STEVENS’ HANDBOOK OF EXPERIMENTAL PSYCHOLOGY
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Chapter 10

THE ADAPTIVE-EVOLUTIONARY POINT OF VIEW IN EXPERIMENTAL PSYCHOLOGY

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INTRODUCTION

Charles Darwin and Psychology

Charles Darwin is undoubtedly one of the most influential figures in the history of experimental psychology. Boring (1960) ranks him with Helmholtz, Freud, and James. Darwin made two great contributions of relevance to psychology, but only one had a significant influence on the field; his insight into the historical continuity of animals and man. Expressed most clearly in The Descent of Man (1871), this idea influenced the growth of comparative psychology and the psychology of animal learning (Jenkins, 1959; Lockard, 1971). Because it emphasized the similarity of structure among organisms, it implied that mechanisms and principles of animal psychology might apply as well to human behavior and mental life.

Darwin's (1859) more fundamental insight dealt with the diversity of biological species and their remarkably adaptive fit with their environment. To explain this, he combined the principle of heritable variation with the principle of differential reproductive success of more fit varieties, and formulated the theory of evolution by natural selection. These principles and the

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simple fact that environments vary greatly between, adaptive diversity of living things, whereas the principle of continuity emphasizes the similarity among organisms.

In psychology, the face of continuity has overshadowed the drive of diversity. At best, these two perspectives made little contact with each other; often they were seen as antagonistic. However, the last few decades have seen some reconciliation. A major goal of this chapter is to combine the confrontation and reconciliation of these two perspectives in a number of areas of psychology, especially animal learning, where the historical and contemporary issues are most clearly drawn (see Boakes's *From Darwin to Behaviorism* [1984] for a history of the period).

Behavior Theory

An early response to the principle of continuity was the evolution of amoebas adapted to demonstrate human-like intelligence and cognition in animals (Romanes, 1882). Inspired by the ideal of objectivity, later researchers achieved the impression of "higher mental processes" to animals and humans and sought to show that human performance could be explained by the same basic processes as in animals. Morgan, 1984; Thorndike, 1898; reviewed in Gottlieb, 1976). From the turn of the century, some models of human learning were mere blind chance. Although it was launched and justified by the principle of continuity, this enterprise was modelled on physics and biology, rather than evolutionary biology. Species differences, especially in receptors and effectors, were acknowledged, but psychologists were primarily interested in those saline and associative mechanisms which "lower" animals shared with that most reflective species, man. They emphasized the arbitrariness of the components of associations, and their procedures were designed to eliminate those species-specific traits of their subjects which might interfere with the extraction of general principles. Thus, Thorndike designed his apparatus to be arbitrary, so that it "could not have been previously experienced or provided for by heredity." (1898, pp. 7-8). (Jenkins, 1978; Timbrell, 1983). The study of learning became the dominant enterprise in experimental psychology, and its proponents included many of the leading psychologists of the century: Watson, Tolman, Hull, and Skinner. It was vigorous and it was vigorous.

The principle of association and continuity, and strong views on the nature of science as an objective enterprise (Jenkins, 1978) contributed to a general set of attitudes toward research known as behavior theory in general process theory (Logan, 1986; 1989; Rachlin, 1978; Schwartz & Lacey, 1989). Its major tenets were linked by history more than by logic. We offer here a distillation, closest to the position held by Skinner (1953, 1986, 1979), of the major principles underlying the general process assumptions:

1. (a) The underlying principles of learning are the same across species. (b) The underlying principles of learning are the same across species (e.g., reproduction, feeding, different perceptual systems) within a species. Those comprise the general process assumptions.
2. Learning is decomposable into one or a few basic associative processes.
3. Most behavior is acquired by "environmentalism" or "expedience.
4. Behavior, and only behavior, can be the proper basis for an objective psychological experimentation.

These four assumptions have their own roots: the general process assumption traces to Darwin, and yet it is ironic the only one that conflicts with the Darwinian expression of Darwin’s second assumption: that within the animal’s reproductive (McGhee, 1987). This widely held view is based on the hypothesis that learning because it did not fit into the associative framework; it was passively acknowledged as a special mechanism in experimental, psychophysics and overly-

Cognition, Language, and Perception

Although the adaptive-evolutionary approach is applicable to all psychological phenomena, it has been notably absent from the area of cognitive science. Since the study of cognition has focused on human beings, the general process claim has assumed that across species (different perceptual or conceptual systems) the same mechanisms are at work. Two of the major approaches to cognition—verbal behavior and psycholinguistics—correspond in some ways to the general process and colloquial approaches. Like behavior theory, the verbal-learning approach: (1) adopted an empiricist and associative account of human memory and thinking (but was markedly less behavioristic); (2) emphasized general
procedures that span all domains of human information processing; (5) acknowledged specificity in sensory systems but tended to ignore it elsewhere; and (6) emphasized laboratory studies, with only limited forays into natural settings (see Noe, 1978). The more recent information processing approach, although quite different from verbal learning, still shares some degree all but the first attitude.

Like ethology, linguistics challenged some of these assumptions. One major claim was that domain-general processes could not account for what animals and people actually do. Chomsky (1970) argued that there must be innate "constraints" on language learning that render tractable a task that would otherwise be hopelessly difficult for a child endowed only with a "general process" inductive system (Weiner & Pullin, 1960). These constraints are assumed to be embodied in specialized neurobiological mechanisms (Lemur, 1970), as part of our (human) species-specific endowment. Within this framework the study of language has prospered, developing, for example, models of speech perception that assume special phonological processing modules (Liberman & Stedt-Kennedy, 1978).

The case for species-specific and domain-specific innate predispositions or constraints has been made for other areas of cognition. Fodor (1975) and Rotin (1974) Rotin & Kalat, 1971) called attention to modules or adaptive specializations in animals (e.g., bhe navigation) and humans (e.g., language, spatial representation). These inputs, outputs, and interconnections to other systems are limited. These are theoretically required, because the world under determins the possible interpretations of experience (as with language) and because an unconstrained general inductive system would be too slow to handle the complexity of these inputs and connections to other systems.

Constraints This historical review provides a context for critically evaluating a term which has, perhaps unfortunately, come to stand for the study of special psychological processes.

Although many specializations are species-specific aspects of concepts (e.g., on-organism specializations in particular domains (e.g., phonological processing in auditory linguistic conditioned taste associations in food selection).

The crossover, within-species emphasis has always predominated. Comparative psychology in the United States has always been centered on human beings as the reference point, and has sought to discover the rudiments of mind in lower creatures (Gettlin, 1979). In the 1930s and 1940s, comparative psychologists assumed that psychological abilities were domain general and sought to document their species-specific limitations. This approach, exemplified by the work of Bitterman (1952), adopted a standard certain general procedures that hold true in humans and apply (e.g., the partial reinforcement effect). Three abilities were assessed in a number of widely separated vertebrate species in an attempt to identify the point in phylogeny at which the species appeared. Although this approach did uncover interesting interspecies differences in abilities to perform in arbitrary situations, it did not take into account the branching nature of evolution. While this approach did uncover interesting interspecies differences in abilities to perform in arbitrary situations, it did not take into account the branching nature of evolution.
Environment (Jenkins, 1979). Strange (unanticipated) environments do occur in the world, and it is important to know how a system's response to a particular niche can perform in others.

Furthermore, arbitrary environments can be considered natural for humans. Hence examination of an animal's behavior in such environments as of comparative interest and might serve as a model for human learning (if not for animal learning) (Schwartz, 1974, 1981). In addition, exploration of an animal's capabilities, whether it is in a tank or a Skinner box, might be expected to reveal some fundamental general adaptive features, perhaps adapted to universal features of environments. The law of effect is an example. Another is the fact that contingency is critical for association formation (Besicca, 1976), since (as opposed to contiguity) it relates to the prediction of the occurrence of events.

Adaptive principles have emerged from general process research in part because behavior theorists have often been concerned with accounting for adaptation in general to the environment in general, sometimes quite explicitly, as in the work of Hull (1939) and Skinner (1938). The Darwinian principle of adaptation by selection has had a central role. Instrumental years, as was explicitly conceived by its proponents to be analogous to natural selection. In the life of the organism, the principle of selection selects those behaviors which produce beneficial consequences, just as in the evolution of species, the principle of natural selection selects those behaviors which increase survival (Skinner, 1981; Staddon & Simmelhag, 1971, Thorpeke, 1989, as cited by Gluckin, 1983, p. 149).

Behavior theorists, in turn, have two criteria of the adaptive-evolutionary approach. One is that it is irrelevant to their interests, a claim we try to refute in this chapter. A second is that the evolution of the organism, the principle of selection selects those behaviors which increase survival (Skinner, 1981; Staddon & Simmelhag, 1971, Thorpeke, 1989, as cited by Gluckin, 1983, p. 149).

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The major impetus for a reconsideration of general process theory came from within the field, in empirical and theoretical papers dating from the 1960s and early 1970s. The early work challenged the basic validity of some accepted basic laws of learning and prompted consideration of the evolutionary relevance of the behaviors and organisms under study.

The most direct challenge came from research on learned taste aversion, as in John Garcia and Koelling (selective association) study. In the classic "balsamgusa" (selective association) study, Garcia and Koelling (1960) showed that rats could avoid an electric shock. This finding directly challenged the principle of contingency.

In the same year, Garcia, Ervin, and Koelling (1960) reported that taste aversion could link two classic intervals of over one hour (long delay learning), a finding grossly off base from traditional learning procedures and contradicting the principle of temporal contiguity. They suggested that

...animal learning mechanisms do not operate randomly, associating stimuli and reinforcers on the basis of recency frequency, and interest. The consequences rules display a bias, probably established by natural selection, to associate satiation and olfactory cues, with internal stimuli when these stimuli are separated by long time periods (p. 129).

These experiments were stark demonstrations of abilities that were less salient in prior and simultaneous research on poison avoidance (Barnett, 1961; Richter, 1960; Rauka, 1960), avoidance of taste stimuli associated with X-radiation (Garcia, Kinselorde, & Hunt, 1967; Melancon, 1960; Smith, 1971), ingestion of food and the acquisition of food preferences (Cagert, 1964; Harris, Clay, Hargreaves, & Ward, 1956; Richter, 1960; Ross, 1960; Smith, 1971; Taylor, 1964). These studies demonstrated fundamental general process principles and they fit well within an adaptive framework: work the behavioral specificity and long delay learning capability are particularly suited to the problem of avoiding poisons and learning about nutritious foods (Garcia & Ervin, 1960; Ross & Koelling, 1972).

Another basic tenet, the law of effect, was challenged at about the same time. In 1961, Keller and Marion Breland, former students of Skinner's who had been using the technology of reinforcement to train animals for commercial exhibits, reported that animals given food Reinforcement for arbitrary behaviors began to perform specific-spatial digestive behaviors so vigorously that these responses interfered with the original operant. In one case, a pig which had been trained to deposit overflow corn in a pig slop bowl eventually became loyal to part with the corn, ceasing to eat and rooting with it instead. Despite the fact that the pig thereby forfeited the food reward. The Brelands noted that this behavior was "an example of the law of effect and gave their paper the provocative title "The Misbehaver of Organisms." In more controlled experimental situations, Bollin (1976) demonstrated that avoidance learning was much more rapid, and perhaps qualitatively different, if a species-specific defensive response was used as the response. Brown and Jenkins (1980) and Williams and Williams (1969) showed that the paradoxically arbitrary operant, the pigeon's key peck, could be elicited by response-independent food presentations with a brief illumination of the barrier ("counterlighting"), with such vigor as to override reward contingencies. These studies suggested that Pavlovian processes and species-specific behaviors could induce into arbitrary instrumental situations.

Thus, all of these studies argue for nonarbitrary relations among stimuli, responses, and reinforcers. They provoked a variety of theoretical and empirical responses.

Theoretical Responses to the Anomalies

The phenomena described in the 1960s are now generally accepted, but this was not always so. Garcia had great difficulty publishing his original findings, and they were ignored for some years, except by "pioneers" working in other areas with related problems (Reevsky & Bedford, 1967; Ross, 1961; Smith & Boll, 1971). At least one general theorist (Rivoire, 1972) claimed that the results were artifactual (Reevsky, 1977). This position is now behind us. The most work on conditioned taste aversion has been done by animal learning researchers working within some kind of general process framework. Our review will progress from views that sought to preserve the core of general process theory to those that departed most radically from it.

Preserving the Core of General Process Theory

These positions had their goals. First, many textbooks of the 1970s characterized conditioned taste aversion as an anomalous exception to otherwise general principles. Second, many learning theorists tried to assimilate the findings as parametric variations in general laws. By this view, the anomalous results represented quantitatively different from basic general principles (Logue, 1978). This is true to some extent, though some aspects of
conditioned taste aversions, such as one trial learning with long delays, arguably stretch the modified "behavioral plasticity" excessively (Lange, 1979). A third view is that, qualitative or quantitative differences are not produced by differences in associative processes per se, but rather by restriction of inputs or variations in "response rules" (Sears & Holland, 1970). We shall see that at least some anomalous results probably can be accounted for in this manner.

Accepting Limited Modifications of General Process Theory

Seligman & Hager (1972) explicitly invoked a selective association principle to bolster general process theory. Seligman rejected associative equipotentiality and suggested that traditional laws of learning hold only for arbitrary events. He postulated a dimension, "preparedness," which ranges from the most readily learned (prepared) associations (specific evolutionary adaptations such as conditioned taste aversions) to the least readily learned (unprepared associations). Seligman operationalized preparedness as the "amount of input" (e.g., number of trials, amount of information) necessary to produce a given level of conditioning. He also suggested that prepared associations might have different physiological substrates and be less influenced by cognitive factors. Preparedness predisposed to both explicit and instinctual alternative to equipotentiality.

Seligman's credentials in animal learning, the straightforward simplicity of his conceptualization, and its compatibility with much of general process theory all made preparedness the most influential of his anomalous findings. In their book, *Biological Boundaries of Learning*, Seligman and Hager (1972) endorsed the preparedness hypothesis, and localized lower order differences within the nervous system. By the mid-1970s, the idea that the nervous system has specific adaptations to particular environmental stimuli had become mainstream, and Seligman's preparedness hypothesis was no longer the primary focus of research in this area.

The classical ethologists viewed learning as just another adaptive feature of behavior. Their focus was on the variety of situations in which the organism is exposed to the environment, and the interplay of prestructured and acquired components.

The student of innate behavior, accustomed to studying a number of different species and the entire behavior pattern, is repeatedly confronted with the fact that an animal may learn some things more easily and some things more rapidly than other behaviors. In other words, some behaviors are more strongly associated with particular stimuli. Different species are predisposed to learn different sets of the patterns. So far as we know, these differences between species have adaptive significance (N. Tinbergen, 1953, p. 145).

Rozin and Kalat (1971, 1972, 1976a) emphasized the adaptive aspects of behavior. They did not rule out the possibility of general laws, but emphasized that such laws would be the product of general features of learning situations. They used the term "constraint" to describe specialization in learning, classifying and analyzing them by considering the way behavior in traditional learning situations may be influenced by the nature of the stimulus, the response, or the reinforcer. Rozin and Kalat call attention to the wide range of plastic adaptations in nature. Their claim that mechanisms of association may differ across situations remains tenable but unproven.

Starting Over: Extreme Ecological Positions

Lockard (1971) and Johnston (1985; Johnston & Turvey, 1980) stressed the adaptive and general perspectives already discussed. But whereas Shuttleworth and Rozin and Kalat appreciated both adaptive and general perspectives in their research, Lockard and Johnston doubted that much of value could come from the study of animals outside of their natural context. They called for a new start. Johnston and Turvey (1980) take a Gibsonian ecological perspective. They view the reception of information (invariances) from the environment as transactional and insist that organisms and environments must be studied together because they are part of the same system. Johnston differs from most other researchers in that he is interested exclusively in functional-adaptive (and not mechanistic) principles (Hinde, 1981). In our opinion, the view of value information gained from the study of animal learning in arbitrary situations (Schwartz, 1971, 1981; see Introduction). Johnston also criticizes the "ecological boundary" approaches for failing to provide an alternative paradigm for research on learning, and proposes that
Selective Association: A Case Study

Because behavior theorists have paid special attention to the anomalous findings on selective association, we will now consider the evidence on the existence and nature of selective associations. Since there is dispute as to whether selectivity resides in associations themselves, or opposed to inputs or outputs, we will use the term "selective association" in quotes, to refer to the outcome of the anomalous studies, as opposed to their interpretation. The literature is vast, and our review is relatively brief (see Donjan, 1980, 1982; Riley & Baril, 1976). We will first discuss evidence for the existence and extent of "selective associations," then consider whether the associative process itself is selective, and finally consider the related phenomenon of potentiation.

The Existence and Extent of "Selective Associations"

Garcia and Koelling's (1966) original brightness-increase experiment illustrated the now paradigmatic "cross-over" design for demonstrating "selective associations." One group of rats received a conditioning pairing of two conditioned stimuli (CS, CS2) with unconditional stimulus (US), and another group receives pairing of the two stimuli with a different US (US2). The critical results is that when US (illness) the animal's reaction to CS (taste) changes monotonically, which with US2 (peripheral shock) the animal's reaction to CS2 (taste) changes more. Differences between the two groups in responses to the various CSs cannot be attributed to CS or US properties per se, and must therefore be due to CS-US relations (although Garcia's original studies did not control for non-associative CS-US relations; see LoLordo, 1979; Roscorla & Holland, 1976; Schwartz, 1974 for discussions of this and related designs). In reviewing instances of selective association, we will follow Shettleworth (1975) in examining relations among stimuli, responses, and reinforcers.

Selective In Stimulus-reinforcer Relations

The "selective associability" of extraneous cues with shock, and of tastes with visceral malaise has been reported many times by many investigators (Donjan, 1980, 1982). While non-associative factors may contribute to "selective association," it is generally recognized as associative (see Donjan, 1980, for alternative interpretations), since it obeys many of the laws of associative learning (e.g., extinction and extinction and extinction) (LoLordo, 1979). There are a few other examples of this type. pigeons were exposed to auditory and visual compound stimuli paired with food or shock; with food, light elicited more pecks than did sound; with sound, shock elicited more conditioned freezing than did light (LoLordo, 1979). There is also evidence for "selective association" based upon stimulus valences and valences (e.g., color) in higher order conditioning (Roscorla & Cunningham, 1976; Roscorla & Furrow, 1977).

Selective In Stimulus-reinforcer Relations

The first (crossover design) evidence for selective stimulus-valence relations would be in 1966 (Doboszczuk, Szwajkowska, & Konosko, 1966; Konosko, 1967; see Shettleworth, 1975). It would be in a food reward discrimination where different frequencies of sound produced better learning of a "go, no go" discrimination than did differences in the location of the same stimulus. When the response to be learned was elicitation of the left versus right leg, location differences in the stimuli were more effective.

Selective In Response-reinforcer Relations

Relatives...
ingness" is confined to an affective expression system, where causal attributions in the same way, and so show a different pattern. There is the unexamined possibility that learning and/or performance may be specialized and constrained differently in different "response systems" (p. 9).

Some claim that conditioned taste aversions involve hedonic changes in the taste CS, whereas in taste-bud pairing the tastes serve as a sig- nal for shock but does not change in hedonic (affective) value (Garcia, Koznss, & Green, 1970; Gordon & Jane, 1974; Ronis & Rakov, 177). Question- naire data on human food aversions indicates that when food ingestion is followed by nausea, there is a strong tendency for the food to become disliked, whereas most other postigestional symptoms (e.g., heavein, gas pains, respira- tory distress) usually produce avoidance with- out negative hedonic change (Pelchat & Ronin, 1985).

Comparable results have been obtained with rats, using tastes as CSs, and nausea (LIC) versus a variety of other negative effects as USs (Parker, 1962; Pelchat, Grill, Ronin, & Jacobs, 1985). While animals learn to avoid tastes paired with any of the USs, they show negative facial responses (Grill & Norgren, 1971) when shown only to bitter tastes to tastes paired with nausea. Thus, in rats and humans, affective food rejection responses are apparently sensitive to nausea associations.

In summary, it is clear that performance fac- tors play a significant role in selective assor- tations, although they may not be sufficient to explain the phenomena.

SELECTIVITY IN ASSOCIATIVE PROCESSES

Since we do not have detailed formulations of the associative process at physiological or psychological levels, it is not clear how one would know that "selective associations" did operate at the very mechanistic of association, rather than at inputs or outputs. Defining the domain of association as "what is, there is always an epsilon small enough that any demon- strated site of specificity falls on either side of it.

The difficulty is illustrated by the response potentiation interpretation of "selective associa- tion" (Shettleworth, 1975, 1983; Timberlake, 1983). By this account, motivational or situ- ational stimuli activate certain appropriate re- sponse systems and make them more available for association. (Responses which increase with food deprivation are generally those that are effectively increased by positive reinforcement [1975]. It is easier to increase ear- scratching in dogs with food reinforcement if cotton, a submissive discomfort of the ear (Konzak, 1967). If these biases operate only at the performance level, they represent selectivity in outputs. If they brighten reactivity to stimuli that elicit the behaviors, they are input biases. But if the associative process itself preferentially inor- ments and reinforced the responses, the selectivity would be in the associative process.

A similar problem arises with Konzak's (1967) suggestion that there are preexisting subthreshold connections between certain inputs and outputs. LeDuc and Jacobs (1985) have carefully scrutinized CSs or any tendency to produce the relevant responses. Their find- ings favor selectivity in the associative process itself.

The only other explicit attempt to account for "selective association" is the neuropeptide theory of Garcia et al. (1974). They point to the "close apposition of taste and gastro- intestinal inputs involved in conditioned taste aversion in the medulla and argue that only neighbors can meet. Unavailability of non-taste and non-illness inputs to certain sequences or inappropriate devices could lead to "select- ing association," and would constrain outputs from those loci. But here too, one could argue the selectivity occurs at the input or output stages.

SELECTIVE ASSOCIATION: Summary and Evaluation

We conclude that "selective association" is a false and probably widespread phenomenon (Domm, 1983; LeDuc & Jacobs, 1983). The case for prepotentiation is de- scribed in everyday language in many in which selectivity at one locus does not preclude the existence of selectivity at others. The appeal of prepotentiation notwithstanding, multiple, some- what redundant mechanisms are common in associative processes. Furthermore, while selectivity in the associative process is the behavior theorists' explanation of last resort, an adaptive perspective on the associative process. From an ecological point of view, the essential outcome is that the animal avoids the objects which are most likely to have pinioned it, and this is probably achieved by multiple input, output, and association mechanisms. There is no compelling reason why the burden of proof should go to those who favor selectivity in the association process.

Potentiation and "Selective Association"

A well-established feature of associative learn- ing is the overshadowing effect (Pavlov, 1927). When two stimuli are simultaneously paired with an event, the more salient stimulus detracts from, or overpowers, conditioning of the other. Work on taste aversions in animals has discovered the reverse phenomenon: potentia- tion. The presence of a taste (a particularly salient CS) during the pairing of olfactory or visual stimuli with illness cannot enhance condi- tioning of this other less readily conditionable stimulus (Clark, Westbrook, & Irwin, 1979; Domm, 1972; Duffie & Droschl, 1980; Gauld & Osborne, 1976; Rantin, Hanks, Garcia, & Bello, 1976; see Garcia & Rantin, 1980, and Domm, 1985, for review). A similar phenome- non has been reported in an autosprinting experi- ment in which a flylight was paired with injections of water into a pigeon's crop. The keylight came to elicit pecking only if the injections were accompanied by oral stimulation (Woodruff & Williams, 1970).

From an ecological point of view, animals must be able to respond in the event in the world, not isolated inputs in particular modalities (Gibson, 1966). For feeding, the relevant stimuli are potentially edible objects, and the critical event is ingestion—that is, the experi- ence of the object in the mouth. Such "mouth objects" produce stimulation in a number of modalities (taste, olfaction, temperature, touch, pain) but are perceived as unitary entities, which we term in common speech as "taste." The salience of taste as a CS related to gastro- intestinal events is highly adaptive, since the great majority of gastrointestinal disturbances are caused by ingested items, and the system seems to be predisposed accordingly: stronger responses result from tastes which are actually ingested and not just placed in the mouth (Domm, 1980; Domm & Wilson, 1972). How- ever, it would also be adaptive to associate more than just the aspects of the object (appearance, smell) with gastrointestinal events, if the object in question were something actually ingested. In this context, potentiation makes sense; taste could flag these normal stimuli as food related. In keeping with this idea, odors that emanate from food are potentiated more strongly than the ambient odors merely present at the time of ingestion (Domm, 1972; Garcia & Rustinik, 1980; see Gauld & Droschl, 1981; Logue, 1993; and Becsora & Cunningham, 1987, for com- parable demonstrations involving vision).

We do not yet know whether potentiation is limited to ingestion learning systems, whether it is a property of the associative process per se, or what the underlying mechanisms might be, although there is some evidence that it can be understood within the framework of higher-order conditioning (Duffie & Droschl, 1980). Whatever the underlying mechanisms, they seem to be tuned to ecological features.

PRINCIPLES OF "SELECTIVE ASSOCIATION"

We now ask about the psychological and eco- logical organizing principles of selective associa- tion. Shettleworth (1985) and Timberlake (1983) suggest that situationally relevant responses are more readily acquired as operators. Inter- ested ecologically, "relevant" refers to those responses which are effective in the real world for obtaining the reinforcement. Interested biologically, "relevant" refers to those responses facilitated by the current motivational state. (Interpreted adaptively, these two senses should overlap.)

"Reinforced" or "similar" stimuli may be selec- tively associated. Tests and Tests (1976) sug- gested that taste and illness go together because they have similar temporal patterns. There is evidence for other determinants of similarity, including common modality (e.g., visual stimuli) or submodality (e.g., two colors or two shapes); (Becsora & Farrow, 1977) and in spatial location (Becsonora & Cunningham, 1987; Tests & Tests, 1975). From a psychologi- cal perspective, "relatedness" corresponds to common perceptual features.

However, "ecological relatedness" could also be due to common origins (as suggested for potentiation) or casual relationship. Common loci in space and time are ecological markers for objects and events. The acquisition of object representations would often be based on simul- taneous association, as opposed to the success- sive associations traditionally studied in conditioning. Simultaneous associations have
only recently come under investigation and are relatively little understood, especially in terms of their adaptive roles. The presence of certain traits can be influenced by various genetic and environmental factors. In the context of evolutionary psychology, the study of the selective pressures acting on species is crucial to understanding their adaptation to specific environments. The concept of niche construction, which highlights the role of organisms in shaping their environment, is a central theme in this field.

**Genetic and Specificity**

**General Processes and Specific Adaptations**

The pursuit of laws of the greatest generality is a major goal of natural science. In this spirit, behavior theory assumes generality across species and across domains within individuals. Our concern in this section is to examine the conditions under which this assumption holds. Natural selection directs attention to both general processes and specific adaptations. A general-specific antagonism arises only if one believes that everything falls into only one of these categories, a proposition for which there is no basis in the facts of biology or the principles of evolution. We will examine the reasons for specificity first, and then those for general processes.

**Forces for Specificity**

Fish swim, birds fly, lions pursue antelopes, ants scrape earth. Diversity is such a fundamental feature of life that it must be explained. It results from diversity in environments and selective pressures, diversity in the mutations and genetic combinations upon which selection acts, diversity of phylogenetic histories, and from accidents of history. Habitual differences make specific demands on organisms, which are reflected in sensory, perceptual, motor, and other capacities. Within-organism diversity is, in turn, produced by the different types of interactions organisms have with their environments in various domains. Predator avoidance, nutrient procurement, and parental all require different abilities. Similarly, the different sources of information (e.g., contact, audition, or vision), and within the visual domain, color, objects, etc., have specific cognitive properties (e.g., the importance of spatial mapping in vision but not gravity reception). It would be a serious error to assume that in the particular areas of plasticity and cognition the force for diversity was suspended.

**Forces for Generality**

General process approaches in biology (from molecular genetics to body fluid physiology) have been very successful; this approach should succeed in psychology as well. Why should we expect generality principles?

**Universal Properties of Environments**

The laws of physics testify to the operation of many general conditions of relevance to animals across all earthly environments: the operation of gravity, the laws of mechanics (relevant to any animal) tracking prey or actively avoiding predators), the validity of the laws of physics in all situations (inertial objects, the laws of optics. On ecological grounds alone we would expect (analogous or homologous) adaptations to these universal features of the world to hold across species and across domains. The existence of such highly general features as inertia in the operation of the vertebrate and cephalopod eye (analog) or contour exaggeration in vision speak to these general conditions. But what about generality for plasticity? Are such universals as (1) the importance of spatial and temporal constancy in mechanical causation, (2) the temporal direction of causation (presumably related to the propensity of forward versus backward conditioning), and (3) the constraints on the diversity of objects (providing the grounds for conditioning processes which generally from past to future events and from part to whole).

**Universal Prerequisites for Life**

Organisms must maintain certain essential physiological processes. Homeostatic mechanisms are universal. Other universal goals, such as nutrient location and consumption and reproduction, constrain or direct similar adaptations across species.

**Commonalities Due to Common Ancestry**

(Homology)

Just as common environmental factors tend to promote common adaptations, so does the common ancestry of organisms. For example, the universality of the neuron as a unit and the context of the nervous system by networks of these units constrains possible adaptations; the temporal properties of action potentials prevent individual neurons from tracking high-frequency stimuli. Common ancestry can produce widespread (although not universal) commonalities within taxonomic groups, such as the design of the eye throughout the vertebrates (Walls, 1942). The fact that animal displays can be used as indicators of phylogenetic relatedness demonstrates the relevance of common ancestry to behavior (Brown, 1972; Lorenz, 1971).

**Constraints on Adaptation**

**Environmental Constraints.** The necessity for an orderly and precisely timed process of development, especially of a structure as complex as the nervous system, makes many types of reorganization biologically practically impossible. Simon (1967) argues that construction of complex multi-component systems must be based on assembly of stable subsystems in a hierarchical structure. As a consequence, viable changes are likely to involve either modest changes in individual components or in the pattern of assembly of components. In addition, the path of development is such a way as to resist a wide variety of perturbations (this is Waddington's, 1966, concept of developmental homeostasis).

**Constraints from Common Components and Their Interaction.** Common components—whether derived from common ancestry (homology), similar selection pressures (analog), or both—lead one to expect general principles to apply across species and across domains. This is true both because the components offer certain opportunities for adaptation while precluding others and because they constitute part of the environment to which new genes must adapt. Thus the internal environment is a feature of the organism, which is very similar in most animals, must give rise to a set of selection pressures that constrain the range of viable physiological mechanisms. Such constraints, for example, would restrict evolutionary changes that disturb homeostasis. Parthenogenetic conditioning mechanisms based on presumed primordialization (in which the CR resembles the TR) would often be selected against in homostatic systems, since it would be adaptive to generate a response capable of neutralizing the anticipated disturbance (Hoch, 1982; Scholl, 1978; Siegel, 1979).

The constraints we have discussed in this section suggest that if a given mechanism has evolved to instantiate a particular principle, then there is a greater likelihood that it will evolve again in a different domain or species. This is simply because its existence indicates that it has a higher probability of occurring than other solutions. Within a species, a mechanism present in one domain is more likely to appear in other domains both for the reasons mentioned above, and because the physical presence of the solution in a particular animal allows for direct utilization (success) of the mechanism in other domains (Roth, 1976).

**Universal Models of Problem Solving**

There may be only one generic way to increase knowledge or competence: the generation of alternatives (behaviors, hypotheses, etc.) and the rejection or retention of them based on feedback from the environment (rewards, data, etc.). (Campbell, 1974, Dennett, 1976; The TOTE of Miller, Gelman, & Pribram, 1960). Something of this sort is seen even in the Protococci, Stent (1974), a model which according to pondering situation has a sequence of environments (trials and error), construction of the perceptual world, and problem solving in primates. In humans, the process is often conscious and voluntary. The universal value of this procedure explains its generality.

In sum, the factors discussed often work in concert to produce similar adaptations among all animals, among groups of animals, and across domains within species. Thus the structural and behavioral similarities of kangaroo rats and desert rats reflect selection pressures produced by the common desert environment, common ancestry, and conservative constraints on evolution and development.

**The Existence of Domain-Specific Adaptations**

There are many examples of plastic adaptations
that are both species-specific and domain-specific (Griffith, 1982; Hundt & Stevenson-Hinde, 1973; Milner, 1964, 1980, 1981, 1982), are not able to subsequent systems only at their final output. Modulars are also mandatory (they operate involuntarily and automatically) fast, and typically have a fixed neural circuitry and a characteristic developmental pace and sequence. Fodor holds that these features of modules are adaptive because of the underdetermination of the world and the necessity of fast action (of memory and perceptual arrays) independent of these modules, modules differ from the open-ended general central system. Fodor holds that because of their predispositions or constraints, modules are much more than the central system, with its multiple inputs and outputs, and unstructured operation (which he takes to be similar to the process of scientific confirmation). His claim that the rich collection of features listed above tends to co-occur in systems that analyze sensory input and language is unconfirmed, though there is suggestive evidence.

Degrees of Generality and Specificity

The arguments for generality and specificity reviewed at the beginning of the section suggest that a species possesses a particular generalization. The question should be whether the ability appears in any or all domains.

The logic of domain-specific specialization is elaborated in Fodor’s (1980) book, The Modularity of the Mind (see Schwartz & Schwartz, 1984, for a critical summary). Fodor, in his book, specializations in perceptual and linguistic input systems which serve to "separate the world into pieces that are not hard to grasp or to think" (Fodor, 1980, p. 40). Their outputs feed into a central general process system which accommodates a variety of input systems. A general process system is constructed general systems, in keeping with the general embryological process of differentiation. With respect to the nervous system general initial states might be a network of multi-connected neurons which are winnowed to achieve constrained systems. This is known to occur in development (e.g., developmental stages), and there is no evidence that the earlier systems have the competence of a general process system. A clearer example is the mechanization of motor routines, which are mediated by a general (conscious, voluntary) system at first, but which become progressively less accessible as they become more routinized. In the evolutionary frame, the prior appearance of a general system would require that produce adaptive systems wide changes, as for example, if a single change in all neurons or all of a certain class) could enforce them with more plastic properties. By skin pigmentation, for example, a mutation might affect melanin regulation so as to make all the skin darker.

On the other hand, the facts of evolution and development suggest that in many cases, specialized adaptations appear first and then become more accessible over time. Thus, in many vertebrate species, Pavlovian conditioning is present only in very well-defined domains, whereas in some mammals it is a widely accessible adaptation, which functions to connect arbitrary events.

Accessing to accessibility theory, the evolution and development of general functions involves an increase in accessibility of initial specialization (Roit, 1976a; Roit & Kalat, 1972; see also Gelman & Gallistel, 1979). With respect to many organisms, the child’s ability to adapt to the environment and to available to all systems, including cognitive and emotional processes. Moderately accessible adaptations operate in a narrower range of domains (e.g., spatial arrays in memory, vision, and touch). More accessible adaptations operate in single domains (unlike some of Fodor’s modules).

From Specificity to Generality: Evolution and Development of Intelligent Systems

Evolution and development may proceed either from the general to the specific or vice versa. On the one hand, modules or inaccessible adaptations could be carved out of a pre-existing network, in keeping with the general embryological process of differentiation. With respect to the nervous system,
Summary

Systems and capacities vary in the extent to which they are domain limited, modular, or accessible. Both domain-general and domain-specific systems are worthy of study, as is the evolutionary development transition from one degree of domain specificity (accessibility) to another. Their study will reveal some principles shared by both and others unique to each.

FUNCTION, PRINCIPLES, AND MECHANISMS

In this section, we try to show that mechanistic and adaptive approaches are complementary and can enrich each other. Our presentation owes much to a stimulating discussion (in the paper) by Shettleworth (1983).

Integration of adaptive and mechanistic approaches would enhance understanding of the phenomena and principles of psychology in two ways. First, it would extend the psychologist's traditional mode of explanation (description of principles and mechanisms), which is simply inadequate. Second, the adaptive-evolutionary theory perspective interacts with, and can enlighten, the type of understanding psychologists normally seek. This latter point will lead us into discussions of the relation between function and mechanism.

Biological Explanation

Research usually begins with the selection and characterization of a phenomenon to be explained, a reference phenomenon. In this case, a phenomenon can be described at different levels of integration, depending largely on the researcher's discipline. Thus, psychologists might describe a predator as a group of behaviors, or the avoidance of a specific predator, or in terms of the releases for identification of the predator. Neurophysiologists might describe the same phenomenon in terms of the neural circuits that mediate the recognition. We refer to the level at which a phenomenon is described as its reference level and define principles as statements about relations or regularities at that level. For most psychologists, principles would be statements of some generality relating environments to behaviors or mental events, or relating behaviors to motor events) to each other (Shettleworth, 1983). A first principle in the investigation of learning, for example, is the discovery of principles such as extinction, higher order conditioning, and the like.

The second goal of psychologists is typically the analysis of underlying mechanisms that account for reference phenomena or principles (Shettleworth, 1983). (As a starting point for analysis of mechanisms, we will take reference phenomena and principles to be equivalent.) The immediate precursors (cause) and consequences of the reference phenomenon are investigated, and/or it is analyzed into simpler units, or "mechanisms", that are usually both smaller (involving less behavior or neural circuitry) and fewer (than the reference phenomenon or principle).

Thus, avoidance behaviors might be studied with regard to their immediate environmental causes and consequences or analyzed into component learning processes, reflexes, or neural programs.

As N. Tinbergen (1951, 1966a) pointed out, a complete understanding of a behavioral phenomenon requires an answer to four questions, of which "What are the mechanisms?" is only one. The others are: (1) How does it develop in the life of the individual? (2) What is its evolutionary history? and (3) What is its adaptive function?

Roth and DeWit (1983) define two dimensions of explanation. The analytic-synthetic dimension spans levels of organisation and relates to the analysis of mechanisms or principles into smaller units (the search for mechanisms) or the synthesis of larger units from smaller ones (Tinbergen, 1967, Tinbergen's first question). The temporal-historical dimension places the reference phenomenon in time and includes Tinbergen's other three questions, dealing with development, evolution, and adaptation (function). These two dimensions of explanation are orthogonal: each type of explanation can be applied to phenomena at different levels of organisation, and every explanation occurs at a particular level of integration and includes a particular time frame. (Even mechanistic explanations include a brief time frame.) From immediate cause to immediate consequence.

We believe that by limiting ourselves to mechanistic and developmental (cause-and-effect) explanations, psychologists have limited the breadth of their understanding. But even if the psychologist's search for mechanistic (analytic-synthetic) explanations is accepted as the goal of research, adaptive-evolutionary perspectives can provide insights into the mechanisms that underlie behavior.

Relations Among Functions, Principles, and Mechanisms

Psychologists frequently suggest alternative physiological or psychological mechanisms to account for a behavioral principle. Thus, for the principle of habituation, three alternative physiological mechanisms are: (1) sensory adaptation (e.g., depletion of photoreceptor pigments); (2) transmitter depletion at a specified synapse; or (3) active presynaptic inhibition at a specified synapse. In nature, redundant mechanisms may underlie the same principle in a single organism, and, as Lehmari (1970) and Shettleworth (1983) have noted, even closely related species often achieve the same adaptive function by different mechanisms. Therefore, they conclude, what matters about a behavior, from the point of view of natural selection, is how it functions, not how it is achieved (its mechanism). Lehmari (1970) holds that "nature selects for outcomes" not mechanisms (p. 25). Shettleworth (1983) concludes that function makes contact with principles of learning at the level of principles, not behavioral mechanisms per se, and concludes the chapter that "considerations of learning as an adaptive phenomenon have no relevance at all to the traditional concerns of learning theory" (p. 13). However, the nature of this conclusion is a central theme of her paper and of this chapter.

The Problem of Equivalent Mechanisms

Two different mechanisms very rarely generate exactly the same result--the same principle. Indeed, finding different behaviors that follow from equivalent hypothetic mechanisms is the deplorable state of contemporary psychology. For example, different possible mechanisms of language delay--learning-interference, trace decay, learned safety, and aftertaste--may predict different behaviors. For example, the effects of frequency and type of taste experiences in the interval between ingestion of the target substance and the next instigation of the negative US (Domjan, 1983; Rotin & Kalat, 1971). Since these different behavioral outcomes can be discriminated by psychologists, they could also be discriminated by natural selection (except in the unlikely case that the alternative outcomes are of equal net adaptive value, and, even then, they would likely produce different behaviors). Nor is the actual evolution of a particular mechanism or set of mechanisms on its consequences (functions). Which mechanism ultimately appears is also constrained by genetic accident (mutations, recombinations, etc.), environmental events (some of which may be unpredictable and unique), and the feasibility of evolving, developing, and executing the mechanisms. Mechanisms may differ in the amount of genetic material, neural tissue, and attentional resources that they require and, hence, in the extent to which they cause abandonment or postponement of other potentially valuable activities.

Because of the rarity of truly equivalent mechanisms and different costs and likelihoods of evolving different mechanisms, it is unlikely that evolution is indifferent to mechanism.

Function and Mechanism as Different Aspects of the Same Principle

The question that function is linked to principles but may be unrelated to mechanisms (Shettleworth, 1983) depends on the distinction between principles and mechanisms. But this distinction is epistemological, not ontological. It depends on the investigator's perspective or discipline. Put simply, one researcher's principle may be another's mechanism. Pavlovian conditioning is both a mechanism of avoidance learning and a principle whose mechanism is sought. It follows that functions can be assigned to mechanisms as well as to principles, since principles and mechanisms are often interchangeable. Temporal (adaptive, evolutionary, or ontogenetic) explanations can be posited for any level of analysis.

Similarly, the same activity or principle can often be described as a mechanism or function. When an activity is viewed as a component of some more complex activity, it is a
mechanism. When the activity is viewed as a fitness-promoting trait, it is called a function. Natural selection is a function of imprinting, and a mechanism of mate selection. Thus, one cannot even hold the view that evolution acts on functions but not mechanisms, because many activities are simultaneously functions and mechanisms. In some cases, a principle or mechanism may not have a function. For example, the principle that the time required for a serial search through memory is linearly related to the size of the set being searched is a by-product of the particular search mechanism. It is unlikely that there was selection for linearity.

This conception and its implications can be made more concrete with an illustration which depicts an individual organism as a hierarchy of interacting, fitness-promoting activities (a functional hierarchy) (Figure 10.1). At the top of the hierarchy is the activity which is the ultimate function of all adaptations, behavioral or otherwise: the promotion of inclusive fitness. At the same time, this highest node spans all of the behavioral systems of the organism. As we move down the hierarchy we encounter functional activities which are more and more molecular, and of decreasing duration. (Figure 10.1.) For the organism psychologist typically study, certain broad categories of fitness-promoting activities can be recognized, such as parenting, reproduction, nutrient procurement, predator avoidance, sheltering, and so forth (Figure 10.1). The next level of activities would include, in nutrient procurement for example, detection of energy or nutrient deficits, food search patterns, food recognition, food capture, and so forth. These basic activities are built up of yet smaller activity units such as feature detectors, specific motor skills, and long delay learning. Obviously, this hierarchy can be extended downwards for many more levels and will vary from species to species. But we believe that all animals are organized in a hierarchical structure which is the basis for the construct of the psychologist's principles (e.g., the law of extinction) but not their mechanisms come from the fact that extinctions are more salient: the higher one is in the hierarchy, because it is easier to relate it to the promotion of inclusive fitness. In this sense, mate selection is more functionlike than recognition of one's own species, which is in turn, more functionlike than the underlying recognition mechanisms (e.g., imprinting or feature detection). But we must remember that natural selection produces whole organisms whose adaptations can be described at many levels.

Using Function to Study Principles and Mechanisms

Given the intimate connection between functions and mechanisms, it is surprising that adaptive considerations are so rarely applied to behavioral investigations. They could be of use in the selection of problems, in the search for principles and in the exploration of mechanisms.

FUNCTION, PRINCIPLES, AND MECHANISMS

1. It gives the investigator a general idea of what the system under study is about. A beginning student of football would be well advised to know the purpose of the game before delving into mechanisms. Consider the relation of conditional response (CR) to unconditional response (UR) in Pavlovian conditioning. According to Hollis (1962), conditioned responses are adaptive. Given that URs have evolved to improve the animal's adaptive measure with the US, it will often (but not always) be adaptive for the animal to prepare for the US's arrival by beginning to emit the same response in advance of the US. If motivation helps one-vestibulate and digest food, it may help even more if one has begun anticipating before dry food has a chance to gum up the mouth. The virtue of this formulation is that it can account for (and even predict) situations in which CRs will fail to mimic URs on the grounds that other responses constitute more adaptive alternatives. Thus chicks approach, peck, and struggle up to visual CRs which signal warmth, whereas they twitter and crouch (UR) in response to the warmth US itself (Wasserman, 1971). Why? Because in the chick's natural environment, the warm-producing event is the mother hen and approaching, pecking, and struggling up to her elicits brooding behavior (Hogan, 1974). Twittering and crouching when exposed to distal visual CRs given off by the hen would honor the principle of stimulus substitution but would be maladaptive.

2. Function can help in the discovery of principles of behavior. Principles can be discovered by use of three routes: (a) observation of empirical relations, (b) working up from mechanisms (e.g., making assumptions about mechanisms and drawing implications from those
natures, nurture, and the evolution of plasticity

Nature and Nurture

No issue has generated more controversy in psychology than the nature-nurture issue, and contemporary debate about sociobiology shows that the question is far from settled. It is still often assumed (1) that species-specific behaviors are necessarily innate, (2) that demonstrably learned behaviors are not naturally selected adaptations, and (3) that the behaviors that genes code for are necessarily unlearned and invariable. Each of these assumptions is incorrect and worth examining briefly.

The first two assumptions were countered in Hallman's (1967) study of "how an instinct is learned." Hallman showed that learning plays an important role in the development of the species-typical help-seeking response of young gulls. His conclusions in no way contradicted Tinbergen and Perdeck's (1959) findings that the response was triggered by very specific specific stimuli, nor that the specificity was adaptively tuned to the gull's way of life. But they did show that much of that specificity and adaptiveness was based upon experience, albeit experience which was a reliable aspect of the gull's niche (i.e., stimulus produced by the parent's beak and movement). Similarly, human language is a quintessential species-specific adaptation that relies heavily on experience.

Conversely to the second assumption, the fact that learning is often adaptive is itself strong evidence for the importance of innate, naturally selected determinants of behavior. Just as the vast majority of mutations are disadvantageous, many effects of experience on development would be maladaptive, if not for adaptive constraints on plasticity. According to Lorenz (1965, p. 200), "an explanation is needed for the inductive fact that learning practically always results in an improvement of the teleonomic function of behavior." That explanation certainly involves natural selection. If natural selection had made tissue damage rewarding or the hunger-reduction punishing (rather than the reverse), the law of effect would often lead us astray.

With regard to the third assumption, innate behaviors are often easily modified (the cat's innate preference for sugar solutions can be reversed by pairing one of such a solution with nausea), and genetically programmed behaviors are often learned. The "gene for" a given behavior may cause that behavior to appear, for example, by predisposing the animal to learn it or by promoting other behaviors which induce conspecifics to teach the behavior in question.

Effects of Plasticity on Evolution

In the next section we will examine selection pressures favoring learned vs. unlearned adaptations. However, it is often forgotten that plastic adaptations have important effects upon selection pressures and on the evolution of other characteristics. Learning can enable an individual with a novel mutation or characteristic to learn how to exploit new traits that might otherwise be maladaptive. Learning abilities can enable a species to invade new niches, thereby exposing itself to new selection pressures (Bisher & Morris, 1985; Piveteau, 1976). By enabling subpopulations to develop adaptations to local circumstances, learning may promote diversity, racial variations, and speciation. This is especially true when cultural transmission of learned behaviors is involved. In birds, the learning of local song dialects may have led to the evolution of the ability of adults in some dainty cultures to digest milk sugar (lactose) (Simons, 1970).
Learning can be a first stage in the programming of innate behaviors. If an organism is capable of a particular form of adaptive learning (e.g., associating X and Y), selection pressures would subsequently favor genes that would improve this learning (e.g., a predisposition to associate X and Y). As the evolutionary psychologist James Mark Baldwin (1866) pointed out, this could ultimately lead to hard wiring of this initially learned relation. Therefore, in species with general learning abilities, learning may have a multiple purpose predisposition that can evolve without the need for Lamarckian inheritance. If so, this would be an important and relatively uninvestigated benefit of plastic abilities (Baldwin, 1866; G. Batson, 1963; Rescorla, 1971; Schull, in preparation).

The Evolution of Plasticity

In this section, we apply the adaptive-evolutionary approach to a central issue in the nature-nurture controversy: When will evolution promote behavioral adaptation which depends importantly on learning or experience, and when will it promote nonplastic adaptation? Our discussion combines our own thoughts with those of Johnstone (1982), who has written the only systematic evaluation of the costs and benefits of learning (also see Paliam & Dunford, 1980). Mayer (1974) observes:

"Considering the great advantage of learning, it is remarkable how relatively few of its advantages have traditionally been generally accepted; few behavior patterns have been replaced by the capacity for the storage of individual acquired information." (p. 205).

Besides the obvious advantages that learning enables individuals to adapt to their particu- lar environment (i.e., learning may be a key advantage in making their own parents, which would be difficult to program genetically. This allows the individual to choose mates that are sufficiently dissimilar to achieve optimal outbreeding.

In some other situations, behavior must be genetically programmed. Cuckoo and cowbirds have near relatives. Since they are reared by other species, species recognition (required for mating) must be innate, and it is. Furthermore, learning carries costs. It tends to require a period of dependency, vulnerability, and inconstancy while the young or naïve organism acquires the appropriate recognition. It may also require more parental investment.

Learned solutions may also be more fallible than fixed solutions; environmental quirks can magnify overly plastic organisms. This consideration leads Finklin and Odling-Smee (1975) to distinguish three temporal frames within which adaptations occur: The phylogenetic frame involves adaptive change in the organization of the gene pool. At the organism level, it responds more rapidly to changed circumstances, and involves environmentally induced changes in the developmental history of the organism. Finally, learning involves even more rapid (and often reversible) change in the organization of the individual's nervous system. Relatively rapid and unpredictable changes in the environment will promote more adaptive change at the level of learning. Unpredictable changes that occur several times in the individual's lifetime would promote plastic adaptations; relatively slow (e.g., environmental) changes and predictable rapid changes (such as during the diurnal cycle) would favor genes for adaptations which do not involve plasticity. In addition to unpredictable environmental variation, unpredictable spatial variation will also promote plastic adaptations.

Too little is known about the ontogeny of plasticity to make detailed arguments about the relative costs of plastic versus nonplastic adaptations. In some cases (e.g., mates with 40 different kinds of prey. Even in a stable, predictable environment, the genetic and developmental plasticity inherent in the food selection system might be larger than simply programming the narrow niche to which your parents "fed you." Given that the general purpose of learning is to acquire adequate learning, not just an "easy" solution, requires more resources, the cost of plasticity is relatively high. If the plastic adaptation is purely a chance event (e.g., the Carnivora and Insecta), indeed, outside of taxonomic classification, the most informative piece of information about an animal is often the type of food it eats.

For some species, such as the large mam- mals and carnivores, the most complex adap- tations involve capture. For others, the most complex adaptations involve eating, such as grazing mammals, capture is less significant than identification. We will concentrate on identification and choice of appropriate foods, one portion of an integrated sequence.

The general problem in food selection is to obtain adequate amounts of energy and nutrients, while avoiding dangerous levels of food-associated toxins. This requires recognition and evaluation of objects in the environment and detection of internal metabolic states (ranging from negative energy balance to positive nutrient deficiency) (see Root, 1979, for a review). A variety of strategies have evolved to deal with this problem, they can be arrayed along a dimension that varies from specialist (limited range of foods, with specific adaptations to recognize and obtain them) to a generalist (wide range of foods with a higher degree of plasticity).

The specialist strategy is often the least com-plex, psychologically. At its extreme are ani- mals that consume only one type of food, such as the highly specialized insectivores and the Kalsi bear, which eat only a few species of eucalyptus leaves (Deshmukh, 1988). In such "unicorns," food recognition is typically programmed in the brain and based on unique stimulus properties of the food. Detecting the need for food is correspondingly simple: finding the simple hunger stimulus is adequate to the animal, not the hunger stimulus must be adequate to the animal, not the hunger stimulus but animals need only that "raw" signal is required. Other animals consume a few types of food, with multiple programmed recognition systems and one or a few internal nutrient-deficit detectors. The best studied example is the bow- er bird (Ptilonorhynchus minor). Carnivorous or invertebrate animals show many commonalities with the "unicorns" in food selection strategy. Since animal food is usually an adequate source of all nutrients, a single metabolic-state detector may suffice. And, at least in some cases, it is possible to pro- gram recognition of the food category; thus, some species of insect-eating frog code small moving objects. The psychological aspects of food selection are of more interest for general herbivores and omnivores, whose broad range of acceptable food
THE ADAPTIVE-EVOLUTIONARY POINT OF VIEW IN EXPERIMENTAL PSYCHOLOGY

reduces the impact of biologic, climatic changes, and more specialization competed for particular foods. In some animals it would be almost impossible to genetically program recognition and acceptance of all potential foods and rejection of all nonfoods. These generalizations must deal with food via open programs (Mayr, 1974), which acquire information about the edibles and toxics in the environment. The wide range of potential foods carries a risk of nutritive imbalance or deficiency since few plants ever contain all nutrients. The wide range of foods also increases the chances of poisoning, since plants often evolve toxins as a defense against predators. For these reasons, food selection presents problems that are complex and difficult problem.

Consider the large grazing mammals. Their food is easy to obtain but low in energy density, so they must spend much time consuming large quantities (Westoby, 1974), to minimize nutritive imbalance, they select appropriate proportions of various plant types (Belyaev, 1978). To cope with plant toxins, there are multiple mechanisms. Grazers may learn to avoid toxins and utilize various consequences of eating different foods (Westoby, 1974; Zehorik & Haupt, 1975). Insect atten activity, such as avoidance of bitter, hop through the appropriate consuming too much of certain toxins. However, low levels of bitter toxins are so common in the foods plants that general herbivores easily can afford to select bitterer foods completely. Many natural toxins can be tolerated at low levels because detoxification occurs in the gut and/or liver and toxins can be excreted. In this context, the common general herbevory strategy of “spreading the risk” (Freudental & nutritionally, to not consuming too much of any single food source make adaptive sense.

The Rat: A Study in Omnivory

The laboratory rat and its wild progenitor (Rattus norvegicus) have been the subject of much research on food selection. The omnivorous nutritional requirements are very similar to the requirements for humans. Its ability to consume both animal and plant products was demonstrated conclusively in the classic work of Curt Richter (1943) and others, as was its ability to avoid poisons, many of which were specifically connected with the rat in mind (Barnett, 1960; Richter, 1960; Richardson, 1963). More recent work has elucidated some of the mechanisms underlying these abilities (Barret, 1975; Barnett, 1960; Belyaev & Milgram, 1960; Kremer & Alloway, 1977; Ronin, 1968).

Until tasting, one totally avoids food, milk, is provided by the mother: This permits survival and growth while basic regulatory, selection, or other behavior (Bals & Teichler, 1960; Galaf, 1961). However, even in the first few days of life, the rat pup can learn how and where milk is to be obtained (Bals & Teichler, 1960; squire aversions to odors (Rudy & Chattia, 1975). The weaning period is a sequence of changes in food selection, and that effect transitions to independence (Galaf, 1961).

The rat has innate equipment for dealing with the bewildering array of potential foods. It has an innate tendency to prefer sweet tastes (an ecological correlate of a particular natural energy source, sugar) and to avoid bitter tastes (correlated with toxins in nature). Furthermore, of refers to at least three distinct and internal: energy, water, and sodium deficiencies. The sodium deficit is innately linked to sensory dissonance in rats (Hoff, 1969; Kieckhefa & Wolf, 1966; Richter, 1966; Schull, 1969). This is a rat that has responded to the sodium food shown to enhance preference for sodium salts the first time it becomes sodium deficient (Flinkmann, 1966; Richter, 1966; Schull, 1969). There may be an equivalent training of water intake linked to the internal signal of water deficit ( thirst) and an innate signal of energy deficit: that is, for sodium, and perhaps water and energy, there are undifferentiated specialist subsystems within the generalist (Ronin, 1969).

Fifth, there is an important sociocultural source of information about dangers and beneficial foods. Wasting rats develop preferences for foods that adult rats consume, hence profiting from the experience of the older rat (reviewed in Galaf, 1977). The information is transferred by a number of routes, all mediated by the rat’s preference for familiar, safe foods. Wastings prefer to eat at food sources where adults have eaten, feasting on rot where adults are eating, and are exposed to some of the characteristics of adults’ diets through mother’s milk and the experience of an adult who has previously lived in a particular diet (Galaf, 1977; Gailef & Wigmans, 1983; Povas-Andrews & Roper, 1983). Most of these affect seems to be mediated by olfactory cues.

The rat’s well-documented ability to select foods that correct a variety of nutritive deficiencies was originally attributed to innate recognition of specific substances; for the development of acquired preferences (Richter, 1948; Young, 1949). The discovery of learned taste aversion led to the suggestion that specific hunger was primarily aversive to deficient diets (Rout & Kalat, 1971). While it is clear that aversion does play an important role in specific hunger, there is also evidence that animals and probably positive preferences based on postdigestive benefic; rapid satiation has been identified as the most potent US (Booth, Stoddard, & Neuber, 1943). Toxic aversions are often learned much more readily than preferences (Rout & Kalat, 1971; Zehorik, 1975; cf. Booth, 1982), perhaps because, due to the threat posed by many noxious stimuli (e.g., poisons, predators), there may be only one opportunity to learn.

Thus, as an ensemble of integrated behavioral, physiological, and psychological mechanisms helps the rat select an adequate and safe diet. For most nutrients, the rat’s general ability to learn about the consequences of foods obviates the need for innate recognition of specific dietary substances. In comparison to many other organisms, dietary deficiencies are relatively. Rather, when ill from any variety of deficiencies), it learns what foods relieves or alleviates its duties.

Why, then, is there a built-in system for sodium (reviewed by Denton, 1962; Rodger, 1967; Rout, 1975; Rout & Kalat, 1971)? Sodium is a major and essential constituent of body fluids, and its level is homostatically regulated. It is produced by processes of recovery from sodium deficiencies, sodium deficiency is rather common in nature. The prior existence in many ani- mals of taste receptors tuned to sodium reflects the importance of sodium and may have made the evolution of sodium hunger easier. Furthermore, because the initial phases of recovery from sodium deficiency may not be reinforcing, it may be that the preference acquisition processes discussed above will not work for sodium.

We cannot yet explain how rats successfully maintain balanced diets in the cafeteria situation, and how they avoid, rather than choose, nutrients.
Adaptive-Optimization Approaches: Foraging

We presented a qualitative and functional approach to food selection. More quantitative analyses of function are possible through the application of optimization theory. This new approach has been applied most extensively to the analysis of food selection, in the form of optimal foraging theory. While it has developed independently of mechanism-oriented approaches, McNab and his colleagues have studied both aspects of foraging (McFarland 1977a, 1977b), and the two approaches are currently converging.

Optimality Theory

Mechanistically oriented investigators often attempt to generate quantitative predictions of behavior by modeling underlying mechanisms. However, prediction-via-mechanism is very difficult to carry out in complex systems (McFarland 1977b). Optimality theory is an alternative prediction-via-function. It assume that natural selection has produced animals which behave in the most adaptive way possible when faced with the kinds of choice typical of their niche. This approach encourages analysts of opportunities and constraints to be allowed by the environment and of the animal's capacities and limitations. One can then estimate costs and benefits of the various behavioral options facing the animal and determine the optimal behavior. If the prediction in not confirmed, one can review the model of costs and benefits. Optimality theory assumes, but does not test, the hypotheses of optimality (cf. Dawkins, 1982: Gould & Lewontin, 1977; Krebs & Davies, 1984). Rather, it is a discipline program for identifying and quantifying selection pressures, organismic constraints, and behavior.

The advantages of foraging for optimality theory are more important: Nutritional requirements are quantifiable and there are clear measures of success: intake, weight, growth, and so forth. In most species, feeding occurs frequently (unlike predator avoidance or copulation) and is easily observable. Finally, because operant psychologists have developed sophisticated methods for the control and analysis of food-presentation behavior, a large data base with which to test quantitative optimization predictions is rapidly accumulating. Here we will emphasize the implications for the psychologist (for reviews of theory and data, see Collier, 1983; Commons, Herrnstein, & Rachlin, 1982; Kamal & Sargent, 1981; Krebs & Davies, 1981, 1984; Lea, 1981; Pashler, 1984; and Staddon, 1983).

A first problem to decide upon a criterion of organismic success. Ultimately, natural selection's criterion is inclusive fitness, but the animal and the optimal foraging theorist may adopt a more proximal and measurable index of success, such as minimization of time spent foraging or maximization of energy intake or net rate of intake. Which index is appropriate depends upon some extent upon circumstances, but for example, whether time spent foraging increases the risk of predation (Schwartz, 1979).

Basic problems facing foragers have been investigated (Pyke, Pulliam, & Charnov, 1977). Which food items should be eaten? Which foraging sites ("patches") should it choose? When should it abandon a patch? What path through a patch should it take? The detailed answer to these questions depends on the specific case under consideration and can frequently involve laborious computerization. However, Lea (1981) points out that the first three questions have a general and simple solution: accept an encountered prey type (or enter a patch, or stay in current patch) "so long as the net gain of doing so exceeds the 'opportunity cost,' the possible return for doing something else" (p. 381). Thus, when high quality prey are available, the animal should be selective. For example, rate prefer shelled to unshelled sunflower seeds, but when the ratio of shelled to unshelled drops below about one to five, they begin to consume unshelled seeds as well (Collier, 1985). More practically, Charnov (1976) showed that if fruits are valued as the nutritional value of the food divided by the total time spent obtaining and ingesting it, then the animal should eat an all-inclusive diet in an all-ornothing fashion if its net food value is greater than that of the diet without. Similar formulations hold for patch choice and abandonment of patches.

An Example

The optimal foraging approach has been applied to the selection of muscles by shore crabs (Carcinus maenas) (Elder & Hughes, 1970). The crabs must break the musel shell. Calculations
of the energy value of different sized muscles and the time spent breaking the shell indicates that the optimal behavior is to eat intermediate sized muscles—larger muscles take too long to break and smaller muscles don’t have enough muscle (energy/handling time) is highest for intermediate size (Figure 10.2). Thus by assuming that the crab is an optimal forager, one can predict its preferences, and the predictions are approximately correct (Figure 10.3), although crabs do consume sizes quite deviant from the optimal. As predicted, crabs are more likely to select the matching law than size, since the existence of a patch is critical to the foraging animal, more attention must be paid to the fact that the matching law sites became depopulated as the animal foraged, while unforaged patches are replenished. The costs of switching must also be considered; too broad a frame would make an animal insensitive to small changes; too narrow a frame would produce erratic responses to random fluctuations. The answer should vary across species, environments, and prey types (see Shettleworth, 1984).

**Optimality and Operant Approaches**

Threaten the operant and optimality approaches emphasize the functional economics of steady-state behavior, underlying mechanisms and acquisition processes are of interest as well. Herrnstein and Vaughan (1980) have suggested that steady-state preferences develop through “mediation”—continuous preference shifts toward the alternative with the highest rate of reinforcement. Pashino (1981) and Aversa and Faridel (1981) argue that pigeons do not evaluate rates of reinforcement in terms of net energy intake per se, but in terms of rates in duration in this case the two are identical. The pigeon can sometimes result in choices which are far from optimal, as when animals choose immediate small rewards over delayed large rewards (Pashino, 1981). But in nature, this rule of thumb may, nonetheless, make adaptive sense for species whose prey are likely to become unavailable with delay (through escape or prediction by a competitor).

**Mechanisms of Optimization**

Theorists have proposed that optimal performance often requires that agents acquire the information on which optimal performance depends has yet to be explored. Plasticity will be involved in learning about densities, nutritive values, and the searching and handling costs of different prey types. The animal’s experience of the variability of the environment (time or space) might have influenced the time spent gathering information to deviations in rates and baselines. Special representations of patches and associated travel times may be used to decide how and when to move between and within patches. Decision rules may themselves be learned (see Staddon, 1980, 1983, for a signal detection treatment of this problem). Furthermore, there may well be decisions about the costs and benefits of searching for one or more prey which depend upon constraints in cognition (see discussion of search images below).

Optimality theory may also help us understand why plastic abilities are so common in various species. Over what time frames should animals be integrating the information they sample? Too broad a frame would make an animal insensitive to short-term changes; too narrow a frame would produce erratic responses to random fluctuations. The answer should vary across species, environments, and prey types (see Shettleworth, 1984).

**Varieties of Complex and Plastic Adaptations**

One of the virtues of a functional perspective is that it brings into play phenomena and mechanisms which might otherwise be overlooked in process-oriented or paradigm-oriented classifications (e.g., Björklund & Holland, 1976). In this section we try to highlight the complexity and diversity of plastic adaptations in aspects of feeding other than food selection and foraging and in other domains.

**Plastic and Complex Adaptations to Feeding**

Search

Food search involves strategies (which may not
be learned), the ability to represent the spatiotemporal environment and its food sources, and movement for this representation. Olson’s (1970) laboratory studies on rats illustrate all of these capabilities. In an eight-arm radial maze, with each arm baited only once, rats show a strong win-shift strategy, rarely revisiting an arm before sampling all of the others. Contrary to reinforcement theory, they do this more readily than learning to return to a previously baited arm. On reflection this makes sense having depleted the food supply in one arm, the least likely place to expect to find food in the same location. Even more impressive, chimpanzees, after watching an experimenter in an outdoor enclosure hide nine preferred food items, and nine less preferred items, visit the locations with the more preferred food first, in a path that minimizes the total distance traveled (Meenail, 1979).

March tits (Parus palustris), who store food in the wild, have similar capacities (Shettleworth & Krasa, 1980). The birds are allowed to cache 12 seeds in 97 sites on large trees ("trees") in an experimental room. Later, they recover the seeds without exploring too many empty holes, which is more than any other species of birds (Stavisky, 1975; Menzel & Erber, 1978). Honey bees (Apis sp.) will learn to visit up to nine different dishes marked with scents at different times of the day (related to different flowering times). When the bee approaches a feeding source, it identifies and remembers the color for the period of some seconds leading up to and including landing on the flower, the scent while on the flower, and the location (landmarks) in the first few seconds after departing (Menzel & Erber, 1978; Oponent, 1981). These are among the best examples of temporarily constrained learning.

**Capture and Handling**

Capture and handling of food, inexperienced red squirrels (Sciurus vulgaris) open hand nuts by gnawing a nutcracker (Dobie, 1967; Eibesfeldt, 1979). Experienced squirrels gnaw one or two long-billed furrows and then cruch and such a sophisticated specialization as apparent movement. Learning is not typical instrumental learning, since the skill is acquired even if the kernels are removed from the nuts.

**Skill Acquisition**

Skill acquisition can also lead to subspecialization within a species. Learning (1979) reports that a number of bird species are capable of ingesting nectar from particular types of flowers, becoming more specialized and more efficient as they learn. The birds have developed different techniques for opening nectar and these skills are transmitted from parents to young (Norton-Grioffth, 1969).

**Varieties of Complex and Plastic Adaptations**

The wide range of adaptations present in one domain (such as mechanisms, such as the spatial and temporal representation of objects) is not unique to one domain. Many mapping abilities involved in food search and storage, also subserve other major functions, such as reproduction, social, and gene transmission. For example, some learning processes, as well as, although other mechanisms, such as, along the way, might be unique to one domain. This illustrates two points made earlier: (1) Adaptations exist over a range from the specific to the very general. The second (2) they are organized in a lattice hierarchy (Figure 1), in which the nodes at each level can fall under a number of higher nodes in which the same element may serve more than one function. Adaptive specializations described for homing and migration in a number of bird species, including learning of complex navigational systems, can be translated into analogous terms for navigation. The role of magnetic, visual, and sun position systems can be translated into analogous terms for time of day and season (see Kesten, 1981).

**Animals and Evolution**

One of the most intriguing areas of natural selection is the existence of a wide variety of adaptive specializations (Newman, 1970). Important observations of primitive behavior in the field (e.g., Kummer, 1960) and laboratory studies of behavior in chimpanzees (e.g., Premack & Woodruff, 1978) on test such problems as the perception of others, the "personalities" of conspecifics, and interactional (impersonal social roles). Perception

Just as navigational and social competencies involve both feeding and reproductive functions, so do many perceptual and motor abilities subserve adaptive behavior in virtually all domains. Universal features of perceptual systems are the obvious ones, and include the representation and extraction of information in the environment. For example, the ability to detect and avoid predators is often linked with spatial representation abilities. For example, herbivores have mechanisms for identifying and avoiding predators, and are thus capable of navigating through the environment. However, this ability is not dependent upon the same mechanisms that are involved in identifying and avoiding predators. The ability to recognize objects in the environment is vital for survival. This ability is not limited to visual perception, but also includes auditory and tactile perception. Audiovisual perception is also important for survival, and includes the ability to detect and avoid predators, and to recognize objects in the environment. Audiovisual perception is also important for survival, and includes the ability to detect and avoid predators, and to recognize objects in the environment.
CONCLUSIONS

It is ironic that by aspiring to account objectively for all behavior of all organisms in terms of a few all-encompassing principles, behavior theory narrowed its scope unnecessarily, in the belief that any organism and situation would suffice for the discovery of universal laws. Behavior theorists tended to avoid phenomena which did not emerge from within the established paradigm and so did not explore many important and tractable plastic phenomena. Their rejection of mental representations and other cognitive processes further limited their scope (see criticism by Griffin, 1976). This was particularly unfortunate because the study of plasticity was not a major concern of any other subfield of psychology or any other discipline. Nonetheless, behavior theory did establish and explore at least some special ability to perform well in arbitrary situations and did develop highly refined techniques to analyze adaptive behavior.

The study of animal learning and behavior could only be enriched if behavior theorists would bite off more than they could chew. Increased attention to diversity would not impede the pursuit of general laws of learning. On the contrary, truly general laws (learning will necessarily encompass principles of diversity. The generality of some associative laws has in fact been confirmed by the discovery of irrelevant or irreconcilable to general process premises. Our basic point in this chapter is that the study of principles and mechanisms of behavior and mind is enriched and facilitated by adaptive and evolutionary considerations. It is enriched because a full understanding must include adaptive and evolutionary explanations and because ecological perspectives reveal a much wider range of plastic and complex behaviors than have been previously studied by psychologists. It is facilitated because knowledge of function (adaptive value) can directly and indirectly guide research on principles and mechanisms under study by anthropologists and biologists and make specific predictions about behavior. We discuss principles grounds on which one can predict the relative value of genetic programming and experience in the determination of particular behaviors and the likelihood that a particular adaptation or principle will be general or limited to particular species or domains. Ecological perspectives reveal a much wider range of plastic and complex behaviors than have been previously studied by psychologists.

The evidence for adaptation and evolution in general is overwhelming, but at the same time the data explicitly support it in the domain of behavior are meager. It is a well justified art of faith that those principles are powerful determinants of behavior. Adaptive explanations are easy to abuse. With a modest amount of cleverness, one can concoct an adaptive explanation for anything. But this need not be confused with reasoned predictions, based on knowledge of evolution and ecology, as illustrated by research on foraging.

We are espousing an adaptive-evolutionary approach, we do not mean to imply that this area of biology provides a completely firm foundation to be trusted uncritically. Evolutionary biology is itself in great ferment (Kenen's College Sociobiology Group, 1983). While the facts of evolution are universally accepted, there is still debate about whether all characteristics are naturally selected biological adaptations (Dodd & Lewontin, 1970). There are also questions about the pace of evolution and the levels of selection: When are genes, individuals, groups, and species units of selection? These are questions to which psychologists have much to contribute, because these processes often hinge on the role of pay- ing phenomena, which were initially seen as irreconcilable to general process premises. Our basic point in this chapter is that the study of principles and mechanisms of behavior and mind is enriched and facilitated by adaptive and evolutionary considerations. It is enriched because a full understanding must include adaptive and evolutionary explanations and because ecological perspectives reveal a much wider range of plastic and complex behaviors than have been previously studied by psychologists. It is facilitated because knowledge of function (adaptive value) can directly and indirectly guide research on principles and mechanisms under study by anthropologists and biologists, and they frequently draw upon the psychological literature since psychological phenomena mediate the interaction of culture and biology (Lounet & Wilson, 1981; 1982; Pullum & Danford, 1980).

Perhaps our major point is that psychology is a particularly interesting branch of biology. Thus, while this chapter has emphasized the contributions that biological perspectives can offer psychologists, the potential contribution of psychology to neighboring disciplines in the life sciences is very great, if psychologists recognize their kinship to those disciplines, and if they recognize that evolution necessarily gives rise to both human and natural regularities. Regularities in the world and constraints in the origins, structure and, development of organisms create a small number of recurring themes. Competency, diversity in environments and chance span diversity and variation on those themes. To quote from the last line of Darwin's The Origin of Species, "Whilst this planet has gone according to the fixed law of gravity, from so simple a beginning so much beautiful and so wonderful have been evolved."

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In this chapter motivation will be studied from the point of view of both neuroscience and psychology. Given that psychology is the dual study of behavior and mental processes, this chapter is designed to meld these traditions: the study of the nervous system, the study of behavior, and the study of mental processes. A dominant theme in this field has been the effort to understand drive and reinforcement in neural terms. This research is becoming more cognitive and more clinical as the neurotransmitters we are studying—for example, monoamines, opiate, and brain-gut peptides—are proving to be involved in both specific behavior categories, such as feeding, drinking, mating and aggression, and in general categories, such as stress, drug seeking, depression and psychosis. These categories involve both motivation and cognition, and many of the neurotransmitters appear to play similar roles in animals and humans.

The neurochemical correspondence between animals and people was the discovery of the century. Human specialization seems to lie in the complexity of brain anatomy more than in brain chemistry. Most human neurotransmitters have been found in animals and even in microorganisms as primitive as the amoeba. Opiates induce feeding in rats and amoeba. The human of today is the result of a chemical inheritance that is relatively unchanged in spite of an extraordinary anatomical evolution. There seem to be only dozens, or perhaps hundreds, of transmitters for billions of neurons. Evidence will be presented to suggest that certain

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