

# A SKETCH OF AN ECOLOGICAL METATHEORY FOR THEORIES OF LEARNING<sup>1</sup>

*Timothy D. Johnston*

NORTH CAROLINA DIVISION OF MENTAL HEALTH, RESEARCH SECTION  
RALEIGH, NORTH CAROLINA

*M. T. Turvey*

UNIVERSITY OF CONNECTICUT, STORRS, CONNECTICUT AND  
HASKINS LABORATORIES, NEW HAVEN, CONNECTICUT

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## I. Introduction

For about the first half of this century, the psychology of learning was unified by a set of metatheoretical concepts and beliefs that may loosely be termed the general process view of learning (Seligman, 1970). Although the major general process theorists (Pavlov, Thorndike, Watson, Guthrie, Tolman, Hull, Spence, and Skinner) differed sharply on a number of theoretical issues, they all shared a set of common assumptions about learning that allowed those issues to be clearly defined and that enabled workers in the field to agree on the nature of important questions to be asked about learning. The issues that were debated included those of S-S versus S-R learning, reinforcement versus contiguity, the nature and role of drive states, and the importance of cognitive processes in learning. Underlying these theoretical arguments was a common set of metatheoretical beliefs that, within the general process tradition, were not called in question. These included the belief that there are general principles of learning that apply to all learning situations, that the same learning processes are involved in all animals, and that learning is to be equated with the formation of associations of some kind.

The last 25 years have seen a gradual retreat from the general process view of learning as its underlying assumptions began to be questioned. The view that learning is explicable by a single set of general principles has given way to a belief in a multiplicity of principles, a development that was anticipated by Tolman (1949). Thus we have seen a proliferation of "minitheories," each dealing with a restricted range of learning phenomena such as classical conditioning (Rescorla, 1972; Rescorla & Wagner, 1972), expectancy (Kamin, 1968, 1969), discrimination learning (Mackintosh & Sutherland, 1971), and avoidance learning (Bolles, 1970, 1971, 1972). The phylogenetic generality of learning processes has been questioned by proponents of the "biological boundaries" approach to learning (Bolles, 1970; Kalat, 1977; Rozin & Kalat, 1971; Seligman, 1970; Shettleworth, 1972). In the literature on human learning in particular, associationism is on the wane and cognitive theories of learning are preeminent (Haugeland, 1978).

The current state of the psychology of learning, in short, is one of great conceptual diversity in which little attention is being paid to the prospects for a unified approach to the study of learning. It may perhaps be argued that such diversity is in fact just what is required to free the study of learning from the remnants of the general process view and to provide a broader data base on which to build new theories. An alternative argument, however, is that without a competing metatheory to set against the general process view, theoretical unification of the field will be greatly

retarded, because there will be no basis for agreement on the theoretical issues to be resolved and on the important questions that must be asked (see Kuhn, 1962, for arguments and examples supporting this philosophical position). Our aim in this article is to sketch the outline of such a competing metatheory. To do this, we have chosen to stand outside the mainstream of much current psychology of learning and to consider learning within the conceptual framework of evolutionary and ecological biology. The biological boundaries approach to learning has set an important precedent for taking ecological considerations seriously in the study of learning, but we shall attempt to offer a more radical alternative to general process theory than is provided by the latter approach (see Johnston, submitted).

The distinction between *metatheoretical* analysis, which primarily concerns us in this article, and *theoretical* analysis, with which we shall be more peripherally concerned, is perhaps worth making explicit. Briefly, the distinction is this: Theoretical analysis provides answers to questions that are posed on the basis of metatheoretical analysis. Metatheory is concerned with justifying the asking of certain kinds of questions in a particular area of inquiry, in our case, the area of learning, and putative answers to those questions are presented in the form of theories, hypotheses, and models. One may arbitrate among competing theories by pointing to data that conflict with some but not with others, but competing metatheories cannot be evaluated in this way. Asking certain kinds of questions about learning may be unprofitable but the questions asked are not "wrong" in any factual sense. A metatheory can thus be properly evaluated only after some of the research that it mandates has been carried out, so that its profitability may reasonably be assessed. In the interim, a preliminary judgment may be made on the basis of criteria such as how well the metatheory articulates with those of other, related fields of inquiry, how wide a range of phenomena is opened up for analysis under the metatheory, and whether the questions asked seem to be *prima facie* amenable to experimental study. These criteria are in addition to those of a logical kind that apply to any form of intellectual inquiry, such as logical consistency and coherence, a minimum number of unproven assumptions (which should be unproblematical), precise definition of central terms, and so forth.

The distinction between metatheory and theory has much in common with Kuhn's (1962) distinction between a paradigm and the normal science that it sanctions, and the concept of metatheory is very similar to Lakatos' (1970) "scientific research programme." This is not, however, the place for a detailed comparison of these various concepts. The aim of this brief philosophical digression has been to characterize the nature of

our endeavor and to suggest partial criteria by which it might reasonably be judged.

## II. The Nature of Ecological Inquiry

Ecology, as a branch of science in its own right, studies the relationships between living organisms and the world in which they live. Thus defined, ecology encompasses almost all of the disciplines that include an organism as part of their concerns, but tradition and necessity have combined to give the field a somewhat more restricted scope (Elton, 1927; Emlen, 1973; Odum, 1953). The *ecological approach*, however, is one that may usefully be applied to any of a wide range of problems that lie outside the scope of *ecology* as traditionally defined. Taking our cue from the above definition, we may say that an ecological approach is one that studies some aspect of an animal<sup>2</sup> in relation to the environment that it inhabits, or, in complementary fashion, that studies some aspect of an environment in relation to the animal that lives in it.

### A. ANIMAL AND ENVIRONMENT

The nature of ecological inquiry depends, evidently, on how one construes the relationship between an animal and its environment; and the nature of this relationship will depend, again, on the interpretation placed on the two terms, "animal" and "environment," that enter into it.

#### 1. *The Animal as Actor*

The conventional and intuitive interpretation of the term "animal" is as a morphologically defined entity, bounded by an epidermis that sets it off from the rest of the world, conventionally its "environment." As long as our interest in the animal is appropriately pursued in morphological terms, such an interpretation may be appropriate. The study of learning, however, is not concerned with questions of morphology, but rather with questions of behavior and of change in behavior, and so we may question the suitability of a morphological interpretation of the term "animal" for the study of learning.

<sup>2</sup>Throughout this article we will be using the terms "animal" and "actor" in the sense of "species-typical individual." That is, we will be thinking of the animal or actor as possessing certain definite (though perhaps unspecified) characteristics that make it typical of a species or population. The phrase "individual animal (actor)" will be used when we wish to denote a particular individual, which may or may not be species-typical.

In morphological terms, we might observe that an animal may be described as possessing certain structures, such as limbs, organs, tissues, and cells. In behavioral terms, then, let us observe that an animal may be described as effecting certain actions, such as feeding, walking, raising its head, and moving its eyes. Thus we may say that from a behavioral point of view of animal is an *actor*, defined in terms of a set of *effectivities* (Turvey & Shaw, 1979), that is, of actions that effect consequences for the actor.

In choosing the term "actor" in preference to "animal" our aim is draw attention to the fact that more than one kind of description may be given of an organism. The description that we choose must be appropriate for the kind of analysis we wish to pursue and, having chosen a particular style of description, it is important not to confuse its terms with those of other styles of description. Such confusion leads to what philosophers call "category errors," in which properties appropriate to the elements of one style of description are inappropriately applied to those of another style. The usual result of such errors is that questions are asked that are unhelpful and misleading: "What color is the Law of Effect?" is a blatant example of a category error. A more famous example is provided by Gilbert Ryle's (1949) foreign visitor to Oxford who was shown the various colleges and who then asked to be taken to the University; "colleges" and "the University" are elements of different styles of description of Oxford and only colleges can be assigned the property of physical location within the town. More subtle, and hence dangerous examples from the study of behavior are discussed by Fodor (1968) and by Purton (1978).

Behavior and morphology are alternative styles of description of an organism. By selecting a term such as "actor," which is both descriptive and relatively unfamiliar in this context, to apply to the results of a behavioral description, we hope to keep the two styles clearly distinct and so avoid unintentionally committing category errors.

## 2. *The Environment as Econiche*

Under the conventional definition of "animal" as a morphological entity, "environment" is construed as a physical entity, namely, that part of the world outside the animal's skin. Defining the animal as an actor, in terms of a set of effectivities, raises difficulties for this definition, however, for an effectivity is a description of an actor *relative* to some environment. The effectivity of flight, for example, can be realized by a particular actor only under certain circumstances (which will vary between actors) and to say that an actor possesses the effectivity of flight is

necessarily to imply an environment in which those conditions are realized.

A description of an animal as an actor possessing a particular set of effectivities, or an *effectivity structure* (Turvey & Shaw, 1979), identifies, in short, an *econiche*, which is an environment possessing the necessary support for those effectivities. A description of the ecological support for an effectivity defines an *affordance* (Gibson, 1977; Turvey & Shaw, 1979), which is a specific combination of physical properties of an environment taken with reference to a particular effectivity. A description of the physical properties of an environment, taken with reference to the effectivity structure of an actor, defines the *affordance structure* of an econiche for that actor. It is important to appreciate the significance of the phrase "for that actor" since a structure that affords climbing, say, by an actor of one kind (such as a tree frog) may not afford climbing by some other actor (such as an alligator).

The term "econiche" is derived from the ecological concept of the niche, originated by Grinnell (1924) and greatly elaborated by Hutchinson (1957, 1967; see Vandemeer, 1972, and Whittaker, Levin, & Root, 1973, for more recent discussions). As proposed by Hutchinson (1967), the niche is a volume of  $n$ -dimensional hyperspace, each of the dimensions corresponding to some physical factor of ecological relevance to the organism; points within the niche space define conditions under which the organism can survive. The concept of econiche, as we shall employ it, is limited to factors of behavioral relevance to the animal and, in particular, it is an animal-relevant description of the environment.

The concept of affordance is discussed at greater length in Section IV,B. For the moment, we wish to emphasize some of the implications of the preceding discussion. It will be apparent that effectivities and affordances are complementary descriptions of actors and econiches, respectively, taken with respect to each other. Just as describing an actor in terms of its effectivity structure implies an econiche with a particular affordance structure for it to inhabit, so describing an econiche with a particular affordance structure implies an actor with the requisite effectivity structure to inhabit it. This statement must not be read as a claim that the existence of the physical world is dependent on the existence of animals; as previously remarked, the term "econiche" refers to a *description* of the physical world with respect to some actor. "Actor" and "econiche," as we shall use these terms, are coimplicative and cannot be defined independently of one another. Figure 1 illustrates the relationships among the various terms defined in this section.

This discussion by no means exhausts the problems inherent in the concept of the econiche; indeed the development of an adequate theory of

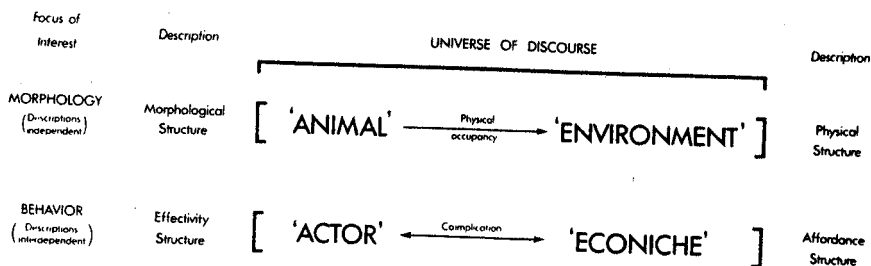


Fig. 1. Two styles of description of the animal and the environment, one from a morphological point of view, in which the descriptions given are independent, and one from a behavioral point of view, in which they are interdependent or coimplicative.

environments taken in relation to their inhabiting animals remains an important desideratum for ecological theory in general (Mason & Langenheim, 1957). For the present, we will content ourselves with supplementing the above account with two further considerations. First, since the term "econiche" refers to a description rather than to a locality, any specific locality will not necessarily provide all of the affordances required by a particular actor. We may speak, therefore, of a locality as providing an *econiche* for *S*, where *S* is some subset of the effectivities of an actor. There must be a set of localities, however, such that together they constitute an econiche for the actor and such that they are *connected* for the actor. Two localities are connected for an actor if it possesses an effectivity permitting it to move from one locality to the other.

The second consideration involves the problem of ontogeny, which is obviously of prime importance in any discussion of learning. As the actor develops, its effectivity structure changes. It acquires capabilities that it previously did not possess and it loses others. Concurrently, the affordance structure of its environment changes. This does not mean, of course, that the physical characteristics of the localities it occupies change (although they may do), but that those characteristics change in relation to the changing effectivity structure of the actor. Mason and Langenheim (1957) express this important point as follows: "The life-span of the organism is the duration time of its environment [econiche] [and] . . . the environmental relation [affordance structure] is ordered by the ontogeny of the organism" (pp. 331-332).

## B. THE ECOSYSTEM—UNIT OF ECOLOGICAL INQUIRY

The close and complementary relationship between actor and econiche that is established by our analysis means that the focus of inquiry into learning must broaden to include more than just the animal. The ecologi-

cal approach to learning is concerned with mutually defined actors and econiches and so the minimal unit of our inquiry must be the whole actor-econiche system, which we will term the *ecosystem*. This term was proposed by A. G. Tansley in 1935 and has become a prominent component of ecological theory, especially in the work of Odum (1953, and subsequent editions). Our use of the term differs somewhat from that of Tansley and of most subsequent writers but it preserves the essential ingredient of their thinking: that of an integral system of animal and environment.

Odum (1959, p. 10) defines the ecosystem as follows:

Any area of nature that includes living organisms and nonliving substances interacting to produce an exchange of materials between the living and nonliving parts is an ecological system or ecosystem.

As examples of ecosystems, Odum (1959, p. 11) lists "a pond, a lake, a tract of forest or even a small aquarium." In ecological theory, the various organisms that inhabit a locality such as a lake comprise a community and the term "ecosystem" as used by most ecologists refers to the community and its environment. We will use the term however to refer to a single (kind of) actor and its econiche, as we have previously defined those terms.

The utility of allowing the concept of ecosystem to apply at various scales of biological organization (individual, group, population, species, or community) was pointed out by Evans (1956), who also stressed that the ecosystem, rather than any of its components, is the minimal unit of ecological inquiry. Where necessary, we shall adopt Evans' suggestion that "the particular level on which the ecosystem is being studied can be specified with a qualifying adjective—for example, community ecosystem, population ecosystem, and so forth" (p. 1128). Since our main concern is with individual kinds of actors, the unadorned term "ecosystem" will be used for this scale of analysis.

The focus of our ecological approach is somewhat more restricted than that of the traditional ecologists, for our concern is with the ecological support for behavior and, crudely, with the ways in which an actor learns to exploit that support in the course of its development. The more traditional issues of the flow of matter and energy through the ecosystem will not concern us.

### C. A STYLE OF INQUIRY FOR THE ECOLOGICAL STUDY OF LEARNING

What and where is behavior? The location of behavior is literally in naturally evolving life on earth. It is literally in organism-environment. These sentences are not verbal



generalities about some generality of behavior. They are intended as literal report upon the specific instance of specific behavior. (Bentley, 1941, p. 485)

In putting forth the ecosystem as the minimal unit for the ecological analysis of learning, we make the same claim for learning as Bentley makes for behavior in the above quotation: Learning goes on in ecosystems, not in animals. The ecological approach adopts a style of inquiry that Dewey and Bentley (1949) call "transactional," a style that, "assumes no pre-knowledge of either organism or environment as adequate . . . but requires their primary acceptance in common system" (p. 123). This style of inquiry Dewey and Bentley (1949) contrast with "interactional" inquiry, which "assumes the organism and its environment objects to be present as substantially separate existences or forms of existence, prior to their entry into joint investigation" (p. 123).

Traditional approaches to the study of learning have adopted an interactional style of inquiry. The animal is described as the possessor of a set of responses and the environment as the emitter of a set of stimuli, each of these sets being described independently of the other, and then means are sought of mediating between one set and the other by recourse to constructs such as reinforcement, contiguity, expectancy, and so forth. By contrast, we seek a style of inquiry that respects the integrity of the ecosystem and that exploits the coimplicative relationship between actor and econiche in an attempt to dispense with the need for mediation between the two (see Shaw & Turvey, in press).

In pursuit of this end, we require a system of concepts that will permit us to treat the integrity of the ecosystem as a primary datum, not as derived from an interaction between animal and environment. This is the task to which we turn in the following section.

### III. The Nature of Biological Adaptation

Having described the nature of ecological inquiry, we now focus on the nature of the relationship between actor and econiche that is the crucial element in any such inquiry. In the course of this discussion we shall consider a number of important concepts that provide the conceptual tools required for the ecological analysis of learning.

#### A. THE CONCEPT OF ADAPTATION

Central though it is to modern biological theory, few concepts have generated more confusion or proven more resistant to analysis than that of

adaptation (Ghiselin, 1966; Medawar, 1951; Williams, 1966). We will not attempt to provide a full-scale explication of the concept here, since to do so would carry us well beyond the scope of this article. Rather, we shall provide a more limited discussion, aimed at resolving certain issues that are particularly relevant to arguments that we wish to make later. The reader interested in a more complete discussion may wish to consult some of the very large literature on the topic, of which the following may be cited as especially valuable: Bock and von Wahlert, 1965; Dobzhansky, 1942, 1956, 1968; Ghiselin, 1966; Lewontin, 1978; Medawar, 1951; Slobodkin, 1968; Slobodkin and Rapoport, 1974; Sommerhoff, 1950, 1969; Williams, 1966.

In the first place, we must distinguish between *adaptation* and *fitness*, two closely cognate terms that are frequently, though incorrectly, used synonymously (for example by Lewontin, 1956, and by Stern, 1970; cf. Dobzhansky, 1956, 1968; Ghiselin, 1974). Fitness is the more easily defined term, being the relative reproductive contribution that an individual makes to the next generation, in comparison with that of other individuals in the population, under a defined set of environmental conditions (Lewontin, 1974; Mettler & Gregg, 1969). It is differences in reproductive fitness that give rise to natural selection (Darwin, 1859), since in a stable population, those individuals that contribute most offspring to subsequent generations will increase their genetic representation at the expense of those that contribute least.<sup>3</sup> There is a close and nonarbitrary relationship between adaptation and fitness, and we discuss this relationship in Section IV,A.

By contrast with the concept of fitness, adaptation is to be assessed more in terms of individual *survival* than in terms of individual *reproduction*. We shall first develop the concept of adaptation with regard to the animal and its environment, after which it will be seen that a transition to the concepts of actor and econiche may be accomplished quite naturally. If an animal *A* can survive in an environment *E*, then we may say that *A* is adapted for survival in *E*. This formulation is acceptable as far as it goes but it does not go very far; it leaves "survival" as a primitive, unanalyzed term, but it is the means whereby survival is ensured that must concern us. If we are to make sense of learning in the context of

<sup>3</sup>This formulation is somewhat inaccurate, for it neglects the concept of inclusive fitness (Hamilton, 1964), which has come to play an important role in modern evolutionary theory. If we ride roughshod over such subtleties (as we do here and in other parts of this article), it is not because of a lack of appreciation of their theoretical importance, but rather out of sympathy for our psychological readership, whose interest is primarily in learning rather than in evolution. We have not, of course, adopted this cavalier attitude when to do so would introduce distortions into the substance of our arguments.

biological adaptation then we require a formulation that recognizes the complexity of animal-environment relationships underlying survival and that will allow us to elucidate the role of learning in maintaining those relationships. Let us see how this might be accomplished, adopting a strategy based on that originated by Sommerhoff (1950).

One way of expressing  $A$ 's adaptedness for survival in  $E$  is to say that  $A$  can attain the goal of survival in  $E$ . With this formulation, the way is open for us to unpack the concept of adaptation: Let us define survival as an ultimate goal of  $A$ , in the sense that all of  $A$ 's activities are adaptively significant only to the extent that they contribute to survival. There are then a number of subgoals, varying in detail between animals of different kinds, that must be attained if survival is to be assured. Thus  $A$  must be able to obtain food, avoid predators, move through space, orient, acquire a mate, care for its young, and so forth. Each of these requirements defines a goal that contributes to eventual survival and reproduction. If  $A$  is able to attain a goal  $G$  under some set of conditions  $E$ , then we may say that  $A$  is adapted for  $G$  in  $E$ .

Defining adaptation in terms of the attainment of goals does not represent a retreat into either vitalism or teleology. " $A$  can attain goal  $G$  under conditions  $E$ " is a descriptive, not an explanatory statement and it is hence not teleological. We must still account for the fact of goal attainment and such an account need not (and should not) appeal to an *élan vital* or other inexplicable entity. Rather, an explanation must be given in terms of publicly observable characteristics of the goal-directed system, in terms of its "objective system properties" (Sommerhoff, 1950, 1969). Equally important, the concept of goal-directedness does not require us to assume that  $A$  is conscious of its goal, that it is acting purposefully, or indeed that it has any internal representation at all of the goal state. Any of these conditions *may* hold, but they need not. What is important for the animal is that it be able to attain the goal—articulating or representing the goal is a problem for the theorist, along with the deeper problem of explaining the process of goal attainment. We shall have more to say of these problems, especially the latter, in the following section.

In defining  $A$ 's adaptedness in terms of both  $G$  and  $E$  we have given explicit recognition to an important aspect of the concept of adaptation, namely, that it is a *relational* concept (Bock & von Wahlert, 1965; Slobodkin & Rapoport, 1974; Sommerhoff, 1950). An animal does not possess adaptation in the sense in which it possesses mass, length, or limbs. Rather, it may stand in an adaptive relationship to some environment and the environment must be defined in order for us to discuss the animal's adaptation. It makes no sense to say that  $A$  is adapted for some  $G$  without specifying the environment  $E$  for which such adaptation holds.

Adaptation (more precisely, adaptation for some  $G$ ) is a property of *ecosystems*, of animal–environment systems, not of animals alone.

The definition of adaptation in terms of goal attainment makes it undesirable to speak, as did Henderson (1913), of an environment as also being adapted to the animal that inhabits it (although we are naturally sympathetic to the ecological tenor of Henderson's thesis). Since we now wish to incorporate the mutually defined concepts of actor and econiche into our analysis, however, we must have some way of referring to the complement of the adaptive relationship of the animal to its environment. We shall speak, therefore, of the *appropriateness* of an environment for an animal that is adapted to it (by implication, in relation to some goal  $G$ ). It is just as legitimate, although it may be less familiar, to inquire into the source of an environment's appropriateness as it is to inquire into the nature of an animal's adaptation. In the latter case we seek to understand the biological characteristics that enable  $A$  to attain  $G$  in  $E$ ; in the former, we seek to explain the ecological support that  $E$  provides for the attainment of  $G$  by  $A$ . Note that appropriateness is a relational concept in the same way as adaptation: An environment is not appropriate per se, but only in relation to the animal that is adapted to it. It will now be apparent that the biological characteristics of interest are the effectivities that permit us to describe  $A$  as an actor and that the ecological support is provided by the affordances that allow us to describe  $E$  as an econiche. Figure 2 illustrates the complementary relationship between an adapted animal (the actor) and its appropriate environment (the econiche).

Several authors (e.g., Medawar, 1951; Stern, 1970) have pointed out that the term "adaptation" may be used in a number of different senses. To avoid confusion, we will define the three most important senses as follows:

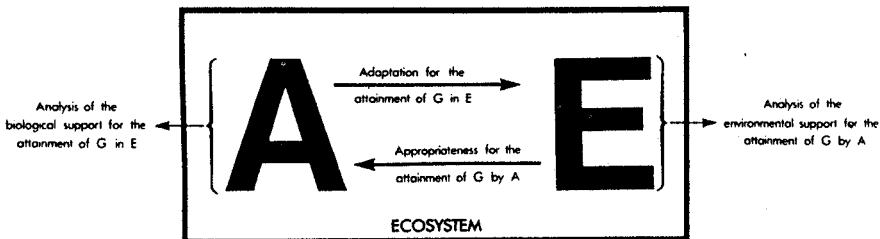


Fig. 2: The actor ( $A$ ) and its econiche ( $E$ ) together constitute an integrated system, the ecosystem. The relationship of  $A$  to  $E$  is one of adaptation for the attainment of goals ( $G$ ); the relationship of  $E$  to  $A$  is one of appropriateness for the attainment of those goals. Both the actor's adaptation and the econiche's appropriateness may be analyzed in terms of the support they provide for goal attainment.

1. As a *relation*. This is the sense in which the term has been used in the preceding discussion;

2. As a *characteristic*. An adaptation, or adaptive feature, is some characteristic of *A* that enables it to survive (and reproduce) in *E*. An adaptation for some goal *G* (e.g., a "feeding adaptation") is one that enables *A* to attain *G* in *E*. Determining whether a particular characteristic of an organism is in fact an adaptation, and if so in what way, is an extremely difficult problem for which there is no general solution (Bock & von Wahlert, 1965; Hinde, 1975; Lewontin, 1979);

3. As a *process*. An adaptive process is one that gives rise to an adaptive relationship between *A* and *E* in regard to some *G*. Adaptations [in sense 2 above] are a product of (a process of) adaptation.

The aim of our analysis is to provide an understanding of learning in relation to adaptation construed in all three senses. First, we want to understand learning as a *process* of adaptation that is manifest over relatively short periods of time, within the lifespan of an individual actor. Second, we wish to understand learning as itself a *product* of adaptation, in this case of the process of evolutionary adaptation, acting over much longer periods of time. Finally, our analysis of both of these aspects of the problem will be guided by the nature, already outlined, of the adaptive *relationship* between the actor and its econiche, for it is the maintenance of this relationship that is the *raison d'être* for learning as both product and process.

## B. A FORMAL MODEL OF GOAL ATTAINMENT

Having provided, in the preceding section, an account of adaptation as a relationship, we now turn to an account of adaptation as a process. Here we shall be concerned not with particular kinds of adaptation, such as learning, nor with the problem of how adaptation occurs, in the sense of providing hypothetical mechanisms. Our analysis remains in the domain of metatheory, in that we are concerned with the question of *what* adaptation is as a process, seeking to answer that question in precise and formal terms. Once the formal model has been expounded, we shall see that it has important implications for the subsequent analysis of learning in relation to adaptation.

The model we shall present is a simplified version of one that has been worked out in detail by Sommerhoff (1950, 1969). Our account of it will necessarily be brief; we will emphasize those aspects of the model that are of greatest relevance to our present concerns and, in particular, we will omit much of Sommerhoff's mathematical development. We will develop

the model with respect to an example of goal-directedness from the field of insect behavior, namely, prey capture by the praying mantis. The mantis catches small insects by means of its long, clawed forelimbs, a process that has been described in some detail by Maldonado, Levin, and Barros Pita (1967), Mittelstaedt (1957), and others. We will deal here with only a few selected aspects of this behavior. Figure 3 shows the position of the mantis' forelimbs at two instants: just before the strike (time =  $t_0$ ) and just after the strike (time =  $t_k$ ). Consider two variables describing the relationship between the mantis and its prey: the bearing of the prey ( $\phi$ ) and the bearing of the claw tip ( $\beta$ ), both taken with regard to an arbitrary line drawn through a fixed point on the mantis' body (Fig. 3). These variables take the values  $\phi_0$  and  $\beta_0$ , respectively, at  $t_0$  and  $\phi_k$  and  $\beta_k$  at  $t_k$ .

The mantis' claw tip must be aligned with the prey in order for capture to be successful and so we may say that the goal of prey capture will be attained only if the following condition holds just after the strike (Fig. 3):

$$\phi_k - \beta_k = 0 \quad (1)$$

Equation (1) defines the *focal condition* of adaptation; it specifies the condition that must be satisfied if the goal is to be attained. In this example there will be many values of  $\phi_0$  (the initial bearing of the prey) for each of which the mantis can produce a specific, adapted value of  $\beta_k$  at  $t_k$  satisfying the focal condition. This range of values defines a set  $S_0$ , which may be either an interval on a continuum or a set of discrete values. Sommerhoff (1950) claims, with some justification, that  $S_0$  must have at least two members in any instance of adaptation. However, we will consider some examples below (see Section V,A) in which there is but one member of  $S_0$  and yet which are incontestably examples of adaptation.

In the case of the mantis,  $S_0$  includes a range of values of  $\phi_0$  and we may say that the mantis possesses a "strike aiming system" such that on detecting the value of  $\phi_0$  at  $t_0$  it produces a corresponding, or adapted value of  $\beta_k$  at  $t_k$  such that  $\phi_k - \beta_k = 0$ . It is the correspondence of  $\phi_k$  and  $\beta_k$  that defines the adaptiveness of the aiming system and this correspondence is effected by virtue of a specific sensitivity of the system in regard to the value of  $\phi_0$ . Following Sommerhoff (1950), we will refer to  $\phi_0$  as the *coenetic variable* of adaptation.

In the example we have been discussing, the relationship between  $\phi_k$  and  $\beta_k$  that defines the focal condition is one of simple equality. Suppose, however, that  $\phi$  is the size of the prey and  $\beta$  is the angle of the claw. Then there will be some more complex relationship between  $\phi_k$  and  $\beta_k$  that must be satisfied if the prey is to be grasped securely and the goal of prey

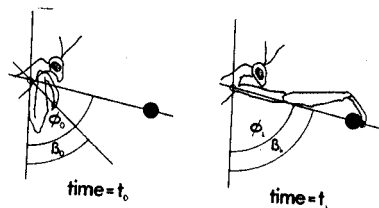


Fig. 3. Two instants in the predatory strike of a praying mantis, just before the strike (time =  $t_0$ ) and just after the strike (time =  $t_k$ ). The bearing of the prey ( $\phi$ ) and of the claw tip ( $\beta$ ) are equalized as a result of adaptation over the interval  $t_k - t_0$ .

capture attained (see Holling, 1964, for details). We may describe this relationship by some function  $F$  and rewrite the focal condition in Eq. (1) more generally as:

$$F(\phi_k, \beta_k) = 0 \quad (2)$$

So far, we have considered only one variable describing the environment ( $\phi$ ) and one describing the animal ( $\beta$ ), but in many instances of goal-directedness, several variables describing the animal ( $\beta_1, \beta_2, \dots, \beta_n$ ) must be adapted to several variables describing the environment ( $\phi_1, \phi_2, \dots, \phi_m$ ). For example, not only must the bearing of the prey and of the claw tip be equalized by the striking mantis, but the claw tip must also be positioned at an appropriate distance, just behind the prey (see Fig. 3). Thus Eq. (2) may be written still more generally as:

$$F(\phi_{1k}, \phi_{2k}, \dots, \phi_{mk}, \beta_{1k}, \beta_{2k}, \dots, \beta_{nk}) = 0 \quad (3)$$

To simplify discussion, we will employ the notation of Eq. (2) and allow  $\phi$  and  $\beta$  to stand for any of several variables that we may wish to consider. Since we are concerned only with the formal and not the quantitative nature of the relationships between the animal and the environment, this simplification will not limit the generality of our arguments.

Two assumptions have been made in the preceding discussion: first, that the coenetic variable ( $\phi_0$ ) and the variable to which  $\beta_k$  is adapted ( $\phi_k$ ) are the same; and second, that the environment does not change between  $t_0$  and  $t_k$  (i.e.,  $\phi_0 = \phi_k$ ). We may relax both assumptions, increasing the power and generality of the model. In many instances of biological adaptation, as we shall see, the coenetic variable may be different from  $\phi$ , the variable to which adaptation is effected at  $t_k$ . For example, diapause in insects is a physiological adaptation to cold weather, but it is initiated as a response to short day length, not to low temperature (Beck, 1968). Here the coenetic variable is day length and the adaptive relationship holds between temperature (high or low) and the insect's physiological state

(normal or diapause). In the sequel, we shall let  $y$  stand for the coenetic variable, taking the value  $y_0$  at  $t_0$ . The nature of the insect's environment is such that between  $t_0$  and  $t_k$  short day length ( $y_0$ ) maps on to low temperatures ( $\phi_k$ ) and the constitution of the insect is such that, in the same interval, short day length maps on to diapause ( $\beta_k$ ).

Formally, we may define two functions, one ( $P$ ) defined on the environment, the other ( $B$ ) defined on the animal, such that:

$$P(y_0) = \phi_k \quad (4)$$

and

$$B(y_0) = \beta_k \quad (5)$$

Notice that since the value of  $\phi$  at  $t_0$  ( $\phi_0$ ) does not appear in Eqs. (2)–(5), we may relax the assumption of an unchanging environment. This is replaced by the assumption that there is a coenetic variable  $y$  (possibly though not necessarily equal to  $\phi$ ) satisfying Eqs. (4) and (5). Notice also that the value of  $\beta_0$  does not appear in Eqs. (2)–(5), implying that the initial state of the adapting organism does not affect the process of adaptation. This may be a limitation of the model, especially in regard to adaptive processes involving evolution and individual development. In these cases, the initial state of the system (at  $t_0$ ) may be of crucial importance in determining the range of subsequent states that it can attain (at  $t_k$ )

The characteristics of a goal-directed, or adaptive system may then be summarized as follows (see Sommerhoff, 1969, pp. 174–175):

1. At some time  $t_k$  it is a necessary condition for the subsequent occurrence of a goal event  $G$  that the two sets of variables  $\phi_1, \phi_2, \dots, \phi_m$  and  $\beta_1, \beta_2, \dots, \beta_n$  should satisfy the focal condition in Eq. (3).

2. There is a coenetic variable  $y$  and two sets of functions  $P_1, P_2, \dots, P_m$  and  $B_1, B_2, \dots, B_n$  such that:

$$P_i(y_0) = \phi_{ik} \quad i = 1, 2, \dots, m \quad (6)$$

$$B_i(y_0) = \beta_{ik} \quad i = 1, 2, \dots, n \quad (7)$$

where  $y_0$  is the value of  $y$  at  $t_0$ .

3. There is a set  $S_0$  of values of  $y_0$ , often containing at least two members, but sometimes only one, for which the above conditions hold.

Figure 4 presents a diagrammatic representation of the various elements in Sommerhoff's model, in the form we shall employ in subsequent discussion. This figure may be referred to when the model is employed in the analysis of particular examples of adaptation in Sections IV and V.



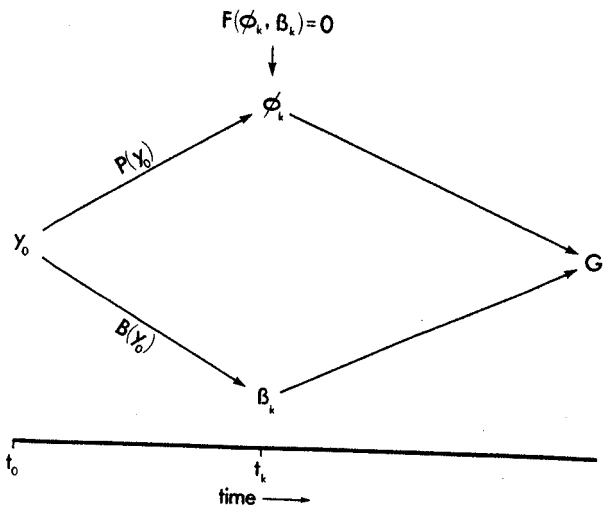


Fig. 4. Sommerhoff's formal model of goal attainment. See text for discussion.

### C. THE BACK-REFERENCE PERIOD

We now single out one element of the model for special consideration, since it will play an important part in subsequent discussion. This is the interval  $t_k - t_0$ , called by Sommerhoff (1969) the *back-reference period*. The back-reference period is the operation lag of the adaptive mechanism that implements the response  $\beta_k$ . During this period, two events occur: the function  $B$  maps  $y_0$  on to  $\beta_k$  and the function  $P$  maps  $y_0$  on to  $\phi_k$ . In order for  $\beta_k$  to be an adaptive response to  $\phi_k$  at  $t_k$ , the function  $P$  must be determinate and single valued; that is  $P$  must always map a given value of  $y_0$  on to the same value of  $\phi_k$ . If this were not the case,  $B$  would often map  $y_0$  on to a maladaptive value of  $\beta_k$ , since the value of  $\phi_k$  would be inappropriate. Another way of saying this is that *given an adaptive mechanism with a back-reference period  $t_k - t_0$ ,  $y$  and  $\phi$  must be invariantly related over at least the span  $t_k - t_0$* . Alternatively and equivalently, *given an environment such that  $y$  and  $\phi$  are invariantly related over a span of no more than  $t_k - t_0$ , adaptation to  $\phi$  can be effected only by an adaptive mechanism with a back-reference period of  $t_k - t_0$  or less*.

This is a formal expression of a boundary condition on the relationship between a variable environment and an adapting animal: Different rates of variation, measured by the invariance between  $y$  and  $\phi$ , require adaptive responses with different back-reference periods. Table I illustrates this point with reference to four kinds of variability and the adaptive response

TABLE I

THE CORRESPONDENCE BETWEEN ADAPTIVE RESPONSES AND THE TIME-SCALE OF ENVIRONMENTAL VARIABILITY

Kind of variability	Back-reference period	Adaptive response
Obstacles in the path of locomotion	Fraction of a second	Adjust direction of movement
Appearance of predator	Few seconds	Effect avoidance or defensive behavior
Location of food, water, shelter, etc.	Several days to a few years	Learn appropriate routes of travel
Availability and nature of substrates for locomotion	Many years	Evolution of locomotor system by natural selection

that is appropriate to each. It is the time-scale of the change and the back-reference period of the response that determine whether the response can be adaptive with regard to the change.

#### D. UNIFICATION IN A THEORY OF ADAPTIVE RESPONSE

It has been pointed out before, for example by Plotkin and Odling-Smee (1979), Slobodkin (1968), and Slobodkin and Rapoport (1974), that animals must be able to adapt to environmental change occurring on different time-scales and that in order to do this, different adaptive mechanisms are required. Perceptuomotor coordination, learning, and evolution by natural selection are three of the most prominent such mechanisms, effective in regard to short-term, medium-term, and long-term environmental change, respectively. A unified theory of adaptive response would provide an account of adaptation general enough to cover all of these (and other) cases, while at the same time providing an explicit statement of the differences between different styles of adaptive change. Sommerhoff's model provides just the framework for such an account and in Section IV,C we shall employ it in our discussion of learning as a mode of ecological adaptation.

The generality of Sommerhoff's model lies in its explicit formalization of several crucial elements in any form of adaptive response: a goal event ( $G$ ); a focal condition [ $F(\phi_k, \beta_k) = 0$ ]; a coenetic variable ( $y$ ); one (or more) environmental variables ( $\phi$ ); and one (or more) response variables ( $\beta$ ). In addition, it provides grounds for explicit distinctions between different forms of adaptive response. We have stressed the back-reference period ( $t_k - t_0$ ), but it should also be realized that the function mapping  $y_0$  on to  $\beta_k$  [i.e.,  $B(y_0) = \beta_k$ ], which corresponds to the *mechanism* of

adaptive response, is a further important basis for distinction. The model leaves many of these elements unanalyzed for, as Sommerhoff (1969) remarks, he is concerned primarily "with the general aspect of *what* a [goal-directed] system does and not *how* it does it" (p. 152). That is also our concern in this metatheoretical article. As remarked in Section I, we wish to motivate the asking of certain kinds of questions about learning by presenting the case for a particular, ecological account of *what* learning is. The answers to some of those questions will constitute putative accounts of *how* learning occurs.

The generality that is provided by this model is bought at the expense of certain restrictions on the account that we can give of particular kinds of adaptive response. The most important of these restrictions is that by accepting the generality of the model, we deny ourselves the option of setting up different forms of adaptive response, such as perception, learning, and evolution, as distinct categories, as phenomena *sui generis*, each to be accounted for on different principles. Instead our strategy must be to identify the various elements of the model in each instance of adaptation and to use the model to explicate the relationship among those elements. This does not mean that we see no important differences among the various forms of response, or that we see no opportunity for the separate development of theories of perception, of learning, and of evolution. We do not deny that important differences exist, particularly in regard to the mechanisms of response, but we claim that much is to be gained by seeking to construct theories of different forms of response that are closely compatible with each other.

The question may be raised whether the unified account at which we aim is an accurate reflection of reality. We believe that it is. If we take any temporal scale of description of the environment, from milliseconds to millenia, we observe that at each scale some aspects remain invariant while others vary. Insofar as these aspects of the environment describe an *ec niche* for some actor, adaptation to both variant and invariant features at all relevant scales of description must be achieved. Such adaptation cannot be achieved by incompatible processes operating at odds with one another; adaptation must be an integrated response by the entire biological system and it must be effected concurrently at all levels of biological organization. This integration of response is perhaps the most remarkable feature of biological systems and it is often obscured by the necessity of isolating particular responses for experimental examination. One of the major goals of biological and psychological theory must be to account not just for particular forms of response, isolated in the laboratory, but for the overall *unified* adaptation of the organism to its environment. Such a goal is more likely to be realized if a unified approach to the problems of

adaptation is adopted at the outset than if it is attempted only when several disparate theories have already established themselves.

Adopting a unified approach to the various forms of adaptation is consonant with an epistemological position that we might call "pragmatic realism" (see Shaw, Turvey, & Mace, in press). Adaptation, of whatever kind, is effective only if it works in some real environment. Consider the case of evolutionary adaptation: Evolutionary change works as an adaptive response only if it is a change in regard to some real feature of the environment actually inhabited by the animal. It would be absurd to maintain that natural selection effects adaptation to some *representation* of the environment and that this representation relates only equivocally to the real environment, yet this is the position adopted by the majority of current theories of short-term, perceptuomotor adaptation (see Section IV,B). A unified approach to adaptation requires us to eschew such disparate conceptual positions. Perception works as an adaptive response because it permits the coordination of action in regard to a real environment, not because it delivers an equivocal central representation of that environment. Similarly, learning works because it permits the development of effectivities that are supported by affordances in a real environment, not because it allows the animal to build an internal model of the world (whether of cognitive or of S-R elements). Section IV consists largely in an elaboration and defense of these assertions.

#### E. LEARNING AND ADAPTATION—AN OVERVIEW

Before passing on to a detailed consideration of adaptation over the long, short, and medium term, it may be as well to review briefly the vantage point that we have gained thus far with regard to an ecological account of learning.

Our first concern was to give a description of the ecosystem, the fundamental unit of ecological inquiry, and of the two components that comprise it: the actor and its econiche. Actor and econiche were seen to stand in a very intimate relation to one another; indeed, we argued that each must be defined *in terms of* the other. An ecological account of learning, on this view, would appear to be more concerned with relationships between actor and econiche than with either alone. More precisely, we argued that learning should be construed as a process defined over the entire ecosystem, rather than the animal alone in the style of traditional inquiry into learning. It becomes just as important, therefore, to analyze the ecological support for learning that is provided by the econiche as to analyze the biological support provided by the actor.

Given that the relation between actor and econiche is crucial to our

understanding of learning, our next step was to consider the nature of this relationship in more detail. Biologists have made use of the concept of adaptation in defining the animal-environment relationship and so an explication of this concept provided us with a useful starting point. Adaptation was analyzed in terms of the attainment of adaptive goals and it was pointed out that the appropriateness of the econiche for the attainment of such goals by the actor is as important an element of the whole process as is the adaptedness of the actor for such attainment. As already discussed, the presentation of Sommerhoff's formal model of adaptation provides us with a powerful logical tool for the analysis of particular instances of adaptation, including learning, and it is that task that we now turn.

#### IV. Adaptation on Three Time-Scales

The environment of any organism is a dynamic system, characterized by a multitude of ecological factors that change on innumerable time scales. In order to preserve its adaptive relationship with the environment, the organism must be able to adapt concurrently to all relevant scales of change in the environment. Only some such adaptive responses may reasonably be thought to fall in the domain of a theory of learning and in subsequent discussion we shall seek to characterize those responses in ways that are revealing of the kind of theory that will be required to account for them. We are mindful, however, of our broader aim of seeking a theory of learning that can ultimately stand as part of a general theory of the unified adaptive response of an organism to its environment. Our strategy will therefore be to compare and contrast learning with other forms of adaptive response in an attempt to uncover both important similarities and differences between them. Our aim will be, in the spirit of metatheoretical inquiry, to raise illuminating questions about learning that may be answered by some future ecological theory of learning.

##### A. LONG-TERM ADAPTATION—EVOLUTION BY NATURAL SELECTION

All biological individuals exist as members of more or less extended populations and it is in such populations that evolutionary adaptation is effected. The structure of the gene pool of the population, by which is meant the relative frequencies of different alleles, the distribution of pleiotropic effects, dominance relationships, and so forth, is determined by the nature of the selection pressures that have acted on the population in the course of its evolutionary history. We can perform a thought-

experiment in which a genetic population is placed in a situation in which there are no selective pressures acting on it. Under such circumstances the genetic constitution of the population is free to vary in a manner determined by the essentially random factors of mutation and drift. (For the sake of discussion, we will assume the population to be genetically isolated, ignoring the phenomena of migration.) A source of selection pressure, we might say, is some property of the environment that exerts a *constraint* on the free variation in the gene pool. This constraint is exerted because, given the environmental property of interest, some individuals reproduce more successfully than others. Reproductive success depends on the ability to attain the goal of self-reproduction and attaining this goal is, as we have argued (Section III,A), dependent on the ability to attain other adaptive goals that contribute to individual survival and eventual reproduction. Goal-attainment is a function of an individual's phenotype and so differences in reproductive success are attributable to phenotypic differences. A constraint on the free variation in the gene pool of a population, however, can be effected only if certain *genotypes* reproduce more successfully than others. Therefore it follows that natural selection can act in a population only to the extent that differences between genotypes are correlated with phenotypic differences in reproductive success.

In attempting to understand the adaptation of an animal to its environment, we must be concerned not only with its adaptation for reproduction but also with its adaptation for other adaptive goals, such as feeding, locomotion, orientation, and so forth. In order for adaptation in regard to feeding (for example) to be effected by natural selection, there must be a constraint on free variation in the gene pool such that those genotypes whose phenotypes develop the necessary feeding adaptations are reproductively more successful than other genotypes. This can occur only if possession of the adaptation(s) in question is correlated with greater reproductive success. Note that natural selection does not necessarily produce adaptations (Dobzhansky, 1942; Ghiselin, 1966, 1974; Lewontin, 1979; Williams, 1966): *Any* phenotypic characteristic that is correlated with greater reproductive success will be selected, whether or not it contributes to adaptation. Similarly, possession of a phenotypic adaptation is not in itself sufficient to guarantee natural selection in favor of those genotypes that develop such phenotypes: Possession of the adaptation must, in addition, be correlated with greater reproductive success. Our present concern, however, is with those instances in which natural selection does produce adaptation to the environment and with the proper analysis of such events.

We may now identify the elements of Sommerhoff's model of adapta-

tion in the preceding account of natural selection. For clarity, we will employ the following hypothetical, but quite realistic example: At time  $t_0$ , a food-limited population gains access to an area containing a new food source not found in its original range and, as a result of natural selection, becomes able to exploit this food source at some later time  $t_k$ . First, there is an environmental property ( $\phi$ ), namely, those characteristics of the food source relevant to its exploitation by the animal in question, that takes the value  $\phi_k$  at  $t_k$ . Second, there is a phenotypic characteristic ( $\beta$ ) of a population-typical individual (see footnote 2) that takes the value  $\beta_k$  at  $t_k$ . In this example,  $\beta$  might be some aspect of tooth structure and there is some value of  $\beta$  ( $\beta_k$ ) that enables an animal to penetrate a hard shell ( $\phi$ ) covering the new food source. The goal event  $G$  in this example is the ability of a population-typical individual to exploit the food source and  $G$  is attained when the focal condition  $F(\phi_k, \beta_k) = 0$  is satisfied.

The coenetic variable  $y_0$  in this case, as in most (if not all) cases of evolutionary adaptation, is the same as the environmental variable  $\phi$  to which adaptation is effected. Certain characteristics of the food source (its hard shell,  $\phi$ ) constrain free variation in the gene pool because those genotypes whose phenotypes develop values of  $\beta$  equal or close to  $\beta_k$  are reproductively more successful than other genotypes. If the characteristics of the food supply do not change over the course of the population's adaptation,<sup>4</sup> then the mapping function  $P(y_0) = \phi_k$  is the identity function (i.e.,  $y_0 = \phi_k$ ).

The response of the adapting system,  $B(y_0) = \beta_k$ , requires more extended analysis than we can provide in this article. As we have seen, the constraint provided by  $y_0$  is on the variation in the gene pool, expressed as differential reproduction among the genotypes that comprise it. But the characteristic  $\beta$  that enables the population-typical individual to exploit the new food supply is measured in the phenotype. The mapping function  $B$  is thus composed of two functions. The first of these ( $S$ ) we may call a *selective function*, which maps a constraint,  $y_0$ , on to a population-typical genotype ( $\Lambda$ ) at time  $t_k$ :

$$S(y_0) = \Lambda_k \quad (8)$$

The second function ( $E$ ) is an *epigenetic function* that maps the population-typical genotype on to a population-typical phenotype (charac-

<sup>4</sup>This is clearly a rather unrealistic assumption, since the population whose adaptation we are considering will itself exert selection pressure on the prey population, causing the latter to make an adaptive response in turn. These reciprocal effects are, however, too complex to permit their incorporation into this discussion. Nonreciprocal change in the environmental variable  $\phi$  is considered below.

terized by  $\beta$ , among many other features) in the course of individual development at  $t_k$ :

$$E(\Lambda_k) = \beta_k \quad (9)$$

The nature of functions such as  $S$  is fairly well understood and such functions figure prominently in population genetic theory (e.g., Lewontin, 1974). Functions such as  $E$ , on the other hand, are very poorly understood and hardly figure at all in contemporary evolutionary theory. A few authors have attempted to bring developmental considerations into evolutionary theory (e.g., Baldwin, 1902; DeBeer, 1958; Ho & Saunders, 1979; Løvtrup, 1974; Schmalhausen, 1949; Waddington, 1957; see Gould, 1977; Stearns, 1977), but these must be regarded as very preliminary steps. Lewontin (1974, pp. 12-16) provides a brief but insightful assessment of the shortcomings of current theory in this regard. Processes of learning are clearly involved in epigenetic functions and further discussion of this issue will be deferred to Section IV,C.

Finally, we come to the back-reference period,  $t_k - t_0$ . It will be recalled from previous discussion that the back-reference period is the operation lag of the adaptive mechanism. The precise back-reference period for the process of natural selection will vary depending on a number of factors, in particular the genetic variability of the population and the strength of the selection pressure exerted by  $y_0$ . If the genetic variance associated with the phenotypic character  $\beta$  is large, then selection may act rapidly to move the population-typical phenotype from  $\beta_0$  to  $\beta_k$ . Similarly, if the difference in reproductive fitness between  $\beta_0$  and  $\beta_k$  is high, producing strong selection pressure, then the population-typical phenotype may shift rapidly.

However rapidly natural selection is able to act, the back-reference period must be at least one generation time, since a change in the population-typical genotype can occur only between successive generations. Generally speaking, natural selection requires much longer than a single generation to effect any adaptive change in a population, often tens or hundreds of generations. The establishment of complex adaptations, such as those required for terrestrial locomotion or flight, may require very much longer periods of time (Frazzetta, 1975). The back-reference period of adaptation by natural selection will, for the sake of discussion, be assumed to be about  $10^2$  generations, give or take one order of magnitude.

The ability of natural selection to effect adaptation to any feature of the environment is limited by a number of factors. In the preceding example, the adapting population was subject to only one source of selection pressure but in all real situations, populations are subject to a constellation of



selection pressures, many of which may tend to operate in opposition to one another. The result is selection for the best available (i.e., reproductively most successful) adaptive compromise and the precision of adaptation that can be made to any one feature of the environment is therefore limited by the adaptive demands of other features. Other limitations include the lack of appropriate genetic variation, the influence of pleiotropic and correlated growth effects, and insufficiently strong selection pressure. We cannot discuss these limitations in detail but they constitute an important and often overlooked aspect of evolutionary adaptation (see Darwin, 1859; Dobzhansky, 1942; Ghiselin, 1966; Gould & Lewontin, 1979; Lewontin, 1979; Williams, 1966).

For our present purposes, the most important limitation of natural selection as a mode of adaptation to the environment lies in its very long back-reference period. The preceding example envisaged a change in the environment from one invariant state (absence of the food source) to another (presence of the food source). Unless other limitations (see above) are in effect, adaptation to this new environmental feature may clearly be achieved through natural selection, since there will be continual selection in favor of phenotypes close to  $\beta_k$  until the population-typical phenotype equals  $\beta_k$  and the focal condition is satisfied. If the environmental variable  $\phi$  changes in the interval  $t_0 - t_k$ , then it appears that the focal condition  $F(\phi_k, \beta_k) = 0$  will never be satisfied and that adaptation cannot be attained until  $\phi$  reaches some stable value.

A moment's reflection shows that one reason for this implausible conclusion is that the focal condition defines too strict a criterion for most real examples of adaptation. In firing a gun at a target (a simple example of goal-directedness) a hit may be scored within some small but finite area around the center of the target. If we designate a hit on the exact center as satisfying the focal condition  $F(\phi_k, \beta_k) = 0$ , then a hit on the target may still be scored provided the focal condition  $F(\phi_k, \beta_k) \pm d = 0$  is satisfied, where  $d$  (the *tolerance* of the focal condition) corresponds to a small area close to the target's center. In a similar vein, there will usually be some range of values of an animal's phenotype close to  $\beta_k$  that permits the adaptive goal (i.e., feeding on a new food source) to be attained. This is true for almost all examples of biological adaptation but to simplify notation and discussion we will omit further reference to the tolerance of the focal condition. Tolerance is a quantitative rather than a qualitative addition to the model and its detailed consideration lies outside the scope of our analysis.

We see, then, that natural selection may effect adaptation to environmental variables that are either invariant or that change only slowly in relation to the generation time of the adapting population. Note that the

invariance in question may be an invariant *pattern* of change in the environment. Light intensity, for example, changes on a rapid, diurnal cycle but since the pattern of diurnal change remains invariant, natural selection may effect adaptation to this pattern.

Where the relation between the coenetic variable  $y_0$  and the environmental variable  $\phi_k$  is such that the mapping function  $P(y_0) = \phi_k$  is indeterminate (corresponding to rapid variation in  $\phi$  over a back-reference period on the order of  $10^2$  generations), natural selection will be ineffective in producing the requisite adaptation. In each generation there will be selection in regard to  $\phi$ , but the constraint imposed on free genetic variation will change irregularly with the value of  $\phi$ . Over periods of time comparable to a back-reference period of  $10^2$  generations, there will be only stochastic genetic change in regard to the phenotypic variable  $\beta$ . Adaptation to a rapidly changing environmental variable can be effected only by an adaptive mechanism with a back-reference period comparable to the time-scale of the change. We turn now to consider two such mechanisms.

## B. SHORT-TERM ADAPTATION—COORDINATION OF PERCEPTION AND ACTION

Let us first of all consider situations in which the back-reference period of adaptation is brief—on the order of seconds or minutes (see Table I). Such situations comprise almost all of the day-to-day interactions of animals and their environments and so occupy a prominent position in any unified account of adaptation. To illustrate: A person sitting with arms resting on a desk top cluttered with books and papers adjusts the posture of the body in general, and of the arms in particular, to reach for, grasp, and retrieve a book from beneath a pile of papers toward one edge of the desk. Such short-term adaptations have been the focus of considerable analysis in philosophy and psychology; they subsume what are commonly called “perceptions” and “actions.”

### 1. *The Phenomenalist Tradition*

What we intend in this section is to review briefly (but, we hope, adequately) the epistemological issues to which the study of short-term adaptation is heir. Those issues reduce fundamentally to one question: Are the objects of an animal's perception, with reference to which it behaves, the same as the objects of the animal's environment? The weight of argument over the centuries has tended to be that they are not—that the

objects of perception and the objects of the environment are in fact quite distinct. The British philosopher, John Locke, for example, argued that there is an environment that exists independently of the perceiver, who is linked to that environment by means of "ideas"; these ideas, which in some but not all cases represent actual properties of the environment, constitute those things of which the perceiver is directly aware. Locke's "ideas" might be termed "between things" for he intended them as entities that intervene between, or coordinate, the animal and its environment. The traditional generic term for a "between thing" in philosophy is a "phenomenal object," of which some specific contemporary examples are representations, models, reference signals, propositions, and schemata. The term "phenomenalism," therefore, applies to those interpretations of perception in which phenomenal objects, not environmental objects, are what an animal directly experiences and with respect to which it directs its behavior.

Phenomenalist interpretations of perception are of two kinds: those that deny the existence of any but phenomenal objects; and those that admit both phenomenal and environmental objects but claim that only phenomenal objects are involved in the coordination of perception and action. The former view, whose foremost proponents were Berkeley and Hume, has held little attraction for psychologists—it would be a strange science of behavior that attempted to explain adaptation to a nonexistent environment! The latter view, which might be more judiciously termed representative or *indirect realism* (see Cornman, 1975; Mundle, 1971), has, however, been the staple philosophical diet for much of psychology, sensory physiology, and cognitive science. This Lockean view of perception has two major themes: first, that there are environmental objects that exist unperceived and that are unaffected by being perceived (hence "realism"); second, that such environmental objects are not perceived directly but only through the agency of phenomenal objects or "between things" (hence "indirect").

The indirect realist's account of perception distinguishes between what an object *is* (in itself) and what that object *means* (to an animal). A description of what an object *is* is given in conventional physical terms (such as mass, length, velocity, etc.); such a description is not specific to any particular animal and so it is not a description of what the object *means*. An animal behaves with respect to objects in its environment in terms of what they mean for it, however, rather than what they are as crass physical entities, and conventionally it is supposed that the animal ascribes meaning to the physical description of its environment. In other words, the animal interprets the physical description of an object, producing thereby a different

kind of (phenomenal) object, describable in terms that are animal-relevant and with respect to which it can behave adaptively.

If we consider the phenomenalist interpretation of perception in terms of Sommerhoff's (1950, 1969) formal model, we see that it yields a most curious account of adaptation over the short term. Under this interpretation, the environmental term,  $\phi_k$ , in the focal condition,  $F(\phi_k, \beta_k) = 0$ , refers to an extraordinary (in the sense of nonreal) property, one that is attributed by the animal to its environment and hence that does not persist unperceived. To illustrate this phenomenalist interpretation, take the case of an animal traversing natural terrain. As the animal encounters obstacles to locomotion and configurations of surfaces that necessitate jumping over, climbing over, or going around, it must adjust its locomotor behavior accordingly. The animal traverses those surface configurations that can support its locomotor activity and skirts those that cannot. It steers through openings that are large enough and around those that are too small. The animal's adaptive acts are with reference to environmental properties such as jump-over-able, walk-on-able, and run-through-able. Yet the time-honored theories of perception, buttressed by the hypostatizing of the basic variables of physics, inform us that such properties are phenomenal rather than real. In short, and this is the larger point, under a phenomenalist interpretation of perception some of the variables over which the focal condition is defined are *not real variables*. The implications of this point for the explanatory scope of contemporary cognitive science have not gone unremarked. Fodor (in press), for one, has argued cogently (and unregretfully) that the current and traditionally popular phenomenalist approach to the knowings of man and animals is a "methodological solipsism" and that questions of what these knowings refer to are beyond its purview.

## 2. *The Ecological Alternative*

The outcome of the phenomenalist tradition, at all events, is that it leads to a nonunified view of adaptation. The account of long-term, evolutionary adaptation, if it is to be at all sensible, must be given in a vocabulary of real terms on both the animal and environment sides. The account of short-term adaptation, as conventionally construed, is, as we have seen, given only partially in real terms. The conclusion to be drawn, therefore, is that adaptation over the short term is radically different in kind from adaptation over the long term, requiring analysis as a separate phenomenon, *sui generis*. On the phenomenalist view, then, whereas the focal condition of long-term adaptation may be written as  $F(\phi_k, \beta_k) = 0$ , that of short-term adaptation is to be written as  $F(\psi_k, \beta_k) = 0$ , where  $\psi_k$

is in the codomain of some function  $M(\phi_k)$ . The function  $M$  is construed as a psychological operator that translates meaningless animal-neutral descriptions (such as  $\phi_k$ ) into meaningful animal-relevant ones (such as  $\psi_k$ ). This proliferation of variables is not in itself overly disturbing; what is disturbing is that the additional variable  $\psi_k$  is ontologically distinct—it is nonreal, or phenomenal. In order to reconcile adaptation over the long and short terms and to establish a unified account of adaptation, we must eliminate from the focal condition variables of the type  $\psi_k$ .

It is not difficult to see that phenomenalism follows in large part from assuming the independence of animal and environment (see Fig. 1) and adopting an interactional style of inquiry. If the animal term and the environment term are logically independent then a third term (the phenomenal object,  $\psi_k$ ) must be introduced to coordinate the two. The ecological perspective, adopting a transactional style of inquiry, produces a different outcome. As argued at length elsewhere (Shaw & Turvey, in press; Shaw *et al.*, in press; Turvey & Shaw, 1979) and as outlined in Section II,C, the ecological perspective assumes a logical dependence of animal and environment, a dependence that is reflected in the account that we have given of the relation between the actor and its econiche. Because these two terms are mutually dependent, there is no encouragement for a third class of terms to bind them together.

It is here in particular, in eliminating the need for mediation between animal and environment, that the concept of affordance becomes especially significant. As we have said (Section II,A,2), an affordance is some property of an environment taken with reference to an actor; it is thus an animal-relevant property, a component of an econiche, but it is not a phenomenal object. It does not come into and go out of existence with fluctuations in an animal's needs and abilities. An affordance is a *real* property of an environment but it is a part of ecological, not physical, reality (see Gibson, 1977, 1979; Shaw & Turvey, in press; Shaw *et al.*, in press; Turvey & Shaw, 1979). If, then, we describe the environment in animal-relevant terms, we accomplish two things. First, we dispense with the need for mediation between animal and environment by considering instead mutually defined actors and econiches. Second, we preserve the unity of our account of adaptation by defining the focal condition of adaptation over a real environmental variable, an affordance.

### 3. *Describing the Environment—Dimensions of Ecological Physics*

In brief summary, casting our account of short-term adaptation in terms of affordances allows us to replace the nonreal variable  $\psi_k$  by a real

variable, an affordance,  $\phi_k$ . It will be clear from the foregoing discussion that this latter variable is not the same as the physical variable from which  $\psi_k$  was derived by the psychological operator  $M$  [i.e., by the function  $M(\phi_k) = \psi_k$ ]. To illustrate the distinction, consider the notion of distance, a property that animals perceive and in regard to which they regulate their behavior. In conventional analyses of perception, "distance" is an animal-neutral dimension, measured in some standard, universal metric, such as feet or meters. On such an analysis, the physical distance ( $\phi_k$ ) between an animal and an object is translated into the phenomenal variable  $\psi_k$  by the function  $M$ ;  $\psi_k$  is what the distance  $\phi_k$  means to the animal in the present context (for example, whether the object is reachable and, if so, how much force is needed to propel the body to it). On the ecological analysis, "distance" is an ecosystem dimension, measured in an animal-relevant metric that is defined by the behavioral capabilities, the effectivities, of the actor. Hence the perception of "distance" and the perception of "the behavioral implication of distance" are one and the same.

The nature of distance as an ecological dimension is illustrated by the behavioral relation between a predator and its prey. (This discussion is owing to T. Alley, personal communication, August 1979.) A predator must be able to perceive the maximum distance between itself and a prey animal at which a pursuit can be successfully initiated; and a prey animal must be able to perceive the minimum separation, a "margin of safety," beyond which it need not make defensive or flight maneuvers with reference to a predator. These "distances" are defined, not in reference to an arbitrary metric (such as feet or meters), but in reference to the effectivities of the animals involved and what the current terrain affords them in the way of pursuit and evasive behavior, respectively.

Let us now elaborate this point further with respect to two examples of the coordination of perception and action, basing our analysis on Sommerhoff's formal model of adaptation.

*a. Prey Capture by the Praying Mantis.* During postlarval growth, the praying mantis goes through several ecdyses (shedding of the exoskeleton), each ecdysis being followed by a rapid growth spurt, after which the exoskeleton hardens again. Each of these developmental stages is called an instar. In each instar, the mantis strikes at prey only within a maximum catching distance (MCD) which bears a definite relation to the maximum extension of the forelimbs (Balderrama & Maldonado, 1973). Striking at prey outside the MCD is presumably wasteful of time and energy and may alert other prey to the mantis' presence, or reveal the mantis to its own predators. In this instance of short-term adaptation, the goal ( $G$ ) is to strike only at catchable prey and for convenience we may assign the following values to  $\phi_k$  and  $\beta_k$ :

$\phi_k = 1$  if mantis-prey distance  $\leq$  MCD and 0 otherwise;  
 $\beta_k = 1$  if the response is to strike and 0 otherwise.

Then the focal condition may be written as:

$$\phi_k - \beta_k = 0 \quad (10)$$

and  $G$  is attained when this condition is satisfied. Since the MCD changes with each ecdysis, the question arises how the mantis is able repeatedly to attain  $G$  throughout development, as it passes through the successive instars. Answering this question amounts to identifying the coenetic variable,  $y_0$ , that maps on to an adaptive response  $\beta_k$ , regardless of the current MCD.

Maldonado, Rodriguez, and Balderrama (1974) argue that at each instar, perception of the distance between the mantis and its prey is based on a triangulation system involving three dimensions of the head: the head breadth (HB), the ocular globe breadth (OGB), and the ocular prominence (OP). The coenetic variable is thus some function  $D$  of these three variables:  $y_0 = D(\text{HB}, \text{OGB}, \text{OP})$ . During postlarval growth, these head dimensions maintain a constant relation to the MCD so that *perceptions of distance that are based on them are automatically scaled to the growing animal's behavioral capabilities*. In short, perception of the distance to the prey animal and perception of what that distance means behaviorally are one and the same. This direct adaptive relationship between the mantis' behavior ( $\beta_k$ ) and its environment ( $\phi_k$ ) is made possible by the involvement of a coenetic variable that describes the environment in terms of the capabilities of the perceiver.

*b. Host Tree Location Behavior in a Tropical Vine.* Our second example of short-term adaptation is drawn from the plant rather than the animal kingdom. We have selected this example because it demonstrates with particular clarity the importance of analyzing adaptation in terms of the actor and its econiche, rather than in terms of the animal (or plant) alone. It also illustrates the wide range of phenomena that may be embraced by the unified approach to problems of adaptation that we have adopted. Strong and Ray (1975) have described an interesting pattern of behavior in *Monstera gigantea*, an arboreal tropical vine whose seeds germinate on the ground after falling from the parent plant. Immediately following germination, the seedling grows toward the nearest tree and, after making contact, loses its roots as it ascends the trunk. Here we have an instance of adaptation in which the direction of growth ( $\beta_k$ ) is adapted to the bearing of the nearest tree ( $\phi_k$ ), enabling the plant to contact the trunk ( $G$ ) and complete its life cycle as a mature, arboreal plant. The focal condition is satisfied when the plant grows toward the tree (i.e., when  $\phi_k - \beta_k = 0$ ).

In analyzing this instance of adaptation we seek to characterize the coenetic variable,  $y_0$ , and the function,  $B(y_0) = \beta_k$ , that effects a response adapted to  $\phi_k$ . Strong and Ray (1975) demonstrated experimentally that the seedling's behavior is an example of positive skototropism, a positive growth response toward darkness: A seedling always grows toward the darkest sector of its horizon. The nature of the response function  $B$  remains to be elucidated but, by analogy with other instances of plant tropisms (Bell, 1959), we might suppose that it involves the differential transport of auxins (plant growth hormones) to or from various points on the circumference of the seedling.

In the plant's natural environment, a physical description of the environment would define  $\phi_k$  as "bearing of nearest tree." However, adaptation is effected not in relation to the tree as a physical (i.e., organism-neutral) object but rather as an object that affords climbing for the plant. Adaptation could not be effected if we were to populate the plant's environment with objects that, while conforming to the *physical* description of a tree, did not conform (perhaps because of their surface properties) to the *ecological* description of a climbable object (climbable, that is, by the plant). It is only by carrying out the analysis in respect to the integrated ecosystem, in which actor and econiche are inseparable and defined in terms of each other, that the adaptiveness of this behavior can be understood; and this requires that our descriptions be given in ecological, not physical dimensions.

An understanding of the adaptiveness of the response to the coenetic variable likewise requires that we adopt an ecological description of the plant's environment. Under a physical description of the environment, the darkest sector on the plant's horizon yields "bearing of lowest light intensity" and light intensities do not, of course, support climbing. Under an ecological description, however, the darkest sector yields "bearing of nearest tree" (more precisely, "nearest climbable object") which does support climbing. In the terms of Sommerhoff's model, the ecological description may be given as  $P(y_0) = \phi_k$ ,  $P$  being an ecological function, mapping dark sectors on to climbable objects. Once again, we could populate the plant's environment with objects whose properties were such that dark sectors no longer mapped on to climbable objects. Strong and Ray (1975) accomplished this by using the open ends of opaque tubes to produce dark sectors on the plant's horizon. In this situation, the physical description of the environment as an array of light intensities is preserved but the ecological description has been changed because the mapping function  $P$  no longer holds. Not surprisingly, the plant's response is now found to be nonadaptive and it grows into the open end of the nearest



tube. (This response, incidentally, provides an interesting demonstration of an optical illusion in this species.) We see, then, that the adaptive relationship between the plant's behavior and its environment can be discerned only by adopting an ecological scale of description and respecting the mutual dependence of the actor and its *ec niche*.

#### 4. *The Adaptive Response to Environmental Structure*

It has become common practice, in many contemporary discussions of short-term, perceptuomotor adaptation, to speak of a plan or program that controls an organism's behavior with respect to perceptually delivered information about the environment (see Miller, Galanter, & Pribram, 1960; Turvey, 1977a). Such an entity is one variety of phenomenal object that mediates between the animal and its environment on the output rather than the input side of perceptuomotor adaptation. Like the phenomenal objects of perception, the motor program threatens the unity of our account of adaptation by its implication of additional nonreal variables in the focal condition of adaptation. In conventional terms, a program is a nonreal, phenomenal object created by the organism to stand in an adaptive relationship with the environment and so permit the adaptive control of behavior.

The status of a program in the phenomenalist account of behavior is that of an explicit, *a priori* description of the orderliness or adaptiveness of behavior. There are two possible ways to view the process by which this description might serve to control behavior. One is to view it as a recipe that is followed by some executive component of the system that directly controls the animal's behavior, in much the same way that one might follow a set of instructions for building a boat. The obvious drawback to this view is that it replaces one problem (accounting for the animal's ability to behave adaptively) with another (accounting for the executive's ability to follow instructions) that inherits all of the logical and psychological problems of the first and so initiates the first step in an infinite regress. The second and less objectionable way is to view the program as being intrinsic to the structure of the behaving animal and as being implicitly rather than explicitly followed.

Cummins (1977) has pointed out that this strategy, which is adopted by most proponents of the metaphor of a motor program or action plan, leaves little or no room for distinction between the structure of the program and that of the system that, by appearances, is executing it. He points out that, on this view, the program is simply a description of those aspects of the structure of the animal that enable it to behave adaptively.

This argument eliminates the program as an explanatory entity, as an a priori prescription for the system, and reconstrues it as an a posteriori description of the system.

The structure of the animal alone, however, cannot guarantee the adaptiveness of behavior for, as we saw earlier (Section III, A), adaptation is a *relation* between the actor and its econiche. To account for the adaptiveness of behavior, we must therefore describe the animal's structure in terms of its environment. Such a description is provided by the response function in Sommerhoff's model, which maps the coenetic variable of adaptation on to a behavioral variable:  $B(y_0) = \beta_k$ . The form of this function is defined by the constitution or structure of the animal and it provides a description of that structure with respect to the environment, that is, with respect to the coenetic variable,  $y_0$ .

Let us then construe the concept of a "program" as an environment-relevant description of the animal that is provided by the function  $B(y_0) = \beta_k$ . On this account, perceptuomotor adaptation does not involve the coordination of the animal and its environment through the agency of phenomenal objects. Rather, it involves a *direct adaptive response* to environmental structure ( $y_0$ ) that constrains the animal's behavior to some particular response,  $\beta_k$ ; this constraint is adaptive when the focal condition,  $F(\phi_k, \beta_k) = 0$ , is satisfied. In the case of the tropical vine *Monstera gigantea*, the directness of the adaptive response is revealed with particular clarity, because of the simplicity of the adaptive system. The plant's perception of its environment (in particular, of the bearing of the nearest tree) is based, let us say, on the differential transport of auxins around the circumference of the stem. But this is also the means by which the plant effects an adaptive response to the layout of the environment, growing in the direction of the nearest tree. We may say, therefore, that the short-term adaptive response is effected by a constraint, specific to the layout of the environment, on the plant's behavior (direction of growth) and that this constraint arises as a direct response to perceived environmental structure.

In the case of more complex organisms, the directness of the adaptive response is obscured by the elaborate physiological support required for its implementation. The response function nonetheless provides a formal, albeit abbreviated description of those aspects of the organism's structure whose sensitivity to the coenetic variable ( $y_0$ ) produces a response ( $\beta_k$ ) over the back-reference period of adaptation. Let us adopt the term "perception/action system" to refer to the relevant aspects of organismic structure. [For further discussion of this and related concepts, see Fitch and Turvey (1979), Fowler (1977), Johnston (1978), Turvey (1977a), and Turvey, Shaw, and Mace (1978).] The perception/action system may be

in any of an indefinite number of states and the state of the system determines the current behavioral performance ( $\beta_k$ ) of the organism (e.g., striking or not striking at a prey, or growing in any one of an indefinite number of directions). The value of  $\beta_k$  thus reflects a constraint on the state of the system that is specific to the coenetic variable  $y_0$  and that is adaptive when the focal condition is satisfied.

While the *state* of the system (specific to  $\beta_k$ ) is relatively transient, being specific to the organism's current perception of its environment, the *structure* of the system, as described by the response function,  $B(y_0) = \beta_k$ , is relatively more enduring. This structure arises in the course of individual development and it is here, in the epigenetic processes that constrain the course of development, that we encounter the subject matter for the study of learning.

### C. MEDIUM-TERM ADAPTATION—LEARNING

In preparation for our discussion of learning as a form of adaptation over the medium term, let us briefly review the story we have told thus far of the nature of adaptive response to the environment. On both the long and the short terms, we spoke of constraints, specific to certain features of the environment, arising in the course of adaptation. In the case of evolutionary adaptation over the long term, constraints arise on free genetic variation in the gene pool that are specific to slowly changing features of the environment, essentially invariant over periods of time comparable to the life span of an individual. In the case of perceptuomotor adaptation over the short term, the constraints are specific to much more rapidly varying features of the environment, in particular to the affordances whose availability changes over time as the animal moves about.

On both the long and the short term, constraints arise as a direct adaptive response to environmental structure. In evolutionary adaptation, they do so by virtue of a sensitivity of the gene pool to sustained selection pressure, a sensitivity that is expressed as the differential reproduction of genotypes. In perceptuomotor adaptation, they arise by virtue of a sensitivity of the perception/action system to information in the form of structured energy (such as light and sound), a sensitivity that is expressed as a modification of the state of the system, hence in the form of the actions that it specifies. It is neither remarkable nor problematical to speak of the adaptive response of the gene pool as direct. No theory of indirect evolutionary adaptation (in which a representation of the environment is constructed, the adaptive response being specific to that representation) has ever been proposed; indeed, it is hard to see what might be meant by an indirect response in the context of evolutionary adaptation.

Theories of indirect perception, on the other hand, are commonplace in psychology but we have argued for a theory of direct perception, a position commensurate with our earlier arguments (Section III,D) in favor of a unified theory of biological adaptation.

Our approach is consonant with a philosophical position that we have called "pragmatic realism," and this position will guide our inquiry into the medium-term adaptation provided by learning. Particular environments place particular adaptive demands on the animals that live in them. Natural selection ensures that those individuals that effect pragmatically successful responses to those demands, responses that ensure survival and eventual reproduction, will come to be typical of the population. Insofar as such responses entail adaptation to certain rapidly varying aspects of the environment, then perceptual abilities will evolve that are specific to those aspects of the *particular* environment in which the population is evolving.

Standing between the long-term constraints on the gene pool effected by natural selection and the short-term constraints on the state of the action system effected by perception is a set of constraints that arise as a result of relatively prolonged epigenetic processes. Some of these medium-term constraints reflect adaptive responses of the kind that we would wish to identify as learning and the account of learning that we will give parallels those already given for adaptation on both shorter and longer time-scales. We will argue that learning, like the other forms of adaptation we have been discussing, is a direct adaptive response, in this case to aspects of the environment that change over periods of time that are short in comparison with evolutionary time-scales but long in comparison with the events of perception. Furthermore, the learning abilities that are typical of a population are those that are "pragmatically successful" in the particular environment in which the population evolves. Our account of learning will be guided by these two principles of direct adaptation and pragmatic realism.

An ecological account of learning as a direct adaptive response to a particular environment faces two central problems. First, it must provide an appropriate description of the environment that is being adapted to. In the terms of Sommerhoff's (1950) model, this means identifying the environmental variable ( $\phi$ ) to which adaptation is effected, the coenetic variable ( $y$ ), and the mapping function [ $P(y_0) = \phi_k$ ] that relates the two over the back-reference period of adaptation,  $t_k - t_0$ . Second, it must provide an account of the adaptive response that the animal makes to the coenetic variable, identifying the phenotypic basis of adaptation ( $\beta$ ) and defining the mapping function [ $B(y_0) = \beta_k$ ] that is implemented by the adaptive response.

## 1. Describing the Environmental Support for Learning

The current, nonecological approaches to the study of animal learning adopt a very different attitude toward the problem of environmental description than does the ecological approach. In the associationist account of learning (which still largely dominates current thinking in the field; see Jenkins, 1979) the environment is seen as an array of stimuli and, in some versions, of reinforcers. The concept of stimulus in such theories is entirely nonecological and its definition is not specific to any particular organism. Anything to which an animal can be persuaded to respond by an experimenter counts as a stimulus in association theory. An ecological approach to learning, however, must treat the problem of environmental description quite differently and indeed must accept it as a significant component of the overall research endeavour.

In discussing the structure of the ecosystem in Section II,B, we argued that the *ecoiniche* is a description of the environment taken with respect to some actor. Specifically, it is a description of the ecological support for behavior and in the preceding discussion of perception we showed how this support may be exploited by a suitably attuned actor. In the same manner, we now argue that an ecological approach to learning must begin with a description of the ecological support that an environment provides for a suitably attuned learner. Such a description cannot be phrased in animal-neutral terms. Animals become attuned, in the course of evolution, to particular aspects of environmental structure that support learning. They evolve the particular attunements (i.e., learning abilities) that they do because such adaptations are pragmatically successful in the environment in which the population has evolved. To the extent that relevant aspects of environmental structure are unique to particular ecosystems, then we expect to find specialized learning abilities, limited to one or a few species. To the extent that these aspects of structure characterize many ecosystems, then we may expect to find large numbers of species attuned to them. Any animal's learning abilities, however, are collectively a complex adaptation to *particular* aspects of environmental structure, namely, those that characterize its particular ecosystem, whether these are of widespread or restricted occurrence. An ecological account of learning requires a description of environmental structure as an integral part.

The ecological support for learning referred to in the preceding paragraph is, of course, the coenetic variable of adaptation (Sommerhoff, 1950). It is that aspect of the environment to which the adaptive response is made and that therefore provides the ecological support for the learning ability in question. In many cases of learning the coenetic variable will be

the same as the environmental variable ( $\phi$ ) to which adaptation is effected as a result of learning. This will not necessarily be the case however and in Section V we discuss some instances of learning in which  $y$  and  $\phi$  are different variables; that is, adaptation to one aspect of the environment ( $\phi$ ) is effected by virtue of a developmental sensitivity to some other aspect ( $y$ ).

It is perhaps worth stating explicitly that the description of  $y$  and  $\phi$  is an empirical problem that can be solved only by studying particular environments in relation to the particular animals that live in them. No general answer can be given to the question "What constitutes the environmental support for learning?" This question must be posed separately for each instance of medium-term adaptation in a specific ecosystem, and answered on the basis of empirical investigation. We can, however, offer some general considerations to guide such investigation.

In our discussion of evolutionary adaptation in Section IV,A, we pointed out that long-term adaptive responses are effective only in regard to slowly changing features of the environment. Suppose that we were interested in the evolutionary response of a population to change in environmental temperature. We can describe change in temperature at any number of "grains of analysis" (Fitch & Turvey, 1979), from the very small, moment-to-moment changes that are produced by wind currents and shadows, to the very gradual shifts in mean annual or decadal temperature that are produced by climatic changes operating over continental expanses. If, in searching for the coenetic variable of evolutionary adaptation to temperature (that is, the ecological support for this form of adaptive response), we focused on the microclimatic changes in temperature to be found at a very fine grain of analysis of the environment, one of two situations might arise. In the first place, we might fail altogether to detect the gradual changes in temperature that support evolutionary adaptation—a case of being unable to see the forest for the trees. On the other hand, we might detect the gradual changes by recording very many small changes in temperature and integrating these over long periods of time. In the latter case, we would then be faced with the problem of explaining how the adapting population performs an analogous integrating operation, identifying the nature and location of the computational machinery, and how it produces an adaptive response based on the outcome of this integration. Evidently, this is an artificial problem that arises because we have adopted an inappropriately fine grain of analysis of the environment. It is only when we provide a description at a coarser grain of analysis, appropriate to the long-term nature of evolutionary change, that we detect the gradual shifts in temperature that provide the ecological support for a direct adaptive response, unmediated by any form of integration.

In searching for the ecological support for medium-term processes of adaptation such as learning, we must adopt a similar strategy of focusing at an appropriate, intermediate grain of analysis. This same strategy has been proposed by Humphrey (1933) in a remarkable and neglected book, *On the Nature of Learning*. Humphrey pointed out that an animal may respond adaptively to a wide range of environmental events (or aspects of structure), some of which are of very brief duration, others much more prolonged. He suggested, as we have done, that the attempt should be made to account for all such adaptive responses under the same theoretical rubric, rather than treating each one as a phenomenon *sui generis*. In pursuit of this aim, we must describe the ecological support for each form of adaptation at an appropriately fine or coarse grain of analysis. If our description of the environment is provided at too fine a grain, then we may either fail to detect the ecological support for learning, or we may be forced to postulate constructs such as memory and associations to mediate between the apparently unconnected elements of our description. If, on the other hand, we seek a coarser grain of description of the environment, one that is more appropriate to the medium-term adaptive response of learning, the need for such constructs may well not arise. In that case, we shall have uncovered the ecological support for learning as a direct adaptive response. In Section V, we will discuss some examples of learning that meet these expectations.

Note the similarity between this orientation to the problem of learning and that of Gibson (1966) toward the problem of perception. Gibson's program was initiated with the claim (Gibson, 1950) that far greater environmental support for perception could be discovered than had previously seemed to be the case. Rather than postulating epistemic mediation (Turvey, 1977b) to account for the elaboration of impoverished sensory data into richly structured perceptual experience, Gibson claimed that the environment itself provides a source of richly structured stimulative energy, to which an appropriately attuned perceiver might respond. Uncovering this structure, however, requires that an appropriate style of description be employed, one that focuses at a suitably coarse grain of analysis (Fitch & Turvey, 1979). We claim, together with Humphrey (1933), that the need for epistemic mediation in learning might likewise be eliminated if we were but to employ appropriate descriptions of the situations in which such adaptive responses occur.

## 2. *The Adaptive Response to Environmental Structure*

In Section III,A we pointed out that the response function involved in evolutionary adaptation [ $B(y_0) = \beta_k$ ] may be resolved into two functions: a selective function [ $S(y_0) = \Lambda_k$ ], which maps the coenetic variable

(selective pressure) at  $t_0$  on to a population-typical genotype at  $t_k$ ; and an epigenetic function [ $E(\Lambda_k) = \beta_k$ ], which maps the genotype on to a population-typical phenotype. In that discussion, the epigenetic function was implicitly assumed to operate instantaneously at  $t_k$ . In fact, this function is itself composed of a number of adaptive processes, with back-reference periods covering the life span of the individual, some of which fall in the domain of an ecological theory of learning. In this section we will consider the nature of the medium-term adaptive responses that implement the epigenetic function. We will continue to use the notation of Sommerhoff's model and the reader should note that, for the remainder of this section, the variables of this notation ( $y_0, t_0, t_k, \beta_k$ , etc.) will apply to the medium-term adaptive responses of learning, unless explicit mention to the contrary is made.

The epigenetic view of development is widespread among modern students of development and is associated especially with the names of Kuo (1967), Lehrman (1953), Schneirla (1956, 1965), and Waddington (1957). Our presentation will be brief and is intended to provide a basis for our account of learning, not as a comprehensive treatment of the issues. The developing organism is subject to two sets of constraints that mutually determine its organization; one of these sets originates in the genome, the other in the environment. The genetic constraints specify what we might call a "life-strategy" for the individual, to which the environmental constraints provide a set of tactical modifications. In some respects, the genetic strategy may be quite strictly defined, providing what Waddington (1957) calls strongly canalized development, relatively insensitive to the nature of the environment. In other respects, the genetic strategy may be less tightly constraining, permitting the nature of the individual's experience to play an important role in determining the course of development. In the latter case, Waddington (1957) speaks of weakly canalized development, the extent of canalization being, of course, a matter of degree.

The development of a particular phenotypic character may, if it is relatively weakly canalized, be sensitive to only a very narrow range of environmental input. For example, isolating the young of many species of songbirds early in life results in a form of adult song that is quite differently structured from the song of conspecifics that have received exposure to an adult song model as youngsters (Marler & Mundinger, 1971; Nottebohm, 1970). In some species, development of normal song organization results only from exposure to conspecific song (i.e., only the species-typical song will be learned), whereas in other species a much wider range of songs will be accepted as song models. Thus while song development in many species is relatively weakly canalized (since song



and no-song experience lead to different phenotypic outcomes in adulthood), the selectivity of the developmental response may be much greater in some cases than in others.

Insofar as the question of the selectivity of developmental responsiveness is concerned only with the degree of potential developmental plasticity, it is not an issue of primary concern for the ecological study of learning (see Gottlieb, 1976, for an expression of a similar point of view). We are more concerned with the individual's adaptive response to the *typical* environment of development, although its response to atypical, experimental environments (as in the selective deprivation or selective exposure experiment) may clearly make an important contribution to our understanding of the former. The question of primary interest as regards plasticity is therefore whether an animal will respond to any of a range of experiences (i.e., values of  $y_0$ ) *typically* encountered in development, or to only one or a few of these experiences. This emphasis follows directly from our identification of the ecosystem (i.e., an actor and its niche) as the unit of inquiry, rather than the animal, considered in isolation.

Let us suppose, then, that under normal (i.e., species-typical) circumstances, the individual develops some phenotypic character ( $\beta$ ) such as the species-typical song of an adult songbird. At some particular time in development ( $t_k$ ) the organization of the character ( $\beta_k$ ) is such that a focal condition [ $F(\phi_k, \beta_k) = 0$ ] is satisfied and some adaptive goal ( $G$ ), such as the acquisition of a mate by a vocally competent male bird, can be attained. In this example,  $\phi_k$  might be the tendency of conspecific females to mate with a singing male. If this is an example of medium-term adaptation, then it will be possible to identify a coenetic variable ( $y_0$ ) and a response function [ $B(y_0) = \beta_k$ ] that maps the coenetic variable on to the phenotypic character at  $t_k$ . In the example of song development, the coenetic variable is exposure, early in life, to an adult song model.

The function  $B$  covers a multitude of important issues concerning the mechanisms of adaptation that cannot be properly addressed in this article; we will, however, discuss some of them briefly. First, many instances of medium-term adaptation can be effected only, or best, during a restricted portion of the individual's lifetime, generally in early life. For example, white-crowned sparrows (*Zonotrichia leucophrys*) will learn the characteristics of an adult song to which they are exposed during the first few months of life but not those of songs that they hear thereafter (Konishi & Nottebohm, 1969). In some cases, therefore, it is necessary to assign a range of permissible values to  $t_0$ , defining a sensitive period within the life cycle when adaptation can be effected.

Second, the response to the coenetic variable may be such as to affect the course of development in any of several possible ways. Gottlieb

(1976) has defined three roles that experience may play in the development of behavior: maintenance, in which experience is required for the continued development of a preexisting characteristic; facilitation, in which experience acts to speed up development; and induction, in which absence of experience precludes development of the characteristic altogether. In its present form, the model we have employed offers no way of distinguishing among these three roles of experience (and others that might be proposed). Elaboration of the model in this regard will require attention to the relationship between  $\beta_0$  and  $\beta_k$  and to the nature of the continuous transformation in  $\beta$  over the course of the back-reference period.

Finally, there is the problem of deciding which instances of medium-term adaptation count as examples of learning and hence form part of the subject matter for an ecological theory of learning. At the outset, we would caution against the temptation to delineate hard and fast categories of "learning" and "not-learning." In Section III,D we pointed out that the adaptive response of the animal to its environment is a *unified* response. Particular "kinds" of adaptive response, such as those we have identified in this article, are probably best regarded as modal points on a fairly densely populated continuum of response. If the unified approach that we advocate to problems of adaptation is indeed appropriate, then attempts to make sharp delineations between categories are bound to be theoretically unproductive. On the other hand, we would certainly accept the heuristic value of recognizing paradigmatic or typical examples of what we have called short-term and medium-term adaptive responses, and using the analysis of such examples to sharpen our appreciation of both similarities and differences among these various forms of response.

Let us briefly consider, then, one or two criteria that seem particularly important in determining the typicality of putative examples of learning. In the first place, we would recognize that the study of learning is concerned with change in an animal's behavior rather than in other aspects of its organization such as its morphology or biochemical make-up. Typical instances of learning are therefore those in which the outcome of medium-term adaptation ( $\beta_k$ ) is some measure of the behavioral phenotype. It should be emphasized, as pointed out in Section II,A, that this requirement specifies a choice of a particular *description* of the phenotype; all instances of learning presumably have some physicochemical basis and so may in principle be described in morphological (or physiological or biochemical) as well as in behavioral terms. The primary concern for a theory of learning, however, is to account for the behavioral description of an adaptive change and typical instances of learning will be those in which the behavioral change is regular, consistent, and demon-

strably adaptive, rather than being secondary to some other, say physiological, change. Accounting for the physiological basis of learning is, of course, a different matter, with which we cannot attempt to deal here.

A second important criterion concerns the specificity of the relationship between  $y_0$  and  $\beta_k$ . There are many effects of experience that influence an animal's behavior in ways that are indeed adaptive but that are also highly nonspecific. To give but one example, adequate nutrition is well known to be required for proper behavioral development in many species (Leathwood, 1978) but the extreme nonspecificity of such effects precludes their acceptance as typical or illuminating instances of learning. We would not, however, wish this criterion to be interpreted as license to erect two mutually exclusive categories of developmental response to the environment, one specific, the other nonspecific. Rather, we suggest that there is a continuum in the specificity of response, with the more typical instances of learning being located toward the "most specific" rather than the "least specific" end (see Bateson, 1976, for further discussion). Again, we urge that an ecological approach to learning respect the unity of the adaptive response to the environment and be prepared, at least in its early stages, to embrace a fairly wide range of developmental phenomena in the search for general theoretical principles. For example, the effects of enriched experience on behavioral development (Rosenzweig & Bennett, 1978) seem to lie toward the middle of the continuum just described and are the kind of nontraditional, borderline effects with which a unified, ecological approach to learning should be prepared to deal.

## V. Learning as Medium-Term Adaptation—Analysis of Three Examples

Having given an account of some of the conceptual issues involved in an ecological approach to learning as medium-term adaptation, let us now turn to consider some concrete examples of such an approach. In selecting examples of learning to present in this section we have restricted ourselves to cases in which the phenotypic characteristic whose development is being analyzed is of clear adaptive significance to the animal that possesses it. Many of the learning tasks that are employed in conventional studies of learning are of questionable adaptive relevance to the animal outside the artificial setting of the laboratory. Their contribution to the understanding of learning as a form of biological adaptation is therefore not readily apparent. This is not to say that we see laboratory investigation as irrelevant to the ecological study of learning. On the contrary,

nothing can be learned about the identity of coenetic variables and the ways in which they influence development without perturbing the natural course of development in some manner. The use of artificial or atypical rearing environments must obviously play a major analytic role in any study of learning, whether ecological or otherwise. But in the ecological approach, such experimental intervention must be designed to analyze an ecosystem rather than an animal (see Section II), seeking to explicate the ecological support for learning and the means by which such adaptation is effected.

An ecological analysis of learning proceeds from the observation that at some point in an animal's life ( $t_k$ ), some aspect of the animal's phenotype ( $\beta_k$ ) and some aspect of its environment ( $\phi_k$ ) stand in a particular relationship to one another [i.e.  $F(\phi_k, \beta_k) = 0$ ], such that some adaptive goal ( $G$ ) may be attained. Analysis of the medium-term adaptation that gives rise to  $\beta_k$  involves identifying the coenetic variable ( $y$ ) that provides the ecological support for adaptation and describing the function [ $B(y_0) = \beta_k$ ] that produces the characteristic in the course of normal development. The response function  $B$  has evolved in an ecosystem in which there is a *specific* relationship between  $y$  and  $\phi$  [namely,  $P(y_0) = \phi_k$ ] and between  $\phi$  and  $\beta$  [namely,  $F(\phi_k, \beta_k) = 0$ ]. Analysis of  $B$  cannot therefore be based on an arbitrary selection of  $y$ ,  $\phi$ , and  $\beta$ ; selection of these variables must reflect the structure of the particular ecosystem under analysis.

One example of an ecological approach to learning, the development of bird song, has already been discussed, in Section IV,C,2. Three more examples will now be considered.

#### A. SPECIES IDENTIFICATION IN DUCKLINGS

The young of many species of precocial birds show a strong and specific tendency to approach a species-typical call, the maternal assembly call, which is uttered by the mother to lead the young off the nest after hatching and to ensure cohesion of the brood following nest exodus (Collias & Collias, 1956; Gottlieb, 1965). Thus, at about the time of nest exodus ( $t_k$ ), the adaptive goal of brood cohesion ( $G$ ) is attained by virtue of a tendency of the young ( $\beta_k$ ) to approach the maternal assembly call ( $\phi_k$ ). The specificity of the approach tendency is such that only the call of the young's own species will be approached, and this specificity is defined by a focal condition,<sup>5</sup>  $F(\phi_k, \beta_k) = 0$ . An analysis of the medium-term adaptation underlying this state of affairs involves identifying the

<sup>5</sup>In this and the following examples we will use the formalism provided by Sommerhoff's model without specifying the nature of the function that defines the focal condition. In principle, the necessary specification can always be provided, but it will depend on a number of considerations that

coenetic variable ( $y_0$ ) and describing the function  $B(y_0) = \beta_k$  that effects the adaptive response.

If mallard (*Anas platyrhynchos*) or Peking (a highly domesticated form of mallard) ducklings are raised in an incubator, with no exposure to the maternal assembly call, they will nonetheless show a strong and specific tendency to approach the call after hatching (Gottlieb, 1971). The mallard call is preferred to those of a variety of other species, including the pintail (*Anas acuta*), the wood duck (*Aix sponsa*), and the domestic chicken (*Gallus gallus*). The fact that prior exposure to the maternal call is not required for the development of a specific approach tendency indicates that the coenetic variable of adaptation is in this case not the same as the variable (the maternal call) to which adaptation is effected (see Section III,B).

Identification of the coenetic variable has been achieved on the basis of experiments in which the ducklings' prenatal experience was artificially modified. During embryonic development, the duckling begins to vocalize approximately 3 days before hatching, when it moves into the airspace at the large end of the egg (Gottlieb & Vandenberg, 1968). If the embryo is surgically devocalized before this time and reared in auditory isolation, so that it can hear neither its own vocalizations nor those of siblings, then a less specific tendency to approach the mallard maternal call will be evident when the duckling is tested postnatally. Specifically, devocal ducklings approach the chicken call about as often as the mallard call in a choice between the two (Gottlieb, 1971). Experiments using artificially altered mallard calls in choice tests revealed that devocal ducklings are relatively insensitive to two acoustic features that differentiate the mallard and chicken calls: a high-frequency component that is lacking from the chicken call (Gottlieb, 1975a) and the repetition rate of the individual notes that make up the call (Gottlieb, 1978).

The specificity of approach shown by normal ducklings to mallard calls containing the high-frequency component may be reinstated in devocal ducklings by exposing the embryo, after devocalization, to a recording of the contact-contentment call (Gottlieb, 1975b), one of the calls that a normal embryo utters during the last 3 prenatal days. This result clearly identifies exposure to the contact-contentment call as the coenetic variable in this instance of medium-term adaptation. There is considerable specificity between  $y_0$  and  $\beta_k$  in this example, as shown by the fact that exposure to either recordings of distress calls (also uttered by the embryo)

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lie outside the scope of this article, particularly the choice of suitable measures for  $\beta$  and  $\phi$ . The example of prey capture by the praying mantis discussed in Section IV,B shows one strategy for defining the focal condition that could be employed in any of the examples discussed here.

or to suitably pulsed bursts of white noise is not effective in reinstating the specific approach tendency in postnatal tests (Gottlieb, 1975b).

The tendency of normal ducklings to approach calls pulsed only at the species-typical rate of about four notes/sec may also be reinstated in devocal ducklings by exposing the embryos to the contact-contentment call (Gottlieb, in press). The embryonic call also has a repetition rate of about four notes/sec and the specificity of the developmental response to it is demonstrated by the fact that exposure to the same call pulsed at either 2 or 5.8 notes/sec does not reinstate the specific postnatal approach tendency (Gottlieb, in press).

Gottlieb's research has made it possible to give a very complete account of both the coenetic variable and the function that defines the adaptive response in this instance of adaptation. The former has already been sufficiently discussed; the nature of the response to the coenetic variable is shown by other results reported by Gottlieb. The sensitivity to the high-frequency component of the mallard call, which, in devocal ducklings exposed to the contact-contentment call, appears at about 24 hr after hatching, emerges even in the absence of such exposure by 48 hr (Gottlieb, 1975c), showing that experience plays a facilitative role in its development (Gottlieb, 1976). The role of experience in the development of the repetition rate preference, on the other hand, appears to be one of maintenance, since the embryo exhibits a specific motor response to calls pulsed at the species-typical rate of four notes/sec even before the normal onset of vocalization (Gottlieb, 1979).

## B. STELLAR ORIENTATION IN THE INDIGO BUNTING

Many species of birds migrate over considerable distances between their summer and winter ranges, an accomplishment that depends on navigational skills of a high order of refinement. In general, these skills require that a migrant's direction of movement be controlled with respect to some source of information in the environment that specifies the direction of the terminus of migration with respect to the migrant's present position (Emlen, 1975a). Thus, by the time of its first migration season ( $t_k$ ) the migrant's navigational skill ( $\beta_k$ ) is such that it can utilize the available sources of directional information ( $\phi_k$ ) to navigate with the required accuracy ( $G$ ). The focal condition [ $F(\phi_k, \beta_k) = 0$ ] is satisfied when the migrant can select a seasonally appropriate direction in relation to the available ecological information.

The indigo bunting (*Passerina cyanea*) is a nocturnal migrant that uses the information present in star patterns as the basis for its navigation (Emlen, 1967a). From experiments using projected star fields in a planetarium, Emlen (1967b) concluded that configurational information

in groups of stars (rather than the bearings of individual stars) provides the basis for navigation. Since blocking out arbitrary portions of the star field does not affect the birds' directional preferences, the relevant information must be widely distributed over the sky, rather than being inherent in particular groups of stars.

Birds that are denied exposure to the night sky until the start of their first migration season do not show the orientation preferences of normally experienced birds (Emlen, 1969). Acquisition of this skill is therefore an instance of medium-term adaptation, information present in the night sky being identified as the coenetic variable. One month of exposure just prior to the migration season is sufficient to establish a weak, although appropriate directional preference. Further experiments (Emlen, 1970, 1972) showed that definition of the axis of rotation of the sky is required to specify the coenetic variable fully. In order for a bird to orient in a particular direction appropriate to the season, rather than just in a constant arbitrary direction, it must have a directional reference and the axis of rotation of the sky provides such a reference, pointing north in the northern hemisphere. Emlen (1970) reared two groups of birds, one exposed to an artificial (planetarium) sky rotating normally about Polaris (the pole star), the other exposed to the same sky rotating about Betelgeuse. When tested for directional preferences in their first migration season, birds in the first group showed normal directional preferences with respect to Polaris whereas those in the second group showed equivalent preferences with respect to Betelgeuse. Subsequent reexposure of the second group to a normally rotating sky failed to modify their preferences, suggesting the existence of a sensitive period for the acquisition of the navigational skill.

Emlen's analysis of the medium-term adaptation underlying the navigational ability ( $\beta_k$ ) of adult indigo buntings has identified the environmental variable ( $\phi_k$ ) to which adaptation is effected (configurational information in star groups) and the coenetic variable ( $y_0$ ) that supports the adaptive response. In contrast to the example discussed previously,  $\phi$  and  $y$  refer in this example to the same aspect of the environment (the star field). However, specification of  $\phi$  and  $y$  requires different descriptions of the star field; specifying  $y$  requires that the axis of rotation be defined, whereas adult birds will orient correctly under a stationary sky ( $\phi$ ) (Emlen, 1967a). Note also that whereas in the preceding example only one value of  $y_0$  (a contact-contentment call pulsed at the species-typical rate) would support adaptation, in this example there is some range ( $S_0$ ) of values (i.e., range of rotational axes), to each of which an appropriate adaptive response is made. Birds raised under skies with different axes of rotation orient differently with respect to configurational information in the stars but all choose an equivalent direction with respect to "celestial north," as defined by the axis of rotation.

As mentioned above, Emlen's (1970) results hint at the existence of a sensitive period in this instance of adaptation. They also suggest that the role of experience is inductive (Gottlieb, 1976) rather than maintaining or facilitative. Inexperienced birds show no directional preference and specific preferences may be induced with respect to any of some range of axes of rotation. This research thus provides at least a partial characterization of the function  $B$  that effects the adaptive response.

### C. VISUALLY GUIDED REACHING IN MAMMALS

Optical information provides perhaps the most prominent source of control on behavior, as demonstrated in experiments by Lee (1976; Lee & Aronson, 1974; Lee & Lishman, 1977), Schiff (1965), Warren (1976), and others (see Turvey, 1977a; Fitch & Turvey, 1979). Consider a simple example of visuomotor control such as reaching for an object in the visual field. In Section III,B we analyzed a similar example as an instance of short-term (i.e., perceptuomotor) adaptation; here we are concerned with the development of the skill itself as an instance of medium-term adaptation rather than with the short-term analysis of its components. Gibson (1958) proposed that an animal might control its behavior by responding appropriately to the patterns of texture gradients and texture flow fields that are present in the optic array (Gibson, 1950), that richly structured optic medium made available by the multiply reflected light in a complex natural environment. Mathematical analyses by Johansson (1974), Lee (1974), and Nakayama and Loomis (1974) have confirmed Gibson's intuition that specificity does indeed exist between patterns, both static and dynamic, of optic texture and the layout of objects and surfaces in the environment. It is significant that in Lee's (1974) analysis, the optical patterns of relevance are scaled to the perceiver's body size; for example, height of the eye above the ground appears as a variable in the equations describing patterns specific to the control of locomotion.

Taken together, the theoretical and experimental results permit the following assessment of the situation at some time  $t_k$  in an animal's life: As a skilled perceiver, the animal has the ability ( $\beta_k$ ) to use ecological (i.e., body-scaled) information in the optic array ( $\phi_k$ ) to coordinate its behavior with respect to the layout of objects and surfaces in its environment ( $G$ ). Several studies demonstrate that acquiring this ability is dependent on specific visual experiences that define the coenetic variable ( $y_0$ ) in this instance of medium-term adaptation. Precise definition of the coenetic variable depends on what component of visuomotor coordination is under consideration. For example, normally reared kittens, when held in the air, show a "visual placing response" (extension of the forelimbs) that is elicited by an approaching surface and, if the surface is interrupted



by gaps, they will guide their forepaws to meet the solid parts of the surface. Hein and Held (1967) found, in kittens reared in a normal visual environment but denied sight of their limbs by a collar worn around the neck, that the elicited component develops normally but that the guided component is absent. The coenetic variable of adaptation apparently differs in the development of these two components of the placing response: For the elicited component, exposure to patterned light is sufficient for normal development (see Hein, Gower, & Diamond, 1970); for the guided component, visual experience of the limbs is also required (Hein & Held, 1967). This specificity between the coenetic variable and the behavioral skill whose development is being considered shows this example to be a relatively typical instance of learning, as previously characterized.

The visual placing response is an example of closed-loop reaching, in which the animal can see both its paw and the target. Under open-loop conditions, by contrast, the position of the target is indicated by a visual marker but the animal can see neither its own paw nor the target. Monkeys that are reared without sight of their hands show deficiencies in open-loop reaching that are similar to those shown by deprived kittens in the closed-loop task (Bauer & Held, 1975; Held & Bauer, 1967, 1974; Walk & Bond, 1971). Whereas normally reared animals reach directly for the target, guiding their reach with reference to the visual marker, deprived animals flail their arms wildly until they hit the target accidentally and then grasp it.

The open loop situation is interesting because the coenetic variable in the development of this skill (sight of the arms) is not the same as the environmental variable to which adaptation is later effected (specification of a hidden target position by visual information). This was also true, it will be recalled, in the case of species identification in ducklings, previously discussed in Section IV, A. A further point of interest is that the environmental variable  $\phi$  is a complex relation between the pattern of optic texture and the position of graspable objects *with regard to the perceiver*; a full understanding of this instance of adaptation therefore awaits an animal-relevant style of description of the environment and of the optical structure that it generates, along the lines of that provided by Lee (1974) for the case of locomotion.

#### D. MEDIUM-TERM ADAPTATION AND ENVIRONMENTAL VARIABILITY

We have pointed out that learning permits adaptation to be effected to aspects of the environment that change rapidly in relation to evolutionary time-scales (see also Plotkin & Odling-Smee, 1979; Slobodkin, 1968;

Slobodkin & Rapoport, 1974). Identifying variation in  $\phi$  is thus an appropriate concern for an ecological approach to the study of learning, since it indicates the possible selective value of particular learning skills and so helps to account for their evolution in the animals that possess them. The terms "indicates" and "possible" are used deliberately, for establishing the selective value of any phenotypic characteristic with any degree of certainty is fraught with difficulty, both conceptual and empirical (see Hinde, 1975; Lewontin, 1979).

In some of the cases we have discussed, it is possible to identify the environmental variability that might account for the adaptiveness of these learning abilities. Thus the relatively rapid speciation of waterfowl and songbirds might be offered as a reason for the involvement of learning in species identification and in song development, respectively (see Immelmann, 1975). In the case of stellar orientation in the indigo bunting, Emlen (1975b) has pointed out that the precession of the earth's axis of rotation, which changes the relationship between celestial and geographic directions at the rate of about  $3^\circ$  every 1000 years, might be identified as the evolutionary reason for the involvement of learning in the development of this skill.

We must, however, guard against the "adaptationist fallacy" of assuming that all characteristics of an organism *must* be explained by appeal to their possible adaptive benefits to their possessor (Gould & Lewontin, 1979; Lewontin, 1979). We have already pointed out that natural selection and evolutionary adaptation, while intimately related processes, are not identical. The ability of natural selection to produce precisely the adaptations that an animal requires and to make those adaptations optimally efficient is limited in a number of important ways (see Section IV, A). Consider, for instance, the limitation imposed by a lack of appropriate genetic variation in the population. A population that experiences a change in its environment, such as a new food source, may not possess the kind or amount of genetic variation required to evolve, say, a different adaptive tooth structure. It may, however, possess more genetic variation associated with the development of its feeding behavior, so that a learning skill can evolve enabling individuals to adapt to the characteristics of the food source on the basis of their own experience, *even though those characteristics may remain invariant over long periods of time*. In this case, the evolutionary reason for the possession of a learning skill has more to do with past genetic variation in the population than with the nature of environmental variability.

It is quite possible that different kinds and amounts of past genetic variation account for the different styles of song development in passerine birds (Marler & Mundinger, 1971); while some species show a strong

dependence on exposure to a song model for normal song development, others develop almost completely normal adult song when raised in auditory isolation. No convincing adaptive explanation of these differences has yet been offered and it may be that none is needed or possible. They may simply reflect equivalent adaptive responses to similar selection pressures by genetically different populations (Lewontin, 1979).

This is not to say that attempts to provide adaptive explanations for the possession of learning skills are always misplaced. Where environmental variability is such that long-term adaptation cannot be effected, natural selection will tend to favor those individuals capable of effecting medium-term adaptive responses in the course of development and such learning skills may clearly be given an adaptive explanation. Providing such explanations, however, is far from straightforward and alternative, nonadaptive explanations should always be borne in mind. Perhaps the greatest danger of adaptive explanations is that while they are very easy to construct, they are usually very difficult or impossible to test. This increases the temptation to accept plausible adaptive stories in lieu of experimental demonstrations (Gould & Lewontin, 1979; Lewontin, 1979). Much more could be said on this important topic and these brief remarks are intended merely as a caveat for future work on this problem.

#### IV. Concluding Discussion

In this article we have presented a sketch of a metatheory, or conceptual framework, that can serve to guide an ecological approach to the study of learning. Our aim has been to set the problems of learning in a broader context, a context supplied largely by ecological and evolutionary theory, and to indicate the kinds of questions that might be asked about learning from the perspective thus provided. Foremost among the issues that emerge from this undertaking is an overarching concern with the relationship between the animal that learns and the environment that is learned about. This relationship is not an arbitrary one; each animal stands in a special, ecological relationship to a particular environment, one that it encounters as a result of its phylogeny and normal ontogeny. Defining the "natural environment" for particular species may be a difficult and demanding task, but the difficulty of this endeavor should not be allowed to overshadow its importance.

The theoretical significance that we attach to the relationships between animals and their (natural) environments is reflected in the account that we have given of the ecosystem, not the animal, as the minimal unit for the ecological study of learning. Within the ecosystem, animal and envi-

ronment are defined in interdependent, coimplicative terms, as actor and econiche. We intend the unity of the ecosystem to be taken quite literally, not merely as an expression of good intent to be forsaken when attention is turned to the analysis of concrete examples of learning (see also Bentley, 1941), but this does not mean that we see the ecosystem as analytically impenetrable. Analytically, our attitude toward the ecosystem is somewhat akin to that of a modern neurophysiologist toward the brain: It is a unified system, with richly structured, nonarbitrary relationships among its many components but its complexity is such that experimental "dissection" is the only possible route to understanding its systemic properties. The implementation of this strategy toward the study of learning is clearly shown by the examples analyzed in Section V, in which experimental interference with the normal processes of development provides the key to understanding those processes.

A second issue that has concerned us deeply is that of the animal's adaptation to its environment and, in particular, of the unity of that adaptation. It is commonplace in biology to observe that the animal is an adapted whole, not an assemblage of adapted elements, and we would extend this observation to include the fact of temporal as well as spatial unity: An animal is not a succession of instants; it is an extended *event* and in striving for a unified account of adaptation on different time-scales, we have given explicit recognition to this fact.

As a conceptual tool for achieving our goal of a unified account of adaptation we have employed the formal model of adaptation developed by Sommerhoff (1950, 1969), a model that has suffered undeserved obscurity during the 30 years since its first publication. We have employed the model as an analytic rather than a predictive tool, analysis being the aim of this article as well as Sommerhoff's original intent. The advantages of employing this formalism are, we hope, evident. It allows us to define, in precise and unambiguous terms, the elements of any instance of adaptation and the relationships between those elements. Most importantly, it provides a vocabulary in which to phrase questions about adaptation, and about learning in particular, that are both ecologically motivated and amenable to experimental investigation. As noted in Section I, the primary aim of metatheoretical inquiry is to raise particular kinds of questions, in our case ecological questions about learning, and Sommerhoff's model provides an admirable tool in that regard.

As far as we have been able to define them in the space of this article, the questions and issues that are raised by the ecological approach to learning are importantly different from those raised by more traditional approaches. Questions concerning the relationships of learning to other forms of adaptation, including those on both similar and different time-

scales, are given a prominence by the unified view of adaptation that is largely lacking in traditional approaches. The problem of description of the environment, as an empirical rather than a logical problem, is not one that has traditionally been raised but it assumes major significance in the ecological approach.

Traditional approaches to the study of learning emphasize, often to the virtual exclusion of other considerations, analysis of the mechanisms of learning. While we have paid rather little attention to questions of mechanism (an emphasis in line with our metatheoretical aims) it is clear that this is an important area for future investigation. It is important to recognize, however, that since we have proposed a view of learning as a *direct* adaptive response, the kinds of mechanism that might be proposed to account for it will probably look very different from the *indirect* mechanisms (involving association, memory, propositional structures and the like) that are currently popular. Gottlieb's (1976) three roles of experience represent an important step toward understanding the mechanisms of direct learning and further work on this problem is urgently needed.

The difference between the two approaches may also be seen in the traditionally important questions that are not raised by the ecological approach. Most of the important issues in current psychology of learning presuppose an associationist account of learning (see Jenkins, 1979). The ecological approach does not involve associationism and so issues such as the role of reinforcement, the nature of Pavlovian-operant interactions, and stimulus-response specificity simply do not arise. Some traditionally important issues (of which the learning-performance distinction may be one) do seem likely to be raised as an ecological account of learning develops, but we doubt that they will take the same form as they do in association theory.

We make no claim to have considered in this article all of the issues that are involved in an ecological approach to the study of learning, nor to have exhausted the problems inherent in those issues that we have considered. Our main hope is that by taking a broad perspective view of the nature of learning we have at least been able to cast some important issues in sharp relief, and so point in the direction of their resolution.

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