Emerging Mechanisms

It has been found in science that when a sub-universe of discourse can be dissociated from a larger universe and a means of studying behavior found which is but slightly affected by uncontrollable factors, the results usually have a high value in prediction.

—E. M. East 1934

Every organized being forms a whole, a unique and closed system, whose parts mutually correspond and concur to the same definite action by a reciprocal reaction. None of its parts can change without the others also changing; and consequently each of them taken separately, indicates and determines all the others.

—G. Cuvier 1812

INTRODUCTION

In Chapter 1 we emphasized that our investigation is directed at identifying the cognitive constraints affecting theory development, and in Chapter 2 we introduced decomposition and localization as the central heuristics figuring in our treatment of the development of mechanistic explanations. We turn now to developing a more detailed analysis, one grounded in historical analyses, of how scientists actually develop mechanistic models. As we proceed, we will focus on *choice-points*, points at which decisions are made that shape the explanatory endeavor. The decisions scientists make are affected by their own cognitive characteristics (for example, the fact that they are agents with bounded rationality); theoretical considerations that suggest that one or another sort of explanation might be viable for the particular problem; and available empirical data. In this part we will identify some of the initial choice-points that are confronted before actually developing an explanation that would qualify as fully mechanistic. These focus on the identification of discrete systems in nature, the assignment of activities to them, and the determination of whether these systems can be functionally decomposed.

Before it is possible, or even relevant, to develop a fully mechanistic explanation of *how* a system performs some function—and, therefore, before the heuristics of decomposition and localization are properly brought into play—it is necessary to identify *what* functions are preformed and *what* system performs these functions. We speak of this as isolating the *locus of control*. A locus of control is not necessarily a system that operates in isolation; rather it is one that carries out a transformation of inputs into outputs that *is* what constitutes realizing a specific function. Although such an identification of a locus of control is critical to any attempt to develop a mechanistic explanation, claims to have identified such loci are often controversial.

We start in Chapter 3 with a discussion of two domains in which controversy is still alive. One involves identifying the locus of control for behavior. The other involves the locus of control in evolution. In each case there are prominent scientific traditions placing control in the environment. Radical behaviorists argue that organisms are not loci of control for behavior—that such control lies outside the organism. Likewise, the Darwinian explanation of evolutionary adaptations looks to the forces of selection operating on individuals of the species, rather than to factors internal to such individuals. Each of these positions can be placed in counterpoint to another which sees the system as, in an important sense, serving as a locus of control. Cognitive psychology, as a recent mentalist turn, rejects the

claim that one can understand behavior without looking inside the organism, and so treats the cognitive system itself as the locus of control. A similar argument has been made in the case of evolutionary theory. This is particularly true of Haeckel's and other orthogenetic programs in the nineteenth century, which view evolution as an internally directed process leading to increasingly complicated forms of organization.

There are other cases in which such controversies have been resolved. One was the nineteenth-century controversy over the locus of control for respiration. Although experimental evidence was marshaled, this alone was not sufficient to settle on tissue cells as the locus of respiration. Theoretical issues, including a variety of questions such as the role the tissues actually play in living organisms and the factors determining the rate of respiration, were also important. Bernard and Ludwig offered essentially theoretical arguments which they took to show the role of the blood in respiration. These were countered by Pflüger, who offered a convincing account of how the cells figure in respiration and how they are able to control the rate of respiration. In section 4 we explore how Pflüger was able to bring this controversy to an end and establish the tissue cells as the locus of respiratory phenomena.

Determining the locus of control is the first critical choice-point in the development of the mechanistic program. The cases we examine in Chapter 3 show some of the arguments that figure in controversies over this issue. As will be true of additional choice-points explored in subsequent chapters, one seldom has definitive evidence for the decision one makes; to some extent it will be made on the basis of other factors. Yet the choice is critical, for it determines the course of subsequent research. If one rejects some proposed locus of control, the task becomes one of identifying an appropriate alternative source of control—a challenge still confronting those who have stressed external factors in explaining behavior and evolution. If one accepts the identification of one locus, the next task is to seek the mechanism that operates within it and allows it to produce the function.

In Chapter 4 we explore what is frequently the first strategy pursued after a system has been identified—or accepted—as a locus of control. This is to identify a component within the system as itself responsible for the phenomenon, without yet inquiring how that component produces the effect. This, as we have said, we term simple or direct localization, because it involves localizing responsibility for an effect in a single constituent component of the system and then showing a direct link between the behavior of the system and that of the component. In developing a direct localizationist research program, what investigators look for are *correlations* between the performance of the system and the activities of one of its components. We consider two sets of cases in sections 2 and 3 of Chapter

4: Gall's localization of cognitive functions in the brain, and the attempt to localize responsibility for cellular respiration in different enzymes within cells.

Both examples of direct localization we consider are ones later researchers came to reject. This choice of cases is deliberate: As we said in Chapter 1, heuristics are strategies prone to failure. It is precisely where heuristics fail that their role in the development of science is clearest. Moreover, when decomposition and localization are deployed in the development of direct localizations, we observe the simplest and least demanding cognitive strategy. Given that scientists have finite problem-solving resources, it is not surprising that this strategy is where they often begin. Moreover, although it is probably seldom conceived of in this way by scientists themselves, the use of direct localization represents the pursuit of a strategy that, when it does fail, is likely to provide the most useful information about how the actual system is organized. This is a point we will develop more fully in Chapter 7.

The fact that direct localization was rejected in the cases we examine should not be taken to mean that it is never correct. Sometimes there *is* a single component responsible for the function of the system, and the direct localization program will be successful. Even when localization is successful, though, it is important to note that it does not itself produce a fully mechanistic explanation, because it does not explain *how* the function is performed by the component. At best it is a preliminary step, though one that is often taken in the research community and is important for the development of a field. The decision to use a different strategy would set an entirely different research agenda. Given a successful localization, perhaps confirmed by subsequent research, the next task is to explain how the localized function is realized. This requires a shift to a lower level. We consider such a case in Chapter 6. Research may also show that other components are involved and lead to a different kind of explanation, involving multistep models, at the same level. This is no longer simple localization. We consider such a case in Chapter 7. What is significant is how frequently investigators begin with a direct localizationist program, and what can lead to its abandonment or displacement.

In choosing whether to engage in such a program, researchers confront a second choice-point: Can one component account for the system's behavior? In answering this question affirmatively, investigators have implicitly affirmed that the system is decomposable. The mechanistic program depends on direct localization, proof of which will be given in Chapter 5 when we examine the arguments of the most radical critics of this approach. These critics claim that the correct explanation of a function requires that a system be nondecomposable, and they therefore reject decomposition and localization as strategies; this is an antimechanistic

stance. Those objecting to these strategies offer a variety of positive proposals broadly classed as *dualist* in the case of psychological functions, or *vitalist* in the case of physiological functions.

Again, we look at two sets of issues. The first, discussed in section 2 of Chapter 5, involves the repudiation of Gall's phrenology by Flourens, with the support of Georges Cuvier. In part Flourens's attempt to refute Gall was experimentally grounded in lesion studies, in which Flourens emphasized what he referred to as the "unity of the nervous system." The second set of issues, discussed in section 3 of Chapter 5, focuses on vitalist opposition to mechanistic physiology in the first two-thirds of the nineteenth century. In particular we focus on Bichat's repudiation of Lavoisier's research, and on Schwann's and Pasteur's repudiations of the mechanistic program in fermentation. These attacks emphasize the central weakness of direct localization: its limitation to a correlational method and, consequently, to an impoverished empirical basis. The theories of Gall and Lavoisier *are* mechanistic, but they are not subject to systematic constraints from lower-level theories that could justify the decomposition into functions by demonstrating that there are lower-level components in which the functions could be localized. Indeed, Gall's and Lavoisier's models were developed largely without independent knowledge of component behavior—or even knowledge of the relevant components themselves. The decompositions into functions were a projection from the behavior of the system as a whole. This is mechanistic in inspiration but incomplete in its realization. As a result, the theories of Gall and Lavoisier are attacked by their opponents, such as Flourens and Pasteur, for being speculative and hypothetical.

These challenges to mechanism indicate the existence of an additional choice: whether to accept, even as a first approximation, the decomposability of the system. Researchers are sometimes led to give a negative answer at this choice-point by evidence that they take to show the failure of the direct localizationist program. Such individuals typically have independent grounds for thinking that one cannot develop an explanation by decomposing the system—a possibility we shall explore later. The negative decision, however, is a significant one, as it necessitates abandoning the mechanistic program for a different objective of research—a focus on *describing* the behavior of certain kinds of systems and delineating their properties, rather than *explaining* how such systems function. It is no accident that the major antimechanistic opposition to both Gall and Lavoisier, as well as to Geoffroy and Lamarck, came from within the French Academy. It was within the Academy, under the leadership of Cuvier, that the most strident opposition arose to Enlightenment materialism. The opposition to Gall and to Lavoisier can be seen as an extension of this antimaterialist and antimechanistic stance.

Identifying the Locus of Control

1. INTRODUCTION: IDENTIFYING SYSTEM AND CONTEXT

Before developing a mechanistic explanation of a particular phenomenon, one must identify which system is responsible for producing that effect. Identifying a responsible system presupposes several critical decisions. The scientist must segment the system from its context and identify the relevant functions assigned to it. To substantiate the assignment of a function to a system, the scientist generally must offer theoretical or empirical arguments showing that the physically and functionally independent system identified has substantial internal control over the effect. This is what we describe as treating the system as the locus of control for a phenomenon. That some system or component of a system is a locus of control for a particular phenomenon does not entail that it is able to produce the effect entirely in isolation; causal control is contextual. Moreover, the systems dealt with in the life sciences are typically not closed, but open, systems; and they are not simply decomposable, but interactive. A locus of control for a given effect is a system or a component of a system that carries out the processes relevant to realize the effect. This is, in essence, what it is to be a machine. An example might help: An automobile does not produce motion on its own. It requires gasoline, a driver, a platoon of mechanics, large amounts of money, etc. Yet, it is *in* the automobile that the chemical energy is transformed into mechanical energy, and so the automobile is the appropriate locus of control for this effect.

In distinguishing a system as a locus of control we make the same assumption as when we explain the activity of a system in terms of the functions of its parts. We assume that nature as a whole is decomposable into units and that the system we are identifying is such a natural unit. In treating it as the locus of control, we assume that variations in the mechanism will be reliable indicators for variations in its behavior and will thereby explain them. Finding the right system is often difficult. It is equally difficult to find the right level of organization and the right boundaries to the system. On some occasions nature seems to divide naturally into systems. Generally this reflects what Wimsatt (1980b) calls "environmental grain" and is largely a result of perceptual and information-processing capacities we as researchers have developed and bring to the con-

text. We readily discriminate organisms—at least organisms of a certain size—as entities, though a swarm of insects may be treated as an entity rather than an aggregate. A bat or a bird, by contrast, can recognize individual insects within a swarm. If we have the capacity to identify and isolate a system, this is usually because, for one reason or another, it is important for us to recognize or coordinate our lives in response to it, or at least to objects of the same scale.[1] Most animals are able to recognize individual conspecifics and members of a variety of other organisms in their environment. These natural capacities make the breaks in nature seem transparent, yet the "natural" breaks may be different from the apparent ones, and these are apparent only because they are important to us. The significant boundaries for scientific inquiry may be quite different than those that are important for other human activities; researchers must discover and learn to recognize these boundaries.[2] In most domains of inquiry, such recognition evolves with time and research as scientists develop conceptual frameworks to determine a particular way of decomposing nature into systems. Until such frameworks are developed, or when they are subsequently brought into question, decisions over how to divide nature into systems can be quite controversial.

The fact that disputes often arise over dividing nature into systems, and then over situating the locus of control for various phenomena in these systems, can be helpful in understanding theory development. Briefly examining these controversies will highlight the issues and the character of the decisions that are made when such conflicts are confronted. These issues and decisions are often concealed once the question of identifying a locus of control has been resolved. This is natural, as the decision virtually defines a research program or tradition, and a resolution will preclude alternative lines of inquiry. To explore these issues and decisions, we shall consider the two domains mentioned earlier in which there have been perennial conflicts over where to situate the locus of control: behavior and evolution.

In both cases, common sense offers a fairly natural division of nature into systems. Individual animals and biological species have long been identified as natural units, even if there has been considerable disagreement over their precise character; for example, the contemporary dispute over whether species are natural kinds or historical lineages, and traditional philosophical debates concerning identity across time, are both metaphysical disputes of this sort. The question here, however, is whether these commonsense boundaries mark off loci of control. This question is an *explanatory* one, as we want to explain such things as behavior and evolution. It is with respect to this explanatory question that controversies arise. Some researchers have argued that these systems are

the appropriate locus and that what is outside these boundaries, the environment, can be treated largely as background or as secondary in significance. The consequence of this internal localization is an emphasis on research into the internal mechanics of these systems in order to explain them. Others argue against situating control within the systems themselves and contend that the important controlling variables are to be found outside of these systems. Those who deny that the system is the locus of control commonly argue for the opposite extreme and treat the system as relatively insignificant in producing the phenomenon in question. For advocates of internal localization, the system looms large and the context is of vanishing explanatory value. For their opponents, the context looms large and the system merely processes inputs.

Our purpose is to elucidate the kinds of considerations that are important in settling on a locus of control for a given phenomenon. We do not provide an exhaustive taxonomy. We offer examples only. The brief discussions in sections 2 and 3 of this chapter should illustrate the question and the principal approaches to answering it. In section 4 we will turn to a more extended example from physiology—the identification of the cell as the locus of biological respiration. In this case there was active controversy during the first three quarters of the nineteenth century until the case for the cell as the locus of control was finally established and researchers were able to direct their attention into the cell to explain how it accomplished the respiratory function. Here there was a resolution to the question of the locus of control, and the problems then were transformed, or, perhaps, they evolved. The mechanical question became the focus of investigation.

2. EXTERNAL CONTROL: THE ENVIRONMENT AS A CONTROL

Controversies over the control of behavior and of evolution display many similarities. In both cases there are those who favor extreme environmentalist views, arguing that the mind/brain or the species were basically pliable entities shaped by their environment. Advocates of this view often focus on how adaptive and responsive the system is to external demands. If the system is extremely responsive to environmental variation, then, it is reasoned, differences must be environmentally induced and controlled. The net result of emphasizing the external factors is to reduce the importance of the system, treating it as responding to external factors, or shaped by them, but not itself an important element in accounting for the responses. A variety of arguments are generally offered as to why the system is unimportant and can be skipped over in the quest for an ultimate explanation.

Radical Behaviorism: Watson and Skinner

Behaviorism as a research program in psychology has many roots. Two are crucial: the *associationistic* program derived from Hume and Spencer in philosophy, and the *functionalist* psychology of William James, John Dewey, and James Rowland Angell, which dominated psychology at the turn of the century. Both downplay the importance of mental structures and construe mental activity as largely adaptive to external processes.[3] The associationist program is committed to the view that even the most complex structures constituting our knowledge of the world are constructed from sensory experiences, with simple general mechanisms emphasizing the association of ideas and experiences. The functionalism of James, Dewey, and Angell was born of Darwinism and emphasizes the adaptive role of cognitive processes:

> The functionalist psychologist . . . in his modern attire is interested not alone in the operations of mental process considered merely of and by and for itself, but also and more vigorously in mental activity as part of a larger stream of biological forces which are daily and hourly at work before our eyes and which are constitutive of the most important and most absorbing part of our world. (Angell 1907, p. 88)

By contrast with the *structuralist* views of Wilhelm Wundt and E. B. Titchener, classical functionalism concerns itself with the role of mental processes in regulating behavior, and downplays the importance of introspectionist taxonomies of mental acts and contents, such as those promoted by Franz Brentano. This role, in turn, is to be understood in terms of how behavior is modified and controlled in a natural setting. Functional psychology, Angell tells us, "portray[s] the typical *operations* of consciousness under actual life conditions, as over against the attempt to analyze and describe its elementary and complex *contents*" (ibid., p. 85). For classical functionalism the contribution of the environment in shaping our mental structures is fundamental.

In what is rightly regarded as the manifesto of radical behaviorism, John B. Watson (1913) initiated a movement that was to dominate psychology for roughly the next fifty years. With his functionalist progenitors, Watson emphasized adjustment to the environment as the primal fact of psychology.[4] The internal causes, whether physiological or mental, were unimportant for the purposes of a scientific psychology. Psychology, so understood, is concerned with the ability to modify and control behavior in the face of environmental demands. Behaviorism, Watson declares, "is the only consistent and logical functionalism" (ibid., p. 514). Behavioral changes are under the control of external stimuli: "stimuli lead the organisms to make the response" (ibid.). The only behavioral changes with psy-

chological significance are *responses* to environmental changes; moreover, our behavioral capacities are the result of environmentally induced modifications in learning, and it is in terms of the simple learning mechanisms that complex capacities must be understood.

The emphasis on environmental control, which is characteristic of behaviorism, in no way implies that internal mechanisms are unimportant. Behaviorists only deny internal mechanisms' significance as primary controlling variables for the purposes of psychology. Watson says quite clearly:

> Much of our structure laid down in heredity would never come to light, would never show in function, unless the organism were put in a certain environment, subjected to certain stimuli and forced to undergo training. Our heredity structure lies ready to be shaped in a thousand different ways—the same structure—depending on the way in which the child is brought up. (1924, p. 97)

The pivotal commitment of behaviorism is the view that our complex behaviors can be neither explained nor understood in terms of internal mechanisms. Any given behavior will be a function, inter alia, of the environment together with the capacities we have developed; these capacities, in turn, will be a function of our developmental history together with innate mechanisms. Yet these innate mechanisms are so simple and general that they radically underdetermine the result. The hereditary structure, as Watson says, "lies ready to be shaped in a thousand different ways." As a result, the specific responses or patterns of responses can be explained, if at all, only in terms of environmental variables.

The rejection of *instincts* as determinants of behavior—Watson devoted two substantial chapters to the topic in *Behaviorism* (1924)—is not a denial of the existence of instincts as much as a denial that they are sufficient to explain particular behavioral results. "The central principle of behaviorism," as Watson tells us, is that "all complex behavior is a growth or development out of simple processes" (ibid., p. 137). This is a legacy of associationism. Its heir, in turn, is the learning theory of Tolman and Skinner. So conceived, we are born with simple capacities to respond in determinate ways to determinate stimuli.[5] Over time, these capacities develop into increasingly complex abilities under the influence of simple learning mechanisms. Watson emphasized respondant conditioning, allowing substitution of both stimuli and responses. Skinner (1938) introduced operant conditioning, with the express intention of explaining behavior for which there is no evident elicitation by a stimulus.

The commitments of behaviorism are, thus, varied. They include a modified associationism with simple and general mechanisms of learning, but reconstituted to apply to behavior rather than to ideas; the rejection of instinct as a significant explanatory concept for psychology; and the

commitment to learning theory, with learning mechanisms common to humans and other animals (cf. Watson 1913, p. 507). Together, these commitments constitute a single fabric emphasizing environmental control of behavior. Each requires the others.

Parallel commitments are equally evident in B. F. Skinner's treatment of operant conditioning in *The Behavior of Organisms* (1938). Two of the central "dynamic laws" governing *operant behavior* (that is, behavior that appears to be spontaneous) pertain to conditioning and extinction. In Skinner's own terms,

> If the occurrence of an operant is followed by presentation of a reinforcing stimulus, the strength [of the operant behavior] is increased.
>
> If the occurrence of an operant already strengthened through conditioning is not followed by the reinforcing stimulus, the strength [of the operant behavior] is decreased. (Ibid., p. 21)

These are the "laws" of operant learning in a qualitative form. They describe changes in behavioral tendencies solely as a function of environmental variables. Reinforcement will increase the "strength," understood in terms of persistence, of some behavior; withdrawal will decrease it.

In the cases of both Watson and Skinner, behaviorism emphasizes environmental control. Innate mechanisms are incapable of explaining the adaptive responses of any organisms, or the corresponding range of their behavior. Indeed, variations in whatever innate mechanisms there are should create no qualitative differences: all differences are differences of degree only. Internal mechanisms that mediate the control of learned behavior must themselves be explained; ultimately, this requires an appeal to environmental conditioning or to selection. This emphasis on external control thus depends on the commitment to simple and general mechanisms of learning and, correlatively, rejects the mental system as, in any interesting sense, a locus of control for behavior.

Natural Selection and Adaptation

In a parallel fashion, the Darwinian emphasis on natural selection and adaptation embodies an externalist approach. Darwin was faced with two related problems in *On the Origin of Species* (1859). On the one hand he was confronted with the task of justifying the claim that evolution—or, as he preferred to describe it, the "transmutation of species"—occurred. On the other hand he proposed to defend a particular mechanism for the evolutionary process. That mechanism, in turn, was simultaneously to explain transmutation and the "perfection of structure," which we have since come to think of as adaptation. As Darwin himself wrote in the first edition,

In considering the Origin of Species, it is quite conceivable that a naturalist, reflecting on the mutual affinities of organic beings, on their embryological relations, their geographical distribution, geological succession, and other such facts, might come to the conclusion that each species had not been independently created, but had descended, like varieties, from other species. Nevertheless, such a conclusion, even if well founded, would be unsatisfactory, until it could be shown how the innumerable species inhabiting this world would have been modified, so as to acquire that perfection of structure and coadaptation which most justly excites our admiration. (Ibid., p. 3)

The central problem for Darwin was thus one that was also common to natural theologians in the tradition of Paley and the Bridgewater treatises. Like them, Darwin insisted on taking seriously the adaptation of organisms to their environment. He differed in *how* to explain this adaptation, but the emphasis on adaptation as well as transmutation led him to locate the control of evolution outside the species and in the environment.

Darwin developed the case for natural selection as the prime mover of evolutionary change in the early chapters of the *Origin*. The general argument is straightforward and simple: Organisms exhibit a remarkable degree of adaptation to their environment, as well as to other species, which are factors in that environment. This adaptation, or coadaptation, is explicable in terms of natural selection if it is understood to operate on individuals over large expanses of time. Natural selection, or the differential survival of individuals on the basis of variations in fitness, is capable of explaining the kind of finely tuned adaptation Darwin saw as so central to the natural order, provided that variations are small, many, and heritable.

Darwin himself adopted an eclectic view and incorporated a variety of secondary mechanisms besides natural selection, among them the environmental induction and the inheritance of adaptive variation which is commonly, if misleadingly, referred to as the "inheritance of acquired characteristics."[6] The same commitment to external control can be seen in Darwin's treatment of the variation on which natural selection acts. He consistently maintained, first, that environments will induce variation in organisms when the species is marginally adapted for those environments; and, second, that when variation is induced by the environment, all organisms in the species encountering that environment will vary in the same manner.[7] In discussing the case of an environment undergoing continual change, Darwin claims that individuals of a given species within that environment will tend to undergo similar changes:

Changes in the conditions of life give a tendency to increased variability; and in the foregoing cases the conditions have changed, and this would manifestly be favourable to natural selection, by affording a better chance of the occurrence of

profitable variations. Unless such occur, natural selection can do nothing. (1872, pp. 75–76)

The induction of variation in marginal environments had the advantage of increasing the amount of variation in just those places in which it would do the most good, and thus could increase the rate of evolutionary change as well as the degree to which it could maintain adaptation.

The problem of explaining adaptation, inherited from Paley, thus lies at the center of Darwin's case for natural selection as the mechanism of evolution. Since what is to be explained is adaptation to an environment external to the organism, the control for that adaptation must either lie in that environment or be due to some agent that can anticipate and guide the change. Darwin took the former option without hesitation.

In more recent Neo-Darwinian work there has been a parallel emphasis. The view that genetic variation enters the species through chance-like mutations, is passed on from one generation to the next, and is selected as organisms compete for survival and reproduction became the orthodox account of evolution with the development of population genetics in the 1920s and 1930s. The working hypothesis is the assumption that a structure or behavior is an *adaptation*, something that facilitated survival and was promoted in the population precisely because it did so (cf. Brandon 1978). In theory it is allowed on all sides that not all traits are adaptations; some, at least, will have other sources. In practice, however, many biologists resort to nonselectionist explanations only as a last resort. Without serious consideration of what would otherwise be expected—in short, without attention to qualitative "base rates"—nonselectionist mechanisms are set aside. Questions about how organisms develop, or about the causal processes active in individual organisms, are set aside as if they were of no interest and did not have an important influence on the overall course of evolution. Ernst Mayr (1961), for example, distinguishes between proximate and ultimate causes of evolutionary change, and, while granting that there may be a variety of proximate and local factors that determine the character of members of a species, he argues that these are not the true determining variables. For that, in his view, we must turn to natural selection.

The point may be underscored by turning to one of the more widely accepted cases in recent theorizing, R. A. Fisher's (1930) explanation of the fifty-fifty sex ratio present in most sexually reproducing organisms. Fisher assumes that either parent can induce a bias in the sex ratio of immediate offspring, skewing the frequency of one sex in either direction from the norm, and further assumes that the reproductive investment involved in bringing a male to maturity is different from that necessary to bring a female to reproductive maturity. He then argues that the optimal

strategy would be to equalize total expenditure of reproductive resources on males with the total expenditure on females. (The details of his argument need not concern us here.[8]) We may grant that, under the stated assumptions, a fifty-fifty ratio will be most common. The question is whether this is an adaptation. There are obvious alternatives to the selectionist explanation that are at least as plausible and are not even considered as candidates (cf. Gould and Lewontin 1979; Lewontin 1978). For example, a fifty-fifty ratio will be the natural consequence of gametogenesis—the production of sexual gametes—because this involves the partitioning of genetic material into two reproductive cells. It is in fact possible that a fifty-fifty sex ratio is not an adaptation at all, but the natural, if not inevitable, consequence of the reproductive machinery in bisexual organisms. The assumption that it is an adaptation bespeaks the commitment to natural selection and to external control.

3. INTERNAL CONTROL:
THE SYSTEM AS A CONTROL

Each of these externalist programs has had opponents arguing in favor of internal control. As would be expected, the contrast between contenders is multidimensional. One common thrust to internalist arguments is that the system in question is not as flexible and adaptive as externalist theories require: Response is limited and structured in the face of large variation. The phenomenon that requires explanation is the limitation on the range of response. Limited responsiveness in the face of wide environmental variation is taken as indicative of internal control, and the solution is to search for specialized and complex internal mechanisms. The system makes its own contribution and influences what happens to it.

The Mentalist Program in Linguistics

Just as *behaviorism* has its roots in the associationist program, which limited internal activity to simple and general procedures for associating ideas, the *mentalist* program traces its roots in part to a rationalist account of knowledge, with a corresponding emphasis on the contribution of cognition to the constitution of the world. Just as behaviorism stresses the external control of behavior, mentalism emphasizes the indispensability of psychological determinants in explaining behavior, many of which are argued to be innate, not learned. This means, in principle, that there is an indeterminacy of behavior when only external parameters are included, and, in practice, that there is an inability to predict or explain important dimensions of behavior in environmental terms alone. A theory emphasizing external control will be correspondingly incomplete, and it will be

necessary to adopt an approach that makes the mental system itself the locus of control.

The history of psychology provides ample evidence to support the mentalist contention. Learning theorists, including behaviorists, were committed to the view that animal learning and human learning differed only in degree (see Skinner 1938, pp. 441–42). Yet the sort of simple mechanisms that were constitutive of the various models failed to generalize to more complex behaviors, including many exhibited by humans. Indeed, once removed from the limited setting of psychological laboratories, it became difficult to isolate or describe the variables supposedly controlling behavior. Skinner's own vacillation on the defining characteristics of behavior (see Chomsky 1959; Scriven 1956) in more popular works (for example, *Science and Human Behavior*, 1953), in contrast to more technical works such as *Verbal Behavior* (1957), is explicable as an immediate consequence of the failure to isolate classes of behavior and environmental variables with suitable functional relations. The extension of conditioning models to complex behavior was a failure. The only alternative was to treat the cognitive system seriously as a locus of control.

By the middle of the twentieth century, the shortcomings of behaviorism had become all too apparent and were crystalized by Noam Chomsky in his argument from what he called the "poverty of the stimulus" (cf. Chomsky 1980, pp. 35ff.). In its simplest form, this argument presses that the specific characteristics of human language are underdetermined by, and inexplicable in terms of, environmental variations alone:

> Gross observations suffice to establish some qualitative conclusions. Thus, it is clear that the language each person acquires is a rich and complex construction hopelessly underdetermined by the fragmentary evidence available. (Chomsky 1975, p. 10)

Children have limited information given to them about the language they are learning. What information they do get, moreover, is fragmentary and disconnected. Yet in a matter of months they develop an elaborate and detailed understanding of their native language. The moral Chomsky draws is straightforward:

> The essential weakness in the structuralist and behaviorist approaches to these topics is the faith in the shallowness of explanations, the belief that the mind must be simpler in its structure than any known physical organ and that the most primitive of assumptions must be adequate to explain whatever phenomena can be observed. (1968, pp. 25–26)

If the environment leaves the particular details of language "hopelessly underdetermined," then the explanation of these details must inevitably lie in the structure of the mind. As a consequence, Chomsky is committed

to embracing innate, internal mechanisms underwriting language learning. This is a rationalist program with an internal locus of control; it does not deny the significance of the environment any more than the behaviorist denies the importance of internal mechanisms. We do, after all, *learn* the language our parents speak—the ability to speak as they do does not lie in our genes. Chomsky's point, rather, is that the specific details concerning the what and how of learning can be explained only by placing the explanatory burden on internal mechanisms.

The case for internal control just sketched was given a more precise formulation by Chomsky in *Syntactic Structures* (1957) and *Aspects of a Theory of Syntax* (1965). The argument Chomsky uses is a linguistic variant on one that has driven mentalism from Descartes to Kant: If we think of a grammar for a language as a set of rules, then, at a minimum, an adequate grammar must be capable of producing all (and only) the strings that are acceptable in that language. Primary-language learning will then involve inducing a grammar from some finite and limited set of sentences presented to the child. Since any finite set of sentences can be generated by an infinite number of grammars that are, nonetheless, formally nonequivalent, the task of language learning requires selecting the correct grammar from among the set of abstractly possible grammars. The only alternative is to allow that we incorporate some mechanism that enables us to limit the number of candidate grammars. That is, there must be some innate structure to guide and inform language learning in the child. Moreover, natural languages are sufficiently complex that the grammar we end up with cannot be a simple algorithm.[9] If grammar is not a simple, general algorithm, then, because it will be largely accidental which heuristic we employ, the mechanism for language will likely be species-specific. The nativism that plays such a central role in Chomsky's thought is driven by the need to accept just this sort of complex, innate, internal structure as the foundation for language learning. Thus, in contrast with behaviorism, Chomsky argues for the mental system as the locus of control with respect to linguistic behavior.

Developmental Control of Evolution

Just as the nativism of Chomsky serves as an alternative to the environmental emphasis of behaviorism, so there is an analogous alternative to the environmentalist orientation of Darwinists and Neo-Darwinists. Its roots lie in *preformationist* theories of development, which were prevalent toward the end of the eighteenth century and early in the nineteenth. Whereas *epigenesists* maintain that form emerged gradually, in the developmental process, preformationists maintain that the fully differentiated animal form is predetermined at the earliest stages of development. Epi-

genesists portray development as a transition from an organism undifferentiated with respect to form to a fully differentiated organism—from an *unorganized* entity to an *organism* proper—under the influence of environmental forces. Such forces literally mold the organism into the form it assumes. Preformationists, by contrast, portray development as an unfolding of what is latent in the individual—from one organized form to another—largely independent of the environment. As Jane Maienschein explains the preformationist view, "Development remains strictly internally determined and not subject to external or environmental conditions in any significant way" (1986, p. 4).[10]

Under the influence of theories that viewed individual development as *recapitulating* the evolution of the species, Darwinism became transformed into an analogue of preformationist development (cf. Gould 1977; Maienschein 1978); evolution became the unfolding of developmental patterns that were reflected and revealed in ontogeny. As Haeckel writes, "Phylogeny is the mechanical cause of ontogeny" (1874, p. 5). Just as development reveals increasingly complicated forms of organization, so, too, does evolution. Evolutionary change involves, according to this recapitulationist view, the successive addition of stages to ontogenetic patterns already established, and then the subsequent attenuation of these stages (cf. Gould 1977, ch. 4). Terminal addition and acceleration of development then form the basis for the next round of evolutionary modification.

In the earliest Neo-Lamarckian writings in the United States, the recapitulationist view takes a developmentalist turn under the leadership of Edward Drinker Cope and Alpheus Hyatt.[11] The tradition became one of the first systematic challenges to Darwinism, and it persisted even into the twentieth century. In its earliest years the view was Lamarckian insofar as it was committed to an orthogenetic model of evolutionary change:

> Cope and Hyatt began from Agassiz's view that the growth of the individual offers a model for the history of life on earth. They accepted that the pattern of development revealed by a group's fossil record is recapitulated in the growth of the modern embryo. Evolution proceeds step by step through the addition of stages to individual growth, and the pattern of development is essentially predetermined and regular. (Bowler 1988, pp. 99–100)

The major point of contention between Neo-Lamarckians and Darwinians was the relative importance of natural selection in the evolutionary process, and not the importance of evolution in the origin of species. While Darwin and his closer followers (such as Asa Gray and Thomas Huxley) claim natural selection as "the main but not exclusive means of modification" (Darwin 1859, p. 6), Cope and Hyatt maintain that the crucial feature in explaining evolution is the *origin* of favorable variations rather than their preservation. As Cope writes, "Nothing ever originated by nat-

ural selection, . . . [and] important though it is, [it] is but half the question, and indeed the lesser half" (1887, p. 16). Adaptation to external circumstance is relegated to a secondary role.

According to Cope and Hyatt's view, recapitulation results from developmental mechanisms that would explain the pattern to be found in evolutionary change.[12] Evolutionary progress is marked by the addition of developmental characters that originated in previous phylogenetic stages. Because what develops before maturity can be inherited, an acceleration in development will result in the hereditary acquisition of these new characters. Ontogenetic stages would thus recapitulate phylogenetic changes. Acceleration of development, then, incorporates newly acquired traits and allows them to be inherited. The loss of characters in retrogressive change, in an analogous way, results from a retardation of development, with a resulting reduction of organic structures and complexity.

For our purposes here, the details of the Neo-Lamarckian account, as well as its motivation and development, are less important than the central explanatory strategy adopted by these opponents of Darwinism. Neo-Lamarckians emphasize internal developmental influences on evolutionary change as more important than the environmental influences on development of, at least, generic characters. The explanation for major changes is thus internalist, reflecting the view that evolutionary changes are guided largely by developmental rather than environmental processes. Thus, in contrast with more orthodox Darwinians, Neo-Lamarckians treat the species as a locus of control for evolutionary change. Through the early twentieth century there was a decreasing emphasis on the importance of development for evolution. The environment was on the upswing as an explanatory variable. The issues, however, did not die, and have recently come again to the fore.[13]

4. FIXING ON A LOCUS OF CONTROL: THE CELL IN RESPIRATION

We turn now to a case in which a long-lasting controversy over locus of control was eventually settled. It involves the biological process of respiration; that is, the process employing oxygen in reactions with foodstuff.[14] This controversy was ultimately resolved in favor of structural units within organisms—the cells found in biological tissues. Knowing the physical identity of the cell, however, could not settle that it was the locus of control for the function, or what its function was within the organism. In fact, by the time the controversy over the localization of respiration was sharply focused in the late nineteenth century, cells had been distinguished as both structural and functional units, largely through the investigations of Theodor Schwann (see Bechtel 1984a). The functional consid-

erations most central to Schwann's (1839) account are those concerning growth. He argues that the structures in different tissues of animal bodies are all the same kind of physiological units—that is, cells—on the basis of the fact that they form in the same way. Schwann also argues, though, that basic metabolic processes, which would include respiration, are performed within the individual cell. He contends that because these functions have to be performed *within* the cell in single-celled organisms, and there is no reason for them to be performed within cells in one context and outside of cells in another, the cell has to be the locus of metabolic functions.

Neither Schwann's arguments nor the acceptance of cells as basic structural units of living organisms, however, were decisive on the issue of the locus of control for respiration. Before turning to the later stages of the controversy and its eventual resolution, though, it will be useful to consider its origins. They lie with Lavoisier.[15] After advancing the oxygen theory, according to which combustion (then reconstrued as oxidation) involved the combination of oxygen with hydrogen or carbon, rather than the release of phlogiston, Lavoisier joined with LaPlace in a study of animal respiration. They argued that animal respiration was also a form of oxidation by demonstrating that the heat output of animals (measured by their ability to melt ice) was comparable to that of ordinary combustion:

> By comparing the heat evolved by the combustion of carbon with the quantity of fixed air which is formed in this combustion, we have the heat developed in the formation of a given quantity of fixed air; if we determine next the quantity of fixed air which an animal produces during a given time, we shall have the heat which results from the effect of respiration upon air; it then only remains to compare this heat with that which sustains the animal heat and which is estimated by the quantity of ice which it melts within our machines; and if, as we have found by previous experiments, these two quantities of heat are approximately the same, we can conclude directly and without hypothesis that the 'conservation' of animal heat is due, at least in its major part, to this change of the pure air into fixed air. (Lavoisier and LaPlace 1780/1862, p. 332)

Lavoisier and LaPlace concluded that respiration was "slow combustion," and they proposed that this combustion occurred in the bronchi of the lungs:

> Respiration is therefore a combustion, very slow it is true, but otherwise perfectly similar to that of charcoal; it occurs in the interior of the lungs, without producing perceptible light, because the liberated matter of fire is immediately absorbed by the humidity of these organs. (Lavoisier and LaPlace, 1780/1862, p. 331)

The proposal that combustion occurred in the lungs was not accepted by all. La Grange, for example, contended that the amount of heat pro-

duced by having all oxidation of foodstuff occur in the lungs would have destroyed the organ:

> If all the heat which is distributed in the economy was set free in the lungs, the temperature of the lungs would necessarily be raised so much that one would have reason to fear that it would be destroyed. (quoted in Foster 1901/1970, p. 252)

La Grange's objections, however, were not viewed as decisive. In fact, Berthelot (1889) much later challenged La Grange's calculations, arguing that rapid circulation of blood and air in the lungs would mean a net rise of less than one degree. But those who took objections such as La Grange's seriously sought a different locus for respiration, and most focused on the blood.

The debate over the site of respiration was not just a theoretical issue; it was also addressed at the experimental level. One important experimental strategy (which is an analogue to the analytic strategy introduced in Chapter 2 and which will become especially important in subsequent chapters) was to attempt to show that respiration can occur in particular sites even in isolation from others. It was this line of experimentation that began to point to tissues as a third possible site of respiration. Vauquelin (1792) confirmed respiration in insects using the same model as Lavoisier. Because insects lack lungs, Vauquelin reasoned, there must be an alternative locus for respiration—which he argued was the stomach. Spallanzani, whose work was posthumously published by Senebier (1803, 1807), performed extensive experiments on respiration in molluscs and crustacea. He showed that formation of carbon dioxide could occur in these organisms even when they were deprived of fresh oxygen. He also demonstrated that different organs (lungs, brain, flesh, liver, and skin) absorb oxygen and give off carbonic acid (CO_2). Clearly, this told against the lungs as the sole or primary locus of respiration. Spallanzani also argued theoretically against respiration in the blood on the grounds that blood was incapable of carrying out the reaction.

> The blood is not of all the animal parts the one most suited to the destruction of oxygen gas, although at first, judging from what has been written in the subject relative to the decomposition of air, I believed that it exceeded all the others. Blood, arterial and venous, from warm and cold-blooded animals, has been tested, and I have never had any variation in the results. (1803, p. 86)

Altogether three candidate sites for respiration were available, and the task investigators faced was to find evidence that could rule out one or more of the loci or, conversely, could show that one of the loci did constitute the major site of respiration. Two major considerations figured in the debates during the first half of the nineteenth century: whether there were sufficient thermal differences between the lungs and rest of the or-

ganism to allow for respiration to be localized in the lungs, and whether oxygen could leave the lungs to travel through the blood and potentially into the tissues. Without significant thermal differences, the lungs could not be the sole locus of respiration; without a mechanism of transport, they had to be.

The best evidence available at the time on these two questions pointed in different directions. J. Davy's (1815) failure to find any significant thermal differences between arterial and venous blood stood against the suggestion that respiration occurred in the lungs. On the other hand there were problems explaining how oxygen might get from the lungs to the blood. Ellis (1807) examined the possible modes of transfer and found them all wanting. He noted that the surface of the lungs was covered with absorbent vessels, but contended "that the fineness of these vessels, the mucus perpetually smearing the surface of the cells, the elastic nature of the air itself, and its repulsion by water, so that it neither penetrates moist paper, cloth nor skin—all demonstrate that no air by this route gets in the blood" (1807, pp. 117–18). Ellis also considered the possibility that the transfer of oxygen was effected by the power of chemical affinity, but he rejected the existence of such an affinity, remarking that "even granting to the blood this power of attracting air, or its oxygenous portion, it is not easy to conceive why it should so readily lose it and again give out this air in the form of carbonic acid" (ibid., p. 123).

In the 1820s and 1830s the problem of oxygen transportation was resolved. Dutrochet separated two fluids of different densities with a membrane and showed that a bidirectional flow occurred. Graham demonstrated the same result with gases. Using membranes from fowl, Faust and Mitchell showed that oxygen and carbon dioxide could readily pass between the lungs and the bloodstream, thus overcoming the objection that had been raised against earlier proposals. The mechanism for transferring oxygen from the lungs to the blood, combined with the thermal evidence, eventually led to the rejection of the lungs as a candidate site for respiration. This shift, however, was not immediate: Magendie and Bernard were both still actively investigating the lungs as a possible site of respiration in the mid-1800s. This investigation, in which Bernard (1856) followed up on previous work by Magnus (1837), offered additional thermal evidence that arterial blood was not warmer than venous blood and seems to have finally established that the lungs did not control respiration. One alternative was eliminated.

Of the two remaining options—the blood and the tissues—the blood was favored by most researchers as controlling respiration, as theories then in vogue portrayed the blood as the center of physiological activity. Moving to the tissues as a site of oxidation meant reconsidering the tissues—generally taken to be passive—as active sites for metabolic func-

tion. Several proposals emerged in the 1840s supporting the localization of metabolic processes in the tissues. Liebig, in formulating his general account of metabolic processes, assigned important functions to the tissues. Moreover, Helmholtz (1847) showed that the contraction of muscles produced heat; that, in turn, suggested that metabolic changes were occurring in the muscles. However, the question of *where* metabolic processes occurred turned out not to be fundamental to determining the site of respiration. Researchers considered the possibility that respiration might occur away from the site where metabolic reactions released energy. The primary focus in the arguments over the site of respiration turned on how and where gases could be transported, not on where the metabolic processes associated with respiration occurred (Culotta 1970a, b). Thus, in the 1850s and 1860s a variety of investigators pursued the issue of the locus of respiration by addressing the question whether gases, and particularly oxygen, could move from the blood into the tissue cells.

Georg Liebig (1850), Justus Liebig's son, focused on the movement of gases. He studied respiratory processes in muscles under a variety of conditions—for example, when saturated with water and when kept in a variety of atmospheric conditions—and concluded that muscles do take up oxygen and release carbon dioxide. He argued that the blood acted solely as a means of transport to the tissues, with the carbon dioxide forming within the tissues and passing into the capillaries. The younger Liebig's experiments showed that the gases required for respiration could reach the tissue cells and were therefore a genuine candidate for the locus of control for respiration. Experiments, however, failed to show that they were the actual site of respiration in living organisms. Two major investigators, Claude Bernard and Carl Ludwig, continued to oppose the tissue cells as the site—or, at any rate, as the major site—of respiration. While they based their arguments in very different ways on considerations about what actually controlled the rate of oxidation, both concluded that the blood was the principal locus of respiration.

Bernard was preoccupied with how the blood came to change color; he attributed it to respiration.[16] Bernard's conclusion was that the darkening of the blood resulted from the increase of carbon dioxide resulting from a chemical reaction occurring in the blood itself. He measured tissue respiration in vitro and compared the carbon dioxide production of liver, kidney, muscle, and brain (1859). Bernard, however, did *not* interpret the results showing respiration here as showing that actual respiration was performed by the tissues. He argued that Liebig's work was inconclusive because it did not rule out the possibility that blood corpuscles stored in the tissues accomplished the oxidation.[17] Moreover, he argued that only liquids were transferred between the tissues and the blood. His inability

to liberate oxygen from red blood cells indicated to him that oxygen could not be passed from the blood to the tissue cells:

> If it is true, and we are much inclined to admit it is so, that the venous blood owes its black coloration to carbonic acid, we must recognize that the modification by which its oxygen could be transformed into carbonic acid, can be brought about directly in it and not directly by immediate contact with tissues. (1859, p. 339)

Bernard proposed that the tissues excreted a liquid containing carbon and hydrogen, rather than carbon dioxide, which was then oxidized by the red blood cells. He concluded:

> It is infinitely probable that the carbonic acid of venous blood results from an oxidation which is brought about within the red blood corpuscle itself. When the blood traverses the capillaries, there will be between it and the tissues not an exchange of gases but perhaps one of liquids. Following the new conditions which such an exchange would create, the oxygen of the red blood corpuscle would be partly used for the oxidation of the carbon of the corpuscle itself. (Ibid., p. 342).

Bernard did not regard the question of the site of respiration as an isolated empirical issue; rather, it fit into his developing mechanistic conception of living organisms as able to regulate their own activities without requiring the agency of a vital force. Bernard held that each of the components constitutive of an organism was integrated with other components and was regulated by what happened in them. The result of this interaction was the maintenance of what he spoke of as the "constancy of the internal environment." Given this view, he argued that the locus of respiration—that is, the center in which the crucial processes of respiration transpired—had to be distinct from whatever controlled the rate of respiration, since regulation required one component to act on others. Bernard took the nervous system in particular to determine the rate of respiration, and he attempted to demonstrate this through experiments in which he cut the chorda tympani and sympathetic nerve. He interpreted the results as showing that the respiratory system regulated the rate of respiration by limiting how much hydrogen and carbon the cells excreted into the blood. Reactions with oxygen, he claimed, therefore occurred in the blood. If, on the other hand, the reaction with oxygen occurred within the cell, there would be no regulation of the reaction. Once oxygen entered the cell, there would be nothing to prevent the oxidation of all the carbon and hydrogen available. So, to enable processes within the tissue cells to regulate respiration, it was necessary that the reaction mechanism itself be situated outside the tissues and, hence, in the blood.

Ludwig also opposed tissue respiration—though less adamantly—but his reasons for being reluctant to accept it were quite different. In contrast with Bernard, Ludwig argued that the blood controlled the respiratory process. His arguments (Ludwig and Schmidt 1869) were grounded in his attempts to develop a mechanical model of the exchange of respiratory gases.[18] He proposed that pressure gradients governed the movement of gases between different media, and he thought studies of gas concentrations would settle the issue of where respiration took place: wherever concentrations of carbon dioxide were highest would be the site of respiration, with concentrations decreasing as one moved away from this site. Ludwig, however, was unable to produce sufficiently precise measurements to settle the issue. This was partly because of empirical difficulties in comparing pressures of gases in tissues and in blood, and partly because of problems in accounting for the possibility that some of the gas might be held in a chemically bound state.

Although his primary approach did not yield definitive data, Ludwig came up with an alternative strategy for determining what factors regulated respiration. He developed improved experimental techniques for perfusing organs with defibrinated blood whose gas content could be carefully measured. He noted a correlation between the rate of blood flow, the amount of oxygen consumed, and the amount of oxygen reduced to carbon dioxide. On this basis he claimed that the amount of oxygen in the blood controlled the rate of respiration: "In these numbers the law once more declares itself, that oxygen consumption increases with the velocity of the stream" (Ludwig and Schmidt 1869, p. 38).

Having located the *control* of the respiratory process in the blood, Ludwig went on to argue that the process itself was also likely to occur there. He asserted, in part, that given the rate with which the blood passed through tissues, there was not time for the oxygen to pass from the capillary into the tissue: "If one realizes the time over which the oxygen disappears, it seems scarcely adequate to effect, by way of diffusion, the copious exit of oxygen from the disks through the vessel wall" (ibid., p. 36).[19]

The contrast between Ludwig and Bernard is interesting. While both argued for the blood as the site of respiration, their arguments were incompatible. Both appealed to the factors they took to regulate respiration; however, for Bernard the locus of the process could not be the same as the factor regulating the process, whereas for Ludwig they were the same. Bernard saw regulation as arising from interaction between a regulating entity and that which is regulated, a perspective not shared by Ludwig.

The major proponent of intracellular oxidation was Eduard Pflüger (1872, 1875). Pflüger's task was twofold. He had to show both that respira-

tion did not occur in blood itself and that it could occur in tissues. In pressing that respiration was not carried out in the blood, Pflüger produced evidence that the blood—or the availablity of oxygen in the blood—does not control the rate of respiration. He performed experiments that purported to show that animals were not sensitive to large variations in the availability of oxygen, thus demonstrating that gas was not exchanged in accordance with differences in pressure. He also exposed asphyxiated blood to oxygen, reasoning that if blood contains readily oxidizable material, it should be plentiful in asphyxiated blood. He took the fact that asphyxiated blood did not produce oxidation upon exposure to oxygen as evidence that the blood *in* organisms would not either.

Pflüger went on to contend that cells and tissues do regulate the rate of respiration. In order to argue this it was necessary to counter Ludwig's claim that time constraints would prevent sufficient transfer of oxygen from the blood into the tissues. Pflüger calculated the pressures of oxygen and carbon dioxide at various points in the body and argued that, especially given the enormous capillary surface, oxygen and carbon dioxide could readily diffuse from blood to tissue or vice versa. Pflüger derived major support for his claim that tissues control the rate of respiration from work on insects showing that tracheal tubes filled with air penetrated directly into the tissues and cells and supplied them with oxygen. If blood was not necessary for respiration there, he argued, it must serve no more than a transport function. He concluded:

> I wish to state this once and for all that herein lies the real secret of the regulation of oxygen consumption throughout the entire organism: that the cell alone determines it, not the oxygen content of the blood, not the tension of the aortic system, not the velocity of the blood stream, not the mode of cardiac output and not the method of breathing. (1872, p. 52)

We could hardly hope for a stronger expression of localization.

Oertmann helped further enforce the view that tissues, not blood, were the determinants of the rate of respiration. He replaced the blood of a number of frogs with saline solution and pure oxygen. Their respiratory activity was unaffected for ten to twenty hours, and the frogs finally died after one to three days. Oertmann concluded, with the frogs dissenting, that "the oxidation processes of the frog undergo no change following the removal of its blood. The bloodless frog has the same metabolism as the frog with blood. The site of the oxidation processes is therefore the tissue, not the blood" (1877, p. 395).

Pflüger's work provided convincing evidence for the claim that tissue cells were the locus of respiration: he effectively removed the evidence that suggested that the rate of blood flow was the critical controlling variable in respiration, and his work on insects demonstrated that tissues were

able to carry out respiratory functions without blood as an intermediary. The evidence that tissues can respire, combined with an account of how oxygen could diffuse into tissues and evidence that tissues actually controlled the rate of respiration, established tissue cells as the locus of respiration.

Pflüger recognized that ultimately one needed to explain *how* the cell carried out respiration and was able to regulate the process. It was not satisfactory simply to stop after identifying the cell as the locus. His ideas on this issue, however, were repudiated as speculative (see Glas 1979, pp. 85-87, for further discussion). Even so, he saw the importance of recognizing that the next step was to discover an internal mechanism capable of performing the task assigned to the system.

5. CONCLUSION: LOCALIZATION OF FUNCTION

Defining and isolating a locus of control is one of the first steps in a mechanistic understanding of the behavior of complex systems. The initial task in identifying a locus of control includes segmenting a system from its environment and showing that it is capable of performing the activity assigned to it. Deciding whether a system constitutes a locus of control is thus the first choice-point on the path to developing a mechanistic explanation. If one successfully differentiates a system as a locus of control, the next task is to determine how the system performs the required functions. If the system is not the locus of control, the task is once again one of segmenting an appropriate system that might be the locus of control for the phenomenon under investigation. This process may be represented as in Figure 3.1.

Segmentation of a unit generally requires collateral theories that refer to the system or indicate its structure. Sometimes the theories leading researchers to segment nature as they do and distinguish the system are not made explicit. Individual organisms, at least those of moderate size, are naturally viewed as entities distinguishable from their environment. While it is somewhat less natural to view species as causal entities, they do appear naturally as classificatory units. Even without theoretical or empirical support for treating them as units, we readily group together various organisms on grounds of similarity into units closely resembling those associated with biological species. However, treating species as *causal units* represents a significant conceptual advance, as it requires, at least in part, construing species not as classes but as units capable of affecting other units and being affected by them (cf. Ghiselin 1974; Hull 1976, 1978). Thus, segmenting systems in nature for purposes of developing mechanistic explanations often relies on theoretical considerations. In the last case discussed above—that of biological respiration—the identification of cells
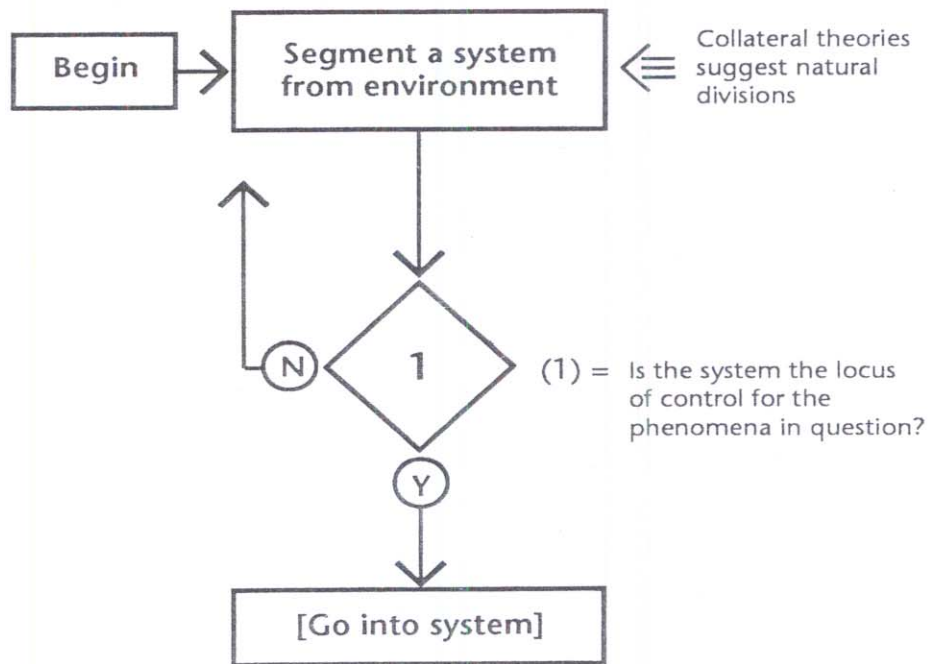
Figure 3.1. The Initial Choice. Defining a locus of control depends on segmenting systems of control from the environment and identifying systemic function. Identifying the locus of control and determining what qualifies as a system are correlative enterprises.

as structural and functional units was itself the product of scientific inquiry. Because the cell theory was already developed by the time some researchers on respiration sought to locate the phenomenon in the cell, it provided the necessary collateral theory.

Having segmented system from environment, one must then locate the locus of control within the system. An array of empirical and theoretical evidence is often brought to bear in settling on a locus of control for a phenomenon. As we have seen, some early investigators, under the influence of evidence suggesting that tissues could respire even without lungs or the circulatory system, concluded that tissues were the proper locus of control. The two most influential researchers opposing this claim, Ludwig and Bernard, tended to discount this evidence, but for quite different reasons. Ludwig produced evidence he thought showed that the circulatory system was really in control of respiration. Bernard thought the tissues and cells actually determined the rate of the reaction, but thought this was incompatible with them also being the locus of the reaction itself. To establish the cells as the locus of control Pflüger countered Ludwig's evidence, showing that cells are the controlling factor in the rate of reaction. He also proposed that cells could simultaneously be the site of the reaction and control its rate. He thereby justified the assumption that cells

were a semiautonomous system in which one could situate the respiration process. Control was successfully localized.

The array of considerations invoked in discussing the locus of control for respiration were varied. Some were essentially theoretical or, perhaps, qualitative. Thus, the appeals to thermal differences and mechanisms of transport in debates over the site of respiration were largely qualitative. Bernard's exclusion of the tissues as the site of respiration rested primarily on theoretical considerations. In other cases the considerations are more narrowly empirical. Some of these are clear exemplars of localizationist experimental strategies, which we will see deployed in many different ways in subsequent chapters. Thus, Pflüger showed that respiration could occur even in the absence of blood to control it; variations in oxygen level did not effect respiration. Moreover, respiratory processes similar to those of animals occurred in insects, where blood could not serve a regulatory function. These empirical appeals are variations on the analytical techniques sketched in Chapter 2. Excitatory studies rely on enhanced activity with increasing stimulation. Varying oxygen levels should affect respiratory rate if it controls it. In Pflüger's case it does not. Inhibitory studies rely on diminished activity in the absence of a structure. Just as the inhibition of a function with the ablation of a structure implicates that structure, maintaining a function in the absence of a structure suggests it is relatively unimportant in the function; for example, if salt water will do, then hemoglobin is not necessary.

In the other two cases considered in this chapter there is still active disagreement. Those advocating internal control of behavior and evolution have tried to show that organisms or species do constitute semiautonomous units in important respects. Such researchers do not maintain that these systems are closed; rather, they acknowledge that in a variety of ways these systems are responsive to environmental factors, but they nonetheless defend an internal locus of control. For example, in arguing for internal control of language and conceptual systems, Chomsky does not deny that the environment influences the development of syntax and concepts, but he maintains that this effect is highly constrained by the internal operation of the system. The impact of the environment is, in his view, one of "prompting" rather than "controlling" behavior. Early advocates of orthogenesis maintained an analogous view, while more recent proponents adopt a much weaker opinion, holding only that the species' internal structure is *one* component with an independent contribution to evolutionary patterns. Function can follow form. Epigenesists, on the other hand, reject internal control, largely by trying to show how development or evolution is primarily ruled by external factors. They emphasize the pliability of the system in responding to these factors, thereby con-

tending that any explanation of the system *must* focus on these factors external to it. The result of a negative verdict on the locus of control is the rejection of the proposed segmentation of nature. What is then needed is a new definition of the system that might be construed as the locus. Thus, the task for the epigenesist, as well as for the behaviorist, is the identification of a more comprehensive system. Only when that is done are they in position to proceed to the next step of inquiry by entering into the system itself to determine *how* it functions.