coloration.

It is made explicit at several points that Tinbergen does not share Skinner's (1938) assumption that the important properties of a single behavioral unit will be shared by all formally identical units. For example, the paper on the grayling butterfly begins with the assertion that some hypotheses about external stimulus control of behavior developed largely from the behavior of birds need to be tested on members of other groups. *The Behavior of Organisms* perhaps never meant to include insects among organisms, but *The Study of Instinct* did. It is of some interest that the way their behavior is controlled by external stimuli and internal states not only is similar to the case in vertebrates but it may display equal complexity, as in the motivational de-

pendence of the response to color and the landmark learning of wasps mentioned earlier.

In the General Papers, which present the most extensive "botanizing" included here, Tinbergen is of course concerned to illustrate general points. Perusal of a few issues of *Behaviour*, *Zeitschrift für Tierpsychologie*, or *Animal Behaviour* might give a more accurate picture of the nature and extent of "botanizing" in contemporary ethology. Nevertheless, the material in these volumes shows that a very wide variety of specific cases can be organized in terms of basic questions about the function, causation, development, and evolution of behavior. At the same time, however, there are reasons to think that accumulating examples does not have limitless usefulness. For instance, is the Godwit's special way of walking any different or more illuminating as an illustration of the adaptiveness of every detail of behavior than the oystercatcher's delayed reproduction or the black-headed gull's carrying away of egg shells? Here, of course, part of the point is that many seemingly trivial aspects of behavior have been found to be closely adapted to multiple and sometimes conflicting environmental pressures. In investigations of the control or development of behavior, the assumption that superficially similar cases are not necessarily the same in details of mechanism would also seem to justify analyzing a large number of examples. Yet, the fact that the basic assumptions about the structure of behavior and methods for revealing it apply so well to cases as diverse as autism and gulls' courtship could obscure the fact that behaviors of a given category like aggressive or displacement activities might depend on different mechanisms in different species. Constructing a truly general account of the causation of behavior could in such cases be hampered by theoretical disputes about what might be species differences.

"One Field"?

The preceding paragraphs assume the obvious point of contact between ethology and the study of experimentally acquired behavior: both deal with the behavior of animals. Concepts and data from one field have often been borrowed by the other, as, for example, when adjunctive behaviors are said to be the same as displacement activities (Falk, 1971;

Staddon and Simmelhag, 1971), when auto-shaping is discussed in terms of "learned release" of species-typical, reinforcer-appropriate behaviors (Woodruff, 1974) or when Tinbergen (Vol. 1, p. 99) refers to the digger wasps' landmark learning as Pavlovian conditioning. Many authors apparently accept that results from ethology can be used to account for phenomena in conditioning and *vice versa*. This seems highly reasonable because it is unlikely that the subjects' behavior depends on who is recording it. However, this way of relating the two areas of inquiry begs the question of how they are properly related to one another on a more theoretical level.

Questions about Behavior: Function and Evolution

Verplanck (1955) asserted that in the study of animal behavior there is really "*only one field*" (his italics). As a starting point for further analysis of this notion, we may take the four areas of ethological inquiry distinguished here by Tinbergen: evolution, function, causation, and development of behavior. Of these, function and evolution have not typically been considered relevant to the analysis¹ of operant or classical conditioning, at least not to the extent of stimulating experimental investigation. "... 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". Skinner's (1966, p. 1211) assertion suggests that the possible function of particular operants in a species' natural environment, past or present, can be ignored. However, a number of recently discovered anomalies in operant and classical conditioning imply precisely that considerations of function are relevant to understanding behavior in laboratory situations. Rozin and Kalat (1971), for example, suggest that a view of learning in which what and how animals learn is expected to reflect contingencies present in nature makes sense of the specificity and long delay of taste-aversion learning. Staddon and Simmelhag (1971) suggest that adjunctive behavior does not seem so strange if we realize that behavior should be organized so that an animal does other things at times when reinforcement is not forthcoming for a particular operant. And Bolles (1970) suggests that extreme cautiousness, rather than the ability to learn to

avoid, should have evolved because predators seldom allow their victims to profit from even one trial. Thus, considerations that are an integral part of ethology and of biology in general are being invoked in discussions of learning, apparently to make us feel more comfortable about findings that are anomalous if considered only in the light of established conditioning principles.

Perhaps because the study of learned behavior does not share ethology's tradition of concern with the function of behavior in the natural environment, discussions like those just referred to sometimes seem to ignore the fact that speculations about the function of certain types of learning (or nonlearning) are not accounts of mechanism. The distinction of questions about function from questions about causation and development that pervades these volumes is thus relevant to attempts to relate behavior in "the box" (Schwartz, 1974) to behavior in "the world". So are the numerous illustrations of how speculations about function can be put to rigorous experimental test. At the same time, the many demonstrations that mechanism so often mirrors functional requirements justify attempts to view learning in the laboratory in terms of the possible function of learning in the wild.

Development

In studies of development and of causation there may be a broader base for integration of psychological and ethological approaches than in the actual study of function or evolution. If behavioral change in the adult animal is seen as an aspect of development, then acquisition and extinction of operants and respondents are part of behavioral development. These volumes include few detailed examples of ethological studies of development, other than the description of the changes in control of the thrushes' gaping response, but the various general descriptions of this area do suggest two things about it. First, ethological studies of development include considerably more than classical or instrumental conditioning. Second, they start from an interest in how the end product, some aspect of normal adult behavior, got to be that way, rather than from an interest in one or another process that might be involved in development more generally. Studies starting from this interest may have uncovered examples of

behavioral development and modification that cannot readily be accounted for by operant or classical conditioning. In fact, if the study of how behavior develops or changes had begun from the range of examples of normal development familiar to ethologists, it might well not have assigned a very prominent role to operant or classical conditioning. Rather than trying to account for such phenomena as imprinting in terms of these types of learning (*e.g.*, Hoffman and Ratner, 1973), we might now be doing the reverse. As well as imprinting, other candidates for behavioral changes not wholly accountable for in familiar terms are imitative behavior (Davis, 1973), learning what song to sing (*e.g.*, Marler, 1970) or what species to mate with (*e.g.*, Klinghammer, 1967), hunting by search image (Krebs, 1973), and homing by landmarks. However, most such cases still require a thorough analysis with an eye to separating the various mechanisms that could be involved. Students of learning in the laboratory have considerably more sophistication in this activity than ethologists, who have not been primarily interested in distinguishing types of behavioral change.

Causation

By causation of behavior, Tinbergen means the immediately preceding conditions for performance of a particular activity. In the study of causation, ethology is essentially behavioristic: antecedent conditions are discovered by observing when a particular activity occurs. In the papers on gulls and on appeasement signals, Tinbergen outlines three convergent methods for inferring motivation in field conditions: observing what the behavior in question alternates with, what other activities its motor elements resemble, and its external stimulus context. The first two of these are especially appropriate for displays, which appear to be the results of conflicts. This statement of how accounts of causation are formulated was arrived at not *a priori* but by analyzing the less formalized approach used intuitively in early studies. One aspect of description that at first seems at variance with a rigorously objective approach to behavior is the frequent summary of certain observable features of behavior in terms of tendencies or states of the animal. How far use of such terms is justified is explicitly discussed

in the comparative paper on gulls (Vol. 1, pp. 55ff.).

In causal analysis in the laboratory, and in favorable situations in the field, external stimuli may be manipulated to define the sign stimuli for given activities. The method is illustrated here in such papers as those on the gaping reaction and on egg shell removal. Although these are formally similar to analyses of the stimulus control of asymptotic operants (*e.g.*, Reynolds, 1961), the behavioral units involved are of different sorts, defined in one case in terms of topography and in the other in terms of consequence. This difference appears to be basic to some differences and even possible sources of conflict between the two areas of psychobiology. These are discussed in what follows.

The bare structure of the causal analysis of action patterns and operants is similar if not identical. (Action patterns are the behavioral units of ethology; the formerly used adjective "fixed" in the term "fixed action patterns" is now often dropped because of its implication of developmental fixity and lack of individual variability). Both action patterns and operants seek to determine how certain behavioral units are controlled in terms of external stimuli and internal states such as hunger, sexual condition, and other "drives". Internal states have received less attention than external stimuli in recent analyses of experimentally acquired behavior. However, Skinner (1935) described his early studies of barpressing as being of a response that had been brought experimentally under the control of a drive, and Herrnstein (1972) traced in detail the roots of Skinner's approach in traditional instinct theories.

Perhaps this similarity of concern is trivial. Maybe the classes of variables both fields study are defined so broadly that they include all the variables that could have immediate effects on behavior. It is of some interest, then, that where similar variables have been manipulated they have proved to have similar functional relations to the two classes of behavior. The most obvious example is stimulus generalization (Verplanck, 1955). There tend to be optimal external stimuli for both types of units, and graded series of physically similar stimuli often have orderly graded effects. Several similarities in the control of unconditioned and explicitly conditioned reflexes, and

their significance, were considered by Skinner (1938). However, there is one phenomenon that may be unique to untrained responses to external stimuli. This is "supernormality": sometimes the most effective stimulus for an action pattern is one other than that which would be present under natural conditions. For example, a very large egg elicits more retrieving by herring gulls than does a normal egg. Hogan, Kruijt, and Frijlink (*in press*) have explored a parallel in an operant situation (*cf.* also Baerends and Kruijt, 1973). To the extent that supernormal stimuli are always larger or more intense than normal stimuli, the phenomenon would be the same as "stimulus intensity dynamism" (Hull, 1949).³

Another interesting similarity is in the ethological "rule of heterogeneous summation", mentioned in the paper on the grayling butterfly: different causal factors that affect a response have additive effects when presented together. Exactly this assumption is made in analyzing the effects of compound stimuli on operant or classically conditioned responses (*e.g.*, Rescorla and Wagner, 1972). The motivational or reinforcer dependence of the most effective class of stimuli, already mentioned, suggests a similarity in a somewhat more complex phenomenon. Most if not all ethological examples involve different responses in the two cases when different elements of a compound stimulus are most effective. Attempts to capture the phenomenon in the laboratory, like that of Foree and LoLordo (1973), can gain better control over the various elements of the situation, as by training the same response with two reinforcers, and thus make an important contribution to its analysis. The developmental history of a behavioral unit is obviously logically independent of how it is controlled in the present. The phenomena reviewed above suggest that this may be true in fact as well. Such parallels should be explored in more detail. Truly approaching the study of behavior as one field, as Hinde does in his *Animal Behaviour* (1970) for example, would seem to lead to this sort of generalized concern with the nature of behavioral control.

Structure and Topography

The many parallel phenomena notwithstanding, important differences between oper-

ant and ethological approaches derive from the types of units whose control is studied. One is that ethological theory goes beyond the study of individual units and attempts to develop an account of how different units are related to one another and how they interact, *i.e.*, an account of the structure of behavior. The hierarchical organization of action patterns is not explicitly discussed in the volumes under review (*cf.* Tinbergen, 1951; and Hinde, 1970), but it is often implicit. Staddon (1967) discussed in some detail the need and possibility for a similar theory of structure in operant behavior.

The ethological account of the structure of behavior is one of interrelations among topographically identified units. In considering how a theory of the structure of operants might be similar or different, an essential point is that any behavioral event can at once be an operant (*i.e.*, described by its consequences) and an action pattern (*i.e.*, described by topography). This duality has some interesting and revealing implications. Tinbergen touches on one in "On Appeasement Signals", when he discusses the different accounts of the outcomes of conflicts. He points out that the outcome of an approach-avoidance conflict is often a display or special posture that depends precisely on the nature of the objects approached or avoided. For example, a herring gull shows the upright threat posture in a conflict between attacking and fleeing from its neighbor, but it never shows this display in a conflict between approaching the nest and fleeing from an observer. It is hard to see how an account purely in terms of consequences, *i.e.*, one that simply labels behavior as "approach" and "avoidance", can encompass the different results of topographically different conflicts (*cf.* also Hogan, 1965). In the comparative study of gulls, Tinbergen considers why a gull species should have so many different displays. This sort of question about the relations of topographically different units does not arise if behavior is considered only in terms of consequence or if inquiry is restricted to the properties of single units.

The need for a topographical, structural account of experimentally induced behavior at least highly similar to that of ethology has recently become apparent in the analysis of autoshaping. Pigeons' pecking in negative autoshaping (Williams and Williams, 1969)

³Thanks to Peter Holland for pointing this out.

cannot be accounted for solely in terms of its consequences, because it persists when it actually prevents reinforcement. It seemed natural in this case to assign a large role to the particular topography (*i.e.*, pecking) and to a special relation of that topography with hunger and/or grain. Indeed, such an account seems to be required by studies in which the topography of key contact is shown to depend on whether the reinforcer is food or water (Jenkins and Moore, 1973). Other studies, similar in their results to the less formal observations of Breland and Breland (1966), have shown how attempts to link arbitrary topographies with arbitrary drives (or, alternatively, to reinforce them with arbitrary reinforcers) meet with difficulties (*e.g.*, Sevenster, 1973; Shettleworth, *in press*). For instance, Sevenster's (1973) account of response-reinforcer interactions in sticklebacks shows how the ethological model of the organization of behavior provides an account of such phenomena. One thing that needs working out here is the relation between what happens when behavior has been reinforced and the elements of the ethological account of structure. This is made the more pressing by the apparent compatibility of anomalous operant results with ethological notions.

The Nature of Behavioral Units

The naturalness and apparent success of substituting topographical-ethological for functional analysis in these few but significant cases, however, may obscure a possible incompatibility of the assumptions underlying the two sorts of analysis. In the cases above, an operant contingency was placed on a pre-existing topographical unit, one that might be referred to as a fixed action pattern (*cf.* Stamps and Barlow, 1973). But *any* feature of behavior on which reinforcement can be made contingent can be an operant (Schick, 1971). However, contingencies of reinforcement, it is claimed, can "shape" complex forms of behavior from relatively undifferentiated material" (Skinner, 1966, p. 1206). As suggested above, such units may be controlled similarly to pre-existing units once constructed, but in terms of an ethological-topographical account of operants, where do such topographically novel units come from? What, for example, is the relation of the stereotypes described by Staddon and Simmelhag (1971) to topographies that would be displayed by an unconfined pigeon in the absence of peri-

odic presentations of food? If such novel topographies bear no relation to action patterns whose pre-experimental causation can be studied and related to their control by contingencies of reinforcement, as was done by Sevenster (1973) for example, then the sort of account suggested for autoshaping and similar phenomena must be limited to *ad hoc* accounts of a few anomalies. This seems an unsatisfactory state of affairs. Moreover, there may actually be a conflict between the two sorts of accounts at the level of data: is the form of behavior infinitely plastic or can it be exhaustively described as sequences of relatively fixed motor units? If each of these accounts is accurate for a certain class of behavior, can these classes be delimited in advance of attempts to shape behavior?

One approach to a resolution of this problem is suggested by some recent analyses of "fixed" action patterns, which show that they can profitably be analyzed as sequences of sub-units that are not always performed in the same order. Stamps and Barlow (1973) have done this for display of a lizard and Fentress (1972) has done so for face-washing in mice (*cf.* also Dawkins and Dawkins, 1973). The relation of these more elementary motor units to Skinner's (1966; Schwartz and Williams, 1972) "minimal units" and their place, if any, in topographies constructed with operant procedures deserves further exploration.

Conclusion

In summary, these two volumes of Tinbergen's original papers should be perused by anyone interested in how ethology and the analysis of experimentally acquired behavior might be related. They provide, first, a view of a science of animal behavior that would superficially appear to "botanize" reflexes and might be so considered in the light of recent suggestions (*e.g.*, Herrnstein and Loveland, 1972) that a similar activity may be unavoidable in the analysis of operants. Second, the fact that ethology embodies a theory of structural interrelations of topographically defined units of behavior and has shown how to study their causation suggests that it may contribute to the elucidation of recent findings in which the effects of contingencies of reinforcement appear to depend critically on the topographical nature and relation of responses and reinforcers (*e.g.*, Breland and Breland, 1966;

Bolles, 1970). Third, suggestions that considering the normal function of certain types of learning in species' natural environments may both illuminate learning in the laboratory and stimulate new sorts of investigations (e.g., Rozin and Kalat, 1971; Shettleworth, 1972) also point to the beginnings of a fuller communication between the two areas.

At present, however, the analysis of operantly and classically conditioned behavior appears to have more in common with ethological questions about the development and causation of behavior than with questions of function or evolution. Future attempts to analyze examples of development and modification of behavior such as those that have been described in the field could be quite fruitful. So could analysis of the many apparent parallels in the causation of behavior. In the past, ethology and the analysis of experimentally acquired behavior have freely borrowed each other's concepts and results when necessary. But little consideration has been given to how each field could suggest directions for a more generalized investigation of the causation and development of behavior. In addition, questions about the basic compatibility of their assumptions about the nature of behavior and its structure—whether, for instance, operants are organized in a way paralleling action patterns—have tended to be ignored. *The Animal in Its World* is recommended to anyone who hopes these questions will be examined more deeply in the future, as well as to anyone who simply wants to know more about why animals behave as they do.

REFERENCES

- Baerends, G. P. and Kruijt, J. P. Stimulus selection. In R. A. Hinde and J. Stevenson-Hinde (Eds.), *Constraints on learning: limitations and predispositions*. London: Academic Press, 1973. Pp. 23-49.
- Bolles, R. C. Species-specific defense reactions and avoidance learning. *Psychological Review*, 1970, 77, 32-48.
- Breland, K. and Breland, M. *Animal behavior*. New York: The Macmillan Company, 1966.
- Davis, J. M. Imitation: A review and critique. In P. P. G. Bateson and P. H. Klopfer (Eds.), *Perspectives in ethology*. New York: Plenum Press, 1973. Pp. 43-72.
- Dawkins, R. and Dawkins, M. Decisions and the uncertainty of behaviour. *Behaviour*, 1973, 45, 83-103.
- Falk, J. L. The nature and determinants of adjunctive behavior. *Physiology and Behavior*, 1971, 6, 577-588.
- Fentress, J. C. Development and patterning of movement sequences in inbred mice. In J. Kiger (Ed.), *The biology of behavior*. Corvallis: Oregon State University Press, 1972. Pp. 83-131.
- Force, D. D. and LoLordo, V. M. Attention in the pigeon: the differential effects of food-getting vs. shock-avoidance procedures. *Journal of Comparative and Physiological Psychology*, 1973, 85, 551-558.
- Garcia, J. and Koelling, R. A. Relation of cue to consequence in avoidance learning. *Psychonomic Science*, 1966, 4, 123-124.
- Herrnstein, R. J. Nature as nurture: behaviorism and the instinct doctrine. *Behaviorism*, 1972, 1, 23-52.
- Herrnstein, R. J. and Loveland, D. H. Food-avoidance in hungry pigeons, and other perplexities. *Journal of the Experimental Analysis of Behavior*, 1972, 18, 369-383.
- Hinde, R. A. *Animal behaviour*. 2nd ed.; New York: McGraw-Hill, 1970.
- Hoffman, H. S. and Ratner, A. M. A reinforcement model of imprinting: implications for socialization in monkeys and men. *Psychological Review*, 1973, 80, 527-544.
- Hogan, J. A. An experimental study of conflict and fear: an analysis of behavior of young chicks toward a mealworm. Part I. The behavior of chicks which do not eat the mealworm. *Behaviour*, 1965, 25, 45-97.
- Hogan, J. A., Kruijt, J. P., and Frijlink, J. H. "Super-normality" in a learning situation. *Zeitschrift für Tierpsychologie (in press)*.
- Hull, C. L. Stimulus intensity dynamism (V) and stimulus generalization. *Psychological Review*, 1949, 56, 67-76.
- Jenkins, H. M. and Moore, B. R. The form of the auto-shaped response with food or water reinforcers. *Journal of the Experimental Analysis of Behavior*, 1973, 20, 163-181.
- Klinghammer, E. Factors influencing choice of mate in altricial birds. In H. W. Stevenson, E. H. Hess, and H. L. Rheingold (Eds.), *Early behavior: comparative and developmental approaches*. New York: Wiley, 1967. Pp. 1-42.
- Krebs, J. R. Behavioural aspects of predation. In P. P. G. Bateson and P. H. Klopfer (Eds.), *Perspectives in ethology*. New York: Plenum, 1973. Pp. 73-111.
- Marler, P. A comparative approach to vocal learning: song development in white-crowned sparrows. *Journal of Comparative and Physiological Psychology*, 1970, 71, No. 2, Part 2, 1-25.
- Morgan, M. J. Resistance to satiation. *Animal Behaviour*, 1974, 22, 449-466.
- Morrison, R. R. *The effects of a negative reinforcement contingency on autoshaped key pecking and on other water-associated behaviors*. Paper presented at the meetings of the Eastern Psychological Association, April, 1974.
- Rescorla, R. A. and Wagner, A. R. A theory of Pavlovian conditioning: variations in the effectiveness of reinforcement and non-reinforcement. In A. H. Black and W. F. Prokasy (Eds.), *Classical conditioning II*. New York: Appleton-Century-Crofts, 1972. Pp. 64-99.
- Reynolds, G. S. Attention in the pigeon. *Journal of the Experimental Analysis of Behavior*, 1961, 4, 203-208.
- Rozin, P. and Kalat, J. W. Specific hungers and

- poison avoidance as adaptive specializations of learning. *Psychological Review*, 1971, **78**, 459-486.
- Schick, K. Operants. *Journal of the Experimental Analysis of Behavior*, 1971, **15**, 413-423.
- Schwartz, B. On going back to nature: a review of Seligman and Hagar's *Biological boundaries of learning*. *Journal of the Experimental Analysis of Behavior*, 1974, **21**, 183-198.
- Schwartz, B. and Williams, D. R. Two different kinds of key peck in the pigeon: some properties of responses maintained by negative and positive response-reinforcer contingencies. *Journal of the Experimental Analysis of Behavior*, 1972, **18**, 201-216.
- Sevenster, P. Incompatibility of response and reward. In R. A. Hinde and J. Stevenson-Hinde (Eds.), *Constraints on learning: limitations and predispositions*. London: Academic Press, 1973. Pp. 265-283.
- Shettleworth, S. J. Constraints on learning. In D. S. Lehrman, R. A. Hinde, and E. Shaw (Eds.), *Advances in the study of behavior*, 4. New York: Academic Press, 1972. Pp. 1-68.
- Shettleworth, S. J. Reinforcement and the organization of behavior in golden hamsters. Hunger, environment, and food reinforcement. *Journal of Experimental Psychology: Animal Behavior Processes* (in press).
- Skinner, B. F. Two types of conditioned reflex and a pseudo type. *Journal of General Psychology*, 1935, **12**, 66-77.
- Skinner, B. F. *The behavior of organisms*. New York: Appleton-Century-Crofts, 1938.
- Skinner, B. F. The phylogeny and ontogeny of behavior. *Science*, 1966, **153**, 1205-1213.
- Staddon, J. E. R. Asymptotic behavior: the concept of the operant. *Psychological Review*, 1967, **14**, 377-391.
- Staddon, J. E. R. and Simmelhag, V. L. The "superstition" experiment: A reexamination of its implications for the principles of adaptive behavior. *Psychological Review*, 1971, **78**, 3-43.
- Stamps, J. A. and Barlow, G. B. Variation and stereotypy in the displays of *Anolis aeneus* (Sauria: Iguanidae). *Behaviour*, 1973, **47**, 67-94.
- Tinbergen, N. *The study of instinct*. London: Oxford University Press, 1951.
- Tinbergen, N. Derived activities: their causation, biological significance, and emancipation during evolution. *Quarterly Review of Biology*, 1952, **27**, 1-32.
- Verplanck, W. S. Since learned behavior is innate and *vice versa*, what now? *Psychological Review*, 1955, **62**, 139-144.
- Wessels, M. G. The effects of reinforcement upon the prepecking behaviors of pigeons in the autoshaping experiment. *Journal of the Experimental Analysis of Behavior*, 1974, **21**, 125-144.
- Williams, D. R. and Williams, H. Auto-maintenance in the pigeon: sustained pecking despite contingent non-reinforcement. *Journal of the Experimental Analysis of Behavior*, 1969, **12**, 511-520.
- Woodruff, G. *Autoshaping: a "learned release" hypothesis*. Paper presented at meetings of the Eastern Psychological Association, April, 1974.