

# NATURAL SELECTION

**Type of animal science:** Evolution

**Fields of study:** Ecology, evolutionary science, genetics

*Natural selection is the process of differential survival and reproduction of individuals resulting in long-term changes in the characteristics of species. This process is central to evolution.*

## Principal Terms

**ADAPTATION:** the process of becoming better able to live and reproduce in a given set of environments

**EVOLUTION:** any cumulative change in the characteristics of organisms or populations over many generations

**FITNESS:** the relative ability of individuals to pass on genes to subsequent generations

**HERITABILITY:** the extent to which variation in some trait among individuals in a population is a result of genetic differences

**POPULATION:** a group of individuals that occupy a common area and share a common gene pool

**SPECIES:** the group of all individuals or populations that interbreed or potentially interbreed with one another under natural conditions

tion was first recognized by Charles Darwin, who provided the first widely accepted mechanism for evolutionary change. Natural selection is one of several processes responsible for changing the characteristics of populations and leading to an increase in adaptiveness. Other processes include genetic drift and migration. These processes interact with the processes responsible for producing variation (mutation and development) and those responsible for determining the rate and direction of evolution (mating system, population size, and long-term ecological changes) to establish the path of evolution of a species.

## The Process of Natural Selection

Natural selection occurs through the interaction of three factors: variation among individuals in a population in some trait, fitness differences among individuals as a result of that trait, and heritable variation in that trait. If those three conditions are met, then the characteristics of the population with respect to that trait will change from one generation to the next until equilibrium with other processes is reached. An example that demonstrates this process involves the peppered moth. It has two forms in the United Kingdom, a light-colored form and a dark-colored form; there is variation in color among individuals. Genetic analysis has shown that this difference in color is caused by a single gene; the variation has a heritable basis. The moth is eaten by birds that find their food by sight. The light-colored form cannot be seen when sitting on lichen-covered trees, while the dark-colored form can be seen easily. Air pollution kills the lichen, however, and turns the trees

**N**atural selection is a three part process. First, there must exist differences among individuals in some trait. Second, the trait differences must lead to differences in survival and reproduction. Third, the trait differences must have a genetic basis. Natural selection results in long-term changes in the characteristics of the population.

As one of the central processes responsible for evolution, natural selection results in both fine-tuning adaptations of populations and species to their environments and creating differences among species. The importance of natural selec-

dark in color. Then, the dark-colored form is hidden and the light-colored form visible. Thus, differences in color lead to fitness differences. In the early nineteenth century, the dark-colored form was very rare. In the last half of the nineteenth century, however, air pollution increased, and the dark-colored form became much more frequent as a result of natural selection.

The characteristics of a population can be changed by natural selection in several ways. If individuals in a population with an extreme value for a trait have the greatest fitness on average, then the mean value of the trait will change in a consistent direction, which is called directional selection. For example, the soil in the vicinity of mines contains heavy metals that are toxic to plants. Individuals with the greatest resistance to heavy metals have the highest survivorship. Evolution leads to an increase in resistance. If individuals in a population with intermediate values for a trait have the greatest fitness on average, then the variation in the trait will be reduced, which is called stabilizing selection. For example, in many species of birds, individuals with intermediate numbers of offspring have the greatest fitness. If an individual has a small number of offspring, that parent has reduced reproduction and a low fitness. If the number of offspring is large, the parent will not be able to provide enough food for all the young, and most, or all, will starve, again resulting in reduced reproduction and a low fitness. Evolution leads to all birds producing the same, intermediate number of offspring. If individuals in a population with different values for a trait have the greatest fitnesses on average and intermediates have low fitness, then the variation in the trait will be increased. This is called disruptive selection. For example, for Darwin's finches, individuals with long, thin bills are able to probe into rotting cactus to find insects. Individuals with short, thick bills are able to crack hard seeds. Individuals with intermediate-shaped bills are not able to do either well and have reduced fitness relative to the more extreme types. Evolution leads to two different species of finch with different bills.

### A Slow and Holistic Process

Natural selection is a slow process. The rate of evolution—that is, response to selection—is determined by the magnitude of fitness differences among individuals and the heritability of traits. Fitness differences tend to be small so that more fit individuals on average may have only a few more offspring than less fit individuals. Heritabilities of most traits are low to intermediate, meaning that most differences among individuals are not a result of genetic differences. So, even if one individual has many offspring and another has few offspring, they may not differ genetically and no change will occur. For example, if all the beetles in a population were between one and two centimeters in length and there was selection for larger beetles, it could take five hundred generations before all beetles were larger than two centimeters. Also, the direction of selection may change from one generation to the next, so that no net change occurs.

Natural selection does not act on traits in isolation. How a trait affects fitness in combination with other traits, called correlational selection, is important. For example, fruit flies lay their eggs in rotting fruit. Considered in isolation, a female should always lay as many eggs as possible. One fruit is not big enough for all the eggs she might lay, however, so she must fly from fruit to fruit. Flying requires energy, and the more energy that is used in flight the less that can be used to make eggs. So natural selection results in the division of energy between eggs and flight that yields the greatest overall number of offspring. This example demonstrates that the result of natural selection is often a trade-off among different traits.

By acting differently on males and females, natural selection results in sexual selection. This form of selection can explain differences in the forms of males and females of a species. In general, because male gametes, sperm, are much smaller and “cheaper” to produce than female gametes, eggs, more sperm than eggs are produced. As a result, it is possible for one male to fertilize many eggs, while other males fertilize few or no eggs. For example, a lion pride usually consists of

## Charles Darwin

**Born:** February 12, 1809; Shrewsbury, England

**Died:** April 19, 1882; Downe, England

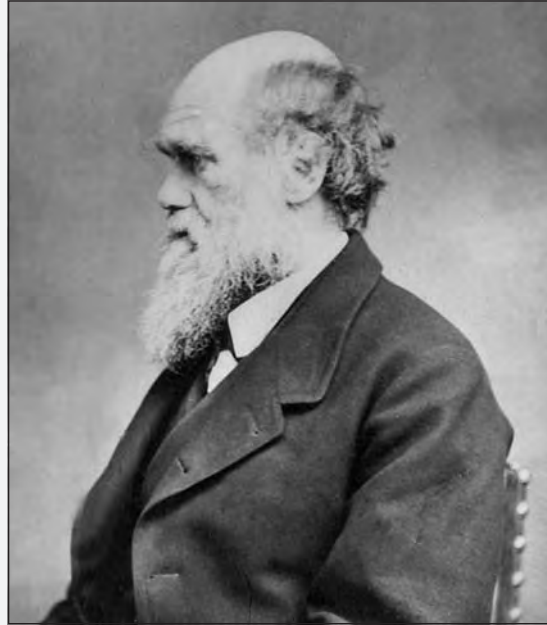
**Fields of study:** Entomology, evolutionary science, human origins, invertebrate biology

**Contribution:** Darwin was not the first philosopher or scientist to posit a theory of evolution, but his theories of natural and sexual selection provided much of the foundation for later scientific evolutionary theory.

Charles Robert Darwin had briefly studied medicine at the University of Edinburgh and attended Cambridge University, intending to prepare for the ministry, when he was offered a chance to sail on the HMS *Beagle* as a naturalist and companion to Captain Robert FitzRoy. The fifty-seven month voyage, from December 7, 1831, to October 2, 1836, allowed Darwin unique opportunities to explore fossils, fish and sea mammals, and coral reefs. Lengthy land excursions allowed him to examine land animals and fossils, primarily in South America.

Returning to England, he first published his findings as *Journal and Remarks*, volume 3 in the series *Narrative of the Surveying Voyages of H.M.S. "Adventure" and "Beagle" Between 1826 and 1836* (1839). This work was revised and published the same year as *Journal of Researches into the Geology and Natural History of the Various Counties Visited by H.M.S. "Beagle"* (1839). His findings caused him to question generally accepted assumptions about animal creation and to posit evolutionary change as occurring mainly through natural selection. In later works, he increasingly stressed the importance of sexual selection. Challenged by peers to examine individual species before generalizing about life as a whole, he began lengthy examinations of such life-forms as beetles and barnacles, which he published.

By the 1850's, despite his aversion to public controversy, he accepted the need to publish his general theories. They appeared in 1859 as *On the Origin of Species by Means of Natural Selection: Or, The Preservation of Favoured Races in the Struggle for Life*. Although he avoided discussion of human origin in this work, the controversy he dreaded was forthcoming. His ideas, however, were adopted by young scientists, most notably Thomas Henry Huxley, who sought to establish the natural sciences as disciplines separate



*Charles Darwin's theory of evolution through natural selection revolutionized not only the scientific view of the world but popular understanding as well. (National Archives)*

from the natural theology that then prevailed in universities. These scientists became his spokespersons, as he continued his experiments at his estate; his theories gained widespread acceptance. In 1871, he dealt directly with the origin of human life in *The Descent of Man*; he followed this, in 1872, with *The Expression of Emotions in Man and Animals*. These works clearly placed man within the animal kingdom, not the product of a separate creation.

Darwin also published on narrower topics involving animal life and fossils, and extensively revised *On the Origin of Species*, ultimately producing six revised editions in the quarter-century after its initial publication. He wrote a brief autobiography, published posthumously in 1887. He was awarded numerous honors in England and on the Continent. At his death, his work was so widely respected that, despite his religious skepticism, England honored him with burial in Westminster Abbey.

—Betty Richardson

one or a few males and many females. Other males are excluded, and they live separately; larger males are able to chase away smaller males. The thick mane on male lions helps to protect their throats when they fight other males. Thus, larger males with thicker manes father more cubs than other males, leading to selection on these traits. Only males are under natural selection since all females, regardless of size, will mate. The result is that males are larger than females and have manes.

### Group Selection

Natural selection can occur not only among individuals but also among groups. This process is generally known as group selection; when the groups are composed of related individuals, it is called kin selection. Group selection operates the same way as individual selection. The same three conditions are necessary: variation among groups in some trait, fitness differences among groups because of that trait, and a heritable basis for that trait. For example, in Australia, rabbits introduced from Europe in 1859 spread rapidly during the next sixty years. In order to control the rabbits, a virus was introduced in 1950. At first, the virus was very virulent, killing almost all infected animals within a few days. After ten years, however, the virus had evolved to become more benign, with infected rabbits living longer or not becoming sick at all. Virulent strains of the virus grow and reproduce faster than benign strains. So, within a single rabbit, virulent strains have a higher fitness than benign strains. The longer a rabbit lives, however, the more opportunity there is for the virus to be passed to other rabbits. Thus, a group of benign viruses infecting a rabbit are more likely to be passed on than a group of virulent viruses. In this example, group selection among rabbits resulted in evolution opposite to individual selection within rabbits; however, group selection and individual selection can result in evolution in the same direction. In general, natural selection can act at many levels: the gene, the chromosome, the individual, a group of individuals, the population, or the species.

Natural selection is the primary process leading to adaptation of individuals. It involves many traits acting together, differences among males and females, and differences among levels. The interaction of all these processes of natural selection determines the path of evolution.

### Measuring Natural Selection

Natural selection is investigated in two ways: by use of indirect measurements and direct measurements. The indirect methods involve observing the outcome of natural selection and inferring its presence. The direct methods involve measuring the three parts of the process and following the course of evolution. Although the direct methods are preferred, as they provide direct proof of natural selection, in most instances, only indirect methods can be used.

Indirect methods involve three kinds of observations. First, comparisons are made of trait similarities or differences among populations or species living in the same or different areas. For example, many species of animals living in colder climates have larger bodies than those living in warmer climates. It is inferred, therefore, that colder climates result in natural selection for larger bodies. Second, long-term studies are done of traits, in particular changes in a group in the fossil record. For example, during the evolution of horses, their food, grasses, became tougher and horses' teeth became thicker. It is inferred, therefore, that tough grass resulted in natural selection for thicker teeth. Third, comparisons are made of gene frequencies of natural populations, with predictions from mathematical models. Gene frequencies are measured using various techniques, including scoring differences in appearance, as with light-colored and dark-colored moths; using electrophoresis to observe differences in proteins; and determining the sequence of base pairs of deoxyribonucleic acid (DNA). The models make predictions about expected frequencies in the presence or absence of selection. Indirect methods are best at revealing long-term responses to evolution and general processes of natural selection that affect many species. The indirect methods

suffer from the problem that often many processes will result in similar patterns. So, it must be assumed that other processes were not operating, or other predictions must be made to separate the processes.

Direct methods involve two kinds of observation. First, there is observation of changes in a population following some change in the environment. There are many types of environmental changes, including man-made changes, natural disasters, seasonal changes, and introductions of species into new environments. For example, from the changes in the peppered moth following a change in pollution levels, one can measure the effects of natural selection. The second type of observation is the direct measurement of fitness differences among individuals with trait differences. For example, individual animals are tagged at an early age and survival and reproduction are monitored. Then, statistical techniques are used to find a relationship between fitness and variation among individuals in some trait. Alternatively, comparisons of traits are made between groups of individuals, such as breeding and nonbreeding, adults and juveniles, or live and dead individuals, again using statistical techniques. For example, lions that breed are larger than lions that do not breed. Direct methods are best at revealing the relative importance to natural selection of the three factors (variation, fitness differences, and heritability). The direct methods suffer from two limitations. It takes a long time for evolution to occur. So, although one can measure natural selection, it is often not known if it results in evolution. Also, for many species, it is impossible or impractical to mark individuals and follow them through their lives.

Many methods can be used to study natural selection and evolution. Each method provides information about different parts of the process. Only through the integration of these methods can the entire process of evolution be revealed.

### **Adaptation and Evolution**

Natural selection is the central process in adaptation and evolution. By understanding how the

process operates and where its limits lie, scientists hope to determine why evolution has proceeded in the fashion that it has. Historically, it was only after Darwin presented his theory of natural selection that the idea of evolution became widely accepted in the nineteenth century. In the twentieth century, much of the work of evolutionary biologists during the 1930's, 1940's, and 1950's was to integrate the fields of genetics, ecology, paleontology, and systematics, using natural selection and evolution as the unifying concepts.

Knowledge of natural selection is still growing; many questions proposed by Darwin and others are yet to be answered. It is still not known to what extent organisms are well adapted to their environments or whether the evolution of the parts of the chromosome that are not translated into proteins are a result of processes that do not involve natural selection. Of the many theories of how natural selection works, it is still unknown which ones are the most important in nature and to what extent evolution is caused by natural selection at the level of the individual, the group, and the species.

Genetic engineering requires knowledge of natural selection. The addition of a new gene into an organism will result in natural selection on that gene and change selection on other genes. Efficiency will be gained if successful and unsuccessful outcomes can be predicted beforehand. If genetically engineered organisms are to be released into nature, scientists need to be able to forecast their fates, such as whether the organism will remain benign or will become a pest. Genes added to one organism could possibly spread to other, native species. The solutions to these dilemmas involve predictions of the outcome of natural selection.

An understanding of natural selection is critical for conservation biology. During the twentieth century, the rate at which natural areas are being destroyed and species are becoming extinct has accelerated tremendously. Conservation biology attempts to stop that destruction and preserve species diversity. For extinction of endangered species to be halted, it must be understood how

## Alfred Russel Wallace

**Born:** January 8, 1823; Usk, Monmouthshire, Wales

**Died:** November 7, 1913; Broadstone, Dorset, England

**Fields of study:** Entomology, evolutionary science, population biology, zoology

**Contribution:** Wallace, a pioneer of the science of zoogeography, proposed a theory of evolution by natural selection in 1855 that predated and stimulated the publication of Charles Darwin's *On the Origin of Species* (1859).

Alfred Russel Wallace grew up in rural Wales and then in Hertford, England. His formal education was limited to six years at the Hertford Grammar School. From 1837 to 1844 Wallace worked in his brother William's surveying business. In 1844, Wallace taught at the Collegiate School in Leicester, England.

In 1848, Wallace and the entomologist Henry Walter Bates embarked on an expedition to Brazil. Wallace and Bates planned to collect and identify biological specimens and then pay for their trip by selling their collections. Wallace spent a total of four

years exploring the Amazon River basin, collecting birds, butterflies and other insects.

Unfortunately, on the return voyage Wallace lost his precious collections when his ship caught fire and sank. Nevertheless, the expedition led to the publication of several articles and two books (*Palm Trees of the Amazon and Their Uses* and *Narrative of Travels on the Amazon and Rio Negro*, 1853). These reports attracted the attention of the Royal Geographical Society, which helped to fund his next expedition. For eight years (1854-1862) Wallace continued his research in the Malay Archipelago (Indonesia). Wallace's research on the geographic distribution of animals among the islands of the Malay Archipelago provided crucial evidence for his evolutionary theories and led him to devise what became known as Wallace's Line, the boundary that separates the fauna of Australia from that of Asia. By the time Wallace returned to England in 1862 he had collected over 125,000 animal specimens.

During an attack of a tropical fever, Wallace experienced a flash of insight in which he realized that natural selection could serve as the mechanism of evolution. Within a few days he completed his essay "On the Tendency of Varieties to Depart Indefinitely from the Original Type" and sent it to Charles Darwin for review and possible publication. Darwin was shocked to find that Wallace had developed a theory of evolution identical to that outlined in his own unpublished 1842 essay. Darwin's friends Charles Lyell and Joseph Hooker arranged for a joint presentation of the papers written by Wallace and Darwin and simultaneous publication in the August, 1858, *Proceedings of the Linnean Society*.

Graciously allowing Darwin to claim priority for the discovery of evolution by means of natural selection, Wallace continued to publish works on natural history and travel, including *The Malay Archipelago* (1869), *Contributions to the Theory of Natural Selection* (1870), *Geographical Distribution of Animals* (1876), and *Island Life* (1880). It was Wallace who called evolution by means of natural selection "Darwinism" in order to distinguish this theory from its predecessors. Unlike Darwin, however, Wallace continued to believe that natural selection could not account for the higher faculties of human beings.

—Lois N. Magner



Alfred Russel Wallace independently proposed a theory of evolution very similar to that of Darwin. (National Library of Medicine)

natural selection will affect these species given massive environmental changes. By discovering how evolution is occurring under natural conditions, researchers will learn how to design nature preserves to maintain species.

—*Samuel M. Scheiner*

**See also:** Adaptations and their mechanisms; Clines, hybrid zones, and introgression; Development: Evolutionary perspective; Ecological niches;

Evolution: Animal life; Evolution: Historical perspective; Extinctions and evolutionary explosions; Gene flow; Genetics; Human evolution analysis; Nonrandom mating, genetic drift, and mutation; Population analysis; Population fluctuations; Population genetics; Population growth; Punctuated equilibrium and continuous evolution; Sex differences: Evolutionary origin.

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# NERVOUS SYSTEMS OF VERTEBRATES

**Type of animal science:** Anatomy

**Fields of study:** Developmental biology, evolutionary science, neurobiology, physiology

*The anatomy of vertebrate nervous systems determines many of the behaviors and adaptive capabilities of animals. Its study is a prerequisite to understanding how it functions.*

## Principal Terms

**AXON:** an extension of a neuron's cell membrane that conducts nerve impulses from the neuron to the point or points of axon termination

**GRAY MATTER:** the part of the central nervous system primarily containing neuron cell bodies and unmyelinated axons

**INTERNEURON:** a central nervous system neuron that does not extend into the peripheral nervous system and is interposed between other neurons

**MYELINATED AXON:** an axon surrounded by a glistening sheath formed when a supporting cell has grown around the axon

**NEURAL INTEGRATION:** continuous summation of the incoming signals acting on a neuron

**NEURONS:** complete nerve cells that respond to specific internal or external environmental stimuli, integrate incoming signals, and sometimes send signals to other cells

**NUCLEUS (pl. NUCLEI):** cluster of neuron cell bodies within the central nervous system

**TRACT:** a cordlike bundle of parallel axons within the central nervous system

**WHITE MATTER:** the part of the central nervous system primarily containing myelinated axon tracts

internal environment, despite fluctuations in the external environment, in order to survive and reproduce. To do so, animals must monitor their external and internal environments, integrate this sensory information, and then generate appropriate responses. The evolution of the vertebrate nervous system has provided for the efficient performance of these tasks.

## The Pattern of the Vertebrate Nervous System

Although the various vertebrates show differences in the organization of their respective nervous systems, they all follow a similar anatomical pattern. The nervous system can be partitioned conveniently into two major divisions: the peripheral nervous system (PNS) and the central nervous system (CNS). These divisions are determined by their location and function. The CNS consists of the spinal cord and the brain. The PNS, that part of the nervous system outside the CNS, connects the CNS with the various sense organs, glands, and muscles of the body.

The PNS joins the CNS in the form of nerves, which are cordlike bundles of hundreds to thousands of individual, parallel nerve-cell (neuron) axons (long tubular extensions of the neurons) extending from the brain and spinal cord. The nerves extending from the spine are called spinal nerves, while those from the brain are called cranial nerves. The elements of the PNS include sensory neurons (for example, those in the eyes and in the tongue) and motor neurons (which activate muscles and glands, thereby causing some sort of action or change to occur). Most nerves contain both sensory and motor axons.

**A**nimals must be able to coordinate their behaviors and to maintain a relatively constant

Thus, the PNS can be divided into two major subdivisions: sensory (or afferent) neurons and motor (or efferent) neurons. There is very little information-processing accomplished in the PNS. Instead, it relays both environmental information to the CNS (sensory function) and the CNS responses to the body's muscles and glands (motor function). Sensory neurons of the PNS are classified as somatic afferents if they carry signals from the skin, skeletal muscles, or joints of the body. Sensory neurons from the visceral organs (internal organs of the body) are called visceral afferents.

The PNS motor subdivision also has two parts. One is the somatic efferent nervous system, which carries neuron impulses from the CNS to skeletal muscles. The other is the autonomic nervous system (ANS), which carries signals from the CNS to regulate the body's internal environment by controlling the smooth muscles, the glands, and the heart. The ANS itself is subdivided into the sympathetic and parasympathetic nervous systems. These are generally both connected to any given target and cause approximately opposite effects to each other on that target (for example, slowing or increasing the heart rate).

The CNS, where essentially all information-processing occurs, has two major subdivisions: the spinal cord and the brain. Virtually all vertebrates have similarly organized spinal cords, with two distinct regions of nervous tissue: gray and white matter. Gray matter is centrally located and consists of neuron cell bodies and unmyelinated axons (bare axons without the glistening sheaths called myelin, created by supporting cells wrapping around the axons). White matter contains mostly bundles of myelinated axons (white because they have glistening myelin sheaths around them). Bundles of axons in the CNS are called nerve tracts. Within the spinal cord, these are either sensory tracts carrying impulses toward the brain, or they are motor tracts transmitting information in the opposite direction.

Interneurons are neurons positioned between two or more other neurons. They accept and integrate signals from some of the cells and then influ-

ence the others in turn. Interneurons are particularly numerous within the gray matter. In the spinal cord, they permit communication up, down, and laterally. Most axons in the cord's tracts belong to interneurons.

### **The Vertebrate Brain**

The brain of vertebrates is actually a continuation of the spinal cord, which undergoes regional expansions during embryonic development. The subdivisions of the brain show more variety among vertebrate species than does the spinal cord. The brain has three regions: the hindbrain, the midbrain, and the forebrain. Their structures are complex, and various systems of subdividing them exist. The major components forming the brain regions are the hindbrain's medulla oblongata, pons, and cerebellum; the midbrain's inferior and superior colliculi, tegmentum, and substantia nigra; and the forebrain's hypothalamus, thalamus, limbic system, basal ganglia, and cerebral cortex.

The hindbrain begins as a continuation of the spinal cord called the medulla oblongata. Most sensory fiber tracts of the spinal cord continue into the medulla, but it also contains clusters of neurons called nuclei. The posterior cranial nerves extend from the medulla, with most of their nuclei located there.

Also in the medulla, and extending beyond it through the pons and midbrain, is the complexly organized reticular formation. This mixture of gray and white matter is found in the central part of the brain stem but has indistinct boundaries. Essentially all sensory systems and parts of the body send impulses into the reticular formation. There are also various nuclei within its structure. Impulses from the reticular formation go to widely distributed areas of the CNS. This activity is important for maintaining a conscious state and for regulating muscle tone.

Prominent on the anterior (front) surface of the mammalian medulla oblongata are the pyramids: tracts of motor fibers originating in the forebrain and passing without interruption into the spinal cord to control muscle contraction. These tracts

cross to the opposite side of the medulla before entering the spinal cord, which results in each side of the forebrain controlling muscle contraction in the opposite side of the body.

Many sensory fibers from the spinal cord terminate in two paired nuclei at the lower end of the medulla, the gracile and cuneate nuclei. Axons leaving these nuclei cross to the opposite side of the medulla and then continue as large tracts (the medial lemnisci) into the forebrain. Thus, each side of the brain gets sensory stimuli mostly from the opposite side of the body.

Immediately above the medulla is the pons. It contains major fiber pathways carrying signals through the brain stem, and a number of nuclei, including several for cranial nerves. Some pontine nuclei get impulses from the forebrain and send axons into the cerebellum, again with a majority crossing to the opposite side of the brain stem before entering the cerebellum.

On the dorsal (back) side of the medulla and pons is the cerebellum, an ancient part of the brain that varies in size among vertebrate species. The cerebellum forms a very important part of the control system for body movements, but it is not the source of motor signals. Its gray matter forms a thin layer near its surface called the cerebellar cortex and surrounds central white matter.

Vertebrates with well-developed muscular systems (for example, birds and mammals) have a large cerebellum, with several lobes and convex folding of its cortex. It is attached to the brain stem by three pairs of fiber tracts called cerebellar penduncles, which transmit signals between the left and right sides of the cerebellum and between the cerebellum and motor areas of the spinal cord, brain stem, midbrain, and forebrain. The cerebellum times the order of muscle contractions to coordinate rapid body movements.

### **The Midbrain and the Forebrain**

The midbrain is the second major region of the brain. The midbrain's dorsal aspect, called the tectum, is a target for some of the auditory and visual information that an animal receives. The paired inferior colliculi form the lower half of the tectum.

They help to coordinate auditory reflexes to relay acoustic signals to the cerebrum. The two superior colliculi, the other half of the tectum, assist the localization in space of visual stimuli by causing appropriate eye and trunk movements. In lower vertebrates, the superior colliculi actually form the major brain target for visual signals. Connecting fiber pathways (commissures) link the individual lobes of each pair of colliculi.

The midbrain's tegmentum contains several fiber tracts carrying sensory information to the forebrain and carrying impulses among various brain-stem nuclei and the forebrain. Two cranial nerve nuclei concerned with the control of eye movements are also in the tegmentum. The reticular formation extends through the tegmentum and regulates the level of arousal. It also helps to control various stereotyped body movements, especially those involving the trunk and neck muscles. Finally, the tegmentum contains the red nucleus, which, in conjunction with the cerebellum and basal ganglia, serves to coordinate body movements. The substantia nigra functions as part of the basal ganglia to permit subconscious muscle control.

The forebrain, the final major area of the brain, differs from the lower areas in the more highly evolved functions it controls. It has a small but extremely important collection of about a dozen pairs of nuclei called the hypothalamus. These control many of the body's internal functions (such as temperature, blood pressure, water balance, and appetite) and drives (such as sexual behavior and emotions). Immediately above the hypothalamus lies the thalamus, another collection of more than thirty paired nuclei. The two thalami are the largest anterior brain-stem structures. Their ventral (front) parts relay motor signals to lower parts of the brain. The dorsal (back) parts transmit impulses from every sensory system (except olfaction, the sense of smell) to the cerebrum.

The limbic system is organized from a number of forebrain structures mostly surrounding the hypothalamus and thalamus. It determines arousal levels, emotional and sexual behavior, feeding behavior, memory formation, learning, and moti-

vation. In general, the limbic system exchanges information with the hypothalamus and thalamus, and receives impulses from auditory, visual, and olfactory areas of the brain.

The basal ganglia function with the midbrain's tegmentum and substantia nigra, the cerebral cortex, the thalamus, and the cerebellum. These paired structures' functions are unclear, but it is known that they are important for adjusting the body's background motor activities, such as gross positioning of the trunk and limbs, before the cerebral cortex superimposes the precise final movements.

The cerebral cortex, like the cerebellum, is an ancient brain structure; however, it shows even more variation among vertebrate species than the cerebellum. It is formed into two hemispheres, which have olfactory bulbs projecting from their anterior (front) ends. The olfactory bulbs receive impulses from olfactory nerves for the sense of smell. The gray matter of the cerebral cortex is at the surface, enclosing the white matter (fiber tracts) beneath. The white matter connects various parts of the gray matter of one hemisphere with others within the same hemisphere and with corresponding parts in the opposite hemisphere. It also connects the cortical gray matter with lower brain structures. The ultimate control of voluntary motor activity resides in the motor areas of the cortex, although this control is heavily influenced by all the previously mentioned motor-control areas of the CNS.

Corresponding to each of the major senses (touch, vision, audition), there are primary sensory areas. These areas get the most direct input from their sensory organs by way of the corresponding sensory thalamic nuclei. Surrounding each primary area are association areas that receive a less direct sensory input but also more inputs from other sensory cortical areas. In general, the more intelligent an animal is, the larger are its association areas.

### **Studying the Nervous System**

Many methods are used in studying vertebrate nervous systems. The level of description desired

often determines the methods employed. For example, the gross structure visible to the unaided eye is usually investigated using the entire brain or spinal cord of the animal under study. It will then be photographed or drawn, sliced at various points either parallel to its long axis or across its long axis, and again photographed or drawn, until a complete series of such "sections" has been assembled.

To see finer structural details requires microscopes and very thin slices of nervous tissue (less than a millimeter in thickness). Preparation of such thin slices of this soft tissue requires that it first be either frozen or embedded in a block of paraffin wax. A special slicing device called a microtome is then used to produce the thin sections. For easy observation of different structural details (such as nuclei and fiber tracts), various chemical stains can be applied to the slices of tissue. These stains specifically color particular structural features green, blue, or some other color, thereby making them more visible.

Nervous tissue can be selectively and painlessly destroyed in an anesthetized animal by cutting a nerve trunk, inserting a fine wire electrode into the CNS and destroying tissue with electricity, or inserting a fine needle and then either injecting a chemical agent that kills nervous tissue or using a suction device to remove areas of tissue. The precision and reproducibility of wire or needle placement within the CNS is possible with a device called a stereotaxic frame. This instrument positions the animal's head and brain in an exact standard position. Then, wires or needles are inserted a certain distance away from (for example, behind, below, or to one side of) common landmarks on the skull. Stereotaxic atlases are books published by investigators for specific animals, with the exact coordinates in three-dimensional space for most CNS structures.

Following such procedures, the animal may be immediately and painlessly sacrificed, its brain or spinal cord removed, and the previously described thin slices prepared and stained. It may be necessary to allow the animal to recover from its surgical treatment, since several days or weeks

must sometimes pass for the severed fiber tracts to degenerate. Then, following a painless lethal injection, the nervous tissue is prepared as above using special staining techniques, which reveal the pathways of degenerating nerve fibers in the tissue sections studied later under the microscope.

Although new techniques are constantly being developed, the preceding methods have revealed that the hundred billion neurons of the vertebrate nervous system form the most complexly organized structure known. Through this knowledge of the structure of the nervous system, it has become possible to study intelligently its functions, to diagnose its diseases, and to devise methods of treatment when it becomes damaged or diseased.

### A Complex Structure

The vertebrate nervous system is the most complex structure known to humankind. The human nervous system, for example, has more than a hundred billion cellular elements, and perhaps a hundred trillion points of information exchange between these elements. It is impossible to understand the details of such a structure in the same way that one can understand the structure of a radio; however, the general organizational plan can be discovered through the application of modern neuroanatomical techniques.

It is a widely accepted tenet of physiology that in order to comprehend the functioning of an organ or an organ system, it is necessary to have a critical understanding of its structure. In fact, physiology and anatomy are inseparable because function (physiology) always reflects structure (anatomy): It is impossible for an organ to perform in any other way than its architecture permits.

The nervous system is the ultimate control and

communication system in the vertebrate body. Its complexity allows the vast range of vertebrate behaviors, as well as the rapid and precise regulation of the body's internal environment. The most complex vertebrate nervous systems display self-consciousness, reasoning, and language capabilities.

There are many reasons for studying the organization of vertebrate nervous systems, ranging from purely theoretical (such as determining the mechanisms of memory recall or clarifying the evolutionary relationships among vertebrate species) to very practical (such as treatments for mental illnesses, precisely defining brain death, or designing better computers).

For many, the ultimate goal is to obtain a better understanding of the relationship between the brain and the mind. It has been proposed that the mind and mental processes are emergent properties that appear when a certain degree of organizational complexity within the nervous system has been reached. The individual elements of the nervous system (the neurons) are not the constituents that think or possess consciousness. These unique capabilities are achieved as a result of the specific connections between neurons and sensory organs, and among neurons themselves.

It does not matter whether one performs an analysis of a machine or of a nervous system; it can never be expected to reveal its soul or its consciousness—if they exist. All that can be done is to admire the intelligence of its designer or the wisdom of nature.

—John V. Urbas

**See also:** Anatomy; Brain; Development: Evolutionary perspective; Habituation and sensitization; Physiology; Reflexes.

### Bibliography

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