

PART ONE INTRODUCTION

Chapter 1 Learning and Behavior: Conditioning

<etym>The English word learning probably comes from an Indo European root, leis, which meant a track or furrow. Before reaching its present form, it went through many changes: læstan, leornian, lernen. At various times in the evolution of our language it might have been understood as following a track, continuing, coming to know, or perhaps even getting into a rut. The verb last, to endure, came from the same root.

The Language of Learning and Behavior
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What is learning? Any satisfactory definition must include learning where things are, learning what has happened in the news, learning how to get along with people, learning definitions, and learning how to play a game or ride a bicycle. But how is learning what to say related to learning what to do and how to do it? How is learning how something works related to learning how to use it? Do these examples have anything in common? There is at least one thing we can say: whatever else goes on, you're different after having learned something than you were before. Something about you is new.

It's usually easy to see what's new. We can say some things we couldn't say before or do some

things we couldn't do before. But how did that happen? What are the sources of our new behavior? This book deals with what we know about the answers to questions like these. Before we can get down to the details, however, we need to cover some preliminaries. We need to worry about the behavior already there before learning begins. Before we can even do that we need to consider what behavior is—not just ours but also the behavior of the many varieties of other organisms with which we humans share our planet. Throughout all of this, behavior will be paramount. We are who we are because of what we can do, and everything about us evolved in the service of our behavior.

We'll start by seeing what behavior is like without learning. We'll examine its origins and its evolution and its development. With that foundation, we'll next consider learning when there are no words. We humans are special particularly because we talk. We talk so much that we find it hard to look at the behavior of the nonverbal creatures with

KEY TERMS: Antecedents, Behavior and Consequences (ABC) in a Three-term Contingency; Behavior Analysis; Behaviorism and Mentalism; Behavior Hierarchy; Function and Structure; Response, Response Class, Sponse; Stimulus (plural = Stimuli).

which we share our world without projecting our words onto them. In many ways they are as alien to us as extraterrestrials. We have to approach them without assuming that they think like us. To make sense of their behavior we must not assume that they do what they do by first talking to themselves about it. Only after we have seen how nonverbal learning works will we be able to appreciate the new kinds of learning that words make possible. We will also see that nonverbal learning provides the underpinnings of verbal learning: we cannot do anything with words unless they are built on what was there before words existed. Once we get that far, we'll be ready to talk more clearly about topics especially dear to us, like human language and memory and cognition.

Now let's get back to learning. Suppose I'm unfamiliar with the word *phenomenon* and then I notice it in a sentence. I may decide from the context that it means something like an event worth noticing. If I look it up I might find it defined as an event that can be observed and probably also as a remarkable or unusual person or thing. The definition might show the word as a singular noun with *phenomena* as its plural, and this form of plural, so different from the usual final -s, might suggest that this is a pretty old word with Latin origins. What I learn by checking its definition could be useful the next time I come across the word even if I hardly ever use it myself.

But what about the definition of the subject matter of this book? What is this phenomenon called *learning*? The word doesn't give us trouble in everyday talk, but a dictionary definition telling us that it means getting to know something or gaining knowledge and skill isn't very helpful. The word *learning* is more familiar than *phenomenon* and yet is much harder to define. Sure, we can usually say whether we've learned something and we can usually agree on what counts as learning. Even so, we run into problems when we try to frame a definition. For example, a textbook might define learning as a relatively permanent change in behavior resulting from experience (e.g., Kimble, 1961 pp. 1–13). But what is meant by *behavior* and by *experience*, and how permanent is *relatively permanent*?

Staring at an eclipse of the sun is an experience and if it damages your eyes it will certainly change your behavior. Yet if I told you this damage was an example of learning I hope you'd disagree.

THE LANGUAGE OF LEARNING AND BEHAVIOR

From the start we must face the fact that we won't be able to define learning. There are no satisfactory definitions. But we won't let that stop us. We can look at how organisms come to behave in new ways. In our study of learning, we'll ask two very different types of questions: (1) What is the nature of these events we call learning? and (2) What is the best way to talk about them? Our main concern will be to show how learning works. What are the conditions under which organisms learn and what happens as they do so? This will give us plenty to do, so we'll only occasionally consider theories of learning or explanations of learning in terms of changes in the brain or other physiological events, though those topics are of interest in their own right.

Words like *learning* or *knowledge* seem obviously important, but they function in different ways in different contexts. For example, sometimes we speak of learning *about* something; at other times we speak of learning *how to do* something. I could learn how a car works without knowing how to drive one; conversely, I could learn to drive a car without being able to say how it works. Some kinds of learning involve deeds and others involve words. Should we treat these two kinds together or separately? Philosophers make this kind of distinction when they debate the difference between "knowing how" and "knowing that" (e.g., Ryle, 1949). Psychologists make it by contrasting *procedural* knowledge or memory with *declarative* knowledge or memory. The distinction is so fundamental that, as the table of contents shows, this book includes two major parts, one concerned with learning that doesn't involve words and the other with learning that does. Learning means different things at different times to different people.

Consider some examples. A pigeon discovers food in its travels and returns to the same place later when hungry. A child becomes able to read a story or to spell simple words. A dog is taught to sit or lie down on command. A patient who once had a bad experience in a dentist's office feels uneasy in the waiting room. A young cat, after its early hunting expeditions, now avoids skunks and porcupines. A shopper sees an announcement for a sale that hasn't begun yet and several days later returns to the store to take advantage of bargain prices. An author who encounters an unfamiliar word later uses it in a short story. You read a chapter in a mathematics text and find a way to solve a problem that had baffled you. I need to check a point in a chapter of this book and find a relevant paper through an Internet search. What do these examples have in common? They involve dogs and cats, children and adults, and we'd probably agree that they are all instances of learning. But is it reasonable to group a pigeon who learns a route to food with a human who discovers a solution to a mathematical problem? Are these examples distantly related just as chipmunks and spiders and clams are distantly related in the realm of animal life?

Can we resolve our problem by adding that learning has to come about through some change in the brain? We might think so, but do we look at an organism's brain to decide whether it has learned? Even if we could watch a brain doing something, how would we know that learning was what it was doing? No doubt the brain does a lot, but except with the aid of sophisticated instruments we see only its products. Ordinarily we see only behavior.

This isn't to say that learning has no physiological basis. Of course it does, and it would be fascinating to find out what neurological changes accompany learning. Yet we'd have trouble figuring out what to look for in the nervous system if we didn't know much about learning. In fact, we can't have an adequate neuroscience of learning unless we understand its behavioral properties. Those properties determine what neuroscientists must look for in the nervous system if they want to know what happens during learning. That's why our

main concern will be with the behavioral properties of learning rather than with its physiological basis.

Furthermore, the brain changes as a function of changes in the interaction of an organism with its environment. For example, when a stroke has partially paralyzed someone's arm, one therapy is to restrain the other arm so that use of the impaired arm will help it to regain full function. This is said to change the brain, but the recovery of the arm and not the change in the brain is the objective of the therapy. Of course the changes in the brain matter, but if the therapy is successful it is important to remember that the behavior, the use of the arm, is what drove those changes. That is why, though we will sometimes consider the nervous system, behavior will always be primary. **Behavior will always be our starting point.**

So far we've hardly worried about the facts of learning; we've mostly worried about how we talk about it. Languages are variable; their vocabularies reflect what is currently important to their speakers. One trouble is that the language that has evolved in our everyday interactions with others isn't necessarily well suited to be a language of learning (that is one reason for the etymologies, or word histories, included at the beginning of each chapter).

We're usually more interested in what other people know and in what they're likely to do than in how they came to be that way. For example, a parent might worry about a child who fights with other children and rarely plays cooperatively. If the child begins to play cooperatively, the parent might not care whether this happened because of the natural rewards of cooperative play or because cooperative play was explicitly taught or because fighting was punished. The child's play might look the same in each of these cases, but it might make a difference how the child got there.

Our language for describing what people do is useful. It is important to know what to expect of others, and that's probably why we describe people in terms of how they are likely to behave. We speak of each other as *outgoing* or *reserved*, *easygoing* or *compulsive*, *trustworthy* or *unreliable*. Describing people with words like *artistic*, *athletic*, *social*, *intel-*

lectural or *musical* specifies their preferred activities. Yet this kind of vocabulary isn't suitable for discussing how someone's particular interests or traits arose or changed.

Consider the difference between lying and telling the truth. If one child learns to stay out of trouble by telling lies and another by telling the truth, should we be surprised if the first child grows up to be less truthful than the second? Yet the behavior of each child is shaped by its consequences: Each child behaves so as to keep out of trouble. This shaping of behavior should concern us, whichever way it leads each child, but our everyday vocabulary doesn't equip us well for discussing it.

Similar problems exist in other fields. When physicists look at events in the world, they don't find the everyday vocabulary adequate. Sometimes it even gets in the way. So they coin new terms or take over existing ones. The latter tactic can create trouble. Words like *work*, *force* and *energy*, for example, mean different things to physicists in their technical talk than they do to most people in casual conversation. Fortunately for physicists, much of what they now study is remote enough from our daily experience that we don't confuse their technical language with our everyday talk.

This isn't so for behavior. We are all inescapably involved with it. We speak of how people grow and change and we speculate about why they do things. If we want to talk about these events in new ways, we must take care not to confuse our new ways of talking with the old ways. We've all spent most of our lives talking about what we do, but those familiar ways may interfere with our new ways of talking, so we must beware of language traps. Some parts of this book will introduce a language of behavior. That language will not be a paraphrase of everyday usages. **It will be fundamentally different.** It will demand new ways of looking at familiar phenomena.

Behavioral and Cognitive Languages

Sometimes we talk about what people do and sometimes we talk about what they know. On the

one hand, what someone does is all we have to go by. We have nothing else to study but behavior. Someone in a learning experiment may describe thoughts or feelings, but these descriptions are still only behavior; verbal behavior may be special, but it is behavior nonetheless. Thoughts and feelings are supposed to be inside of us, but if nobody else can detect them how can anyone teach us how to talk about them? Our words and our theories must ultimately be derived from behavior, from what organisms do. This is another sense in which behavior must come first.

On the other hand, there is more to an organism than shows in its behavior. Two students may sit silently through my class. They aren't behaving differently right now and yet based on their past coursework I may know that one can answer certain questions and solve certain problems while the other cannot. The difference is in what each potentially can do; I might simply say that one student knows more than the other. When we study this knowledge, it is tempting to say that we study the mind.

The debate between those who call themselves behaviorists and those who call themselves cognitivists or mentalists has been long-standing. To a large extent it has been about how we talk. The behaviorist argues that, because behavior is all that is available to measure, the language of mental events can be misleading, especially when a mentalistic account is accepted as explanatory and therefore discourages further inquiry.

For example, we sometimes casually say that an idea, a feeling or a hunch led someone to do something. The behaviorist doesn't dispute the existence of ideas, feelings and hunches, but rather criticizes appeals to them as causes of behavior. It is too easy to be satisfied with an explanation in these terms. For a behaviorist, it isn't enough to say that someone did something because of an idea, a feeling or a hunch. Ideas, feelings and hunches are about the world, and therefore must have their origins in our experiences with the world. We must look further, to these past experiences or, in other words, to past behavior, to account for what we do. If we are successful, we may also have some-

thing useful to say about the origins of our ideas, feelings and hunches.

The cognitivist maintains that such a view is unnecessarily narrow. Things must occur in our dealings with the world that aren't observable in our behavior. When we try to recall a word that is "on the tip of our tongue" or try to solve a problem by "sleeping on it," things are happening that don't show directly in our behavior and we may not even be able to report them. If we can find out something about such events, it is bound to be relevant to our study of learning.

This dispute stems as much from different ways of talking about behavior as from differences in research findings. Some difficulties arise because behaviorists and cognitivists are often interested in very different types of questions. Behaviorists tend to deal with questions of function and cognitivists with questions of structure.

Suppose I'd like to teach a child to read. Where do I start? On the one hand, I could worry about how to involve the child in reading. What will keep the child alert, what will help the child to attend to the words presented, and what will help the child remember what the various words are? Will I be more successful rewarding the child's right answers or penalizing the child's wrong ones? When I arrange different consequences for the child's different answers, I determine the functions of these answers or, more technically, the functional relations between behavior and its consequences.

On the other hand, no amount of worry about the effects of reward and punishment on the child's mastery of reading will tell me the most efficient way to present reading materials to the child. What is the best way to order them? Should I start with single letters, with syllables, or with whole words? When I present these materials in different orders, I'm structuring the subject matter. Are words best taught as units or as structures built up from simpler parts such as letters or syllables? Problems of structure are concerned with the organization of behavior and of the world within which it takes place.

Educators concerned mainly with function might try to improve a school system by changing what happens in the classroom, without worry-

ing much about how the curriculum is structured. Those concerned mainly with structure might try to improve the school system by changing the curriculum, without worrying much about what happens in the classroom. But obviously both are important. Any attempt to improve how children learn to read that ignores either is likely to prove deficient. Any that ignores both, as in concentrating mainly on instilling a vaguely defined trait such as self-esteem, has no hope at all.

Historically, some controversies about learning arose because those interested in functional problems tended to speak a behavioral language whereas those interested in structural problems tended to speak a cognitive or mental language. The problems in which behaviorists and cognitivists were most interested interacted with how they each talked about them. If I'm concerned with function, I study the consequences of particular relations between environmental events and actions; I can conveniently express these in the behavioral language of stimuli and responses. If I'm concerned with structure, I study the properties of particular capacities or abilities; I can conveniently express these in the cognitive language of knowledge and mind. This issue is not unique to psychology. A parallel distinction between structure and function, the separation of anatomy and physiology, was significant in the history of biology (e.g., Russell, 1916).

Let's not be sidetracked by this controversy. We'll consider both function and structure in learning and we'll therefore examine both types of research. In either case, it will often be useful to describe situations in terms of *antecedents*, or the circumstances that set the occasion for behavior, the *behavior* that occurs in those circumstances, and the *consequences* of the behavior (these three terms are conveniently abbreviated as ABC). We can consider either *function*, the relations among the terms (given certain antecedents, what consequences are produced by responses?) or *structure*, the properties of behavior (how are environments and responses organized?).

Though I will usually emphasize the behavioral approach, this book deals with both function and

structure and therefore encompasses both behavioral and cognitive concepts. These two approaches differ in their languages and in what they study, but they have in common the reliance on experimental method, the anchoring of concepts to experimental observations, and the assumption that our subject matter, however complex, is orderly and not capricious.

The World and the Laboratory

How then do we find out about behavior? Our language is not the only problem. We live in a complex world. The events that influence our behavior don't occur in isolation. Thus, to understand a situation we must strip away the unessentials. We must analyze it. To analyze something is simply to break it down into its component parts. To do this we start in the laboratory, studying organisms simpler than ourselves, in simple environments, in a science called behavior analysis. We must face the objection, of course, that a laboratory experiment is artificial and so may be inappropriate for establishing generalizations about learning outside of the laboratory. But starting with simple events helps us to develop techniques and vocabularies applicable to complex ones. Biologists could not have mapped the human genome if they hadn't started with the genetics of simpler creatures, such as the fruit fly *Drosophila melanogaster* or, simpler still (but nevertheless complex), the bacterium *E. coli*.

In the laboratory environment we look at one thing at a time. We arrange circumstances so that we know what goes into a situation; if we're careful enough, we'll exclude distractions that might otherwise obscure what we wish to study. The simplicity of our laboratory environment may also help us to see things more clearly. We must be able to identify events before we can study their properties. Yet even after we've studied behavior inside the laboratory, we can't expect to successfully interpret every instance of behavior outside. There are limits to what we can know. It is tempting to ask why someone did this or that, what led to a certain incident, how someone came to have

certain interests, fears or attachments. But usually we have so little information that giving a plausible interpretation is the best we can do.

In this respect, behavior analysis is not much different from other sciences. If I see a leaf blow across cars on a busy street and land at the foot of someone sitting on a sidewalk bench, I couldn't say how or why it got there. But a failure to account for every twist and turn in the path of that falling leaf doesn't invalidate the principles of aerodynamics. We can't possibly measure the details of air currents, leaf surface, and so on in enough detail. Similarly, the principles of behavior aren't invalidated when we can't account for what someone did on some occasion. Again, we simply can't measure personal history and other factors in enough detail. In our study of learning, we must recognize what remains out of our reach. In what follows, we'll find that the most profitable course is one that stays close to the data. We'll worry less about theory than about properly describing our findings. It will usually be more useful to *describe* what an organism has learned or remembered than to try to *explain* its learning or its remembering.

ANTECEDENTS, BEHAVIOR, CONSEQUENCES

Behavior is no easier to define than learning. We may say glibly that behavior is anything we do, but this definition is too global. Should we count respiration or metabolism along with muscle movements and glandular secretions? We describe behavior with verbs: people walk, talk, think, do things. But we also distinguish between active and passive actions. We may say that someone breathes, but are we likely to say that someone heartbeats? People bleed when cut but do we want to call their bleeding behavior? Let's not try to resolve this problem. The phenomena of behavior are varied, and though they sometimes share common names we'll probably do better by considering examples than by attempting definitions. We can deal with specific examples without much risk of misunderstanding.

Stimuli and Responses

When we observe an organism, we see properties of its environment, *stimuli*, and properties of its behavior, *responses*. In the singular, we speak of a *stimulus* and a *response*. Neither is of interest by itself. An experimental analysis determines what kinds of relations exist between stimuli and responses and how they can be changed. It must also consider the situations or broader contexts within which these stimuli and responses are embedded.

Imagine a pigeon in an experimental chamber. On one wall is an opening to a feeder that can dispense food. Above the feeder opening is a recessed translucent disk or key that can be lit from behind. The pigeon has learned to earn food by pecking the key whenever it is lit. Now suppose the pigeon hasn't eaten for a while, the key is lit, and a peck on the key immediately makes some food available. We need to know the context before we can guess what the pigeon will do. It is one thing if the alternative, not pecking, is never followed by food; it is another if not pecking is followed by a somewhat delayed but much larger amount of food. In each case a response, the key peck, is followed by a stimulus, food. But the contexts are very different. We would expect the pigeon to peck the key in the first case, but what about the second? If the pigeon doesn't peck, we might want to say that it shows self-control, forgoing the small amount of immediate food in favor of the larger but delayed amount. We'll discuss this type of situation in more detail later. For now, the point is that we must look at not only the moment-to-moment details of events but also their contexts over extended times.

Let's examine relations between environment and behavior further by observing a human infant. We might want to start by asking what the infant feels, but that won't work. She isn't yet verbal and can't tell us. Even if she were an older child who could tell us, we'd have to wonder how she learned the words and whether they'd mean the same thing to us as to those who taught them to her. When we get to language, in Part IV, we'll examine the role it

plays in molding our knowledge of ourselves and others, but that won't help us here.

We know the infant is active, learning from the environment and interacting with it. But how do we find out what's going on? We watch for a while and see her move her hands or arms or legs. Perhaps at some point she begins to cry. If the crying stops without our intervention, she may sleep or may lie quietly with open eyes. If we look closely, we may see her eyes moving, although it might be difficult to judge what she is looking at, if anything. We could catalogue what she does and we might discover that some movements usually occur in particular sequences. But if we only watch, we can't say much more than that she does different things more or less often and more or less in certain orders.

We needn't be restricted to watching. We might touch or rock her, move objects in or out of her view, make sounds, or offer a pacifier. We'd expect her to respond to each event in a characteristic way. If we touched her palm, for example, she would most likely clench that fist, grasping whatever touched it. The vocabulary for these events is already familiar: we call the touch to the palm a *stimulus*, and the grasping a *response*. We may notice that this stimulus and this response are correlated (Skinner, 1931); they tend to occur together in sequence.

Besides the grasping produced by a touch to the palm, we could catalogue other examples of stimulus-response correlations: crying caused by a sudden loud noise; sucking produced by a nipple in the mouth; blinking triggered by a flash of light. We see the environment act on this infant when stimuli produce responses, but things may go in the other direction. She can act on the environment. Her crying, for example, often brings her mother's attention. Crying, then, is a response that often produces a consequence: mother's presence. This case involves stimuli and responses, but here the responses come first, not the stimuli; here behavior has consequences.

The relations can get more complicated. If the infant's eyes move while the lights are on, those eye movements change what she sees. Eye movements can't have this effect with the lights off.

Thus, she may come to look around in the light but not in the dark. In the presence of one stimulus, the light, moving the eyes produces other stimuli, some new things seen. Eye movements can't have this consequence in the dark. The relation involves three terms: an antecedent stimulus, the light; a response, eye movement, in its presence; and a consequence, what is newly seen given this response in its presence. This three-term relation, stimulus-response-consequence, is sometimes called a *three-term contingency*. It is important because an organism's behavior depends on both antecedents and consequences.

An *antecedent* is simply something that comes before. A *consequence* is simply what is caused by or what happens as a result of some event. Thus, everyday usage corresponds pretty well to the senses of these terms when we use them technically. It is important to note that **consequences should not be identified with stimuli**. Responses can have many types of consequences. They sometimes produce stimuli that would otherwise have been absent, but they can also prevent things from happening or change the consequences of other responses. For example, food produced by a response is both a stimulus and a consequence, but food presented independently of behavior is a stimulus only; shock prevented by a response is a stimulus, but the consequence of the response is the absence of shock, which isn't a stimulus. Sometimes the consequence of one response is a change in the consequences of some other response, as when a light switch stops working and changing the light bulb restores the usual consequences of operating the switch.

For *stimulus* and *response*, the relations between technical and everyday usages are not so simple. Stimuli are events in the world and responses are instances of behavior. The term *stimulus* is often restricted to specific physical events such as lights or sounds or touches. But organisms respond to varied features of the environment, including relations (e.g., to the left of, on top of), complex behavior (e.g., facial expressions, tones of voice), functional properties (e.g., edible, comfortable),

and so on (cf. Gibson, 1979). We'll often speak of such environmental features as stimuli even when we cannot specify their physical dimensions.

As for the term *response*, everyday usage often implies that it is *to* something (typically a stimulus). The term won't function that way here, however, because an account of what causes responses typically includes other factors along with or instead of the stimuli that precede them. We'll be especially interested in responses that are not elicited by stimuli but are caused in other ways. Such responses are said to be *emitted*. Unfortunately *sponse*, a useful word for such cases, is not a well-established term (but see Provine, 1976).

A stimulus is an environmental event, but such events vary in complexity. When the infant's crying produced the mother's attention, we regarded the mother as a stimulus. An infant's environment is certainly different when the mother is present than when she is absent. Yet what sort of stimulus is the mother? We don't know which aspects of her looks, her voice or her touch are important to the infant early in life. We might guess that the infant wouldn't react to her as usual if she approached wearing a surgical mask, but we couldn't be sure unless we did the experiment. Despite our ignorance with respect to these questions, we don't doubt that the mother is an important part of the infant's environment. It is useful to speak of the effects she has as she comes and goes in the infant's world.

This example again illustrates structure and function. When we try to analyze which of mother's visual, auditory and tactile features are important to the infant, we deal with the structure of this complex stimulus, mother. We might ask how the infant learns to respond to a particular individual as mother despite changes in her dress or hair style, her facial expression or posture. If we concentrate instead on how mother interacts with the infant's responses, we're concerned with the functional significance of mother in the infant's environment. For example, if an infant cries we may not care whether the infant recognizes mother by her face, her hair or her voice, as long as her presence makes a difference; it would be enough to see that

when mother goes to the infant the crying stops. Later we'll often be interested in simpler stimuli: lights, sounds, food in the mouth. But even with simpler stimuli we'll have to distinguish between structural problems, as in analyzing stimulus properties, and functional problems, as in analyzing the interactions between stimuli and responses.

And what about responses? In describing responses, we encounter at least two difficulties. The first is that behavior isn't repeated exactly from one instance to the next. If the infant grasps an object on two different occasions, the grasping won't be the same each time. The difference may be small, in the force of the grasp, for example, or in the exact placement of the fingers. But if there is any difference at all, we must worry whether the two grasps should be regarded as two instances of the same response or as two different responses. We must speak not of individual responses but of classes of responses having common properties.

The second difficulty is that responses are sometimes adequately described in terms of movements, but at other times the description must include the environment in which the responses occur. For example, suppose we want to compare the infant's grasping of an object with clenching a fist. If we look just at muscles, grasping an object with the right hand and clenching that fist have more in common than grasping an object with the right hand and grasping an object with the left hand. Yet sometimes it is more important to speak of the act of grasping an object, no matter which hand is used, than to speak of the movement of closing a particular hand.

An account of behavior must distinguish between *movements*, responses defined by their form or the musculature used, and *actions*, responses defined by their relations to the environment. We'll find that actions are more important for our purposes. Consider how often we speak of doing things, going places or manipulating objects, without regard to the details of how we do them.

Even in the absence of movement we sometimes conclude that behavior has occurred. We do many things that involve no obvious movement. For example, while listening to a song I may shift

my attention back and forth between the vocalist and the accompaniment. Those shifts of attention are behavior even though we can't record them as movements. Many aspects of thinking and imagining involve no movement, but as things we do they count as varieties of behavior. Thus, **not all instances of behavior need be movements.** In fact, we will later find that a useful criterion for whether something counts as behavior is not its form but whether it varies depending on how it affects the environment.

Whether behavior involves movement or not, it typically has consequences, and one of the most significant consequences of behavior is that it provides opportunities for other behavior. For instance, if a child is given a cookie, the cookie affords the child an opportunity to eat. The significance of the cookie is based on the child's eating, its behavior with respect to that stimulus. As we will see again and again, we cannot characterize stimuli independently of an organism's behavior, nor can we characterize responses independently of an organism's environment. **Behavior is the interaction between an organism and its environment.**

Behavior Hierarchies

One way to classify an organism's behavior is to rank responses according to the relative frequencies with which the organism engages in them. For example, if we gave a child an opportunity to eat, to play with toys or to take a bath, we might find that the child plays a lot, eats occasionally, and hardly ever volunteers for a bath. Playing, as the most likely or most probable behavior, comes first in this ranking, followed by eating and then by taking a bath. Such a ranking has been called a *behavior hierarchy* (Hull, 1943). An equivalent way of describing the ranking is in the language of preference: we could say that the child prefers playing to eating and prefers either of these to taking a bath.

Behavior hierarchies are changeable. For example, if we waited until the child's usual mealtime and provided a choice between eating and playing, we might find that eating had now become

more probable than playing. While eating, the child is neither playing nor taking a bath, but we could find out about the relative rankings of those responses by giving the child a choice between the toys and the bathtub. We might discover that this child almost always prefers the toys. We therefore conclude that right now playing with toys ranks above taking a bath in this child's behavior hierarchy. We might even find that this child always leaves the bathtub area even when there isn't much to do elsewhere. Maybe the child recently had a bad experience there. For any kind of behavior, we must consider when it stops as well as when it starts. It is often convenient to speak of stimuli rather than of opportunities for responding. Thus, for this child we might describe food as an *appetitive* stimulus or event and taking a bath as an *aversive* one, with events that are neither appetitive nor aversive categorized as *neutral*. Unfortunately, even though we may be able to use such terms in specific situations, stimuli in general cannot be sorted out so neatly. Context makes too much of a differ-

ence. We cannot just divide the environment into three simple classes of events called appetitive, neutral and aversive. Instead, we must evaluate each stimulus relative to the others available.

With changes in the behavior hierarchy come changes in the significance of stimuli. For example, consider how food may change from appetitive to aversive over the course of an unusually large holiday dinner. In the bathtub example, if the parents handle things carefully this child may begin to tolerate baths and eventually even come to prefer toys in the tub to toys in other places. In any case, as the child's behavior changes we might want to say that the child is learning something about toys and tubs.

So now we've surveyed some general properties of stimuli and responses as they enter into the relations among antecedents, behavior and consequences. With these preliminaries behind us, we are ready to move on to some classic experiments and findings in the study of learning.

Chapter 2

A Behavior Taxonomy

<etym>The word behavior, like habit, inhibit and ability, is related to the Latin habere, to hold or have. The prefix be became attached in such words as the Old English behabban. As a word for how one held oneself, it was closer to the sense of comportment or demeanor than to the more contemporary sense of activity, just as habit was once more commonly what was worn than what was habitually done.

<etym>A taxonomy is a system of classification. The word is derived from the Greek tassein, to arrange, plus the Greek nomia, method. It shares its first root with the grammatical term syntax, with tactic, and with taxis, a kind of movement; it shares its second root with systematic disciplines such as astronomy and economics, with metronome and autonomy, and probably even with number.

Observing Behavior

Presenting Stimuli

Arranging Consequences

Signaling Events and Procedures

Signaling Stimulus Presentations

Signaling Consequences

Establishing the Effectiveness of Consequences

Summary

In this chapter I outline a behavioral taxonomy, a vocabulary in terms of which the various procedures and phenomena of behavior can be organized. Please don't expect explanations of behavior in terms of formal laws. Instead, think in terms of a systematic classification of behavior based on its origins: given any example of behavior, where did it come from? The taxonomy will not be exhaustive, because we can't anticipate everything we'll run into in studying behavior. Like any science,

behavior analysis and its taxonomy are and will remain works in progress. But we can at least aim for a descriptive system that organizes the phenomena we've begun to know while not excluding those we have yet to study. This field has evolved in many ways since I first encountered it. The several editions of this book provide some snapshots of its progress. I hope all of them, and especially this one, have been reasonably well focused.

We study behavior through experimental *procedures* or *operations*. We call the changes in behavior they produce behavioral *outcomes* or *processes*. We study the relation between environmental events and the organism's behavior by changing the environment and observing how this affects what the organism does. In the analysis of behavior, procedures or outcomes are *what the experimenter or the environment does or arranges*, and outcomes or processes are *the changes in behavior that result*. A convenient analogy comes from medicine, where the

KEY TERMS: Taxonomy; Operation or Procedure; Process or Outcome; Reflex, Releaser, Fixed action pattern; Stimulus control, Discriminative stimulus, Signal, Occasion; Elicitation, Emission, Evocation; Establishing operation, Motivation, Deprivation, Satiation.

surgical operation, a procedure, is what the physician does to the patient, and the processes that follow, such as changes in circulation, respiration and so on, are the outcomes of the operation. In this text I'll usually favor *procedure* over *operation* and *outcome* over *process*, but within each pair the terms are somewhat interchangeable.

If you are familiar with the standard sections of experimental papers in psychology you will recognize this distinction as similar to that between the Method section, which describes the procedures and other details of an experiment, and the Results section, which describes the data obtained. We can also interpret changes in behavior once we have observed them, and interpretation corresponds most closely to what happens in the Discussion section of an experimental paper. In distinguishing between procedures, what gets done, and outcomes, what happens as a result, I'll emphasize experimental procedures rather than properties of the environment, mainly because this text is about research findings drawn from the laboratory.

But behavioral events occur in natural circumstances as well as in artificial circumstances arranged by an experimenter. We startle in response to an unexpected loud noise whether it was produced by accident on the street or deliberately in a laboratory. For that reason, these terms are often applied not only to artificial procedures and their outcomes but also to natural sequences of events. For example, Chesapeake, my cat, has learned that he often gets fed after going to his feeding dish in the kitchen. It hardly matters whether I deliberately trained his behavior or it came about as a matter of course during routine feedings. Either way, this was a procedure or operation in which being fed had become a frequent consequence of going to that place in the kitchen. It is convenient to call such circumstances procedures or operations whether or not they were explicitly arranged.

The simplest procedure, of course, is merely (1) to *observe behavior*: just watch. We then discover what an organism can do. But we have no control over events when we simply observe, so we may not be able to draw conclusions about the causes of behavior. To learn more we must intervene, and

the simplest intervention is (2) to *present stimuli*. A more complicated intervention is (3) to arrange the environment so that it is changed by the organism's behavior or, in other words, so that the organism's behavior has *consequences*. Once behavior has consequences it may occur more or less often, and therefore consequential arrangements lead to the outcomes sometimes called *reinforcement* and *punishment*.

We haven't exhausted the possibilities. We can arrange things so that (4) stimuli *signal* the presentation of other stimuli or so that (5) stimuli *signal* the opportunity to produce consequences. We then speak of *signaling* or *stimulus-control* procedures; these can only occur in combination with one of the simpler procedures, either presenting stimuli or arranging consequences. Behavior may then depend on whether the signaling stimulus is present or absent. We must also consider procedures that (6) change the effects of the consequences of behavior, as when food becomes a more potent reinforcer after a period of food deprivation. Such procedures are called *establishing* or *motivating operations*, in that they establish the conditions under which consequences may become effective as either reinforcers or punishers.

Thus, the basic procedures are (1) observing behavior, (2) presenting stimuli, (3) arranging consequences for responses, (4) signaling stimuli, (5) signaling consequences and (6) establishing the effectiveness of consequences. These categories were not recognized all at once. They were gradually added to our taxonomy over the history of this science and have been refined in various ways as their effects on behavior have been more fully understood. For that reason, what follows surveys several classic experiments, not only illustrating these procedures in more detail but also introducing some researchers who played significant historical roles.

OBSERVING BEHAVIOR

What must we do to observe behavior? Interesting behavior depends on interesting environ-

ments. What would happen if we tried to move in the other direction, avoiding the contamination of behavior by the environment? For example, imagine fitting a rat with goggles to exclude visual stimuli and with ear plugs to exclude sounds, and setting up a ventilating system to remove odors. The rat can still touch things, including its own body, so we arrange a suit of hollow tubes that holds the rat's legs, reducing tactile contact at least for its paws. We may still not be satisfied, because the rat's weight produces pressure where the suit meets part of its body and so allows it to orient spatially. Is our next step to send the suited rat up to an orbiting space station, where gravity is eliminated? Yet even if we accomplished this much, what could we say about the rat's behavior? What could we see it doing?

The rat example is hypothetical, but experiments on sensory deprivation place humans in environments approximating the minimal stimulation we imagined for the rat. The problem is that in such environments, for human as well as rodent, there isn't much to do: no place to go and no one to talk to. Humans in such environments report a range of activities during their waking time, from thinking to hallucinating, but—no surprise—they sleep most of the time. So, to observe interesting behavior we have to observe organisms in interesting environments. Let's consider some examples. In early accounts of learning, speculations were typically based upon anecdotal evidence derived from simple observation, as in C. Lloyd Morgan's description of how his dog learned to get through a garden gate:

The iron gate outside my house is held to by a latch, but swings open by its own weight if the latch be lifted. Whenever he wanted to go out the fox terrier raised the latch with the back of his head, and thus released the gate, which swung open.... How did he learn the trick? In this particular case the question can be answered, because he was carefully watched. When he was put outside the door, he naturally wanted to get out into the road, where there was much to tempt him—the

chance of a run, other dogs to sniff at, possibly cats to be worried. He gazed eagerly out through the railings... and in due time chanced to gaze out under the latch, lifting it with his head. He withdrew his head and looked out elsewhere; but the gate had swung open.... After some ten or twelve experiences, in each of which the exit was more rapidly effected with less gazing out at wrong places, the fox terrier had learnt to go straight and without hesitation to the right spot. In this case the lifting of the latch was unquestionably hit upon by accident, and the trick was only rendered habitual by repeated association in the same situation of the chance act and the happy escape. Once firmly established, however, the behaviour remained constant throughout the remainder of the dog's life, some five or six years. (1920, p. 144)

Observing this behavior was perhaps a lucky accident, like the dog's lifting of the latch. More can be learned about learning by arranging the environment within which behavior will be observed. One researcher who did so was Wolfgang Köhler, one of the founders of gestalt psychology. Köhler studied the behavior of chimpanzees maintained from 1913 to 1917 at the Anthropoid Station on Tenerife, an island northwest of Africa (Köhler, 1927). Chimpanzees aren't native to Tenerife and the station was probably a front for German espionage, the observation of Allied shipping, during World War I (Ley, 1990). But Köhler's research does not appear suspect. In some of Köhler's experiments, bananas or oranges were placed in visible but inaccessible locations and the chimpanzees used materials within the area as tools to obtain the fruit. The following describes the behavior of the male chimpanzee, Sultan:

The six young animals of the station colony were enclosed in a room with perfectly smooth walls, whose roof—about two metres in height—they could not reach. A wooden box..., open on one side, was stand-

ing about in the middle of the room, the one open side vertical, and in plain sight. The objective was nailed to the roof in a corner, about two and a half metres distant from the box. All six apes vainly endeavored to reach the fruit by leaping up from the ground. Sultan soon relinquished this attempt, paced restlessly up and down, suddenly stood still in front of the box, seized it, tipped it hastily straight towards the objective, but began to climb upon it at a (horizontal) distance of half a metre, and springing upwards with all his force, tore down the banana. About five minutes had elapsed since the fastening of the fruit; from the momentary pause before the box to the first bite into the banana, only a few seconds had elapsed, a perfectly continuous action after the first hesitation. (Köhler, 1927, pp. 39–40)

In many instances, of course, chimpanzees made fruitless attempts to solve such problems.

Köhler discussed these and other observations in terms of the chimpanzees' intelligence and insight. More important, chimpanzees were much less familiar in those days than now, and Köhler's readers were impressed by his descriptions what chimpanzees could do. But it was impossible to say from observation alone where the behavior came from. Did Sultan solve the problem because of some inherited cognitive disposition? Because the problem had features in common with some situation he had already encountered? Because he'd seen other chimpanzees whose behavior he could imitate? Because of some combination of these and other factors?

The term *insight* seemed appropriate to Köhler because of the suddenness with which a solution to a problem typically emerged. Problem solving that seemed insightful led to further questions: whether learning took place abruptly or gradually, and whether problem solving could be explicitly taught. Debates about how much nonhuman primates can learn continue to the present. But observation alone rarely identifies the sources of behavior and therefore rarely resolves such issues.

Strictly, of course, Köhler did much more than just observe behavior. He arranged environments within which to make his observations. Observation without intervention is difficult to achieve. To observe organisms successfully in the wild, one must know the possible effects of a human presence on their behavior. Even bringing an organism into captivity is itself an intervention. Observation alone is not good enough.

PRESENTING STIMULI

Köhler did in fact present stimuli, by arranging environments for his chimpanzees. So let's turn to procedures that examine the role of stimuli more directly. The following, by the ethologist Niko Tinbergen, describes the first feeding of newly hatched herring gull chicks:

Sometimes the parent stands up and looks down into the nest, and then we may see the first begging behavior of the young. They do not lose time in contemplating or studying the parent, whose head they see for the first time, but begin to peck at its bill-tip right away, with repeated, quick, and relatively well-aimed darts of their tiny bills. They usually spread their wings and utter a faint squeaking sound. The old bird cannot resist this, and if only the chicks persist it will feed them. First the parent stretches its neck, and soon a swelling appears at its base. It travels upward, causing the most appalling deformations and the most peculiar turnings and twistings of the neck. All at once the parent bends its head down and regurgitates an enormous lump of half-digested food. This is dropped, and a small piece is now picked up again and presented to the chicks. These redouble their efforts, and soon get hold of the food, whereupon the parent presents them with a new morsel. Now and then the chicks peck at the food on the ground, but more often they aim at the parent's bill, and although this aiming is not always correct,

it rarely takes them more than three or four attempts until they score a hit. (Tinbergen, 1960, p. 178)

So far all we have are only some observations of chick behavior. But they involve the effects of stimuli and therefore prompt questions. What exactly are the critical features of these special stimuli presented by the parent gull? Are some more important than others? Are they the most effective ones possible? Tinbergen answered these questions by preparing stimuli that resembled the parent gull in various ways. He then measured the pecking generated when these stimuli were presented to recently hatched herring gull chicks. The herring gull parent has a white head and a yellow beak with a red patch near its tip. A beak with a black or blue or white patch produced less pecking than one with a red patch, but a beak with a patch of any color produced more pecking than one with no patch at all. Compared to the red patch, the color of the beak or the head was relatively unimportant in generating pecking. In fact, as long as the model had a beak with a red patch on it even the presence or absence of a head made little difference.

Tinbergen also varied the shape of the beak, as illustrated in Figure 2-1. Next to each stimulus, pecking is shown as a percentage of pecks generated by the normal beak shape at the top. With the red patch and other color differences eliminated, changes in pecking depended solely on changes in shape. Most models produced less pecking than the one with the normal shape. The model with an elongated beak (Figure 2-1, bottom) produced considerably more pecking than any of the others, including the one with the normal shape. Because of its effectiveness relative to the normal shape, Tinbergen called this one a *supernormal* stimulus, but he speculated that its shape might be more like what the chick first sees of its parent's beak, as it looks up from beneath the parent's head, than the profile view used for most of the other models.

Tinbergen varied other properties of the beak, including movement, slant and height above the ground. His analysis enabled him to construct a truly supernormal stimulus, a red pencil-shaped

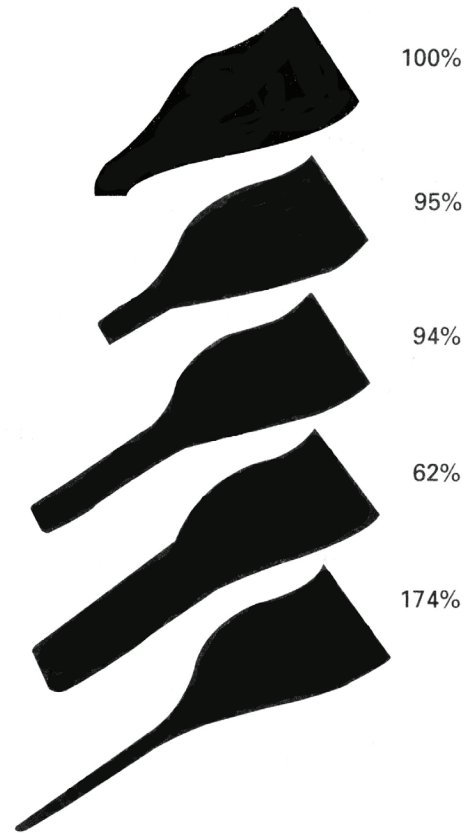


Figure 2-1 A series of models used to analyze which properties of the parent gull's beak produced begging pecks in the hatchling herring gull. Pecks to each model are expressed as a percentage of the reference level (100%) given by pecks to the top model. (Adapted from Tinbergen & Perdeck, 1950, Figure 15)

rod with three narrow white bands that generated more pecking than an accurate model of a herring gull head. More important, he could specify which features of the parent's head were important in generating pecks and which were unimportant. In other words, by presenting stimuli and observing their effects Tinbergen was able to identify the critical *structure* of the stimuli that generated pecking in the hatchling herring gulls.

Stimulus presentations are a common feature of research conducted by ethologists, whose con-

cern is the evolution of species-specific behavior patterns in natural habitats. One effect of stimulus presentations, as we have just seen, is to produce responses. This outcome of presenting stimuli is called *elicitation*; the stimulus is said to elicit a response. In the language of ethology, the critical stimuli or stimulus features are called *releasers*, and the behavior they produce is called a *fixed action pattern*. But variations in vocabulary should not obscure the simplicity of the basic procedure of presenting stimuli.

The eliciting or releasing effects of stimuli can change over time. Data from the laughing gull chick provide an example. Feeding in the laughing gull chick differs in some details from that of the herring gull but includes the begging peck at the parent's beak followed by the parent's regurgitation of partly digested food that the chick then eats. The accuracy of the begging peck was tested by presenting beak models to chicks of various ages. Only about one-third of the pecks of newly hatched chicks struck the model, as opposed to more than three-quarters of those of two-day-old chicks (Hailman, 1969). Did the improved accuracy depend on changes in coordination or visual experience or other factors? Some behavior might be built in ("prewired") whereas other behavior might have to be learned. How do we tell which is which?

The consequences of accurately aimed pecks differ from those of poorly aimed pecks. In the laughing gull's natural habitat, a more accurately aimed peck is more likely to hit the parent's beak and therefore to be followed by the parent's regurgitation of food than a poorly aimed one. Accurately aimed pecks might increase relative to poorly aimed pecks because of their different consequences. Hailman's observations are consistent with that idea:

If an inexperienced chick is too close to the target at first, its pecking thrust against the bill or model is so strong that the chick is thrown backward as much as an inch. If the chick starts out too far from the target, the pecking thrust misses and the chick falls forward as much as two inches. Older chicks

rarely make such gross errors, suggesting that the experience of overshots and undershots has helped the chick learn to adjust its distance. (Hailman, 1969, p. 100)

To study such cases, it isn't enough simply to present stimuli. A more complex procedure must be arranged: stimuli must be arranged as consequences of the organism's behavior.

ARRANGING CONSEQUENCES

Our example this time is from research on animal intelligence by the American psychologist, Edward L. Thorndike. The crucial difference between Thorndike's research and Köhler's was that Thorndike systematically observed changes in behavior over many repetitions of behavior in a given setting rather than looking only at single instances of a problem solution. Thorndike noted gradual changes in behavior over repetitions rather than the abrupt changes typically reported by Köhler, perhaps in part because the problems he studied didn't lend themselves to sudden or insightful solutions. More important, Thorndike's experiments showed how responding often depends on its past consequences. Thorndike described his procedures this way:

I chose for my general method one which, simple as it is, possesses several other marked advantages besides those which accompany experiment of any sort. It was merely to put animals when hungry in enclosures from which they could escape by some simple act, such as pulling at a loop of cord, pressing a lever, or stepping on a platform.... The animal was put in the enclosure, food was left outside in sight, and his actions observed. Besides recording his general behavior, special notice was taken of how he succeeded in doing the necessary act (in case he did succeed), and a record was kept of the time that he was in the box before performing the successful pull, or clawing, or bite.... If, on the

other hand, after a certain time the animal did not succeed, he was taken out, but *not fed*. (Thorndike, 1898, pp. 5–6)

One of Thorndike's problem boxes is illustrated in Figure 2-2. In such devices, Thorndike studied cats, dogs and chicks. He gave the following description as typical of the behavior of most cats:

When put into the box the cat would show evident signs of discomfort and of an impulse to escape from confinement. It tries to squeeze through any opening; it claws and bites at the bars or wire; it thrusts its paws out through any opening and claws at everything it reaches; it continues

its efforts when it strikes anything loose and shaky; it may claw at things within the box.... The cat that is clawing all over the box in her impulsive struggle will probably claw the string or loop or button so as to open the door. And gradually all the other non-successful impulses will be stamped out and the particular impulse leading to the successful act will be stamped in by the resulting pleasure, until, after many trials, the cat will, when put in the box, immediately claw the button or loop in a definite way. (Thorndike, 1898, p. 13)

As a consequence of its behavior, the cat escaped from confinement and gained access to food. We can assume that both escaping and eat-

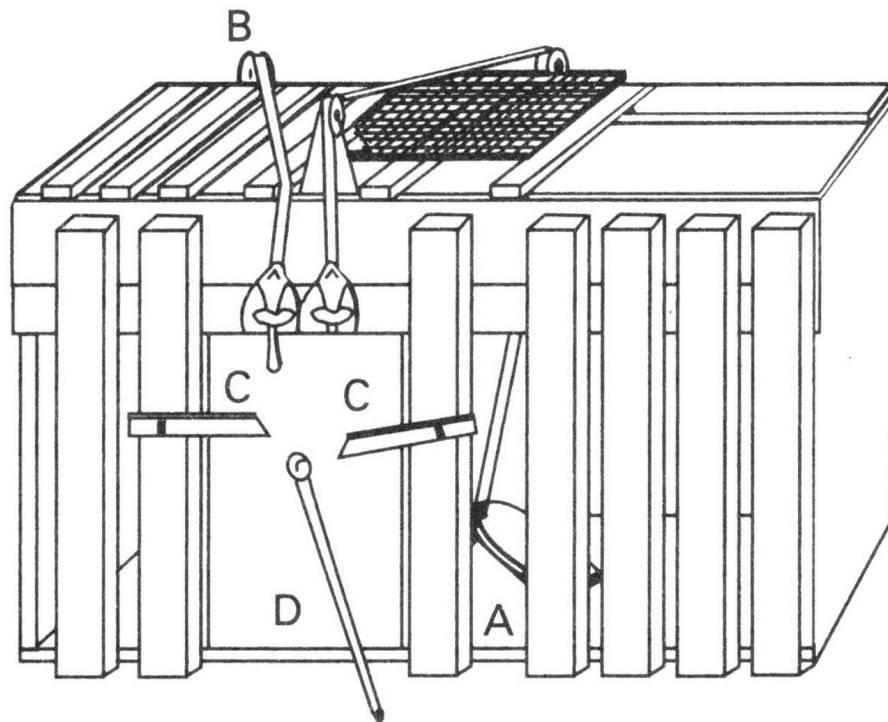


Figure 2-2 In most boxes that Thorndike (1898) used, the animal had only a single way to free the door. In the one shown, three different methods are illustrated: a treadle inside the box (A); a wire or string that can be reached from inside (B); and two outside latches that can be reached from inside (C). The door (D) was usually counterweighted so that it opened by itself once the animal made the appropriate response.

ing helped make the successful response gradually dominate over other, unsuccessful ones. In either case, the procedure cannot be reduced simply to the presentation of stimuli. A new part of the environment was not just presented to the cat; it became available as a consequence of what the cat did. As a result, the cat's behavior changed. Contemporary experiments often examine simpler responses in simpler situations but are similarly concerned with relations between responses and their consequences.

We arrange consequences for responses by constructing environments. If we place food in the goalbox of a maze, for example, we create an environment in which a consequence of a rat's movement from the startbox to the goalbox is finding food. After the rat has reached the food once, we can find out how this consequence affects its behavior by seeing what it does next time we put it in the startbox.

The consequences we arrange can vary from events of obvious biological significance such as presenting food or water to relatively minor changes in things seen or heard or touched. But not all consequences involve producing stimuli: responses can alter stimuli, as when turning a dimmer switch changes the brightness of a lamp; they can remove stimuli, as when operating a switch turns off a light; they can prevent stimuli, as when unplugging a lamp before repairing it eliminates the possibility of an electric shock; they can change the consequences of other responses, as when replacing a burned-out lightbulb makes the previously ineffective response of operating the light switch effective again.

Two classes of consequences are often distinguished on the basis of their effects on behavior. *Reinforcing* consequences are those that increase or maintain responding; *punishing* ones are those that decrease or suppress it. (It is also useful to have a term that doesn't prejudge whether the consequences will reinforce or punish. *Consequation* has been introduced for that purpose, though its usage is fairly uncommon. For example, if we don't know whether gold stars will reinforce the classroom behavior of a kindergarten child, it would still be

appropriate to speak of *consequating* that behavior with gold stars (e.g., Powers & Osborne, 1976).

SIGNALING EVENTS OR PROCEDURES

When stimuli become effective as signals, we speak of them as *discriminative* stimuli. Procedures that involve signals are called *signaling* or *stimulus-control* procedures or operations. The presentation of stimuli and the arrangement of consequences seldom occur in isolation; they are often signaled by other events. A flash of lightning is often followed by a clap of thunder. A traffic light typically alerts drivers to possible consequences of proceeding or stopping at an intersection. These two examples illustrate that the signaling or discriminative effects of stimuli may be combined either with stimulus presentations or with consequential arrangements. Both demonstrate the signaling functions of stimuli, though the two types of signaling can have very different properties.

Signaling Stimulus Presentations

Stimuli that signaled the presentation of other stimuli were the basis for experiments on conditional or conditioned reflexes by the Russian physiologist, Ivan P. Pavlov. Pavlov (1927) studied how stimuli acquired signaling properties by showing that responses to stimuli such as food were sometimes produced by other stimuli that had reliably preceded the food. Pavlov spoke of the effects of food in a dog's mouth in terms of the alimentary reflex (for Pavlov, its components included both the glandular response of salivating and motor responses such as chewing and swallowing). He concentrated on salivation because the technology available to him made salivating easier to measure than motor responses. Through surgery, he brought the duct of one of the dog's salivary glands to the outside of the dog's cheek, where he connected it to a fluid system that allowed drops of saliva to be counted.

For one dog, the sound of a metronome consistently preceded food presentations. Pavlov gave the following account of the conditions necessary to make a stimulus function as a signal:

On several occasions this animal had been stimulated by the sound of the metronome and immediately presented with food—i.e., a stimulus which was neutral of itself had been superimposed upon the action of the inborn alimentary reflex. We observed that, after several repetitions of the combined stimulation, the sounds from the metronome had acquired the property of stimulating salivary secretion and of evoking the motor reactions characteristic of the alimentary reflex.... Hence a first and most essential requisite for the formation of a new conditioned reflex lies in a coincidence in time of the action of any previously neutral stimulus with some definite unconditioned stimulus. Further, it is not enough that there should be overlapping between the two stimuli; it is also and equally necessary that the conditioned stimulus should begin to operate before the unconditioned stimulus comes into action. If this order is reversed, the unconditioned stimulus being applied first and the neutral stimulus second, the conditioned reflex cannot be established at all. (Pavlov, 1927, pp. 26–27)

Pavlov's conditioning experiments demonstrated how a signaling procedure can be superimposed on the simpler procedure of presenting stimuli. We'll discuss his procedures in more detail in another chapter.

Signaling Consequences

Instead of signaling the presentation of stimuli, a stimulus may signal when responses will have consequences. The signaling of consequences played an important role in the history of the study of learning long before it began to be studied experimentally. For example, it was involved in the analy-

sis of the case of Clever Hans, a horse that seemed to have been taught to solve arithmetic problems (Pfungst, 1911). The horse apparently took not only addition and multiplication but also square roots in its stride.

The visitor might walk about freely and if he wished, might closely approach the horse and its master, a man between sixty and seventy years of age. His white head was covered with a black slouch hat. To his left the stately animal, a Russian trotting horse, stood like a docile pupil, managed not by means of the whip, but by gentle encouragement and frequent reward of bread or carrots.... Our intelligent horse was unable to speak, to be sure. His chief mode of expression was tapping with his right forefoot. (Pfungst, 1911, pp. 18–19)

Clever Hans gave his answers by the number of times he tapped. His performance was investigated by Oskar Pfungst, who discovered that the horse performed accurately only in the presence of his master. Furthermore, Clever Hans knew the answers only if his master knew them too. Pfungst therefore turned his attention from the horse to the master, and determined that the horse was responding to subtle cues provided by the master's behavior.

we sought to discover by what movements the horse could be made to cease tapping. We discovered that upward movements served as signals for stopping. The raising of the head was most effective, though the raising of the eyebrows, or the dilation of the nostrils—as in a sneer—seemed also to be efficacious.... On the other hand, head movements to the right and to the left or forward and back... remained ineffective. We also found that all hand movements, including the “wonderfully effective thrust of the hand into the pocket filled with carrots,” brought no response. (Pfungst, 1911, p. 63)

The master had cooperated in the investigation and there was no evidence that he had been aware of the signals he had provided. Pfungst noted that

Hans's accomplishments are founded... upon a one-sided development of the power of perceiving the slightest movements of the questioner.... We are justified in concluding from the behavior of the horse, that the desire for food is the only effective spring to action.... The gradual formation of the associations mentioned above, between the perception of movement and the movements of the horse himself, is in all probability not to be regarded as a result of a training-process, but as an unintentional by-product of an unsuccessful attempt at real education. (Pfungst, 1911, pp. 240–241)

In this case, the master's movements provided the stimuli in the presence of which the horse's taps were followed by food. The case of Clever Hans demonstrates that even very subtle properties of stimuli can signal the consequences of responding, and it is often cited as *The Clever Hans Effect* when critics wonder whether sophisticated behavior depends on cues unwittingly provided by participants.

Facilitated communication, for example, was an attempt to provide therapy for nonverbal children on the autism spectrum. The children's hands were guided on a typewriter keyboard by facilitators, individuals who were supposed to provide emotional support and motor help. Even though the children did not speak, some soon seemed to be producing complex typed messages. When it was discovered that the children could answer questions correctly only when the facilitators knew the questions, however, it became clear that facilitated communication was a modern Clever Hans phenomenon (Montee, Miltenberger, & Wittrock, 1995). The facilitators had been actively guiding the typing, though in many cases like Clever Hans' master they were unaware that they were doing so.

Signaling effects such as those displayed by Clever Hans were eventually examined more sys-

tematically. They came to be called the discriminative functions of stimuli, and differed in many ways from the kinds of signaling functions that had been studied by Pavlov. The research that most decisively established the distinction was conducted by the American psychologist, B. F. Skinner, who arranged an environment in which a rat's lever presses produced food when a light was on but not when it was off, as illustrated in the following passage:

[The apparatus] consists of a dark, well-ventilated, sound-proofed box... containing... a horizontal bar, made of heavy wire, which may be pressed downward approximately 1.5 cm. against a tension of 10 grams. As the lever moves downward, a mercury switch directly behind the wall is closed. We are concerned with the response of the rat in pressing this lever, which we may define as any movement by the rat which results in the closing of the switch. The switch operates a food-magazine, which discharges a pellet of food of standard size into the tray, where it is accessible to the rat. The connection between the lever and the magazine may be broken at will by the experimenter.... The only additional requirement for the investigation of a discrimination is an extra source of stimulating energy... a small (3 c.p.) electric bulb.... The experimenter controls the current to the light and the connection between the lever and the magazine in such a way that the response to the lever-plus-light is always followed by the discharge of a pellet of food into the tray, while the response to the lever alone is never so reinforced. The animal eventually learns to respond to the lever when the light is on but not to respond when the light is off. (Skinner, 1933, pp. 304–305)

In this example, the light signals the consequences of pressing the lever, in that the lever press is reinforced in the presence but not the absence of the light. The light is a *discriminative*

stimulus, and the rat comes to press the lever more often when it is on than when it is off. As the rat begins to respond differently in the presence than the absence of the light, its behavior is said to come *under the control* of the light as a discriminative stimulus; the light is also said to *occasion* the behavior. The development of this differential responding has been called *discrimination learning* (this is a technical usage, but later we'll discuss how it is related to discrimination in social behavior, as in racial profiling and in other differential treatments of people along dimensions such as gender and ethnicity).

The relations between a discriminative stimulus and the consequences of responding are elaborated in the following passage by Skinner (the term *operant* refers to a class of responses having certain consequences, and the term *reinforcement* refers to these consequences):

the operant must *operate* upon nature to produce its reinforcement. Although the response is free to come out in a very large number of stimulating situations, it will be effective in producing a reinforcement only in a small part of them. The favorable situation is usually marked in some way, and the organism... comes to respond whenever a stimulus is present which has been present upon the occasion of a previous reinforcement and not to respond otherwise. The prior stimulus does not elicit the response; it merely sets the *occasion* upon which the response will be reinforced.... Three terms must therefore be considered: a prior discriminative stimulus (S^D), the response (R^O), and the reinforcing stimulus (S^I). Their relation may be stated as follows: only in the presence of S^D is R^O followed by S^I . (Skinner, 1938, p. 178)

Skinner explored this three-term relation experimentally with lights as discriminative stimuli, rats' lever presses as responses, and food pellets as reinforcing consequences, but his next example, reaching for and touching objects in the seen envi-

ronment, illustrates the broad range of situations to which the relation can be applied.

A convenient example is the elementary behavior of making contact with specific parts of the stimulating environment. A certain movement of my arm (R^O) is reinforced by tactual stimulation from a pencil lying on my desk (S^I). The movement is not always reinforced because the pencil is not always there. By virtue of the visual stimulation from the pencil (S^D) I make the required movement only when it will be reinforced. The part played by the visual stimulus is shown by considering the same case in a dark room. At one time I reach and touch a pencil, at another time I reach and do not.... In neither the light nor the dark does the pencil *elicit* my response (as a shock elicits flexion), but in the light it sets the occasion upon which a response will be reinforced. (Skinner, 1938, p. 178)

The three-term relation, discriminative-stimulus—response—consequence, will be a recurrent theme. Each term is critical. Their combination distinguishes them from other, simpler behavioral relations. In the Pavlovian situation, for example, in which a stimulus is signaled, the organism's behavior has no effect on the sequence of events; no consequences are arranged for responses.

Consider the earlier examples. My blinking or startling at the lightning flash won't prevent the subsequent clap of thunder. But if a traffic light is red as I approach an intersection, my stepping on the brakes is occasioned by this stimulus only because I have learned the potential consequences of doing or not doing so. The second of these two examples is the only one that involves all of the terms of Skinner's three-term contingency. An important difference in vocabulary accompanies these distinctions: (i) **when a stimulus is the primary cause of a response, we say that the stimulus elicits the response or that the response is elicited**; but (ii) **when a response occurs in the presence of a stimulus because the stimulus**

signals some consequence of responding, we say that the stimulus occasions the response and that the response is emitted.

Early animal experiments were often concerned not so much with the nature of discrimination learning as with the sensory capacities of organisms. For example, rodent vision was studied by arranging two paths only one of which led to food (Yerkes & Watson, 1911). Where a rat had to choose between left and right, two stimuli were presented (e.g., a black card and a white card). The path to food varied from left to right but was always indicated by the same card (e.g., black). Once the rat learned to take the path indicated by the card correlated with food, the limits of its vision could be studied by substituting other cards for the original pair (e.g., light and dark grays). Such experiments were laborious; demonstrating discrimination learning might take hundreds of trials if the rat learned at all. Several problems existed in this type of study, not least of which was ensuring that the rat looked at the cards when it reached the choice point.

Apparatus improved over time. Figure 2-3, for example, shows the jumping stand developed by Karl S. Lashley (1930). Lashley described its advantages:

it requires the animal to jump against the stimulus patterns from a distance, instead of to run past them.... I have usually trained the animals by placing the stand against the screen and allowing the animals to step through the open holes to the platform, then gradually withdrawing the stand until, in ten or fifteen trials, the distance of 25 cm. is reached. Cards are then placed in position and training in discrimination begun. (Lashley, 1930, pp. 454–457)

In Lashley's apparatus, rats typically learned to discriminate black from white with perfect accuracy within four or five trials, and even more difficult discriminations, such as vertical versus horizontal, could usually be mastered within less than 50 trials.

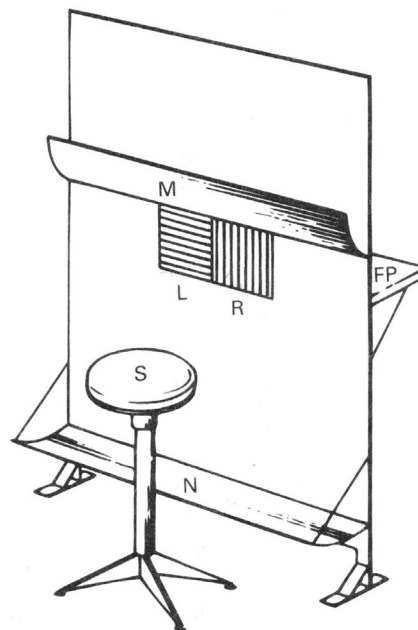


Figure 2-3 The Lashley jumping stand (Lashley, 1930, Figure 1). A rat was trained to jump from the stand (S) to one of two doors (L and R). If it jumped to the correct door, the door gave way and the rat reached the food platform (FP). If it jumped to the incorrect door, the door remained fixed and the rat fell into the net below (N). The projecting metal sheet (M) prevented the rat from jumping too high. In the illustration, the right door (R) would be correct for a rat being trained to jump toward vertical lines.

These cases in which discriminative stimuli signal consequences are more complex than the example in which a rat's lever presses produced food in the presence but not the absence of light. There our concern was only with how often presses occurred when the light was on and when it was off. The jumping stand, however, seems to involve just two responses and their consequences: jumping toward vertical and finding food and jumping toward horizontal and landing in the net. But left and right are not irrelevant to the rat. The situation involves at least four responses, each with its own conse-

quence: jumping to vertical on the left, to vertical on the right, to horizontal on the left and to horizontal on the right. Rats might respond on the basis of position, left or right, rather than on the basis of stimulus cards. For example, if the first three trials of vertical-horizontal training were set up with vertical on the right, as in Figure 2-3, it would be no surprise if on trial 4, with vertical on the left for the first time, the rat jumped right, toward horizontal. Until trial 4, jumping to the right led to food just as reliably as jumping toward vertical.

A discrimination in which stimulus conditions alternate, as in the lever-pressing example, is called a *successive* or *go-no go* discrimination. One in which two or more stimuli are present at the same time and in which each is correlated with a different response, as in the jumping-stand example, is called a *simultaneous* discrimination. Both illustrate signaling procedures superimposed on consequences of responding. Such procedures come in varying degrees of complexity.

ESTABLISHING THE EFFECTIVENESS OF CONSEQUENCES

Some consequences of behavior are more important than others and their effectiveness can vary over time. For example, water is likely to be an effective reinforcer if you've been deprived of water for a long time, but it is less likely to be so if you just drank a lot of water. The things that can be done to change its effectiveness are called *establishing* or *motivating operations*. *Deprivation* and *satiation* are two examples but are not the only possibilities. For example, heavy exertion in a hot and dry climate or a mouthful of very salty food can have the same effect as a period of water deprivation. Establishing operations change the effectiveness of consequences by changing the likelihood of behavior, as illustrated in the following passage from B. F. Skinner:

the probability of drinking becomes very high under severe water deprivation and very

low under excessive satiation.... The biological significance of the change in probability is obvious. Water is constantly being lost through excretion and evaporation, and an equal amount must be taken in to compensate for this loss. Under ordinary circumstances an organism drinks intermittently and maintains a fairly steady and presumably optimal state. When this interchange is disturbed—when the organism is deprived of the opportunity to drink—it is obviously important that drinking should be more likely to occur at the first opportunity. (Skinner, 1953, p. 141–142)

The vocabularies of motivation and establishing operations have become somewhat interchangeable. Skinner also spoke of these phenomena in terms of drives:

The term is simply a convenient way of referring to the effects of deprivation and satiation and of other operations which alter the probability of behavior in more or less the same way. It is convenient because it enables us to deal with many cases at once. There are many ways of changing the probability that an organism will eat; at the same time, a single kind of deprivation strengthens many kinds of behavior. (Skinner, 1953, p. 144)

Behavior that occurs because of establishing operations is sometimes said to be *evoked*. Skinner pointed out, however, that the effects of establishing operations must not be equated with those of stimuli:

A common belief is that deprivation affects the organism by creating a stimulus. The classic example is hunger pangs. When an organism has been without food for a sufficient time, the contractions of the stomach stimulate it in a characteristic way. This stimulation is often identified with the hunger drive. But such stimulation is not closely correlated with the probability of eating. Hunger pangs

are characteristic of only a small part of the range through which that probability varies continuously. We usually eat our meals without reaching the condition of deprivation in which pangs are felt, and we continue to eat long after the first few mouthfuls have stopped any pangs which may have occurred. (Skinner, 1953, pp. 144–145)

As Skinner's example indicates, effects of discriminative stimuli must be distinguished from those of establishing operations. Another relevant term is *incentive*. It is often defined as a motivator or incitement to action, but it usually implies some stimulus correlated with its availability. Food pellets that a rat has not yet seen or eaten may serve as reinforcers but they are not yet incentives. Once the rat has produced and eaten them, however, their sight or smell or predictable availability will function as incentives.

The most straightforward way to distinguish between consequential procedures and establishing or motivational ones is to consider whether the consequences of a response change or stay the same. Consider a flashlight (cf. Michael, 1989). It lights when I press the button that turns it on. It does so whether I press the button in light or in dark, but turning it on matters to me only when it is dark. Thus, changes from outdoor daylight to darkness or from indoor lamplight to the darkness of a power outage are examples of establishing operations with regard to whether I'm likely to turn on the flashlight. In each case, something happened that made it important to turn on the flashlight, but I could have turned it on even if those events hadn't occurred.

If my flashlight battery goes dead, however, pressing the button that usually turns it on no longer does anything. The consequences of pressing the button have changed. It used to work. Now it doesn't. Thus, the dying of the battery is not an establishing operation. It is a consequential operation: it changes whether my button press will be reinforced by the onset of light.

But the dead battery may be establishing or motivational in a different way. It might not have

mattered to me before, but now finding a fresh battery has become important. Once I find one and replace the dead battery, my flashlight works again. In other words, the battery going dead had two effects at the same time: it had a consequential effect, because it changed what happened when I tried to turn on the flashlight, but it also had an establishing or motivational effect, because it made finding a fresh battery important. And if I cannot find a fresh battery, I might start looking for candles and matches; not everything that becomes established as a potential reinforcer will necessarily be available when that happens.

Establishing operations and consequential operations work together. Usually we can't have one without the other, but it is important to be clear about which behavior is related to each. In these examples, turning on the flashlight was a response with consequences, but the light versus dark conditions established whether it was important for me to turn it on; similarly, when the battery went dead, replacing the battery was a response with consequences, but the failure of the flashlight to work established whether it was important for me to change the battery. Another point of this example is that these procedures encompass far more than the physiological effects such as hunger and thirst implied by the language of drive or motivation.

In contrast with the language of stimulus control, in which changes in discriminative stimuli are said to occasion responses, the responding said to be evoked by establishing operations may occur in a relatively constant environment. For example, if you are more likely to check the refrigerator a long time after than right after a meal, it is your behavior and not the refrigerator that changes from one time to another. In this case, checking the refrigerator is said to be evoked by the establishing event, food deprivation. And when we want to talk about such behavior without mentioning either the establishing operations or the discriminative stimuli, it remains okay to say that the behavior was emitted. In other words, establishing or motivational procedures *evoke*, discriminative stimuli *occasion*, and the responses they evoke and/or occasion *are emitted*.

SUMMARY

The study of behavior is concerned with relations between environmental events, *stimuli*, and the organism's actions, *responses*. We can examine these relations by analyzing how changes in the environment produce changes in responding. A critical first step is to *observe* behavior, but just watching is typically not enough. To understand behavior we must intervene by changing the environment. We describe environmental changes in terms of classes of experimental procedures: *presenting stimuli*, *arranging consequences*, *signaling stimuli or consequences*, and *arranging establishing operations*. We'll return to these procedures often throughout this

book, and they will especially help us to organize the topic of learning without words in Part III. They are summarized in Table 2-1.

Behavior is complicated. Different stimuli can have different effects on different responses, and different responses can have different consequences. Nevertheless, as we will see, a wide range of learning situations can be treated in terms of combinations of these basic types of experimental interventions. As our behavioral taxonomy these categories will take us a long way. But later, especially when we consider the transition from learning without words to learning with words, we will find that they do not exhaust the possibilities.

Table 2-1 Behavioral Procedures

<i>Procedure</i>	<i>Description</i>	<i>Examples</i>	<i>Usage</i>
1. Observation	No intervention.	We watch an animal behave.	---
2. Stimulus-presentation procedure	Stimulus <i>A</i> is presented.	<i>Loud noise (A)</i> startles child. Physician shines <i>light (A)</i> in patient's eye.	Stimulus <i>elicits</i> response; response <i>is elicited</i> by stimulus.
3. Consequential procedure	Response <i>B</i> has consequence <i>C</i> (e.g., a stimulus is produced or terminated).	<i>Putting coin in vending machine (B)</i> produces <i>soft drink (C)</i> . <i>Touching hot stove (B)</i> produces <i>burn (C)</i> . <i>Light goes out (C)</i> when <i>switch is thrown (B)</i> .	Response is <i>emitted</i> .
4. Signaling or stimulus-control procedure: Superimposed on stimulus presentation	Stimulus <i>D</i> signals presentation of stimulus <i>E</i> .	<i>Lightning (D)</i> precedes <i>thunder (E)</i> .	Stimulus <i>elicits</i> response; response <i>is elicited</i> by stimulus.
5. Signaling or stimulus-control procedure: Superimposed on consequences	Stimulus <i>F</i> signals that response <i>G</i> will have consequence <i>H</i> .	<i>Red traffic light (F)</i> signals that <i>driving through intersection (G)</i> may lead to <i>traffic ticket (H)</i> . <i>Ringing telephone (F)</i> signals that <i>answering (G)</i> may provide <i>opportunity for conversation (H)</i> .	Stimulus <i>occasions</i> response; response <i>is emitted</i> in presence of stimulus.
6. Establishing operation	Effectiveness of consequence <i>I</i> as a reinforcer or punisher is established.	<i>Food (I)</i> becomes an effective reinforcer after food deprivation. The presentation of shock makes <i>shock removal (I)</i> a reinforcer. When it is important to unlock a door, <i>the key to the door (I)</i> becomes a reinforcer.	An event is <i>established</i> as a reinforcer or punisher. Behavior is <i>evoked</i> by the establishing operation.

PART TWO BEHAVIOR WITHOUT LEARNING

Chapter 3 Evolution and Development

*<etym>Evolution and revolution are descendants of the Latin *volvere*, to roll; they differ in that evolution implies an unrolling or rolling out whereas revolution implies a rolling over or turning around. They appear unrelated to *develop*, perhaps of Celtic origin via *des- plus voloper*, an unwrapping or unfolding. Selection can be traced to the Latin *legere*, originally to gather or to choose; via *logos* it is a relative of logic and lexical. The prefix, *se*, adds the implication of a weeding out from a large number, as contrasted with the bringing together implied by *con*, the root prefix for collection.*

*<etym>Phylogeny, evolutionary history, and ontogeny, the life history of the individual organism, share the Greek root *gen*, in the sense of kind or sort, through which both are related to generalization. *Phylo-* has a Greek root implying a tribe or clan or racial stock and *onto* has one implying being or reality. In their combination with *gen*, each implies origin: the origin of a biological phylum or population or the origin of a living entity. *Memetic* is derived from a 1976 coinage by Dawkins, *meme*, a term that echoes both *gene* as in genetics and *mime* as in mimicry.*

Chaos Theory and Darwin's Butterfly

The Nature of Evolution

Recipes and Blueprints

Variation and Selection

The Origins of Complexity

Evolution and Development

Kinds of Selection

Addendum3A: Phylogeny, Ontogeny and Behavior

It has not been many human lifetimes since Copernicus and Galileo and Kepler pressed their

cases that the earth was part of a system of planets orbiting our sun rather than being at the center of things. However humbling that displacement may have seemed at the time, it pales in comparison with the twentieth-century discoveries that our sun is just one among hundreds of billions of stars in our galaxy and that our galaxy is just one among hundreds of billions of galaxies in our universe.

The cumulative evidence has converged on an estimate for the age of our universe of roughly fourteen billion years. Our galaxy formed within the first billion years or so and our sun ten bil-

KEY TERMS: Evolution; Variation and Selection; Recipe versus Blueprint; Phylogeny and Ontogeny; Development and Evo Devo; Modules, Compartments and Boundaries; Natural Selection, Sexual Selection, Operant Selection, Cultural or Memetic Selection.

lion years or so later (e.g., Marochnik & Suchkov, 1995). Our planet formed not long after. The earth is about four and a half billion years old. That's a very long time. If I tried to count to a billion, I'd take more than thirty years to finish even if I kept up an uninterrupted count of one number per second. If I took time out to sleep, of course, I'd take much longer. The one-per-second estimate, by the way, is very generous: I can easily manage with small numbers, but surely I'd slow down when I got to bigger ones like 9,275,078, especially if I was worrying about losing count.

Life existed on earth for most of those years (Fortey, 1998, provides a detailed account). Chemical and fossil evidence indicates that it began within the first billion years or so. Over most of the next three billion years it consisted of single-celled organisms. Some of those single-celled organisms congregated, but multicellular organisms in which different cells had different functions only appeared roughly 550 million years ago, in the geological period called the Cambrian. An explosion in the diversity of multicellular life during that period provided the major groupings from which contemporary species evolved. One of these was the vertebrates. The evolution from fish to amphibians to reptiles included many significant events, such as the colonization of land. The dinosaurs were a spectacular part of the story, but by 65 million years ago they were gone, surviving only in those forms that have since evolved into birds. The passing of the dinosaurs made room for the evolution of mammals, and by perhaps four million years ago primates had evolved that walked upright. We humans eventually emerged from that hominid line only a little more than 100,000 years ago. We are all cousins, all the descendants of a very long line of survivors.

CHAOS THEORY AND DARWIN'S BUTTERFLY

In the face of these vastnesses of time and space it is all too easy to conclude that we are insignificant. But if nothing else, our planet is a place that

has produced organisms who have begun to see how the world in which they live works. We are those organisms. Writing on the issue of God having created humans from mud, Kurt Vonnegut put it this way: "And I was some of the mud that got to sit up and look around. Lucky me, lucky mud" (Vonnegut, 1963, ch. 99). His point is not novel: "Our word 'human' comes from the proto-Indo-European root *dhghem*, meaning simply 'earth'" (Thomas, 1992, p. 19). So let's look around. There is plenty to marvel at.

In those vastnesses the odds *were* against us, individually as well as collectively. Charles Darwin can give us a sense of how much so. Butterfly collecting was one of Darwin's many interests, and it is safe to assume that in his youth in the summer of 1828 in North Wales he caught a butterfly. Actually, he almost certainly caught more than one, but the capture of any butterfly by Darwin or by any other butterfly collector during the first half or so of the nineteenth century would suit our purposes. Whichever capture we consider, all our lives hung upon it.

This conclusion follows from what in Chaos Theory is called the Butterfly Effect (Gleick, 1987). Chaos Theory is derived from the mathematics of nonlinear systems, which involves recursive computations, computations in which the output of an equation serves as the input for its next iteration. For example, if x_n begins as .50 in the equation $x_{n+1} = 3x_n(1-x_n)$, it first becomes .75, then substituting this as the new x it becomes .56, then .74, and .58, and .73, and so on. Many natural phenomena, including the weather, are best described in terms of such systems. One significant property of some of them is that they are drastically affected even by very tiny changes in initial value. Mathematical models for predicting the weather made significant contributions to Chaos Theory (Lorenz, 1963). The Butterfly Effect refers to the finding that when predicting weather patterns using models that incorporate nonlinear equations, the entry of initial values differing by as little as the energy produced by the flap of a butterfly's wings can alter the prediction of the direction in which a storm system will move some days from now.

Now consider the implications of Darwin's capture of that butterfly. If it had remained free to flap, weather patterns throughout the world, little by little, would have begun to deviate from those in our own history. We could imagine their impact on major historical events. For example, the battle of Gettysburg would probably have gone differently had the weather been different. And even if Darwin had set sail on the *H.M.S. Beagle* in that world as in ours, his voyage might have come to a different conclusion.

But for us there would have been an even more profound effect, because each of us is the product of a particular union of sperm and egg. Would that particular union have come to pass—would any of us have ever come into existence—if our parents' act of procreation had occurred at a somewhat different time or place? Almost certainly not. A lovely sunset where in our world it was overcast; a meeting at an agreed time where in our world a delay was caused by rain; a wedding forced indoors by storm where in our world it occurred in open air; illness following from rain and damp where in our world a parent remained healthy. Spun out over days and weeks and months, these alternative circumstances would very soon extend to every person on our planet.

Long before the twentieth century, things would have differed so much that no individual now alive would have been conceived in that other world. No doubt some individuals would have been given the same names as their existing counterparts, but all would have been different, both in their genetic endowments and in their upbringings. Would an Igor Stravinsky in that world have composed "The Rite of Spring"? Would a Pablo Picasso have painted "Guernica"? Would an Albert Einstein have formulated the Theory of Relativity? Of those who determined the fates of so many in our world, no Roosevelt or Hitler or Churchill or Stalin or Gandhi or Mao. Others in their places and in ours, but neither you nor me. Had that butterfly evaded Darwin's net, we would not be here. Lucky we. And if our being here now sounds improbable enough, think of all the flaps of all the butterflies across all the lepidopteran millenia of our world.

Now some might argue that a single butterfly couldn't have made all that difference, and that whether it flapped or not would have been washed out by other events. But if effects on the weather seem too counter-intuitive to be persuasive and the butterfly effect seems too metaphorical, consider that in taking flight in one direction or another that butterfly might have led Darwin to trip when he did not trip in our world, perhaps resulting in a sprained ankle and so on through a cascade of events ending with someone other than Darwin eventually taking his place on the deck of the *H.M.S. Beagle*. A world without his revelatory trip and his momentous book would have been different enough for the purposes of our example.

THE NATURE OF EVOLUTION

My interest in evolution began early. I was a preschooler when my parents took me to see Walt Disney's animated film, *Fantasia*, not long after its 1940 premiere. Igor Stravinsky had written "The Rite of Spring" as a ballet evoking primitive human rites, but Disney's animations for it instead began with the volcanic spasms of an ancient earth, followed by the emergence of life in the sea and its movement onto land, and culminating in prehistoric scenes dominated by the dinosaurs. The dramatic entrance of Tyrannosaurus Rex scared me at the time, but it was not too long afterward that it was a treat to be taken to see actual dinosaur skeletons in the exhibit halls of the Museum of Natural History in New York City. All of the segments of *Fantasia* were cartoons but on that screen the dinosaurs had a reality not shared by Mickey Mouse as the Sorcerer's Apprentice or the pirouetting hippopotami of "The Dance of the Hours." I was hooked. But it is one thing to have one's interest aroused and another to grapple with real events rather than human creations such as movie cartoons. What kept me hooked was the coherent and persuasive science I later encountered.

We live in a time when some still think evolution is a topic from which schoolchildren must be protected. Evolution is of course hardly the only

example of reluctance to face facts. For example, the evidence for the Nazi Holocaust of World War II remains overwhelming. It happened during my lifetime and I vividly recall the newsreels of the time. But when they came home from the war, many of the US troops who had participated in the liberation of the concentration camps didn't talk much about what they had seen (Hirsh, 2010). Despite the overwhelming evidence, some of those born too late to remember it came to deny that the Holocaust had ever happened. Talk is too often unconstrained by reality. Like everything else we do, human talk is behavior, and as we shall see when we later consider verbal behavior, it is too often shaped more by social consequences than by actual events. Anyway, despite the naysayers, evolution happens.

Evolution has operated throughout the history of life on our world. It is rapid enough that it has been observed within individual human lifetimes (Weiner, 1994). It occurs in natural habitats, such as the Galapagos Islands, where different species of finches continue to evolve with changes in the local habitats on each island. It also occurs as a result of human interventions, for example when disease organisms become resistant to antibiotics or insect pests become resistant to insecticides. Evolution is the foundation of the entire discipline of contemporary biology: "Biology without evolution is like physics without gravity" (Carroll, 2005, p. 294). We are only beginning to reap the fruits of this expanding science, ranging from the legal ramifications of DNA testing to a broad spectrum of medical applications.

The fossil record is inevitably incomplete, but many lines of evidence from biology and geology and other disciplines have decisively shown that evolution has happened and continues to happen. In other words, **evolution is not a theory; it is a name for certain kinds of changes that happen to the biological populations we call species**. Theories of evolution are not about whether contemporary species are descended from the very different ancestors we find in the geologic record. All theories of evolution take that for granted. They differ in what they say about how evolution

came about. The theory that has been most successful in accommodating the facts of evolution is Charles Darwin's account in terms of natural selection. *Natural selection* refers to Darwin's account of evolution in terms of the differential survival and reproduction of the members of a population; the environment selects the individuals who pass on something of themselves from one generation to the next and it thereby shapes the characteristics of those in later populations (Carroll, 2005, 2006; Dawkins, 1976, 1986). Evolution by natural selection requires variations within populations; these variations are the stuff upon which selection operates.

Selection was well-known even before Darwin but was the sort used by humans in horticulture and animal husbandry. People knew how to breed plants or livestock selectively for hardiness or yield or other characteristics. This selective breeding was called *artificial selection*, and it created new varieties of vegetables and flowers and so on. Workhorses were selected for strength and racehorses were selected for speed. One part of Darwin's insight was that a similar kind of selection occurred in nature, without human intervention; that was *natural selection*. Darwin's main arguments were first published in his book, *On the Origin of Species* (Darwin, 1859). They were warmly received in some quarters but in others were strongly resisted. The resistance grew and by the end of the nineteenth century the belief was widespread that Darwinism was dead. It didn't recover until well into the twentieth century. The half century or so that preceded that recovery has been called the eclipse of Darwinism (Bowler, 1983; cf. Catania, 1987).

The reason for the eclipse wasn't simply that evolution itself had temporarily been discredited but rather that other theories than Darwin's became dominant. The main alternatives to Darwin's *natural selection* were *Lamarckism*, *orthogenesis*, and *Mendelian genetics*. Lamarckism was based on the work of an eighteenth-century French scientist who in his time had done much to make a case for the fact of evolution (Jordanova, 1984). Lamarck's guess was that characteristics acquired during an organism's lifetime could be passed

on to its offspring, through changes in its own genetic material or germ plasm. One problem with his theory was that it couldn't show why advantageous acquired characteristics should be any more likely to be passed on than disadvantageous ones such as injuries.

According to the theory of orthogenesis, evolution was a developmental unfolding directed by forces within organisms, without reference to demands of the environment. One of its manifestations was supposed to be the recapitulation of phylogeny by ontogeny. *Ontogeny* is the development of the individual organism and *phylogeny* is its evolutionary history. During ontogeny the embryo was thought to pass through stages corresponding to its phylogeny. But the idea of recapitulation, based on only superficial properties of embryos, is no longer central to evolutionary theory (Gould, 1977).

The work of Gregor Mendel (Henig, 2000) provided a crucial foundation for genetics, but its problem was that it provided no mechanism for variation. In strict Mendelian descent, dominant and recessive genes in one generation determined their proportions in the next. Without variation, natural selection had nothing to work on. To provide for the appearance of new forms, later Mendelian accounts added mutation theory, which held that evolution proceeded through spontaneous and usually large genetic changes. Mutations have since played a pivotal role, but too little was known about them at that time to support a convincing account.

Recipes and Blueprints

In the nineteenth century, genes were theoretical entities. The techniques of cell biology hadn't yet reached the point at which genes had been identified in actual cells; the discovery of the structure of DNA (Watson & Crick, 1953) would follow nearly a century after Darwin's revolutionary book. Nevertheless, all of these evolutionary theories assumed that hereditary material of some sort was passed on from one generation to the next and that evolution was determined by the properties

of this material. A recurrent major flaw was the assumption that genetic material constituted a representation or copy of the organism. In the earliest versions of orthogenesis, called *preformationist*, the embryo was literally a homunculus, a tiny individual complete in all its parts; in later variations it was seen as taking on ancestral forms, as ontogeny was said to recapitulate phylogeny. As for Lamarckism, the transmission of acquired characteristics required that they be preserved in the germ plasm in some way, so the germ plasm had to contain some kind of plan for those parts of the organism to be altered in subsequent generations. In each case the germ plasm could be regarded as a representation or copy of the organism.

A *recipe* is a sequence of procedures or instructions. It describes how to create a product but doesn't necessarily incorporate a description of the product (a recipe for a cake doesn't look like a cake). A *blueprint*, on the other hand, doesn't ordinarily say how to construct the structure that it shows. A blueprint is a representation or copy but a recipe isn't.

A major achievement in contemporary biology was to reinterpret genetic material not as blueprints for the organism's structure but rather as recipes for its development (Dawkins, 1986, Ch. 11). The modern formulation demanded rethinking of the sense in which genetic material contains information, whether about evolutionary history or about the organism's structure (Dawkins, 1982, Ch. 9). Genetic materials provide some information about the past environments in which they've been selected, especially when those materials can be found in many species, but they don't include the genetic materials of all those other organisms that didn't survive. In combination with developmental environments they determine the eventual structure of an organism, but **they do so as recipes for the production of proteins rather than as blueprints for body parts**. One implication was that Lamarckism and orthogenesis were untenable alternatives to Darwinian selection because their implicit copy theories were inconsistent with what we've learned about how the genetic material works.

It is ironic that Mendelian genetics had also been seen as a serious challenge to Darwinian selection. The integration of Mendelian genetics with Darwinian selection in the 1920s and 1930s, known as the *modern synthesis*, became the core of twentieth-century biology. Mendelian genetics had provided no mechanism for variations. Then genetic experiments with fruit flies by T. H. Morgan and others not only elaborated on genetic mechanisms but also brought mutations into the laboratory. With fruit flies, many generations could be studied within a relatively short time. The evidence yielded natural rates of mutation and the magnitudes of mutation effects, which were relatively small compared to the changes assumed by prior mutation theories. The combination of Mendelian genetics with the facts of mutation provided the variability needed for the workings of natural selection. The case has been further strengthened in recent decades as developmental biology has been incorporated into the story, in an account sometimes called *Evo Devo* (Carroll, 2005).

The Darwinian view had to face and overcome other hurdles besides competing theories (cf. Mayr, 1982). One was the incompleteness of the fossil record. Our understanding of prehistoric life depended on finding occasional preserved members of earlier species, but the accidents of their preservation and discovery left inevitable gaps. Furthermore, hard parts such as bones or shells were far more likely to be preserved than soft parts. And even when we found all parts intact, our information about how those creatures behaved was limited. It was often necessary to resort to indirect evidence (e.g., analogies with living species; fossil records of behavior such as fossil footprints).

The age of the earth was another problem. In those days the estimate was too short to make evolution through natural selection plausible, but that age has been revised vastly upward. Another misunderstanding was the likelihood of improbable events coming to pass when many opportunities for those events occur over extended time periods. For example, suppose some organic molecule is a crucial prerequisite for life and occurs

naturally with odds of one-in-a-million only when lightning creates it by passing through some mixture of gases present in earth's early atmosphere. Its creation might seem a very long shot. But many lightning storms over many millions of years during our planet's early history would have repeated those conditions many millions of times, making it a virtual certainty that the molecule would be created not just once but again and again, even though the exact moments of its creation would have been unpredictable (cf. Dawkins, 1986; Gleick, 1987).

Variation and Selection

Variation and selection will be central to much of our later discussion of learning and behavior, in phenomena called shaping and reinforcement. We'll examine it now in the context of natural selection. Let's start with a population of prey animals (e.g., antelopes) the members of which vary in how rapidly they can outrun predators. The reasons might include differences in anatomy (e.g., bone length, muscle size), sensory differences that allow some to get off to a quicker start than others, metabolic differences that affect endurance, and so on. Everything else being equal, the slowest are the ones most likely to be caught.

The proviso that everything else must be equal is important. Speaking only of speed is an oversimplification. For example, an antelope that is fast at the expense of needing more to eat might forage longer and thus run a higher risk of being seen by predators during foraging. If this antelope is more often chased than others, that higher risk might counterbalance its speed advantage. Or, one antelope might run faster than another but the other is harder to catch because it can change direction more unpredictably. As long as the antelope population varies, we can recast our argument in terms of how such factors affect the chances of being caught. Speaking of speed is convenient, but the effective dimensions of escape from predators are more complex than that.

At any time, our antelope population has some mean or average speed, with some members

above that mean and others below it. The ones below are those most likely to be caught and so are less likely to pass their genes on to the next generation. The next generation will then include more descendants of those above the mean than of those below or, in other words, fewer of the previous slow and more of the previous fast runners. The mean speed in this generation will again be higher than in the last one. But the same kind of selection still operates: again, slower ones are more likely than faster to be caught. Over many generations, therefore, the mean speed becomes faster and faster. (Selection will operate similarly on the big cats and other predators, because their effectiveness in catching antelopes will vary across individuals too.)

The evolution of the horse provides striking evidence for such selection (Gould, 1996a; Simpson, 1951). Over the 50 million years or so since *eohippus*, the so-called dawn horse (technically, its proper name is *Hyracotherium*), individuals in the populations from which modern horses are descended gradually became larger. These size changes were accompanied by other changes (e.g., toes becoming hooves), presumably including changes in behavior. *Eohippus* was the ancestor of modern horses, but it is unlikely that an *eohippus* population could survive in contemporary habitats. The fact that *eohippus* is extinct is relevant to our story. Many descendants of *eohippus* must have been the most evasive of their kind in their time, but they are no longer around. When selection operates on some relative property, such as speed relative to a population mean, the mean for the population changes. After capture by predators has repeatedly selected faster escape in a population, few descendants of the originally slow runners will be left even if that slower running speed provided a selective advantage at a time when it was very fast relative to the mean. In other words, as *eohippus* demonstrates, we should not expect to find examples of ancestral forms within current populations.

According to these arguments **the environment does the selecting** (the environments of predators include their prey and the environments

of prey include their predators). It maintains as well as creates and alters the characteristics of organisms. The ancestors of whales were once land mammals. After they moved back into the sea, the environmental contingencies that made legs advantageous no longer selected well-formed legs. Instead, selection began to favor limbs effective for movement through water. The legs of the ancestors of whales gradually disappeared; in a sense it is appropriate to say that the legs had extinguished or become extinct (Provine, 1984; Skinner, 1988, p. 73). Selection operates on species by acting on particular organs and systems and body parts, and all of these become important because of the ways in which they serve an organism's behavior. Sensory organs and nervous systems and muscles and so on determine what an organism can do.

Consider another example. Environments in which a major food source consists of hard nuts favor beaks that work well at crunching nuts. Although Darwin did not recognize the significance of the observation until some time after visiting the Galapagos Islands during his voyage on the *Beagle*, such beaks were a characteristic of one population of finches there (Weiner, 1994). Such selection hadn't occurred with finches on other islands where softer foods were readily available. The hard nuts had set the occasion for the selection of finches with good nut-crunching beaks.

Selecting environments include members of one's own species. In the discussion of natural selection, the neck of the giraffe has often been offered as an example of selection, on the grounds that environments with food high on tall trees selected for long necks. But the neck of the male is typically longer than that of the female though the same selective contingencies should have acted upon both genders. Despite the plausibility of this evolutionary story, the long neck of the giraffe appears not to be a product of selection by such environments. Instead, female giraffes prefer males with long necks, and this sexual selection by the female is more likely what drove the evolution of long necks (Coe, 1967; Gould, 1996b; Simmons & Scheepers, 1996).

The role of *sexual selection* has long been appreciated in accounting for other evolutionary extravagances, of which the tail of the peacock is a familiar example (Darwin, 1871). The peahen, the female of that species, is more likely to mate with a male with a larger and/or more colorful tail. Despite the metabolic and other costs of their elaborate tails, such males are more likely to be healthy and therefore to provide favorable genes to their offspring. There is no inconsistency between these contingencies of sexual selection and those involved in other aspects of Darwin's account of natural selection. We'll encounter a related example later, in an account of how the female cowbird may shape the dialect of a male cowbird's song through differential attention (see Chapter 9).

We've discussed phylogenetic selection involving gradual changes taking place over long periods of time (it has much in common with a kind of selection that occurs within the lifetime of the individual; see Chapter 9 on shaping). Some controversies about evolution have been about whether evolution takes place through *gradual changes*, as in the example of the horse, or in fits and starts (*punctuated evolution* or *saltation*). The fossil record includes evidence of major changes in species over periods of time that are relatively short by evolutionary standards. Examples include the explosion of multicellular life in the Cambrian period, and at the end of the Cretaceous period the extinction of the dinosaurs, perhaps triggered by the impact of a comet or some other planetary catastrophe, and the later proliferation of large mammals. Given the strong evidence for both kinds of evolutionary change, it is reasonable to conclude that evolution can take place either way, with some features selected gradually and continuously relative to a population mean and others selected following punctuated events that produced massive environmental changes.

The Origins of Complexity

Evolution by natural selection involves more than changes along a single dimension. An example is animal mimicry. A stick insect may look so much like a stick that a bird that otherwise would have

eaten it will pass it by. But to get to look like a stick requires changes in surface shape and texture and color accumulating over many generations. As that selection got going, how much good did it do for the insect's ancestors to have merely a 5% resemblance to a stick? In response to this question, Dawkins (1986, pp. 83–84) points out that a 5% resemblance might be just enough to make a difference in twilight or in fog or if the bird is far away. Once individuals in the population vary in their resemblance to sticks, natural selection based even on small differences can drive populations to more and more convincing mimicry.

Another example of organized complexity is the intricate structure of the human eye. Is it reasonable to believe that natural selection could have produced such organized complexity? Using an analogy from aeronautical design, Dawkins (1982) posed the problem this way for engineers designing a jet engine:

Imagine what they would have produced if they had been constrained to “evolve” the first jet engine from an existing propeller engine, changing one component at a time, nut by nut, screw by screw, rivet by rivet. A jet engine so assembled would be a weird contraption indeed. It is hard to imagine that an aeroplane designed in that evolutionary way would ever get off the ground. Yet in order to complete the biological analogy we have to add yet another constraint. Not only must the end product get off the ground; so must every intermediate along the way, and each intermediate must be superior to its predecessor. (Dawkins, 1982, p. 38)

If the eye is a product of natural selection, it couldn't have emerged full blown. But what good is part of an eye? The answer is that even 1% of an eye is a substantial advantage if all of one's contemporaries have even less. Any sensitivity to light is better than none, 2% is better than 1%, 3% is better than 2%, and so on (cf. Dawkins, 1986, p. 81).

But that is only part of the story. Not only have eyes evolved many times in many species. We

now know that the same gene, Pax-6, provided the source of the evolution of all eyes across the entire animal kingdom, from worms and flies and squid and crabs and fish to mammals like us (Carroll, 2006, pp. 194–196). “The eye, far from being one of the most difficult structures to account for by evolution, has become one of the leading sources of insights into how evolution works with common genetic tools to build complex organs... Common genetic tools are used to build the very different hearts, digestive tracts, muscles, nervous systems, and limbs of all sorts of animals” (Carroll, 2006, p. 202).

The earliest light sensitive tissues emerged half a billion years or more ago, during Cambrian times. “Natural selection has not forged many eyes completely from scratch; there is a common genetic ingredient to making each eye type.... These common genetic ingredients must date back deep in time, before there were vertebrates or arthropods, to animals that may have first used these genes to build structures with which to see, sense, eat, or move” (Carroll, 2005, p. 72). With sensitivity to light, predators and prey could begin to orient and move with respect to each other not just in response to accidental contact but also when at some distance from each other. From even those early times, the kind of selection relative to the population mean that we considered for antelopes and horses would have produced rapid evolutionary change, as predators became progressively more efficient in capturing prey and prey in turn became progressively more efficient at evasion (cf. Parker, 2003).

Evolution and Development

Science too evolves. Much of what we can now say about natural selection is based upon research on human and other genomes first reported only within the first decade of this century. The field continues to grow and change. I cannot do the topic justice here, but some parts of it have enough relevance to other parts of our behavioral story that it is appropriate to sketch out some of its fea-

tures (cf. Carroll, 2005, 2006; Kirschner & Gerhart, 2005; West-Eberhart, 2003). The significant developments include demonstrating the modular functions of the compartments of the developing embryo, recognizing the independence of these modules in development and evolution, and working out the roles of the conserved evolutionary processes that built structural support, circulation, neural innervation and other basic biological functions into multicellular organisms.

A key was the integration of embryology with genetics and evolution: “every animal form is the product of two processes—development from an egg and evolution from its ancestors” (Carroll, 2005, p. 4), leading to the conclusion that “the development of various body parts such as eyes, limbs, and hearts, vastly different in structure among animals and long thought to have evolved in entirely different ways, was... governed by the same genes in different animals. The comparison of developmental genes between species became a new discipline at the interface of embryology and evolutionary biology, or ‘Evo Devo’ for short.... Evo Devo can trace the modifications of structures through vast periods of evolutionary time—to see how fish fins were modified into limbs in terrestrial vertebrates, how successive rounds of innovation and modification created mouthparts, poison claws, swimming and feeding appendages, gills, and wings from a simple tubelike walking leg, and how many kinds of eyes have been constructed beginning with a collection of photosensitive cells” (Carroll, 2005, p. 9–10).

The earliest genetic contributions to life on our planet were those involving the genetic system itself, including the replication of DNA and an array of basic metabolic and structural functions called *conserved processes* (e.g., Kirschner & Gerhart, 2005). With the emergence of multicellular forms these processes expanded to determine the structure of the growing embryo, and in particular to geographic arrangements of compartments or modules, each containing genetic material destined to control various body parts and functions (Goodsell, 2009). Compartments remain

important throughout development and manifest themselves in various parts of the mature organism, including the nervous system; furthermore, the boundaries between compartments can be affected by their environments as well as by their genetic context (Bolker, 2000; Irvine & Rauskolb, 2001; Kiecker & Lumsden, 2005). Later we'll see that modules and the formation of boundaries are relevant to behavioral units, such as classes of responses with common functions.

Genes are, in effect, chemical switches, components that can be turned on or off at various stages of development. "A critical property of these switches is that changes in one switch will not affect the function of the other switches. And therein lies a huge insight into how form evolves." (Carroll, 2006, p. 206). "Modularity allows for the modification and specialization of individual body parts..., independent of other body parts... [allowing] evolutionary change to occur in one part of structure, independent of other parts" (Carroll, 2005, p. 195). Modules that isolate various developmental functions are crucial to the evolution of organized complexity. Without them a mutation that influenced, say, the form or size of a limb, would too often have lethal effects on other systems. Within compartmentalized systems, genes can have very specific effects without disrupting other functions.

As such systems play out, the conserved processes that determine skeletal structure and blood circulation and muscular attachment and neural connection and so on each do their job to accommodate to the developing organism within which they find themselves. If a mammalian forelimb changes its form or its size, blood supply will serve it in its entirety based upon chemical gradients produced by metabolizing cells, muscles and tendons will attach to bones and joints at appropriate places, neurons will find their way to sensory cells or to the sites of neuromuscular junctions, and so on, all independently of the details of the developing hindlimbs or other growing parts of this particular organism. The restriction of genetic changes to single sites opens up a vast evolution-

ary potential; effective mutations do not require synchronized changes at other sites.

Thus, the evolution of limbs is independent of the evolution of the nervous system that controls them: "the connectivity of the nervous system can change as the anatomy of the organism changes, without the need to alter the processes that generate that connectivity" (Kirschner & Gerhart, 2005, p. 160; see also p. 203). Earlier conceptions of self-organizing processes in developing organisms, and especially in developing nervous systems, properly appealed to common function, as in the assumptions that cell assemblies would come about because "cells that fire together wire together" (e.g., Hebb, 1949), but those systems were insufficiently concerned with the role of boundaries in the development of functional units.

Another property of these systems is that they too involve varieties of selection. For example, cell death is a crucial component of the developing nervous system. As cells grow from the central nervous system to sensory receptors at the periphery, only some find their way; those others that cannot find a binding site die (e.g., Edelman, 1987). The genes of the developing organism do not give instructions about where structural parts will go; instead, the parts go their variable ways and are selected on the basis of their functional engagement with other parts. This is the sense in which brains and other organs adapt themselves to the bodies within which they find themselves. Though the variable workings of these systems preclude predictions of particular outcomes, once they are in place there is a certain inevitability to the proliferation and elaboration of organized complexity. "This is a general theme in evolution, that one innovation creates the opportunity to evolve additional innovations" (Carroll, 2006, p. 113). Where there is life there is evolution.

KINDS OF SELECTION

The selection we've emphasized so far, the selection of populations of organisms over evolution-

ary time, is called *phylogenic selection*. But it is not the only kind. Of the various kinds of learning we'll explore later, one is the case in which responses are affected by their consequences. For example, if an organism is food-deprived and some response produces food, that response is likely to occur more often. This is an instance of reinforcement. It can also occur in particular environments or settings, when we say that a situation sets the occasion on which responses are reinforced. This is selection operating within the lifetime of the individual rather than over successive generations: the reinforcer selects those responses that will continue to occur.

Such selection has been called *ontogenic selection*; it involves *selection by consequences* (cf. Skinner, 1981). For the food-deprived organism, for example, responses that produce food continue to occur; other responses don't. Food is the consequence that selects some responses and not others. This is a way of saying that the responding is selected by its environment (notice how very different this is from saying that the organism itself selected some way to respond). We could say that responses that produce food survive and others that don't extinguish. Parallels between these two varieties of selection, phylogenic selection or Darwinian natural selection and ontogenic selection or the selection of behavior by its consequences, have been explored in considerable detail (e.g., Catania, 1978; Catania, 1995; Skinner, 1981; Smith, 1986); we'll note some parallels as we explore learning.

Behavior acquired through learning during an individual's lifetime will disappear unless it is somehow passed on to others. A third variety of selection occurs when behavior can be passed on from one organism to another, as in imitation or, more important, in language. For example, what someone has said or written can survive the person's death if it is passed on to and repeated by others. The verbal behavior that survives within and is shared among the members of a group is part of the culture of that group. We'll give special attention to this third kind of selection in the chapters on social learning and on verbal behavior (Chapters 19 through 24). It has been called

cultural selection or *memetic selection*. The term *memetic* is derived from *meme*, a word coined by Dawkins (1976) for an event passed along among individuals, (e.g., a vocabulary item, a catchy melody).

These varieties of selection may complement one another, but selection at one level also may oppose selection at another. For example, drug abuse is behavior that has been reinforced in ontogeny, but it will have unfortunate phylogenic consequences if it damages the fetus. At the level of cultural selection, the celibacy of some of its members may benefit a group, but it disadvantages those individuals at the phylogenic level. Conversely, at the phylogenic level opposition to birth control may benefit individuals who produce more offspring than those who practice it, but if population growth exceeds economic growth then per capita income decreases; the cultural consequences may be spreading poverty and environmental degradation. Phylogeny may have produced the capacity for behavior to be selected by its consequences in ontogeny, but this does not imply that individuals or their progeny will necessarily profit from that capacity. Similarly, beneficial social behavior transmitted from one individual to another only with difficulty may be displaced by competing behavior less likely to be reinforced but more easily transmitted, as when extreme political rhetoric overrides reasoned discussion (Catania, 1994, 2001). "The dilemma of good and evil was created by multilevel selection, in which individual and group selection act together on the same individual, but largely in opposition to each other" (Wilson, 2012, p. 243).

We've considered three kinds of selection: (1) phylogenic selection, the evolution over biological time of populations of organisms and their characteristic features, such as behavior; (2) ontogenic selection, the shaping of behavior by its consequences during the lifetime of an individual organism; and (3) cultural or memetic selection, the survival of patterns of behavior as they're passed on from some individuals to others. These kinds of selection depend on behavior that changes during ontogeny as well as during phylogeny. We must understand each kind of selection to see where behavior comes from.

ADDENDUM 3A: PHYLOGENY, ONTOGENY AND BEHAVIOR

As research in Evo Devo has shown, development and evolution are intricately interrelated. This makes sense because both involve interactions with the environment. Consider the butterfly, *Bicyclus anynana*, and its adaptation to the seasonal swings of its habitat in Malawi (Carroll, 2005, pp. 214–215). In the wet season, broods of these butterflies emerge with big eyespots on their wings, which amidst lush foliage contribute to their evasion of predatory birds and lizards; in the dry season, however, amidst withered foliage and brown leaf litter, those spots make a distinctive target, and broods of these butterflies emerging at the start of the dry season have only flecks of color in place of the eyespots. The system works because these caterpillars have evolved to be sensitive to the ambient temperature in such a way that when they metamorphose into a butterfly, the gene that produces their spots is activated if it develops in warm wet season temperatures but not if it develops in cooler dry season temperatures. Thus, eyespots may vary from one generation to the next, depending on the environment, though the generations share a single gene pool. They have common *genotypes*, or genetic makeups, but different *phenotypes*, in the individual variations occasioned by the different developmental courses in their different environments.

Another instance of the interacting roles of environments and genotypes is the enhancement of the likelihood of functional mutation in a phenomenon called *the Baldwin effect* (Baldwin, 1896). When environments change, organisms adapt, as when a fish population adjusts to an increase in the water temperature of its habitat. Selection will soon work on the fish population in favor of those best fitted to the higher temperature. If a mutation arises that makes the fish even better adapted to the new temperature, then those carrying that mutation will have a selective advantage even though the mutation

followed the adaptations produced by the temperature change. First came ontogenic changes produced by the new environment, with phylogenetic changes following later (cf. Kirschner & Gerhart, 2005, pp. 76, 222). Still another possibility is that the new temperature will select a genetic feature that was long latent in some members of the fish population, becoming effective only after environment change. In this instance, the phylogenetic changes came first and the ontogenic changes later (Kirschner & Gerhart, 2005, pp. 251–252).

Together these examples show how new mutations can become functional even if their origins were unsynchronized with relevant environmental changes. We must also allow the possibility that variability itself can be selected, in what has been called *facilitated variation*: “the capacity for generating a broad range of somatic adaptations is as heritable as anything else” (Kirschner & Gerhart, 2005, p. 83). We will explore a parallel issue when we examine the reinforcement of variable responding in Chapter 13.

So much for our whirlwind tour of evolution and development. Let us now focus again on behavior, which is a joint function of *phylogenetic contingencies*, those operating in ancestral environments during the evolution of species, and *ontogenic contingencies*, those operating during interactions between organisms and their environments within their own lifetimes (cf. Skinner, 1966). Ontogeny does not recapitulate phylogeny, so we cannot trace the evolution of behavior by following the development of behavior in an individual (or vice versa). Whether phylogeny or ontogeny contributes more to behavior has been a common question. How much does behavior depend on evolutionary history and how much on learning? When such questions are addressed to socially significant issues such as the inheritance of intelligence, especially when the alternatives are presented as oppositions (e.g., nature versus nurture, heredity versus environment), heated controversy often follows.

Douglas Spalding, a nineteenth-century British naturalist, provides an elegant example of the role of phylogeny in behavior:

we have only to look at the young of the lower animals to see that as a matter of fact they do not require to go through the process of learning;... chickens, for example, run about, pick up crumbs, and follow the call of their mother *immediately* on leaving the shell.... I have observed and experimented on more than fifty chickens, taking them from under the hen while yet in the eggs. But of these, not one emerging from the shell was in a condition to manifest an acquaintance with the qualities of the outer world.... (Spalding, 1873/1954, pp. 2–3)

Spalding noted that the chicks advanced rapidly. Within four or five hours of hatching they were pecking at objects and preening their wings. But he also recognized that a lot could be learned in four or five hours.

To obviate this objection with respect to the eye, I had recourse to the following expedient. Taking eggs just when the little prisoners had begun to break their way out, I removed a piece of the shell, and before they had opened their eyes drew over their heads little hoods, which, being furnished with an elastic thread at the lower end, fitted close round their necks. (Spalding, 1873/1954, p. 3)

Spalding kept the chicks blind for one to three days and then removed their hoods.

Almost invariably, they seemed a little stunned by the light, remained motionless for several minutes, and continued for some time less active than before they were unhooded. Their behaviour, however, was in every case conclusive against the theory that the perceptions

of distance and direction by the eye are the result of experience, of associations formed in the history of each individual life. Often at the end of two minutes they followed with their eyes the movements of crawling insects, turning their heads with all the precision of an old fowl. (Spalding, 1873/1954, p. 3)

Our primary interest in this text is in behavior that is learned, but we must always entertain the possibility that the behavior we study has phylogenic sources. We can try to create arbitrary environments to minimize the role of phylogeny. For example, a standard pigeon chamber is an arbitrary environment, because natural environments don't include keys on which a pigeon's pecks produce food only when the key is lit. But arbitrary environments aren't always arbitrary enough; they won't necessarily make the behavior that occurs in them arbitrary. Consider a pigeon's key pecks:

Such responses are not wholly arbitrary. They are chosen because they can be easily executed, and because they can be repeated quickly and over long periods of time without fatigue. In such a bird as the pigeon, pecking has a certain genetic unity; it is a characteristic bit of behavior which appears with a well-defined topography. (Ferster & Skinner, 1957, p. 7)

Behavior may start very early in an organism's life, but that in itself is not evidence that its sources are phylogenic rather than ontogenic. Recall that Spalding had misgivings about how much a chick could learn within just a few hours after hatching. Creatures may be prepared by phylogeny to do the same sorts of things that their ancestors have done, but they also may be prepared to start learning right away. Behavior begins in the embryo (e.g., Hall & Oppenheim, 1987). Both prenatally and postnatally some of that behavior is independent of sensory input

and of consequences. But behavior changes even with the organism's earliest interactions with its environment (e.g., Johanson & Hall, 1979; Rudy, Vogt, & Hyson, 1984). By this point it should be evident that the answer to

the question of whether behavior is a product of phylogeny or ontogeny is that it is a product of both. To questions about the relative magnitudes of their contributions, of course, the safest answer is typically, "It depends."