9

Evolution Within the Body:
The Darwinian Lesson Extended

Evolution builds brains using evolution itself as a design tool. As it matures, a brain literally adapts to its body.
—Terrence W. Deacon (1997, p. 194)

Our present understanding of Darwinian evolution offers some answers and suggests others to many ultimate and proximate why questions concerning behavior. However, it must be recognized that the natural selection of organisms has a serious adaptive limitation. Natural selection can lead only to the evolution of organisms whose structure and behavior are adapted to *past* environments, with no guarantee that they will be adapted to the environment in which they live today and will inhabit tomorrow.

To the extent that an organism's environment is similar to that in which its predecessors evolved, we can expect its physical structures, physiological systems, and behavior to fit the demands of its current environment. But if the environment is significantly different in any way from that of its ancestors, we should not be surprised to find the organism maladapted in some way to the demands of living and reproducing. Changes in climate or in a species' food supply, or the arrival of a new predator or parasite may lead to extinction. The consequences of this inability of natural selection to prepare organisms for future environments can be quite serious, as indicated by the fact that the normal fate of a species is extinction; there are many times more extinct species than extant ones.

Psychologist Henry C. Plotkin referred to this as the "uncertain futures problem" (1994, p. 135), and it poses a serious challenge for all living

organisms. Obviously, an organism's chance of surviving and reproducing would be improved if it could somehow solve the uncertain futures problem by changing its behavior to adapt to changes in the environment. Indeed most, if not all, organisms can adaptively modify their behavior to at least some degree, although some species are much better at this than others. In this respect, the human species is distinguished by remarkable flexibility that permits us to survive in a range of environments unmatched by any other species yet encountered (excluding parasites and bacterial companions for which we serve as host), from tropical forests and deserts to arctic tundra and, thanks to modern technological advances, from the ocean floor to the lunar surface.

The ability to change one's behavior (and thoughts, in the case of humans) as a result of environmental experiences is generally referred to as *learning* by psychologists and animal scientists. We surveyed in chapter 3 several attempts to understand how humans and other organisms are able to make adaptive changes to their behavior. But we also noted how these proposals—from behaviorist theories of Pavlov, Thorndike, Watson, and Skinner to cognitive theories of learning—fail to account for the purposeful nature of behavior, relying as they do on one-way stimulus-response or stimulus-computation-response mechanisms.

This chapter considers a more satisfactory materialist understanding of how it is that human behavior and thought can be adaptively modified as a result of experience. In keeping with the book's major themes, the mechanism offered will most assuredly not be one in which environmental stimuli cause behavior, but rather one that extends Darwin's selectionist lesson to processes occurring *within* organisms.

The Immune System as Within-Organism Darwinian Selection

Although it may seem odd to begin our discussion of learning with a look at the mammalian immune system, there are actually very good reasons for doing so. They will not become apparent, however, until we consider some basic facts about the functioning of the immune system.

The human immune system's primary function is to protect our bodies from microscopic pathogens such as bacteria, viruses, and chemical

toxins that are collectively known as *antigens*. It does this by producing cells called *antibodies* that are able to recognize invading antigens and bind with them so that other cells produced by the immune system can find and neutralize or destroy them. What is both striking and essential about antibodies is that they have a very close physical match to the antigens to which they bind. An effective antibody fits an antigen in much the way that a jigsaw puzzle piece fits its neighboring piece (although for antibodies and antigens the fit is in three dimensions, not just two).

For over 100 years scientists puzzled over how antibodies managed to achieve this close fit with antigens. During the 1890s the first important immune system researcher, Paul Ehrlich (1854–1915) of Germany, theorized that mammals were born with a large innate set of antibodies, at least one of which was able to bind to any possible antigen. In this view, information essential for the production of all possibly needed antibodies is contained in the animal's genes (see Ehrlich 1900). Ehrlich's theory was therefore known as a *germ-line theory* of antibody production, with germ line referring to the entire set of genes (or *genome*) that is passed from parents to offspring.

But this theory soon encountered a major difficulty. During the 1900s Karl Landsteiner (1868–1943) of Austria demonstrated that antigens could be produced in response to the introduction of completely new artificial substances. This indicated that the germ-line theory is inadequate since an animal could not possibly possess in its finite genome the information required to produce an infinite number of all possibly needed antibodies. In effect, Landsteiner showed that the immune system somehow manages to solve the uncertain futures problem by producing new antibodies able to bind with antigens never before encountered in its host's life or evolutionary past.

The theory that first attempted to account for the immune system's ability to generate antibodies in response to novel antigens was the *template theory* that appeared in Europe in 1930 and was further developed by Nobel prize-winning chemist Linus Pauling (1901–1994) in the United States. According to the template theory, antigens themselves are used by the immune system to construct well-fitting antibodies, similar to the way that a cookie cutter makes cookies out of dough. Since antibody formation is considered the result of the direct action of antigens on

antibodies, this can be referred to as an *instructionist* theory with anti-gens somehow directly causing or "instructing" adaptive changes in the production of antibodies. In this way the template theory is similar to Lamarck's instructionist theory of evolution that saw the environment as directly causing adaptive changes in organisms (see chapter 7).

Also like Lamarck's theory, the template theory of antibody production ultimately failed. As British-Danish immunologist Niels Kaj Jerne (1911–1994) pointed out in the 1950s, it could not account for several key immunological findings. These include the increasing rate of antibody production during the initial immune response, the system's memory of previously encountered antigens, and the fact that antibodies produced during the latter stages of an immune response are more effective in bind-ing with antigens than antibodies initially produced.

In addition to making strong arguments against the template theory, Jerne offered an alternative for which he received a Nobel prize in 1984. His natural selection theory of antibody production held that a mammal initially possesses a relatively small number of antibodies. Successful binding of an antibody to an antigen—which fortunately does not require an exact fit between them—triggers the antibody to produce a large num-ber of copies of itself. In this way a preexisting antibody is effectively *selected* by the antigen that in turn stimulates the chosen antibody to pro-duce a multitude of clones. Australian virologist Sir Frank Macfarlane Burnet (1899–1985), yet another Nobel laureate, further developed this theory, calling it the *clonal selection theory* of antibody production.

Whereas this rather sketchy account of antibody production has omit-ted much (for a more detailed summary see Cziko 1995, chapter 4), it nonetheless reveals its essentially Darwinian operation. Indeed, the clonal-selection production of antibodies is a veritable microcosm of Darwinian evolution with the three major principles of overproduction, variation, and selection each playing an essential role. Overproduction is evident in the production of far more antibodies than are effective in bind-ing with an antigen; variation is achieved by the random recombination and mutation of antibody genes; and selection occurs as only those anti-bodies that bind with an antigen can reproduce and thus be represented in the next generation.

It should be now somewhat clearer why this chapter on learning and cognitive development began with an introduction to the mammalian immune system. It is because the immune system is an adaptive system that has overcome the uncertain futures problem by employing its own version of Darwinian evolution. This evolution takes place not over long periods of geological time, but rather over the much shorter lifetime of individual organisms as certain antibodies are naturally selected for reproduction and others are eliminated. Whereas adaptive biological evolution proceeds by cumulative natural selection occurring *among* organisms, we now understand that the immune system is able to adapt to new, unpredictable pathogenic threats by cumulative variation and selection occurring *within* organisms. Might it also be the case that organisms are able to devise behavioral and mental solutions to problems posed by uncertain futures using a similar process of within-organism variation and selection?

Darwinian Theories of Behavioral and Cognitive Change

Just such a Darwinian approach to cognitive functioning and behavior played an important role in psychological theory, particularly at the end of the nineteenth century and beginning of the twentieth. In the late nineteenth century, theories involving mental or cognitive variation and selection were used to attempt to understand how scientific discoveries are made. Scottish philosopher and psychologist Alexander Bain (1818–1903) emphasized that scientific discoveries required the generation of a great number of ideas and then trying them out (1868, pp. 593 ff.). Another early cognitive Darwinian was English economist and logician W. Stanley Jevons (1835–1882) who stated that "in all probability the errors of the great mind exceed in number those of the less vigorous one. Fertility of imagination and abundance of guesses at truth are among the first requisites of discovery; but the erroneous guesses must be many times as numerous as those which prove well founded" (1874; quoted in Campbell 1974, p. 428).

Other respected nineteenth-century writers who were quick to apply Darwinian selectionism to the understanding of human thought and behavior included American psychologist James Mark Baldwin (1861–1934), Austrian physicist and philosopher Ernst Mach (1838–1916), and

French mathematician Henri Poincaré (1854–1912). Central to all these men was the notion that useful thoughts (beliefs, ideas) could be found only if the thinker generated a large number of varied guesses that were somehow filtered so that only the better ones were retained and the others discarded.

In the United States, mathematician and philosopher Chauncey Wright (1830–1875) was so taken by the theory of evolution that he visited Darwin in England in 1872 and went on to apply concepts of natural selection to the workings of the human mind. Instead of Darwinian competition among organisms, Wright described a process of mental competition among beliefs, with both other current beliefs and the environment acting to eliminate less fit beliefs and leaving better-adapted ones.

Wright's ideas apparently also had some influence on America's first great psychologist, William James. James, who recognized the purposeful character of animal and human behavior (recall his description of the frog seeking air and Romeo striving to place his lips on those of Juliet), applied the ideas of Darwinian random variation and selection to the psychological realm (1880, pp. 456–457).

. . . new conceptions, emotions, and active tendencies which evolve are originally *produced* in the shape of random images, fancies, accidental outbirths of spontaneous variation of the excessively unstable human brain, which the outer environment simply confirms or refutes, preserves or destroys—selects, in short, just as it selects morphological and social variation due to molecular accidents of an analogous sort . . .

But the rise of behaviorism in the United States during the first half of the twentieth century put a rather abrupt end to James's cognitive Darwinism and replaced it with a Darwinism oriented to overt behaviors. The theory of operant conditioning introduced by Thorndike and further developed and advocated by Skinner was described and critiqued in chapters 3 and 7. It will be recalled that Skinner's dismissal of purpose and his emphasis on the environment's role in determining an organism's behavior resulted in a theory in which external factors cause the organism's behavior and cannot account for the way in which the organism acts to control aspects of its environment. Skinner saw behavior as determined by its consequences (reward and punishment), however, a true appreciation of the purposeful nature of animate behavior must include understanding behavior as a means of controlling consequences.

In retrospect, it is unfortunate that Skinner used an evolutionary analogy for his theory of animate behavior and learning, since this provided a reason for those involved in the cognitive revolution of the second half of the twentieth century not only to reject his narrow focus on overt behavior and environmental control but to purge all Darwinian thinking from psychology as well. The Skinnerian image—organisms (including humans) emitting random behaviors with the environment providing consequences to determine which of these behaviors should be repeated—was (and still is) considered simplistic, unrealistic, and even repugnant to cognitive scientists. They instead attempt to understand behavior and its change by focusing on mental and neural processes that underlie what often appears to be initially highly intelligent behavior, not the randomly emitted fumblings Thorndike and Skinner described.

Perhaps the best example of this anti-Skinnerian and anti-Darwinian attitude among cognitive scientists is that of linguist Noam Chomsky and his innatist theories of language structure and acquisition. Indeed, Chomsky's 1959 review of Skinner's book *Verbal Behavior* is typically taken as the beginning of the cognitive revolution in psychology. Curiously, his anti-Darwinism goes so far as even to deny Darwinian evolution an important role in the evolution of the human capacity for language.[1]

Donald T. Campbell's Cognitive Darwinism

At least one behavioral scientist was able to reject Skinner's narrow focus on overt behavior while recognizing the power of the Darwinian process working within organisms. Donald T. Campbell (1916–1995), who spent most of his academic career at Northwestern University near Chicago, is best known among behavioral and social scientists for his development of research methods (see, for example, Campbell & Stanley 1966; Cook & Campbell 1979). But although this work remains important and influential, Campbell was actually more interested in developing a general theory of knowledge processes that used as its engine the Darwinian mechanism of variation and selection.

Campbell made three major accomplishments in this area. First, he documented and described Darwinian theories of thought and behavior of philosophers, psychologists, and other scientists since the time of Darwin (Campbell 1974). Second, over more than thirty-five years he provided

strong arguments that Darwinian variation and selection underlie all processes by which adaptation of some type is achieved. These include the fit of our perceptions to aspects of the environment they represent, the fit of our thoughts and mental processes to real-world problems we confront and solve, and the fit of our scientific theories and predictions to the universe they describe. Finally, he devised a hierarchy of knowledge processes to explain how the development of all forms of knowledge—whether over long periods of evolutionary time or during the relatively short lifetime of a single organism—can be accounted for by the general Darwinian process of variation and selection.
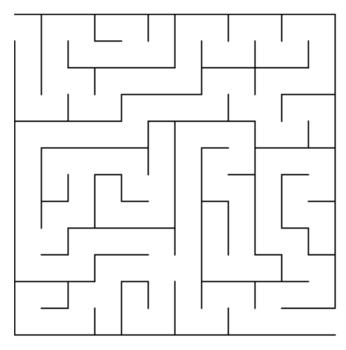
For the purpose of this chapter, it is Campbell's description of what he called "vicarious blind variation and selective retention" that is of most interest. Campbell saw such vicarious processes as adaptive mental processes "substituting for overt locomotor exploration or the life-and-death winnowing of organic evolution" (1974, p. 421). Let us turn to a concrete example for a better idea of what he had in mind.

Imagine that a desired object, such as a piece of food, is placed in view behind a fence so that an animal can obtain it only by first moving away from it to go around the intervening barrier. This is known as the *Umweg* (German for "detour") task and has been used to test the problem-solving abilities of chimpanzees, chickens, and other animals (see Boakes 1984, pp. 184–196).

It turns out that chickens and chimpanzees differ markedly on the Umweg task. Whereas chickens can solve the problem only if their frantic movements bring them by chance to a spot where they can see the path around the obstacle, chimpanzees can more calmly examine the situation and then simply walk around the barrier to obtain the object. So chickens must rely on the variation and selection of overt behaviors, but larger-brained chimps are able to substitute the variation and selection of mental processes for overt behavior.

Here's another example that you can try yourself. Examine the maze shown in figure 9.1 and by visual examination alone (using no pen or pencil or tracing actions) try to find the path from the upper left corner to the lower right one. You should try this now before reading further.

Notice how you were able to solve the maze problem with no overt behavior at all (other than moving your eyes, if you consider that overt). To find the path, you almost certainly made a number of mental errors,

Figure 9.1
Maze

running into cul-de-sacs and backtracking to find an alternative successful route. This is an example of the vicarious variation and selection of mental processes that in humans—and presumably other "higher" animals such as apes and perhaps even dogs and cats—can substitute for the overt variation and selection of behaviors that Skinner emphasized.

As a final example, imagine trying to rearrange the furniture in your living room to accommodate a piano. In looking over the room as currently furnished, you could readily imagine other possible arrangements. You might think, "The sofa could be moved from the back wall to under the window freeing up wall space for the piano, and the armchair currently next to the window could be moved to the empty corner." On second thought, this plan may not prove to be feasible, as the piano would block access to the built-in bookcase. But other arrangements could easily be imagined as you observe the room's current configuration and contents and think about other ways it could be arranged.

The usefulness of this variation and selection of mental processes as a substitute for more costly (in terms of time and energy) and potentially dangerous overt behaviors provides what may be an important clue in understanding the evolution of consciousness itself. While the topic of consciousness and its purpose continues to intrigue and mystify both philosophers and cognitive scientists (for example, see Dennett 1991; Searle 1992), one important use of consciousness is the vicarious mental variation and selection it makes possible. This perspective on consciousness does not provide answers to the question of why we have the particular conscious experiences we have, but it does suggest an important functional role for consciousness. Consciousness as vicarious variation and selection allows us to try out possible solutions mentally using a type of simulated or virtual reality as a substitute for more effortful and possibly dangerous overt behavioral trials.

It is largely because of Campbell's writings that a general Darwinian approach to human knowledge, thought, and behavior survived through both the behaviorist and cognitive phases of twentieth-century psychological theory. Campbell coined the term *evolutionary epistemology* that is still widely used, at least among philosophers, for a general Darwinian account of the emergence of knowledge. For more than thirty-five years he provided important philosophical, logical, historical, and anecdotal reasons for seeing creative thought, problem solving, technological advances, and scientific progress as involving the cumulative blind variation and selection of thought trials. But he did not undertake empirical research to provide evidence for his claims and so his Darwinian account of knowledge processes has not had much impact on mainstream psychological theory. But we will see in the following sections that there is increasing evidence from both behavioral and neuroscientific research for Campbell's cognitive extension of Darwin's lesson.

Evidence for Cognitive Darwinism

When Campbell first proposed his extension of Darwinian theory to psychology, he anticipated difficulty finding empirical support, noting "the unfavorable ratio of hypothesized unobservable processes to observable input-output variables" (1960, p. 397). Thoughts and ideas do not

leave fossils that can be dug up and examined, nor are they readily accessible to other means of scientific observation and measurement. But now, forty years later, a growing body of evidence suggests that some cognitive processes do involve the Darwinian variation and selection of thought trials. These findings are not only consistent with Campbell's theory but are difficult to account for otherwise. Much of this research deals with human creativity and invention and was reviewed by Simonton (1999b). We will now take a look at some of these studies, as well as some others not discussed in Simonton's book.

If it is true that problem solving and other adaptive forms of human creativity depend on blind variation and selection of thought trials, we should expect them to be enhanced by factors that increase the variability and number of such thoughts. This was found in a number of experimental studies. Subjects in one study were provided with shapes and forms to create objects having certain functions (Finke, Ward, & Smith 1992). They came up with the best and most imaginative inventions when both the forms they were given and the target function were randomly selected from a large set of possibilities. In another study, randomly generated associations facilitated problem solving on a marketing task (Proctor 1993).

Other investigations, known as psychometric studies, examined relationships between certain psychological traits and creativity. They found that above a certain basic level, IQ is not related to creative ability (Simonton 1985). Instead, creative individuals tend to produce many varied ideas (see, for example, Eysenck 1993, 1994, 1995). Accordingly, tests that attempt to measure creativity typically do so not by replicating the types of items found on intelligence tests but rather by assessing an individual's ability to generate many diverse ideas. The Remote Associations Test (Mednick 1962) assesses creativity by measuring one's ability to create associations between dissimilar ideas. Other tests assess an individual's ability in what is called divergent thinking, that is, the ability to generate many novel and diverse responses to a problem or question. An example is the Alternate Uses Test in which one attempts to come up with as many different uses for an object as one can.

Other aspects of personality that are associated with creativity also support a within-organism Darwinian view of cognition. Simonton (1999a) summarized this research by noting that:

. . . creative personalities tend to possess those characteristics that would most favor the production of ideas both numerous and diverse. In particular, creative individuals tend to be independent, non-conformist, unconventional, even bohemian; they also tend to have wide interests, greater openness to new experiences, and a more conspicuous behavioral and cognitive flexibility and boldness.

Also of interest are studies of creativity and invention that use historical measures. Historiometric studies conducted by Simonton (1979, 1987, 1997) showed that individuals who are most prolific are also the most successful in creative achievements. This relationship between quantity and quality holds across as well as within individuals and thus provides some evidence that creativity is a function of variations. The more an individual produces, the more likely he or she is to be successful in some creative endeavor, not unlike biological evolution in which organisms that produce the most offspring are most likely to produce a variation that will be better adapted to survival and reproduction. Of particular interest is the finding that the proportion of produced variations that are successful does not increase as an individual gains experience in his or her field. Rather, individuals appear to be most creative around the age of 40, which is when they produce the greatest number of variations. In addition, a Darwinian view of creativity can account for the output of scientific communities (Kantorovich 1993).

Finally, in the field of cognitive development, Siegler (1996) found a high degree of variation in the problem-oriented thinking of children and held that "variability and selection functions seem essential to any developing system. Thus, they may be a basic part of many, if not most, mechanisms of cognitive development" (1989, p. 376).

These are just a few of the studies from the considerable (and growing) body of empirical research that supports a within-organism Darwinian theory of creative thought and behavior as suggested by Campbell. The reader is referred to Simonton's recent book (1999b) for a thorough treatment of this topic.

The Rise of Neural Darwinism

In addition to evidence from psychological studies of thought, personality, and behavior, the rapidly developing field of neuroscience has uncov-

ered findings having clear Darwinian implications for our understanding of the development, structure, and functioning of the human brain.

One of the principal puzzles in the neurosciences is understanding how something as complex as the human brain can develop from a single fertilized egg cell. The adult human brain contains about 11 billion specialized nerve cells, or *neurons*, and each neuron may have up to 10,000 connections, or *synapses*, with other neurons. It is widely believed by neuroscientists, psychologists, and even some philosophers that all knowledge that the brain contains—from knowing how to walk to being able to perform abstract mathematical reasoning—is a function of neurons and their interconnections. Therefore, understanding how the functional complexity of the brain develops is a major goal of behavioral and brain sciences.

It was thought at one time that the brain's complex organization was fully specified in the genome as a result of many millions of years of natural selection. Research findings now cast doubt on such a view. For one thing, it is estimated that the human neocortex alone (the most recent addition to our brain) has about 10^{15} (1 followed by 15 zeros, or 1 thousand million million) synapses (Eccles 1989, pp. 1, 4). Since the entire human genome has only about 3.5×10^9 (3.5 billion) bits of information stored as nucleotide base pairs, some scientists (for example, Deacon 1997, p. 197) have concluded that our genes simply do not have enough storage capacity to specify all these connections, in addition to including information on the location and type of each neuron plus similar information for the rest of the body.

How then is the brain able to achieve the very specific and adaptive wiring required to function in so many remarkable ways? For example, how does a motor neuron know to which particular muscle fiber it should connect? How is a sensory neuron in the visual system able to connect itself to the correct cell in the visual cortex of the occipital lobe of the brain? If this detailed neuron-to-neuron wiring plan is not provided by the genes, from where does it come?

It turns out that the precise wiring of the brain and nervous system is accomplished by a process that *eliminates* many neurons and synapses. As far back as 1906 it was known that some embyronic neurons did not survive birth (Changeux 1985, pp. 216, 217), with later research

finding that of the 20,000 neurons present in a particular location of a chicken embryo's spinal cord, only 12,000 remained in the adult bird (Hamburger 1975).

In addition to entire neurons, countless synaptic connections are eliminated during the development of the mammalian nervous system. But how does the nervous system know which connections to retain and which to eliminate? The work of David Hubel and Torsten Wiesel in the 1970s (who shared a Nobel prize in 1981) provided an important clue. They conducted their ground-breaking experiments by sewing closed the lid of one eye of newborn cats and found that even one week without sight altered the connections of the eyes to the brain (layer 4 of the occipital cortex, to be more precise). Neurons carrying nervous signals from the closed eye made fewer connections with the cortex, whereas those from the open eye made many more connections than was normal. This finding suggests that visual system neurons engage in a form of Darwinian competition for space in the visual cortex, with the result of the competition dependent on the amount and type of sensory stimulation carried by the axons.

We know that normal development of the brain is a function of interaction between genetic inheritance and environmental experience. The genome provides the general structure of the central nervous system, and nervous system activity and sensory stimulation provide the means by which the system is fine-tuned and made fully operational. But this fine-tuning does not depend on adding new components and connections in the way that a radio is normally assembled in a factory. Instead it is achieved by eliminating much of what was originally present. It is as if the radio arrived on the assembly line with twice as many electrical components and connections than it needed. If such an overconnected radio were plugged in and turned on, nothing but silence, static, or a hum would be heard from its loudspeaker. However, careful removal of unnecessary components and judicious snipping of redundant wires would leave just those components and connections that result in a functioning radio. This snipping is analogous to the elimination of synapses in the human brain as part of its normal development.

Psychologist William Greenough of the University of Illinois at Urbana-Champaign has studied in microscopic detail the process by which brain

connections change over time as maturing animals interact with their environments. Using sophisticated techniques to determine the numbers of neurons and synapses in specific regions of the rat's brain, he and his associates found a rapid spurt in the growth of synapses during the first months of the rat's life that occurs regardless of the amount or type of sensory experience (Greenough & Black 1992). This period of synaptic "blooming" is followed by a sharp decline in the number of synapses. That is, elimination or "pruning" of synapses takes place based on the activity and sensory stimulation of the brain, ultimately resulting in the pattern of connections characteristic of the mature rat's brain.

Greenough refers to this initial blooming and pruning of synapses as *experience-expectant* learning, since the initial synaptic overproduction appears to be relatively independent of the animal's experiences. It is as though the brain is expecting important things to happen during the first months of life and is prepared to profit from these experiences with an overabundance of synapses, only a fraction of which will be selectively retained. The work of Greenough and his associates has been limited to rats and monkeys, but autopsy studies of human cortex have also found a decrease to about 60 percent of the maximum number of synapses as the human brain matures (Huttenlocher & Dabholkar 1997, p. 167).

In a recent book on the evolution of language, neuroscientist and biological anthropologist Terrence Deacon (1997, p. 199) summarizes the role of within-organism Darwinism for brain development:

In the same sense that Darwinian processes have created new design information for building organisms during the course of the evolution of life, Darwinian-like processes in brain development are responsible for creating the new information required to adapt large brains to themselves and to their bodies.

Greenough's work also gives a Darwinian explanation for how the adult brain is able to learn new skills, form new memories, and adapt to new environments. According to this theory, experience-dependent learning involves both addition and elimination of synapses. Addition involves growth of new synapses in response to the animal's attempt to control aspects of a new, complex environment. Although the brain does appear to know what part of itself has to be involved in this construction project, it need not (and most likely could not) know which particular individual

connections to make. By forming a large variety and number of new connections, the brain can select the combinations that work best, in the same way that the immature, developing brain retains useful connections from its initial oversupply. The long-term result is an overall addition to the number of synapses.

But the actual selection process that fine-tunes the connections is a subtractive one in which useful connections are selectively retained and less useful ones eliminated. Although clear evidence exists for synaptic increase in learning, as I write this we still have no such evidence in mature learning for overproduction of synapses that are pruned away. However, evidence has been found for overproduction of dendrites in mature rats during readaptation of the brain after injury, suggesting that overproduction of synapses may be involved as well (Jones & Schallert 1992, 1994; Schallert & Jones 1993). These findings fit very nicely with the subtractive synapse findings on brain maturation and provide an elegant solution to the puzzle of how the brain could know exactly which new synaptic connections to establish to enable it to acquire new knowledge, skills, and memories.

Several years ago only a relatively small number of neuroscientists subscribed to the view that the adult brain develops and learns through a Darwinian process of cumulative neural variation and selection. Today, however, such a view is starting to be considered mainstream, although much debate remains (see Quartz & Sejnowski 1997 and following commentaries and response). Neuroscientist William Calvin has referred to the brain as a "Darwin machine" that follows the plan of making lots of random variants by brute bashing about, then selecting the good ones (Calvin 1987; see also Calvin 1996a, b). Gerald Edelman, who shared a Nobel prize in 1972 for his research on the chemical structure of antibodies in the immune system, has written several books describing aspects of his neuronal group selection theory of brain development and learning that he refers to as "neural Darwinism" (Edelman 1987, 1988, 1989, 1992).

Research is underway to find physical evidence for overproduction and elimination of newly formed synapses in the adult mammalian brain as the mechanism underlying learning. New imaging techniques such as mag-

netic resonance imaging are also being used to gain insights into the functioning of the human brain, the universe's most complex known object. Finding clear evidence for Darwinian processes in its structural modification and functioning would place the brain alongside the immune system as a second striking example of how the process of cumulative variation and selection during the lifetime of an organism makes it possible to adapt to new and changing environments.

The Complementarity of Among- and Within-Organism Selection

The discovery of within-organism Darwinian processes involving cumulative variation and selection offers some clear answers and suggests others to a number of vexing problems concerning the functioning of the immune system, the processes involved in human thought and creativity, and the development and modification of the brain. Since these phenomena all require the adaptation of one system to another, we should not be too surprised to learn that Darwinian processes are involved. In effect, through the process of among-organism variation and selection, mechanisms of within-organism variation and selection have evolved to solve the uncertain futures problem that all organisms face.

But this does not mean that all physiological and neural functioning involves variation and selection of some kind. We should be grateful that the human heart does not have to learn to pump blood by within-organism trial and error elimination. And although processes of neural Darwinism may be involved in the development of the human auditory system, once developed, it appears to be able to analyze the sounds of human speech directly and quickly with remarkable accuracy with few if any errors from guessing. The among-organism variation and selection of human evolution (along with, in the case of the auditory system, some fine-tuning involving selective neuronal and synaptic elimination) may have provided us with some systems that are able to function quite well without current variation and selection. But other systems that face continual challenges and new environments, such as other aspects of the mammalian nervous and immune systems, must rely on variation and selection to adapt to these new circumstances.

A clearer understanding of the roles of among-organism and within-organism selection can be achieved by considering figure 9.2, which is a simplified illustration of what is hypothesized to be the relative importance of the two processes for three different types of adaptations.[2] To the extreme left we have what are usually considered inborn instincts, such as a spider weaving a web or a newly hatched gosling following the first large moving object it sees (Konrad Lorenz's imprinting, mentioned in chapter 7). Such behaviors are adaptations that may be entirely due (or nearly so) to among-organism selection of biological evolution.

In the middle of figure 9.2 we have adaptive behavior that is not innate but acquired during the individual's lifetime. One obvious example is a rat in a Skinner box learning to push a lever to obtain bits of food. Here we have what appears to be within-organism selection of behaviors emitted by the rat. But better examples for our present purposes are the types of learning studied by Köhler (1925) in apes, such as learning to stack two or more boxes to reach a suspended banana, or use a stick to pull in a banana placed outside the cage. Such learning often appears insightful; that is, after what appears to be a period of incubation, the apes proceed directly to the solution with no overt variation and selection of behaviors. Thanks to Donald Campbell, we can understand such learning as the result of
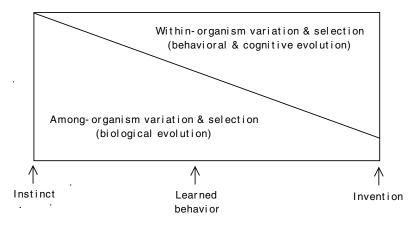

Figure 9.2
Complementarity of among-organism and within-organism variation and selection for three different types of adaptations

within-organism variation and selection involving the generation, evaluation, and selection of thought trials that substitute for overt behaviors.

Note, however, that among-organism evolution still plays an essential part in such learned behavior, as it is responsible for the ape having the necessary equipment (eyes, hands, arms, legs, brain) and motivation (a taste for bananas) for solving the problem. But among-organism (biological) selection is clearly not sufficient since, unlike instincts, what emerges is a new behavior that could not have been naturally selected in the ape's evolutionary past. Such acquired behavior also requires within-organism (cognitive or behavioral) variation and selection.

A useful way of conceptualizing the relative importance of among-organism variation and selection in learning is the degree to which it provides constraints for the blind variations of within-organism variation and selection. For example, young children readily learn the meanings of words spoken to them by their caretakers (as rapidly as one word per waking hour). Although biological evolution cannot in itself provide the child the meanings of these words (in the way that it may provide the meaning of a scream), it appears to set rather narrow (and very useful) limits on the possibilities that a child is willing to entertain. So whereas a child may have little difficulty in learning the meanings of *hand*, *arm*, and *forearm* (the latter referring to both the hand and arm up to around the elbow), she would not expect a single word to refer to both shoulder and hand, or to both knee and foot, or to both red and blue. Such constraints, the results of among-organism evolution, have the effect of usefully constraining or guiding the necessary within-organism variation and selection that must take place to acquire language.

Now we move to the extreme right of figure 9.2. Here we find certain forms of behavioral and/or cognitive adaptations that appear to rely primarily on within-organism variation and selection. Of course, among-organism variation and selection must still play a role since biological brains and limbs are involved (which is why in figure 9.2 the line separating among-organism from within-organism selection never makes it all the way to the lower right corner). But at this end there are fewer useful biological constraints on within-organism variations. Human invention is an example of such an adaptation, since there are apparently few useful biological constraints for the variations that must be considered

for inventing steam engines, light bulbs, transistors, or nuclear fusion reactors.

A second important distinction exists between prior and current variation and selection. Obviously, from the viewpoint of the living organism, among-organism variation and selection of biological evolution is prior, but within-organism variation and selection can be seen as either prior or current. An ape confronted for the first time with boxes and a suspended banana must engage in some form of current behavioral and/or cognitive variation and selection to create a solution for reaching the banana. But the ape who solved the task yesterday requires little or no current variation and selection of behavioral or thought trials since the knowledge gained from that experience remain to guide the ape today. Such prior variation and selection can be of use even if the task is modified so that the boxes are different (such as being open on one end) or a desired object other than a banana (such as a favorite toy) is suspended out of reach. In other words, prior within-organism variation and selection results in knowledge that can be used to constrain current variation and selection for similar types of tasks.

Figure 9.3 indicates the complementary role of prior and current variation and selection for different types of behaviors or abilities. At
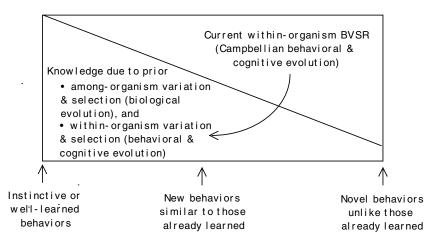

Figure 9.3
Complementarity of prior and current variation and selection for three different types of behaviors

the left end we find both instinctive (for example, bird nest building) and well-learned behaviors (as in a pianist's playing a familiar piece). For such behaviors, no current variation and selection may be necessary. For instincts, among-organism variation and selection supplies the necessary knowledge. For well-learned noninstinctive behaviors, it is a combination of among-organism variation and selection and prior within-organism variation and selection that provides the knowledge necessary for the new behavior or ability.

Moving toward the middle of figure 9.3 we find behaviors and abilities similar but not identical to acquired ones. Prior within-organism variation and selection provides some of the knowledge necessary for these behaviors, but it is not sufficient, thereby making additional current variation and selection necessary. Having created one successful musical composition or invention, one may find creating the next one quite a bit easier. But some additional current variation and selection will be necessary if the next work is not to be just a copy or imitation of the previous one.

Toward the right of figure 9.3 we find novel behaviors unlike those already learned. To learn such behaviors or develop new abilities, current variation and selection must play a major role since little has been learned to constrain or guide new variations that must be generated and tested. The arrow between "current within-organism variation and selection" and "prior within-organism variation and selection" indicates the transformation of current variation and selection to knowledge that may be used to constrain future within-organism variation and selection. This perspective on the complementary role of biological natural selection (that is, among-organism variation and selection) and continuing evolutionary processes (that is, within-organism variation and selection) suggests the universality of the Darwinian process of variation and selection as responsible for all instances of adaptation, indeed, for all knowledge processes broadly conceived (see Cziko 1995; Dennett 1995). If an animal appears to be born already knowing when and how to perform complex behaviors, such as finding food, defending itself, and mating, that knowledge is the result of the among-organism variation and selection of biological evolution. If, however, new behaviors are learned as a result of environmental demands (such as a seal learning to balance a ball on its nose to obtain food from its trainer, or a physicist developing a new

superconductive material), this new learning or knowledge must also rely on a form of variation and selection, but now it is occurring within the organism.

This extension of Darwinian thinking to within-organism processes provides a major conceptual advance for many fields of inquiry, but it is not complete. For among-organism variation and selection, the environment (including other organisms) provides the selective filter to winnow the fit from the less fit. But what provides the selective filter for the within-organism selection of thoughts and ideas and new behaviors? Although biological evolution has no purpose in mind, the within-organism evolution of thoughts, ideas, and behaviors *is* purposeful. So to complete our understanding of how new knowledge and skills evolve within organisms, we have to pay heed once again to Bernard's lesson and combine it with this within-organism extension of Darwin's.