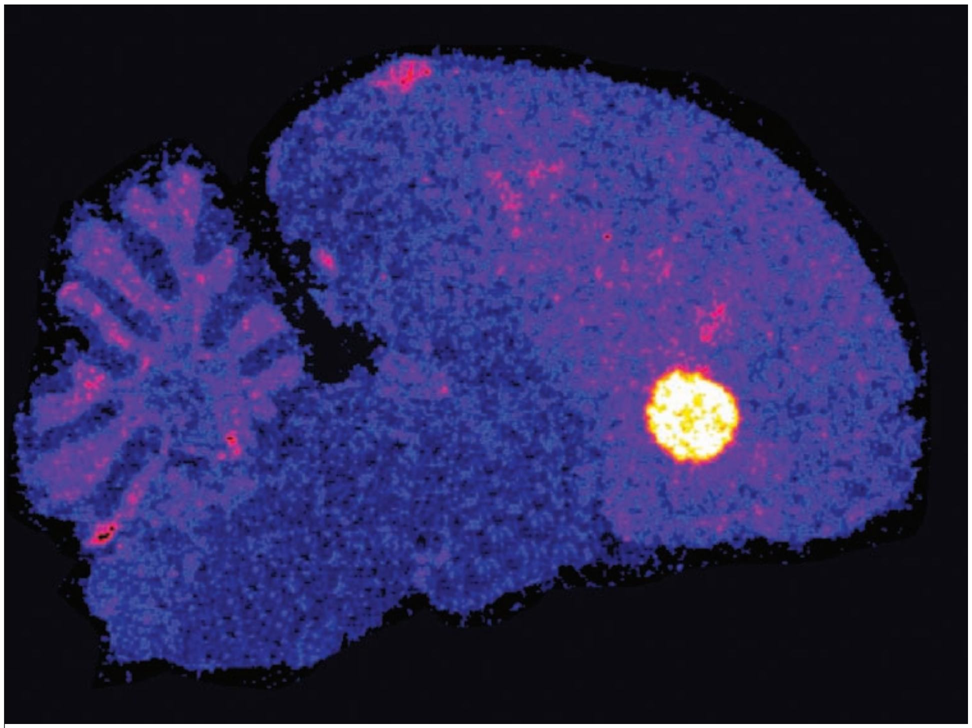

A section of zebra finch *(Taeniopygia guttata)* brain, stained to illuminate expression of the *zenk* gene, which helps a male bird reproduce his species' song.

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54 The Physiology and Genetics of Animal Behavior

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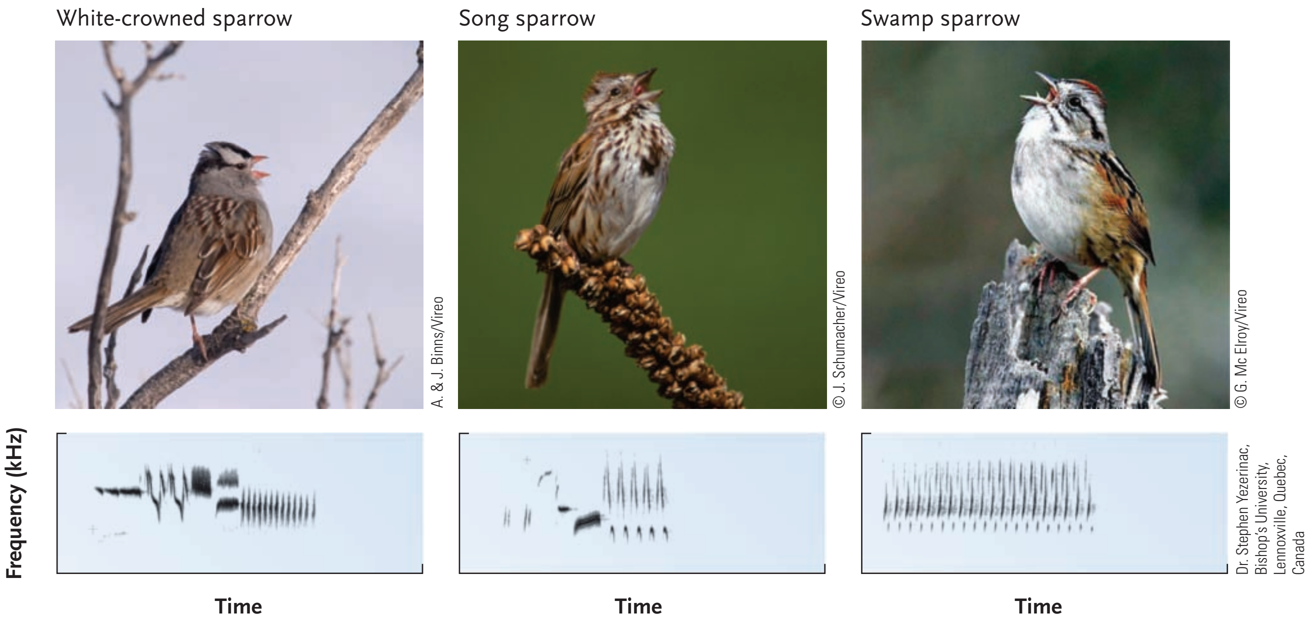
WHY IT MATTERS

Male white-crowned sparrows *(Zonotrichia leucophrys)* are handsome birds with a song that birdwatchers describe as a "plaintive whistle" followed by a "husky trilled whistle." This distinctive song is a critical part of a male white-crown's **behavioral repertoire,** the set of actions that it can perform in response to stimuli in its environment. An adult male sparrow's song is one of the ways he struts his stuff. The song not only announces his presence to rival males, but it also signals to females that he is available as a potential mate. Experienced birders easily recognize this song, which differs from that of song sparrows *(Melospiza melodia)* and swamp sparrows *(Melospiza georgiana),* as sound spectrograms illustrate **(Figure 54.1).** In fact, every songbird species produces vocal signals that are characteristic of its species and its species alone.

The study of **animal behavior** involves discovering how animals respond to specific stimuli and why they respond in predictable and characteristic ways. A comprehensive approach to animal behavior studies first crystallized in the 1930s, when European researchers—notably Konrad Lorenz, Niko Tinbergen, and Karl von Frisch, who shared a Nobel Prize for their work in 1973—developed the discipline



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Dr. Stephen Yezerinac, Bishop's University, Lennoxville, Quebec, Canada

Figure 54.1
Songbirds and their songs. Sound spectrograms (visual representations of sound graphed as frequency versus time) illustrate differences in the songs of the white-crowned sparrow *(Zonotrichia leucophrys)*, the song sparrow *(Melospiza melodia)*, and the swamp sparrow *(Melospiza georgiana)*.

of **ethology,** which focuses on how animals behave in their natural environments. They analyzed how evolutionary processes shape inherited behaviors and the ways that animals respond to specific stimuli. Tinbergen identified four basic questions that any broad study of animal behavior should address: (1) What mechanisms trigger a specific behavioral response? (2) How does the expression of a behavior develop as an animal matures? (3) What is the behavior's function and how does it increase an animal's chances of surviving and reproducing? (4) How did the behavior evolve?

Advances in **neuroscience**—the integrated study of the structure, function, and development of the nervous system—now allow researchers to explore the first and second questions in detail. Comparable advances in genetic analysis and evolutionary theory enable scientists to address the third and fourth questions. In this chapter, we examine the *proximate causes* of behavior—the genetic, cellular, physiological, and anatomical mechanisms that underlie an animal's ability to detect internal stimuli and environmental cues and react to them in species-specific ways. In Chapter 55, we consider the *ultimate causes* of animal behavior—its adaptive value and evolution.

54.1 Genetic and Environmental Contributions to Behavior

For many years, animal behaviorists debated whether animals are born with the ability to perform most behaviors completely or whether experience is necessary to shape their actions. However, extensive research in neuroscience has demonstrated that no behavior is determined entirely by genetics or entirely by environmental factors. Instead, behaviors develop through complex gene–environment interactions. We illustrate such an interaction below with a detailed description of the process through which male white-crowned sparrows learn their adult song.

Most Behaviors Have both Instinctive and Learned Components

Why do adult male white-crowned sparrows sing a song that no other species sings? One possible explanation is that they possess an innate (inborn) ability to produce their particular song, an ability so reliable that young males sing the "right" song the first time they try. According to this hypothesis, their distinctive song would be an example of an **instinctive behavior,** a genetically "programmed" response that appears in complete and functional form the first time it is used. An alternative hypothesis is that they acquire the song as a result of certain experiences, such as hearing the songs of adult male white-crowns that live nearby. In other words, this species' distinctive song might be an example of a **learned behavior,** one that is dependent upon having a particular kind of experience during development.

How can we determine which of these two hypotheses is correct? If the white-crowned sparrow's song is instinctive, isolated male nestlings that have never heard other members of their species should be able to sing their species' song when they mature. But if the learning hypothesis is correct, young birds deprived of certain essential experiences should not sing "properly" when they become adults.

In a set of pioneering experiments conducted at Rockefeller University, Peter Marler tested these alternative hypotheses. He took newly hatched white-crowns from nests in the wild and reared them individually in soundproof cages in his laboratory. Some of the chicks listened to recordings of a male white-crowned sparrow's song when they were 10 to 50 days old; others did not. The juvenile males in both groups first started to vocalize when they were about 150 days old. For many days, they produced whistles and twitters that only vaguely resembled the songs of adults. But gradually the young males that had listened to tapes of their species' song began to sing better and better approximations of that song. At about 200 days of age, they were right on target, producing a song that was nearly indistinguishable from the one they had heard months before. By contrast, males in the group that had not heard tape-recorded white-crown songs never came close to singing the way wild males do.

These results revealed that learning is essential for a young male white-crowned sparrow to acquire the full song of its species. Although birds isolated as nestlings did sing instinctively, they needed the acoustical experience of listening to their species' song early in life if they were to reproduce it months later. We can therefore reject the hypothesis that white-crowned sparrows hatch from their eggs with the ability to produce the "right" song. Their species-specific song—and presumably those of other songbirds—has both instinctive and learned components.

Although early researchers generally classified behaviors as *either* instinctive *or* learned, we now know that most behaviors include both instinctive and learned components. Nevertheless, some behaviors have a strong instinctive component, whereas others are mostly learned.

STUDY BREAK

1. What is the difference between an instinctive behavior and a learned behavior?
2. How did the isolation of young male sparrows in soundproof cages allow Marler to conclude that learning was important to song acquisition?

54.2 Instinctive Behaviors

Instinctive behaviors—which are often grouped into functional categories, such as feeding behaviors, defensive responses, mating behaviors, and parental care activities—can be performed without the benefit of prior experience. We therefore assume that they have a strong genetic basis and that natural selection has preserved them as adaptive behaviors.

Many Instinctive Behaviors Are Highly Stereotyped

Many instinctive behaviors are highly stereotyped; in other words, when triggered by a specific cue, they are performed over and over in almost exactly the same way. Such behaviors are called **fixed action patterns,** and the simple cues that trigger them are called **sign stimuli.** For example, sign stimuli and fixed action patterns govern the transfer of food from herring gull *(Larus argentatus)* parents to their offspring. Researchers found that very young chicks secure food from their parents through a begging response (the fixed action pattern), which is triggered when they see a red spot on the lower bill of an adult (the sign stimulus). This cue "releases" the begging behavior of hungry baby gulls, which peck at the spot on the parent's bill. In turn, the tactile stimulus delivered by the pecking chick serves as a sign stimulus that induces the adult bird to regurgitate food stored in its crop. The baby gulls then feed on the chunks of fish, clams, or other food that lie before them. We know that the spot on the parent's bill releases the begging response of the young gull because the same response is triggered by an artificial bill that looks only vaguely like a herring gull's bill, provided it has a dark contrasting spot near the tip **(Figure 54.2).** Thus, even very simple cues can activate fixed action patterns.

Human infants often respond innately to the facial expressions of adults **(Figure 54.3).** For example, researchers can trigger smiling in even very young babies simply by moving a mask toward the infant, as long as the mask possesses two simple, diagrammatic eyes. Clearly the infant, like a nestling herring gull, is not reacting to every feature of a face; instead it focuses on simple cues, which function as sign stimuli that release a fixed behavioral response.

Natural selection has molded the behavior of some parasitic species to exploit the relationship between sign stimuli and fixed action patterns for their own benefit. For example, birds that are brood parasites lay their eggs in the nests of other species (see *Why It Matters* at the beginning of Chapter 50). When the brood parasite's egg hatches, the alien nestling mimics and even exaggerates sign stimuli that are ordinarily exhibited by its hosts' own chicks: opening its mouth, bobbing its head, and calling vigorously. These exaggerated behaviors elicit feeding by the foster parents, and the young brood parasite often receives more food than the hosts' own young **(Figure 54.4).**

Although instinctive behaviors are often performed completely the first time an animal responds to a stimulus, they can by modified by an individual's experiences. For example, the fixed action patterns of a young herring gull change through time. Although

Figure 54.2 Experimental Research

The Role of Sign Stimuli in Parent-Offspring Interactions

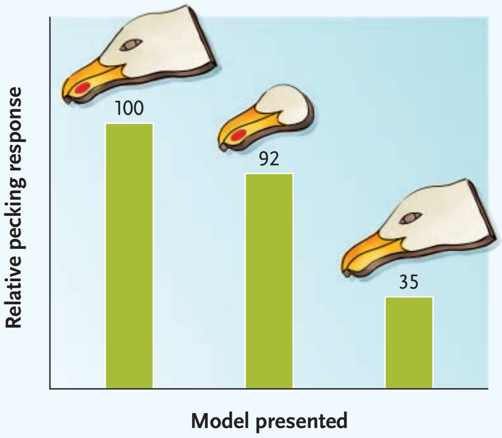
QUESTION: What feature of the parent's head triggers pecking behavior in young herring gulls?

EXPERIMENT: Niko Tinbergen and A. C. Perdeck tested the responses of young herring gull *(Larus argentatus)* chicks to cardboard cutouts of an adult herring gull's head and bill. They waved these models in front of the chicks and recorded how often a particular model elicited a pecking response from the chicks. One cutout included an entire gull's head with a red spot near the tip of the bill; another cutout included just the bill with the red spot; the third cutout included the entire head but lacked the red spot.

RESULT: Young herring gulls pecked at the model of the bill with a red spot almost as often as they pecked at the model of an entire head with a red spot, but they pecked much less frequently at the model of an entire head that lacked a red spot.

Herring gulls *(Larus argentatus)*

© Marie Read Natural History Photography



CONCLUSION: Begging behavior by young herring gulls is triggered by a simple sign stimulus, the red spot on the parent's bill. Experimental tests revealed that herring gull chicks respond more to the presence of the contrasting spot than they do to the outline of an adult's head.

Evan Cerasoli

Figure 54.3 **Instinctive responses in humans.** The smiling face of an adult is a sign stimulus that triggers smiling behavior in very young infants.

the youngster initially begs by pecking at almost anything remotely similar to an adult gull's bill, it eventually learns to recognize the distinctive visual and vocal features associated with its parents. The chick uses this information to become increasingly selective about the stimuli that will elicit its begging behavior. Thus, instinctive behaviors can be modified in response to particular experiences during their early performances.

Behavioral Differences between Individuals May Reflect Underlying Genetic Differences

Because the performance of instinctive behaviors does not depend on prior experience, behavioral differences between individuals may reflect genetic differences between them. Stevan Arnold, then at the University of Chicago, tested that hypothesis by studying the innate responses of captive newborn garter snakes *(Thamnophis elegans)* to the olfactory stimuli provided by potential food items that they had never before encountered. Arnold measured the snakes' responses to cotton swabs that had been dipped in a smelly extract of banana slug *(Ariolimax columbianus)*, a shell-less mollusk. A snake "smells" by tongue-flicking, which draws volatile chemicals into a special sensory organ in the roof of its mouth. If the young snake had been born to a mother captured in coastal California, where adult garter snakes regularly eat banana slugs, it almost always began tongue-flicking at the slug-scented cotton swab **(Figure 54.5).** By contrast, newborn snakes whose parents came from inland California, where banana slugs do not occur, rarely tongue-flicked at the swabs. Thus, although the coastal and inland snakes belong to the same species, their instinctive responses to the volatile chemicals associated with banana slugs were markedly different.

In another experiment, Arnold tested whether newborn snakes would feed on bite-sized chunks of slug. After a brief flick of the tongue, 85% of the newborn snakes from a coastal population routinely struck at the slug and swallowed it, despite having had no prior experience with this prey. By contrast, only 17% of newborn snakes from the inland population ate slugs consistently, even when no other food was available. Arnold hypothesized that coastal and inland garter snakes possess different alleles at one or more gene loci controlling their odor-detection mechanisms, leading to differences in their behavior. To test this hypothesis, Arnold crossbred coastal and inland snakes. If genetic differences contribute to the different food preferences of the two snake populations, then hybrid offspring, which receive genetic information from each parent, should behave in an intermediate fashion. Results of the experiment confirmed his prediction: when presented with bite-sized chunks of slug, 29% of the newborn snakes of mixed parentage consumed them every time.

Many additional experiments have confirmed that genetic differences between individuals can translate into behavioral differences between them. *Insights from the Molecular Revolution* describes a striking example of a single gene that influences the grooming behavior of mice. Bear in mind that single genes do not control complex behavior patterns directly. Instead, the alleles present affect the kinds of enzymes that cells can produce, influencing the biochemical pathways involved in the development of an animal's nervous system. The resulting neurological differences can translate into a behavioral difference between individuals that have certain alleles and those that do not.

STUDY BREAK

1. How do the chicks of brood parasites stimulate unwitting foster parents to feed them?
2. How did Arnold demonstrate that the receptiveness of garter snakes to a meal of banana slugs had a genetic basis?

54.3 Learned Behaviors

Unlike instinctive behaviors, learned behaviors are not performed completely the first time an animal responds to a specific stimulus. Instead, they change in response to environmental stimuli that an individual experiences as it develops.

Learned Behaviors Are Modified by an Animal's Prior Experiences

Behavioral scientists generally define **learning** as a process in which experiences change an animal's behavioral responses. Different types of learning occur un-

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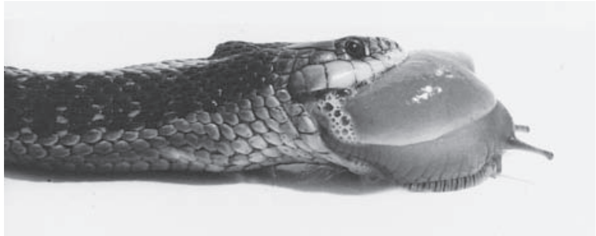
Figure 54.4
Exploitation of a releaser. This young European cuckoo *(Cuculus canorus)*, a brood parasite, stimulates feeding behavior by its foster parent, a hedge sparrow *(Prunella modularis)*. It secures food by displaying exaggerated versions of the sign stimuli used by the host offspring to release feeding behavior by the parents.

a. Banana slug

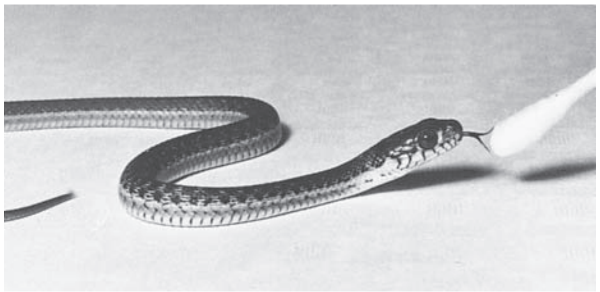
Eugene Kozloff

b. Adult coastal garter snake eating a banana slug



Stevan Arnold

c. Newborn coastal garter snake "smelling" slug extract



Stevan Arnold

Figure 54.5
Genetic control of food preference. (a) Banana slugs *(Ariolimax columbianus)* are a preferred food of **(b)** an adult garter snake *(Thamnophis elegans)* from coastal California. **(c)** A newborn garter snake from a coastal population flicks its tongue at a cotton swab drenched with tissue fluids from a banana slug.

Insights from the Molecular Revolution

A Knockout by a Whisker

Almost all eukaryotic organisms share a series of developmental interactions called the *wingless/Wnt* pathway**.** The name comes from the original discovery of the pathway in the fruit fly *Drosophila melanogaster,* in which mutant genes of the pathway cause alterations in the wings and other segmental structures. Recently, three genes closely related to *disheveled (dsh),* one of the genes of the *Drosophila wingless/Wnt* pathway, were isolated and identified in mice. No functions have yet been identified for the proteins encoded in the three mouse disheveled genes, but tests show that they are highly active in both embryos and adults. Their function must be important, but what could it be?

Nardos Lijam and his coworkers in several laboratories, including Case Western University, the Universities of Colorado and Maryland, and the National Institutes of Health in Bethesda, Maryland, decided to seek an answer to this question by developing a line of mice that totally lacked one of the disheveled genes, called *Dvl-1* in genetic shorthand. First they constructed an artificial copy of the *Dvl-1* gene with the central section scrambled so that no functional proteins could be made from its encoded directions. Next they introduced the artificial gene into embryonic mouse cells. Cells that successfully incorporated the gene were then injected into very early mouse embryos. Some of the mice grown from these embryos were heterozygotes, with one normal copy of the *Dvl-1* gene and one nonfunctional copy. Interbreeding of the heterozygotes produced some individuals that carried two copies of the altered *Dvl-1* gene and no normal copies. Such individuals, in which the normal gene is eliminated, are called knockout mice for the missing gene. (Making knockout mice is described in Section 18.2.)

Surprisingly, the knockout mice grew to maturity with no apparent morphological defects in any tissue examined, including the brain. Their motor skills, sensitivity to pain, cognition, and memory all appeared to be normal. Their social behavior was a different story, however. When housed with normal mice, the knockouts failed to take part in the common activities of mouse social groups: social grooming, tail pulling, mounting, and sniffing. Rather than building nests and sleeping in huddled groups, as normal mice do in the cages, the knockouts tended to sleep alone, without constructing full nests from cage materials. Mice heterozygous for the *Dvl-1* gene—that is, with one normal and one altered copy of the gene—behaved normally in all these social activities.

The knockout mice also jumped around wildly in response to an abrupt, startling sound while the response of normal mice was less extreme. Since it is known that a neural circuit of the brain inhibits the startle response of normal mice, the reaction of the knockout mice suggested that this inhibitory circuit was probably altered. Humans with schizophrenia, obsessive-compulsive disorders, Huntington disease, and some other brain dysfunctions also show an intensified startle reflex similar to that of the *Dvl-1* knockout mice.

The researchers' analysis revealed that the *Dvl-1* gene modifies developmental pathways affecting complex social behavior in mice, and probably in other mammals. It is one of the first genes affecting mammalian behavior to be identified. The similarity in startle-reflex intensity between the knockout mice and humans with neurological or psychiatric disorders also suggests that mutations in the *Dvl* genes and the *wingless* developmental pathway may underlie some human mental diseases. If so, further studies of the *Dvl* genes may give us clues to the molecular basis of these diseases, and a possible means to their cure.


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Figure 54.6
Imprinting. Having imprinted on him shortly after hatching, young greylag geese *(Anser anser)* frequently joined Konrad Lorenz for a swim.

der different environmental circumstances. In this section we consider *imprinting, classical conditioning, operant conditioning, insight learning,* and *habituation.*

Some animals learn the identity of a caretaker or the key features of a suitable mate during a **critical period,** a restricted stage of development early in life. This type of learning is called **imprinting.** For example, newly hatched geese imprint on their mother's appearance and identity, staying near her for months. And when they reach sexual maturity, they try to mate with other geese, which exhibit the visual and behavioral stimuli on which they had imprinted as youngsters. When Konrad Lorenz, one of the founders of ethology, tended a group of newly hatched greylag geese *(Anser anser),* they imprinted on him instead of an adult of their own species **(Figure 54.6).** The male geese not only followed Lorenz about, but they also courted humans when they achieved sexual maturity.

Other forms of learning can occur throughout an animal's lifetime. Russian physiologist Ivan Pavlov's classic experiments with dogs explored **classical conditioning,** a type of learning in which animals develop a mental association between two phenomena that are usually unrelated. Dogs generally salivate when they eat. The food is called an *unconditioned stimulus* because the dogs respond to it instinctively; no learning is required for the stimulus (food) to elicit the response (salivation). In his experiment, Pavlov rang a bell just before offering food to dogs. After about 30 trials in which dogs received food immediately after the bell rang, the dogs associated the bell with feeding time, and they drooled profusely whenever it rang—even when no food was forthcoming. Thus, the bell became a *conditioned stimulus,* one that elicited a particular learned response. In classical conditioning, an animal learns to respond to a conditioned stimulus when it precedes an unconditioned stimulus that normally triggers the response. For example, your cat may become exceptionally friendly whenever she hears the sound of a can opener, another example of classical conditioning.

In another form of associative learning, called trial-and-error learning or **operant conditioning,** animals learn to link a voluntary activity, called an *operant,* with its favorable consequences, called a *reinforcement.* For example, a laboratory rat will explore a new cage randomly. If the cage is equipped with a bar that releases food when it is pressed, the rat will eventually lean on the bar by accident (the operant) and immediately receive a morsel of food (the reinforcement). After just a few such experiences, a hungry rat will learn to press the bar in its cage more frequently—as long as bar-pressing behavior is followed by access to food. Laboratory rats have also learned to press bars to turn off disturbing stimuli, such as bright lights.

A few animal species can abruptly solve problems without apparent trial-and-error attempts at the solution; researchers call this **insight learning.** For example, captive chimpanzees *(Pan troglodytes)* were able to solve a novel problem that their keepers devised: how to get bananas hung far out of reach. The chimps studied the situation, then stacked and stood on several boxes, and used a stick to knock the fruit to the floor.

Animals typically lose their responsiveness to frequent stimuli that are not quickly followed by the usual reinforcement. This learned loss of responsiveness, called **habituation,** saves the animal the time and energy of responding to stimuli that are no longer important. For example, the sea hare *Aplysia,* a shell-less mollusk, typically responds to a touch on the side of its body by retracting its delicate gills, a response that helps protect it from approaching predators. But if an *Aplysia* is touched repeatedly over a short period of time with no harmful consequences, it stops retracting its gills.

STUDY BREAK

1. Dogs typically wag their tails when they see their owners pick up a leash. What kind of learning does this demonstrate?
2. What type of learning allows you to sleep through your alarm clock when it rings to awaken you for biology class?

54.4 The Neurophysiological Control of Behavior

Research in neuroscience has shown that all behavioral responses, even those that are either mostly instinctive or mostly learned, depend on an elaborate physiological foundation provided by the biochemistry and structure of neurons (nerve cells). The neurons that regulate an innate response as well as those that make it possible for an animal to learn something are products of a complex developmental process in which genetic information and environmental contributions are intertwined. Although the anatomical and physiological basis for some behaviors is present at birth, an individual's experiences alter cells of its nervous system in ways that produce particular patterns of behavior. In this section we use examples from research on the singing behavior of songbirds to explore general principles about the physiological basis of behavior that apply to many other kinds of animals.

Discrete Neural Circuits in Specific Brain Regions Control Singing Behavior in Songbirds

Marler's experiments (see Section 54.1) help explain the physiological underpinnings of singing behavior in male white-crowned sparrows. If acoustical experience shapes this behavior, a sparrow chick's brain must be able to acquire and store information present in the songs of other males. Then, months later, when the young male starts to sing, its nervous system must have special features that enable the bird to match its vocal output to the stored memory of the song that it had heard earlier. Eventually, when it achieves a good match, the sparrow's brain must "lock" on the now complete song and continue to produce it when the bird is singing.

Additional experiments have provided detailed information about the nature of the sparrow's nervous system. Young birds that did not hear taped song during their critical period, between 10 and 50 days old, never produced the full song of their species, even if they heard it later in life. In addition, young birds that heard recordings of *other* bird species' songs during the critical period never generated replicas of those songs as they matured. These and other findings suggested that certain neurons in the young male's brain are influenced only by appropriate stimuli, namely the acoustical signals from individuals of its own species, and only during the critical period. Neuroscientists have identified the neurons clusters, called *nuclei* (singular, *nucleus*), that make song learning and song production possible.

Moreover, every behavioral trait appears to have its own neural basis. For example, a male zebra finch, *Taeniopygia guttata* **(Figure 54.7),** another songbird, can

Arco Images/Petra Wegner/Alamy

Figure 54.7 Zebra finches. Native to Indonesia, zebra finches *(Taeniopygia guttata)*, have played an important role in studies of the physiological basis of song learning. The male has a striped throat.

discriminate between the songs of strangers and the songs of established neighbors on adjacent **territories.** (In many bird species, territories are plots of land, defended by individual males or breeding pairs, within which the territory holders have exclusive access to food and other necessary resources. Territories are discussed further in Chapter 55.) The ability to discriminate between the songs of neighbors and those of strangers also involves a nucleus in the forebrain. Cells in this nucleus fire frequently the first time that the song of a new zebra finch is played to a test subject. But as the song is played again and again, these cells cease to respond, indicating that the bird becomes habituated to a now familiar song, although it still reacts to the songs of strangers. The neurophysiological networks that make this selective learning possible enable male zebra finches to behave differently toward familiar neighbors, which they largely ignore, and unfamiliar singers, which they attack and drive away.

The Activation of Specific Genes Fosters the Development of Nuclei That Regulate a Bird's Song

The role of genes in learning has been identified by research using new molecular and cellular techniques that reveal when a specific gene is active in neurons. When a bird is exposed to relevant acoustical stimuli, such as the songs of potential rivals of its own species, certain genes are "turned on" within neurons in the song-controlling nuclei of the bird's brain. For example, when a zebra finch hears the elements of its species' song, a gene called *zenk* becomes active in the brain, producing an enzyme that changes the structure and function of the neurons (see photo on p. 1253). In effect, the ZENK enzyme programs the neurons of the bird's brain to "anticipate" key acoustical events of potential biological importance. When these events occur, they trigger additional changes in the bird's brain that affect its actions. As a result, a territory owner habituates to (that is, learns to ignore) a singing neighbor with which it has already adjusted territorial boundaries; but it retains the ability to detect and repel new intruders of its own species, which represent a real threat to its continued control of its territory.

Study Break

1. What research results suggest that certain neurons in the young male bird's brain are influenced only by acoustical signals from members of its own species and only during a critical period?
2. What happens to cells in the nucleus in the forebrain of a zebra finch after it hears a neighboring bird's song many times?
3. What is the role of the ZENK enzyme in song learning?

54.5 Hormones and Behavior

Research on many animal species has revealed that hormones are the chemical signals triggering the performance of specific behaviors. They often accomplish this function by regulating the development of neurons and neural networks or by stimulating the cells within endocrine glands to release chemical signals.

Hormones Regulate the Development of Cells and Networks That Form the Neural Basis of Behavior

How did the neurons in an adult zebra finch acquire the remarkable capacity to change in response to specific stimuli? In zebra finches, only males produce courtship songs. Very early in a male songbird's life, certain cells in its brain produce the hormone estrogen, which affects target neurons in an area of the developing brain called the *higher vocal center*. The presence of this hormone leads to a complex series of biochemical changes that result in the production of more neurons in parts of the brain that regulate singing. By contrast, the brains of developing females do not produce estrogen, and in the absence of this hormone, the number of neurons in the higher vocal center of females *declines* over time **(Figure 54.8).** Experiments have shown that when young female zebra finches are given estrogen, they produce more neurons in the higher vocal center; but the treated females do not sing later in life unless they are also treated with androgens (male hormones).

Thus, genetically induced hormone production contributes to song learning and singing behavior in male zebra finches by regulating the numbers and types of neurons in the brain centers that produce those behaviors. The development of these neurons primes them for additional changes in response to specific acoustical experiences during the bird's development. Moreover, specific stimuli, such as the songs of either familiar or unfamiliar males, can alter the genetic activity of the neurons that control the behavior of adult birds.

Changing Hormone Concentrations Alter the Behavior of Animals as They Mature

Just as estrogen influences the development of singing ability in zebra finches, other hormones mediate the development of the nervous system in other species. Indeed, a change in the concentration of a certain hormone is often the physiological trigger that induces important changes in an animal's behavior as it matures.

In honeybees *(Apis mellifera)*, worker bees perform different tasks for the colony's welfare as they grow older: bees that are less than 15 days old tend to care for larvae and maintain the hive, whereas those that are more than 15 days old often make foraging excursions from the hive to collect the nectar and pollen that bees eat **(Figure 54.9)**. These behavioral changes are induced by rising concentrations of juvenile hormone (see Section 40.5), which is released by a gland near the bee's brain. Despite its name, circulating levels of juvenile hormone actually increase as a honeybee gets older.

Juvenile hormone may exert its effect on the bee's behavior by stimulating genes in certain brain cells to produce proteins that affect nervous system function. One such chemical, *octopamine,* stimulates neural transmissions and reinforces memories. It is concentrated in the antennal lobes, a part of the bee's brain that contributes to the analysis of chemical scents in the bee's external environment. Octopamine is found at higher concentrations in the older, foraging bees that have higher levels of juvenile hormone. And when extra juvenile hormone is administered to bees experimentally, their production of octopamine increases. Thus, increased octopamine levels in the antennal lobes may help a foraging bee home in on the odors of flowers where it can collect nectar and pollen.

The honeybee example illustrates how genes and hormones interact in the development of behavior. Genes code for the production of hormones, which change the intracellular environment of assorted target cells. The hormones then directly or indirectly change the genetic activity and enzymatic biochemistry in their targets. If the cells in question are neurons, the changes in their biochemistry translate into changes in the animal's behavior.

Hormone Levels Affect Reproductive Activity in Many Animals

The African cichlid fish *(Haplochromis burtoni)* provides an example of how hormones regulate reproductive behavior. Some adult males maintain nesting ter-

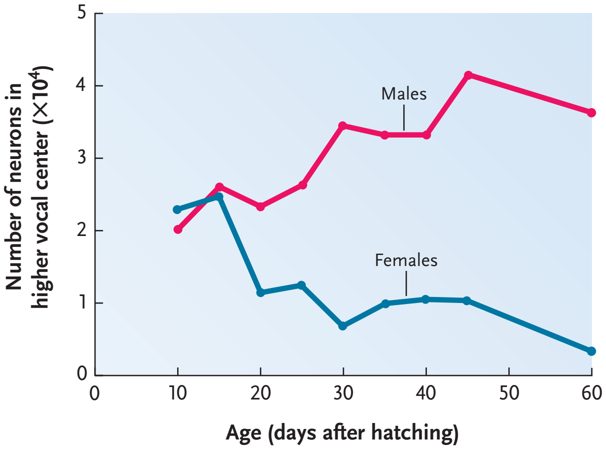


Figure 54.8
Hormonally induced changes in brain structure. The brains of young male zebra finches secrete estrogen, which stimulates the production of additional neurons in the higher vocal center. Lacking this hormone, the brains of young female zebra finches lose neurons in this brain region.

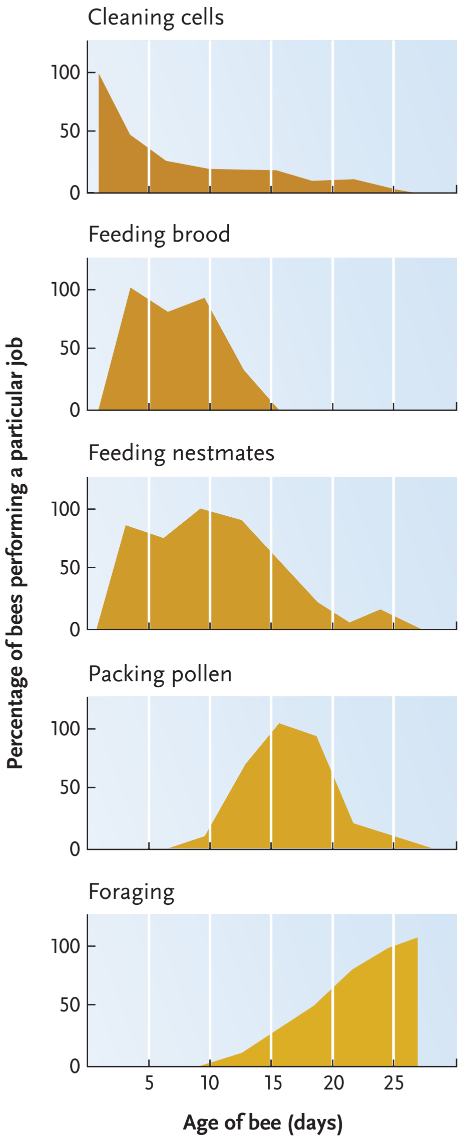
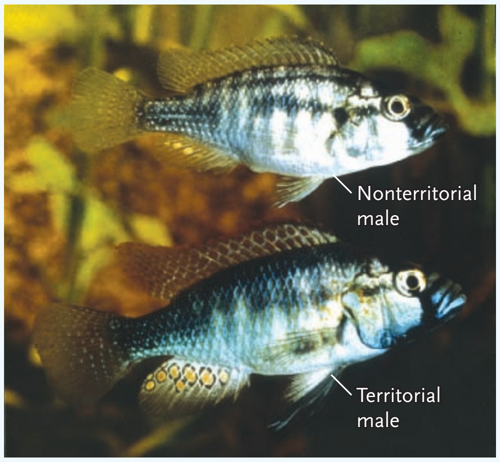


Figure 54.9
Age and task specialization in honeybee *(Apis mellifera)* workers. Young bees typically clean cells and feed the brood; older workers leave the hive to forage for food.

Figure 54.10 Experimental Research

Effects of the Social Environment on Brain Anatomy and Chemistry

a. African cichlid fish *(Haplochromis burtoni)*



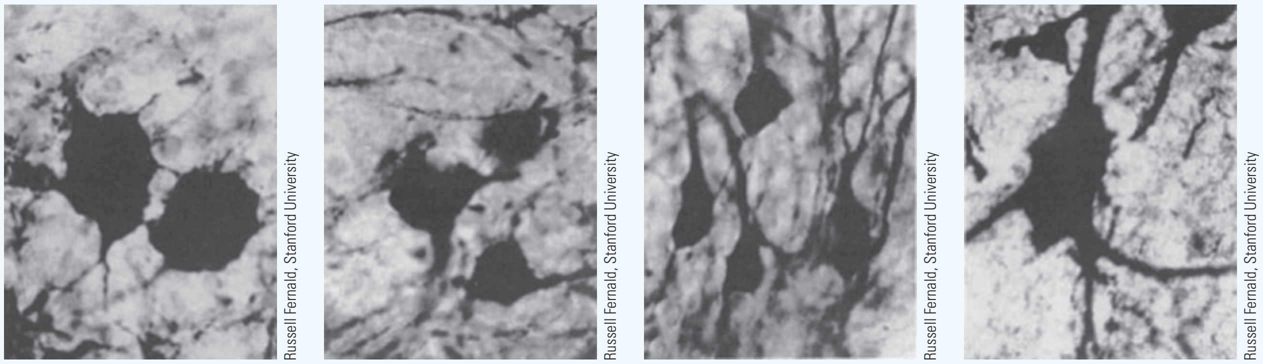
Russell Fernald, Stanford University

QUESTION: How does the acquisition or the loss of a territory affect the brain anatomy and chemistry of an African cichlid fish *(Haplochromis burtoni)?*

EXPERIMENT: Fernald and his students housed groups of male cichlids in aquariums in their laboratory. Males that established and maintained territories in the aquariums were brightly colored, whereas those that could not hold territories were pale and drab. The researchers then moved some small territorial males into tanks where larger males had already established territories. The newly introduced males could not establish and maintain territories under these experimental conditions, and therefore changed status from territorial to nonterritorial. The researchers also moved some large nonterritorial males into tanks with smaller territorial males. Under these experimental conditions, the newly introduced males quickly established and maintained territories, changing their status from nonterritorial to territorial. Other males, left in their original tanks so that their territorial status did not change, served as controls. Four weeks later, the researchers examined the brains of the experimental and control fish and measured the size of the neurons that produce GnRH, a hormone that stimulates bright coloration as well as aggressive behavior and mating behavior in males.

RESULT: The GnRH-producing cells in the brains of experimental males that had lost their territories were much smaller than those in the brains of control males that had maintained their territories. By contrast, the GnRH-producing cells in the brains of experimental males that had gained territories were much larger than those of control males that had never held territories.

b. GnRH-secreting cells



Russell Fernald, Stanford University

Territorial control

Russell Fernald, Stanford University

Territorial to nonterritorial experimentals

Russell Fernald, Stanford University

Nonterritorial control

Russell Fernald, Stanford University

Nonterritorial to territorial experimentals

CONCLUSION: Changes in social status influence the size of brain cells producing hormones that influence the color and behavior of males.

ritories on the bottom of Lake Tanganyika in East Africa. Territory holders are brightly colored, and they exhibit elaborate behavioral displays that attract egg-laden females to their territories. These males defend their real estate aggressively against neighboring territory holders and against incursions by males that have no territories of their own. By contrast, nonterritorial males are much less colorful and aggressive; they do not control a patch of suitable nesting habitat, and they make no effort to court females.

The behavioral differences between the two types of males are caused by differences in their levels of circulating sex hormones. Recall from Section 47.3 that gonadotropin-releasing hormone (GnRH) stimulates the testes to produce testosterone and sperm. When the circulating testosterone is carried to the brain, it modulates the activity of neurons that regulate sexual and aggressive behavior. In territorial fish the GnRH-producing neurons in the hypothalamus are large and biochemically active, but in nonterritorial fish they are small and inactive. In the absence of GnRH, the testes do not produce testosterone; the testosterone-deficient fish do not court females with sexual displays, nor do they usually attack other males.

What causes the differences in the neuronal and hormonal physiology of the two types of male fish? Russell Fernald and his students at Stanford University conducted laboratory experiments in which they manipulated the territorial status of males: some territorial males were changed into nonterritorial males; some nonterritorial males were changed into territorial males; and the territorial status of other males was left unchanged as a control **(Figure 54.10).** Four weeks later, they compared the coloration and behavior as well as the size of the GnRH-producing cells in the brains of the experimental fishes with those of the control males that had retained their original status. Males that had held territories in the past, but had then been defeated by another male, quickly lost their bright colors and stopped being combative. Moreover, their GnRH-producing cells were smaller than those of the successful territory-holding controls. Conversely, males that gained a territory in the experiment quickly developed bright colors and displayed aggressive behaviors towards other males. And the GnRH-producing cells in their brains were larger than those of fishes that had maintained their status as non-territory-holding controls.

The neuronal, hormonal, and behavioral differences between the two experimental groups of males are therefore correlated with a key environmental variable: success or failure in the acquisition and maintenance of a territory. The fish can detect and store information about their aggressive interactions. The neurons that process this information transmit their input to the hypothalamus where it affects the size of the GnRH cells, which in turn dictates the hormonal state of the male. A decrease in GnRH production can turn a feisty territorial male into a subdued drifter, biding his time and building his energy reserves for a future attempt at defeating a weaker male and taking over his territory. If successful in regaining territorial status, the male's GnRH levels will increase again, and the once-peaceful male will revert to vigorous sexual and aggressive behavior.

Note the general similarity of these processes to those described for the white-crowned sparrow's song learning: the fish's brain possesses cells that can change their biochemistry, structure, and function in response to well-defined social stimuli. These physiological changes make it possible for the fish to modify its behavior, depending on its social circumstances. In the next section, we examine how the structure of the nervous system allows animals to respond to important environmental stimuli.

STUDY BREAK

1. What is the effect of estrogen on the development of neurons in the higher vocal center of young zebra finches?
2. How might juvenile hormone production influence a bee's ability to recognize and locate appropriate food sources?
3. How does the loss of its territory change the brain chemistry of an African cichlid fish?

54.6 Nervous System Anatomy and Behavior

Although many behaviors result from gene–environment interactions and changes in hormone concentrations, some specific behaviors are produced by the anatomical structure of an animal's nervous system. Studies on a wide range of animal species demonstrate that the nervous systems of many animals provide rapid responses to key stimuli. In other species, sensory systems are structured to acquire a disproportionately large amount of information about those stimuli that are most important to survival and reproductive success.

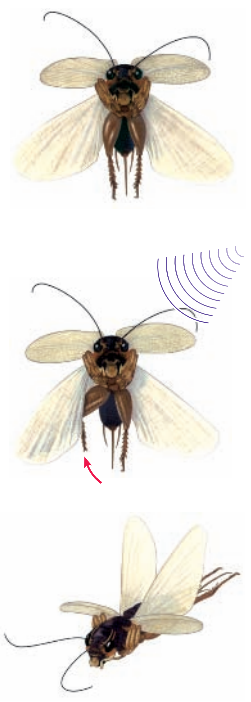
Hard-Wired Connections between Sensory and Motor Systems Provide Rapid Behavioral Responses to Life-Threatening Stimuli

In some animals, important information acquired by the senses is relayed directly to motor neurons. Such a system provides crickets with a potentially lifesaving predator avoidance behavior. Crickets and some other insects fly mainly at night, a behavior that allows them to avoid day-flying predatory birds. But flying crickets aren't safe even at night, because insect-eating bats can detect them in pitch darkness.

Bats detect potential prey by echolocation (see *Why It Matters* at the beginning of Chapter 39). They call almost continuously while flying at night, and the sound waves they produce bounce off items in their path, creating echoes that the bats hear and use to track their prey. Their vocalizations are of such high frequency (up to 100,000 hertz) that they lie outside the upper limit (20,000 hertz) of unaided human hearing. However, a bat's auditory apparatus and brain not only can hear ultrasound, as these high frequency sounds are called, but also can analyze ultrasonic echoes in a way that permits the bat to identify, approach, and capture flying insect prey. With enemies of this sort in its environment, a cricket flying at night is in real danger of being intercepted and eaten.

Crickets are not defenseless, however. Black field crickets *(Teleogryllus oceanicus)*, for example, hear ultrasound through ears in their front legs (see Figure 39.7). The approach of a calling bat causes sensory neurons connected to the ears to fire. However, to be of any use to the cricket, this information must be translated immediately into evasive action—and crickets have the anatomical and physiological equipment to do exactly that.

Imagine that a bat is zeroing in for the kill, rushing toward the left side of a flying cricket. The cricket's left ear will be bombarded with more intense ultrasound than the right ear, and the neurons that receive input from the ears will also be stimulated unequally. The cricket's nervous system is structured to relay



A flying cricket usually holds its hind legs close to the body so that they don't get in the way of its wings.

Sound waves from a predatory bat

When a cricket hears the ultrasonic call of a bat coming from its left side, it automatically lifts its right hind leg.

The raised leg interrupts the right wing's movement, causing the insect to swerve down to the right and away from the approaching predator.

American Scientist 79:316–329 article by M. May 1991

Figure 54.11 A neural mechanism for escape behavior in the black field cricket *(Teleogryllus oceanicus).*

incoming messages from the *left* ear to the motor neurons (muscle-regulating nerve cells) that control the *right* hind leg. Sufficient ultrasonic stimulation on the left side of the body will induce the motor neurons for the right hind leg to fire, causing muscle contractions in that leg. As the right hind leg jerks up, it blocks movement of the right hind wing, reducing the flight power generated on the right side of the cricket's body. The flying cricket then swerves sharply to the right and loses altitude, diving down and away from the approaching bat **(Figure 54.11).** Thus, the anatomical structure of the cricket's nervous system produces a behavioral response that takes the cricket out of harm's way.

If all goes well, the cricket will gain the safety of foliage or leaf litter on the ground before the bat can reach it. Once there, echoes bouncing off the materials all around it will mask any ultrasonic echoes coming from its body. The thwarted bat will be forced to look elsewhere for prey that responds less rapidly.

The Structure of Sensory Systems Allows Animals to Respond Appropriately to Different Stimuli

In some animals, the structure and neural connections of sensory systems allow them to distinguish potentially life-threatening stimuli from those that are more mundane. For example, fiddler crabs *(Uca pugilator)* live and feed on mud flats where they build burrows that provide safe refuge from predators, including crab-hunting shorebirds. But to use its burrow wisely, a crab must be able to distinguish between predatory gulls and its fellow fiddler crabs. Otherwise, it would dash for cover whenever anything moved in its field of vision.

Fiddler crabs possess long-stalked eyes that they hold above their carapace perpendicularly to the ground. John Layne, a neurophysiologist at Duke University, wondered whether a crab might distinguish between dangerous predators and fellow crabs by having a divided field of vision. A large predatory gull sailing in for the kill would stimulate receptors on the upper part of the eye, whereas a fellow crab, whose movements would be slightly below the midpoint of the eyes, would stimulate a lower set of visual receptors. If the receptors above and below the retinal equator relayed their signals to different groups of neurons, the crab's nervous system could be "wired" to provide different responses to the different stimuli.

Layne hypothesized that receptors above the midline of the eye activate neurons that control an escape response, so that stimulation from above would reliably trigger a dash for the burrow. By contrast, a moving stimulus at or below eye level, as when one crab approached another, would provide input to the neurons that allow a crab to behave appropriately to a male or female of its species.

Layne tested this hypothesis by placing crabs on an elevated platform in a glass jar. He then presented the same moving stimulus, a black square, to each crab at two heights; sometimes the stimulus circled the jar above the crab's eyes and sometimes below. Stimuli that activated the upper part of the retina did indeed induce escape behavior, but if the stimuli were below the retinal equator, the animal generally ignored the moving objects altogether **(Figure 54.12).** Thus, specific nervous system connections between a fiddler crab's eyes and brain provide appropriate responses to different specific stimuli.

The Amount of Brain Tissue Devoted to Analyzing Sensory Information Varies from One Sensory System to Another

The match between the structure of an animal's nervous system and the real-world challenges it faces extends beyond the ability to avoid predators. For example, the star-nosed mole *(Condylura cristata),* which lives in wet tunnels in North American marshlands, spends almost all of its life in complete darkness. Like nocturnal insect-eating bats, the mole must find food without benefit of visual cues; and, like the bats, it has a receptor-perceptual system that enables it to feed effectively. The star-nosed mole subsists largely on earthworms, and it uses its nose to locate them—but not by smell. Instead, as the mole proceeds down a tunnel, 22 fingerlike tentacles from its nose sweep the area di-

Figure 54.12 Experimental Research

Nervous System Structure and Appropriate Behavioral Responses

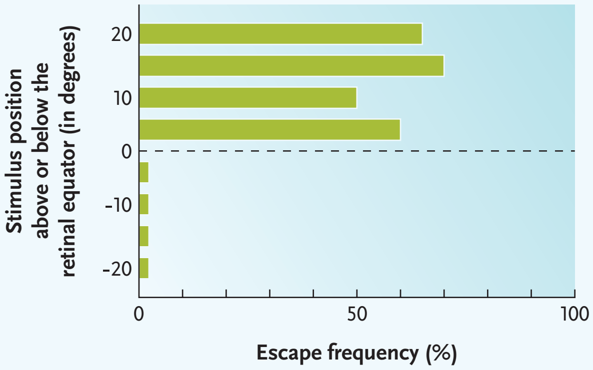
QUESTION: Do fiddler crabs respond differently to stimuli that are presented above the midline of their visual field than they do to stimuli presented below it?

EXPERIMENT: Layne investigated this question by placing crabs on an elevated platform in a glass jar. He then presented the same moving stimulus, a black square, to each crab at varying heights; sometimes the stimulus circled the jar above the crab's eyes and sometimes below.

RESULTS: Stimuli that activated the upper part of the retina did indeed induce escape behavior, but when the stimuli were below the retinal equator, the animal generally ignored the moving objects altogether.

Fiddler crab *(Uca pugilator)*

© Jeff Foott/Dcom/DRK Photo



CONCLUSION: Specific nervous system connections between a fiddler crab's eyes and brain provide appropriate responses to different specific stimuli.

Unanswered Questions

How does an animal choose which behavior to perform?
Animals must perform many types of behaviors in their lifetimes. But what determines which behavior is most appropriate in any particular situation? In some cases, it appears that an animal performs whichever behavior it is most provoked to do at the time. For example, when the Eimer's organs of a star-nosed mole tell it that its tentacles have contacted an earthworm, the mole responds by biting into whatever is in front of its mouth. In other cases, an animal may perform whichever behavior will bring it the most reward. Researchers are studying how animals choose behaviors, using a combination of methods including theoretical modeling, neuroscience, and molecular biology. Male fruit flies often must choose between aggression and courtship, and molecular manipulations that result in the inability of a fly to discriminate between males and females often result in the fly making the wrong choice. Understanding the behavioral choices that animals make will help us understand both the mechanisms and evolution of behavior.

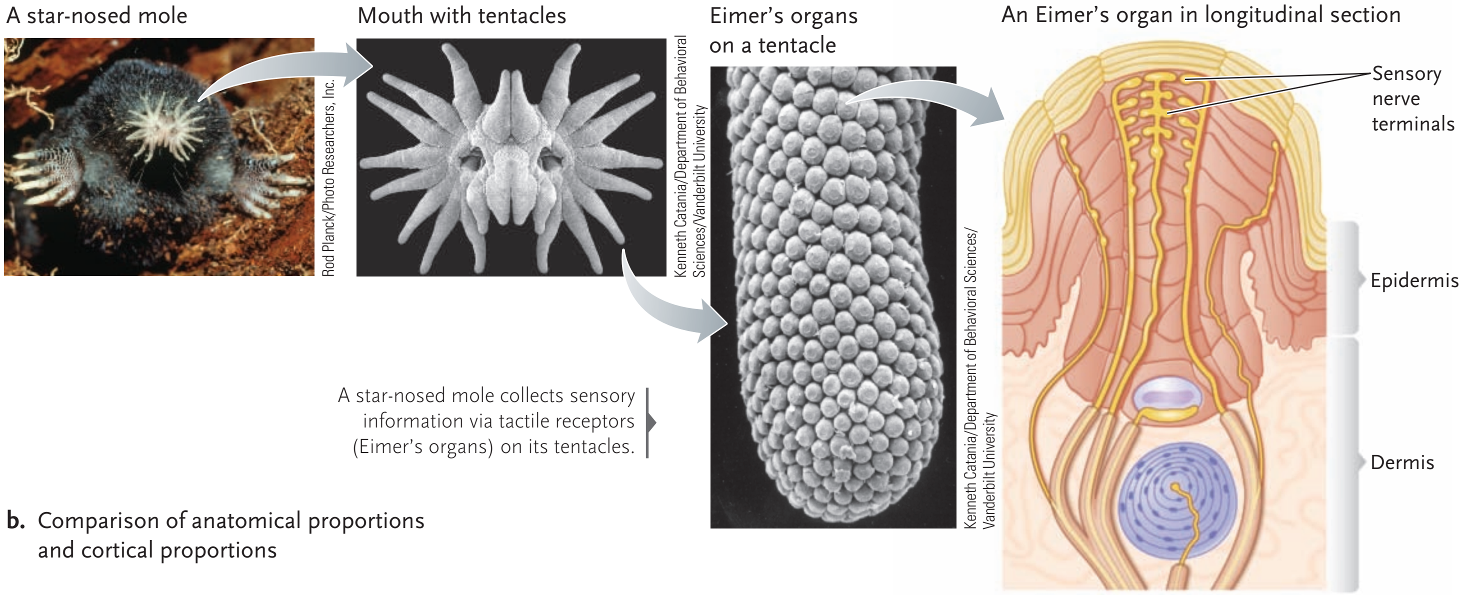
How does experience change the brain to affect behavior?
Some behaviors develop only after an animal has had certain experiences. How does experience translate into a new or improved behavior? Researchers are tracing the paths from stimulus perception, to activation of specific neural circuits and molecular pathways in the brain, to changes in brain structure and chemistry that then lead to behavioral change. This research is helped enormously by the burgeoning field of molecular neuroscience. Knowing how experience translates into a new or improved behavior has broad implications for our understanding of learning and memory, brain plasticity, brain disease, and recovery from stroke.

How do genes influence behavior?
Genetic differences between individuals can translate into behavioral differences between them. But genes encode proteins, and the road between the transcription of a gene and the performance of a specific behavior is a "long and winding" one. Researchers are studying how genetic differences between individuals influence the biochemical pathways that shape the development of the nervous system or later modify its function. Insights into how genes influence behavior have profound implications for our understanding of brain function and perhaps even policy decisions about screening people for genes that may influence their behavior.

John Dixon The Champaign–Urbana News–Gazette

Gene E. Robinson is the G. William Arends Professor of Integrative Biology at the University of Illinois at Urbana-Champaign, where he studies social behavior and genomics using the honeybee. To learn more about his research, go to http://www.life.uiuc.edu/robinson.

a. Sensory organs on the tentacle of a star-nosed mole



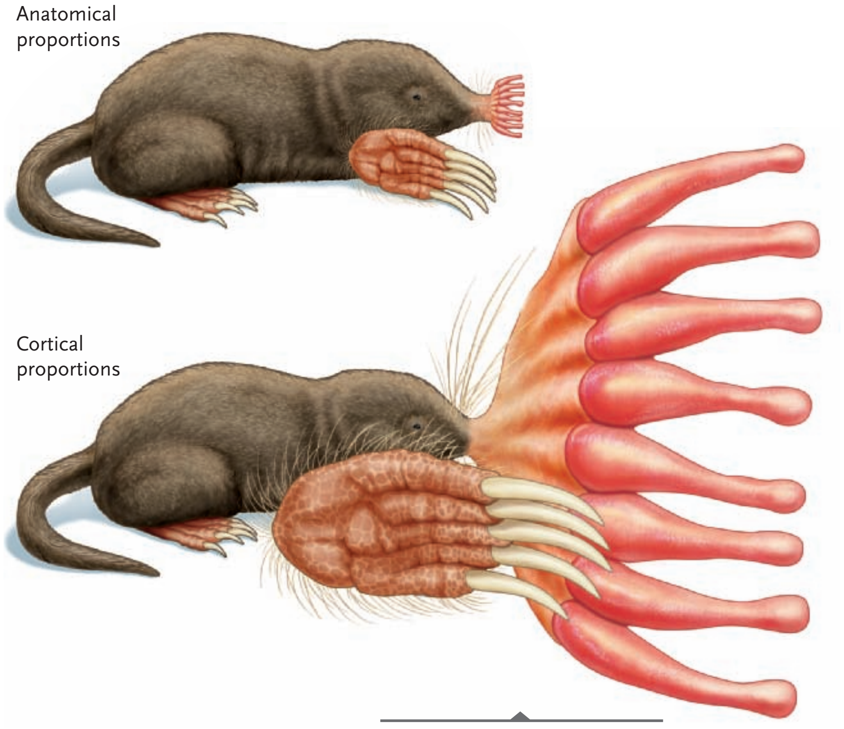
Rod Planck/Photo Researchers, Inc.

Kenneth Catania/Department of Behavioral Sciences/Vanderbilt University

Kenneth Catania/Department of Behavioral Sciences/Vanderbilt University

A star-nosed mole collects sensory information via tactile receptors (Eimer's organs) on its tentacles.

b. Comparison of anatomical proportions and cortical proportions



Most of the mole's cereberal cortex is devoted to the tentacles and front, digging feet.

Figure 54.13
The collection and analysis of sensory information by the star-nosed mole *(Condylura cristata)*. **(a)** The mole's nose has 22 fleshy tentacles covered with cylindrical tactile receptors called Eimer's organs, each containing sensory nerve terminals. **(b)** The star-nosed mole's cerebral cortex devotes far more space and neurons to the analysis of tactile inputs from the tentacles than from elsewhere on the body. These drawings compare the mole's actual body proportions with the relative amount of cortical tissue that processes sensory information from the various parts of the body.

rectly ahead. These tentacles are covered with thousands of tactile (touch) receptors called Eimer's organs **(Figure 54.13a).** Sensory nerve terminals in the Eimer's organs generate complex and detailed patterns of signals about the objects they contact. These messages are relayed by neurons to the cortex of the mole's brain, much of which is devoted to the analysis of information from the nose's tactile receptors.

The structural basis of the mole's sensory analysis is apparent when we consider that the amount of brain tissue responding to signals from the mole's nose contains many more cells than do the tissues that decode tactile signals from all other parts of the animal's body combined **(Figure 54.13b).** Moreover, the brain does not treat inputs from all 22 of the mole's "fingers" equally. Instead, the brain devotes more cells to the tentacles closest to the mole's mouth, and fewer cells to analyzing messages from tentacles that are farther away.

The processing of tactile information in this species is clearly related to the importance of finding food in totally dark underground tunnels. Moreover, the extra attention given to signals from certain tentacles almost certainly helps the mole locate prey that are close to its mouth, allowing it to bite worms before they can move away after being touched.

As these examples illustrate, animal nervous systems do not offer neutral and complete pictures of the environment. Instead, distorted and unbalanced perceptions of the world are advantageous because certain types of information are far more important for survival and reproductive success than others. In the next chapter, we examine the ecological circumstances and selective forces that have promoted the evolution of specific behaviors.

STUDY BREAK

1. How does the anatomy of the cricket's nervous system helps it avoid an approaching bat?
2. What behavioral response is elicited in a fiddler crab when its eyes detect movement above the midline of its visual field?
3. Explain the sensory mechanism that allows a star-nosed mole to locate earthworms in its tunnels.

Review

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54.1 Genetic and Environmental Contributions to Behavior

- Most behaviors have both instinctive and learned components. Some behaviors can be produced only if the animal's nervous system acquires inputs from specific experiences during a critical stage of its development (Figure 54.1).

54.2 Instinctive Behaviors

- Instinctive behaviors are those that an animal performs completely the first time it is presented with a stimulus.
- Fixed action patterns are highly stereotyped behaviors that animals exhibit in response to simple cues called sign stimuli (Figures 54.2–54.4). Fixed action patterns often change through time in response to an animal's experiences.
- Behavioral differences between individuals often reflect underlying genetic differences. Research on garter snakes suggests that certain food preferences are genetically based (Figure 54.5).

Animation: Instinctive behavior in infants

Animation: Adaptive behavior in starlings

Animation: Snake taste preference

Animation: Cuckoo and foster parent

54.3 Learned Behaviors

- Learned behaviors develop only after an animal has had certain experiences in its environment. The different forms of learning include imprinting (Figure 54.6), classical conditioning, operant conditioning, and insight learning. Habituation is a learned loss of responsiveness to specific stimuli.

54.4 The Neurophysiological Control of Behavior

- Animal behavior requires an anatomical, physiological, and biochemical foundation based in the nervous system. An individual's experience alters cells of the nervous system in ways that produce particular patterns of behavior.
- The physiological basis of bird singing behavior resides in specific neuron clusters, called nuclei, that communicate with each other in the bird's brain.
- Bird song and some other behaviors develop only after specific genes are activated within the neurons that produce the behavior.

Video: Development and elicitation of bird song

54.5 Hormones and Behavior

- Hormones can mediate the expression of specific behaviors by activating genes that change the biochemistry, morphology, and number of neurons in specific nuclei. Estrogen stimulates the production of neurons in the higher vocal center of male zebra finches (Figures 54.7 and 54.8).
- Age-related changes in hormone levels can alter the behavior of animals over the course of their lives. Changes in juvenile hormone concentration are correlated with changes in task specialization in honeybees (Figure 54.9).
- Behavioral interactions with other individuals can alter an animal's hormone levels, inducing changes in its behavior. Research on male cichlid fishes suggests that variations in coloration and aggressive behavior associated with territorial status and social interactions are mediated by the production of certain hormones (Figure 54.10).

Animation: Hormonal control of behavior

54.6 Nervous System Anatomy and Behavior

- Sensory information enables animals to make adaptive behavioral responses to their environments. In crickets and some other animals, sensory systems relay information to motor systems, inducing an almost instantaneous response (Figure 54.11).
- Nervous systems can generate prompt and effective responses to those environmental stimuli that may have a large impact on an animal's survival and reproductive success. Fiddler crabs respond differently to movements that occur either above or below the midline of their visual field (Figure 54.12).
- Sensory systems are often structured to provide more information about important environmental factors. A large fraction of a star-nosed mole's brain is devoted to analyzing input from tactile receptors on its nose (Figure 54.13).

Questions

Self-Test Questions

1. Marler concluded that white-crowned sparrows can learn their species' song only:
   a. after receiving hormone treatments.
   b. during a critical period of their development.
   c. under natural conditions.
   d. from their genetic father.
   e. if they are reared in isolation cages.
2. Instinctive behaviors are:
   a. performed completely the first time they are used.
   b. always modified by an animal's experiences.
   c. performed only by very young animals.
   d. often the product of habituation.
   e. sometimes called trial-and-error responses.
3. A stimulus that always causes an animal to behave in a highly stereotyped way is called:
   a. a fixed action pattern.
   b. an instinct.
   c. habituation.
   d. a sign stimulus.
   e. a reinforcement.
4. Arnold's experiments on the feeding preferences of garter snakes demonstrated that food choice is largely governed by a snake's:
   a. early experiences.
   b. genetics.
   c. size and color.
   d. diet while it was developing inside its mother.
   e. trial-and-error learning.
5. Learning in which an animal associates two phenomena that it experiences at approximately the same time is called:
   a. imprinting.
   b. operant conditioning.
   c. classical conditioning.
   d. insight learning.
   e. habituation.
6. The development of the song system in male songbirds depends on:
   a. direct connections between sensory neurons and motor neurons.
   b. a decrease in the number of neurons in the song system.
   c. the behaviors of females, which stimulate hormone production.
   d. the successful defense of a territory.
   e. the production of estrogen early in life.
7. One of the functions of octopamine in foraging honeybees is to:
   a. increase the production of juvenile hormone.
   b. decrease the production of juvenile hormone.
   c. make the bees defend their territory more aggressively.
   d. stimulate neural transmissions and reinforce memories.
   e. increase the time they spend caring for larvae.
8. In cichlid fishes, high levels of the hormone GnRH:
   a. make females more receptive to male attention.
   b. cause males to be sexually aggressive but not territorial.
   c. stimulate a male to defend its territory.
   d. cause males to abandon their territories.
   e. cause males to lose their bright colors.
9. Sensory bias in the nervous system of a cricket ensures that ultrasound perceived on one side of the body will cause:
   a. a movement in a leg on the same side of the body.
   b. a movement in a leg on the opposite side of the body.
   c. the cricket to respond with a vocalization.
   d. the cricket to stop vocalizing.
   e. the cricket to fly toward the sound.
10. In the brain of a star-nosed mole, more cells decode:
    a. tactile information from its feet than from all other parts of its body.
    b. tactile information from the tentacles on its nose than from all other parts of its body.
    c. tactile information from its mouth than from all other parts of its body.
    d. visual information from the top part of its visual field than the bottom part.
    e. visual information from the bottom part of its visual field than the top part.

Questions for Discussion

1. One day, while walking in the country, you see a rooster wade into a pond and begin to court a female mallard duck. What probably happened to the rooster early in life?
2. Using an example from your own experience, explain why habituation to a frequent stimulus might be beneficial. Also describe an example in which habituation might be harmful or even dangerous.
3. Is learning always superior to instinctive behavior? If you think so, why do so many animals react instinctively to certain stimuli? Are there some environmental circumstances in which being able to respond "correctly" the first time would have a big payoff?
4. Cockroaches have two small projections called *cerci* at the tip of the abdomen. You suspect that the cerci might be responsible for the insects' ability to detect predators, such as lizards, rushing toward them from behind. Under the microscope you see that each cercus is covered with fine hairs. What properties should these hairs have if they are part of a system that detects moving air pushed ahead by an approaching predator? How might the roach determine whether the danger was coming from the right or left side? How quickly should cercal information be processed compared with information about the chemicals in a food item?

Experimental Analysis

You find that some fruit flies in your lab are quick to come to a dish containing citrus oils, but others are not as responsive. How could you test whether these behavioral differences are caused by genetic differences among the flies? What should happen if you performed an artificial selection experiment (see Section 19.2) in which you tried to select for quick versus slow responses to citrus oils?

Evolution Link

Some birds that are frequently kept as pets, such as parrots and myna birds, have the uncanny ability to imitate human speech. Develop a hypothesis that explains why the ability to be a good mimic might have evolved in these species. What features of the birds' brains might be involved in this behavior?