The Evolution of the Vertebrate Brain

Dahl Clark
Mr. Lindsey B6
Anatomy/Physiology

The phylum *Chordata* is a large and diversified group containing more than 35,000 species, ranging from small wormlike forms to man. All chordates have three characteristics in common at some stage of their life cycle; a human embryo has the same notochord, a single, dorsal, tubular nerve cord, and pharyngeal gill slits as the lowest ancestral chordates. The primitive notochord, the predecessor of the spinal cord, is the feature that has allowed the development of higher and more complexified forms of life. Instead of a widespread system of nerves, the centralization of nerves has allowed specialization and greater control of body areas.

I. The Evolution of the Notochord in *Branchiostoma*

The lancelets are considered to be predecessors to the vertebrate line. These animals are found in coastal waters, "usually lying partly buried in the sand with only their front end protruding," and are small enough to require a hand lens for observation (Walker 6). All are superficially fishlike animals that have an extremely long notochord extending beyond the nerve cord to the very front of the animal. This extreme extension of the notochord is probably correlated with the burrowing habits of the animal, since rather than being active swimmers like fish or sessile like most tunicates, lancelets are burrowing animals. The notochord consists of "vacuolated cells that are distended with fluid and held tightly together by a firm connective tissue sheath" (Walker 11). The notochord is in the general position of the vertebral column of higher chordates, and it has a comparable function, "to provide support and prevent the body from shortening when the myomeres contract" (Walker 7).

The appearance of the myomere, or primitive muscle segment, correlates with the appearance of cephalochordate central and peripheral nervous systems. In response to its environment, *Branchiostoma* evolved the necessary muscle segments needed to provide digging power and thrust. The average number of myomeres in American species ranges from 55 to 75, all controlled by nerves issuing from the nerve cord. There are dorsal and ventral roots that do not unite but run directly to the tissues; the ventral roots carry motor fibers, and the dorsal roots carry sensory muscles. The nerve cord, parallel and superior to the notochord, extends the length of the body to provide innervation to all myomeres.

Although a brain has not yet evolved in *Branchiostoma*, a filter-feeder with a streamlined, elongate shape flattened from side to side, it exhibits the elaboration of more sophisticated sensory mechanisms. Because it has no brain or individual afferent and efferent nerve fibers, *Branchiostoma* is classified as a lower chordate, approaching but not yet arriving at the status of a true vertebrate. However, by cephalochordate sensory mechanisms, the animal has developed a crude level of association. Surrounding its mouth at the front end are small tentacles called cirri, which contain chemoreceptive cells and aid in excluding large material, permitting only water and small food particles to enter. The animal can "associate" a certain stimulus acting upon its chemoreceptors with food, while disregarding other stimuli associated with non-food particles.

Another sensory mechanism evolved first in *Branchiostoma* is its photoreceptor, made up of dark pigment granules along the ventral edge of the nerve cord. These granules are particularly numerous at the animal's front end since the nerve cord bluntly ends there. There is no expanded brain, but a prominent pigment spot. This pigment spot is the precursor to the vertebrate eye, and is in the exact position where a brain would soon evolve.

II. The Development of the Brain in Aquatic Vertebrates

The brain was born in the primordial sea 500 million years ago. The most primitive vertebrates to possess the brain are jawless fishes of the class *Agnatha*. Small swellings had formed along its embryonic neural tube, the precursor to the nervous system, and insulating myelin sheaths had formed around neurons, speeding their conductivity to 270 mph. The most primitive agnathans were the ostracoderms, which have been found in Ordovician fossils over 4 million years old. Therefore, the true vertebrate brain has been around since that time. The modern cyclostomes, represented today by the hagfishes and lampreys, are the only living descendants.

The name "*Agnatha*" and "cyclostome" refer to "one of the distinctive traits of this group--the circular mouth, which is jawless" (Dillon 192). The oral form is similar to that of *Branchiostoma*, and the large sea lamprey, *Petromyzon marinus*, maintains a functional notochord throughout life. At maturity, the notochord also becomes partly enclosed by the semblance of a vertebral column. Unlike *Branchiostoma*, *Petromyzon* has developed a brain and spinal cord lying above the notochord. This brain, although it has poorly developed acousticolateral centers (for its lateral line system) and a small cerebellum, is highly similar to the brain of *Squalus*, a dogfish belonging to the higher class of sharks and rays, *Chondrichthyes*.

Groups of pores, one group posterior to the top of the newly evolved eye, another extending from the eye anteriorly and dorsally, and another on the ventral side of the head, represent the lateral line system--a group of fluid-filled sense organs functioning as a single sensory mechanism, associated with detecting "vibrations and movements in the water" (Walker 17). The chemoreceptors of *Branchiostoma* have evolved into a dark olfactory sac in front of the brain, led to by a pair of nostrils. Behind the nostril is an oval, depressed, light area called the pineal eye (the precursor to the higher vertebrate eye), which detects changes in light and influences diurnal color changes in larval lampreys, "probably by its effect upon the hypothalamus and pituitary gland" (Walker 17).

The *Petromyzon* notochord has a gelatinous texture, but is enclosed in a strong fibrous sheath. It serves, as in *Branchiostoma*, as an endoskeleton to support the body when the animal's myomeres contract. Cartilaginous blocks lie above the notochord on either side of the spinal cord, making up the foundation for vertebrate neural arches. Other cartilages surround parts of the brain, forming parts of the primary brain case, or chondrocranium--made not of bone, but cartilage.

Unlike *Petromyzon*'s lifestyle as an attached fish parasite, having a small cerebellum since it has no need to swim, *Squalus*, the dogfish, has a nervous system representative of the vertebrate condition. Its nervous system can be divided into central and peripheral portions, the central being the brain and spinal cord, the peripheral composed of various sensory and motor nerves; these are representative of all higher vertebrates, but slightly modified to fit each individual species. These modifications exist mainly in the sensory mechanisms that progressively sophisticate in higher species. The differentiation of the nerve network into central and peripheral systems is the same for *Squalus* as it is for all other higher vertebrates. The spinal cord's basic structure, allowing for the differentiation of afferent and efferent nerve fibers, is universal for all higher vertebrates. The only two evolutionary pathways that continue to develop in exponential complexity from the point of the dogfish onward are the increasing complexity of association and the progressive elaboration of the brain.

III. The Evolution of Brain Areas and Functions in *Petromyzon* and Amphibians

The general development of the brain from *Branchiostoma* to *Homo sapiens* consists of enlargement and complexification of the brain areas. The anterior portion of *Branchiostoma*'s nerve cord contains a secretory area that is the forerunner of the posterior pituitary gland of higher vertebrates, "lying in a comparable region of the brain during embryonic growth" (Dillon 214). Embryology of higher forms suggests that this early brain version enlarged and became subdivided into three major regions. The first versions of the prosencephalon, mesencephalon, and rhombencephalon became associated, respectively, with the sense of smell, vision, and hearing/equilibrium. Later, midbrain outgrowths developed into the two cerebral hemispheres; rhombencephalon outgrowths developed into the cerebellum. In *Petromyzon*, these additions were small but gradually enlarged as neurons migrated into them. This migration of neurons into the brain to promote enlargement is seen in all evolving vertebrates, due to the increase in stimuli and the need for the brain to respond to them.

In each major class of vertebrates, many specializations of nervous system function have been developed independently. For example, in *Squalus* and other shark species, the sense of smell is highly acute; muscular coordination and body position control are highly developed. These adaptations were preceded and made possible by the development of the olfactory lobes, cerebrum, and cerebellum to a degree surpassing most higher fish. Taking these adaptations into consideration, the class *Amphibia* have the "most primitive brains of all living vertebrates" (Dillon 214).

Although in primates and some other mammalian orders the olfactory sense has degenerated, its importance to terrestrial life is reflected as the early tetrapods emerged from the primitive aquatic environment onto land. In the fossils of primitive tetrapods, exemplified by the modern amphibian *Necturus*, most of this pattern of change is seen more clearly in the bones of the skull and brain case; the bones of the snout elongate while those at the base are shortened or lost. This evolutionary adaptation, caused by the tetrapod migration onto land, allowed the anterior expansion of the brain in later vertebrates. In *Necturus*, the shifting of the brain case forward provided several advantages to its early tetrapod ancestors: the eyes, instead of maintaining a lateral position optimal for underwater sight in fish, had shifted towards the top of the skull to allow a better view of the land above. The lateral line system has degenerated due to life away from the main oceans.

The primitive meningeal layer of fish is represented by two layers in *Necturus*--the tough outer dura mater and an inner vascular pia-arachnoid mater applied to the surface of the brain. The anterior region of the brain is formed by the paired cerebral hemispheres and olfactory bulbs. The olfactory bulbs in *Necturus* are the same size as the cerebral hemispheres. The optic lobes are relatively smaller in amphibians and do not bulge dorsally to the extent that they do in *Squalus*. They are located midway between the cerebrum and cerebellum, which is followed by the thick medulla oblongata. As in *Squalus* and other fish, the brain has a horizontal layout parallel to the skull and body.

IV. The Development of the Reptilian Brain

As the early tetrapods adjusted to life on land, they were faced with a number of new stimuli. There were extreme climatic, geological, and biological differences from life in water. Having evolved scaly, dry skin and an independence from water, the class *Reptilia* began to dominate the land. The mesencephalon and rhombencephalon complexified due to the environmental stresses upon these reptiles. These brain parts together make up the reptilian brain, which persisted to the age of the dinosaurs and was inherited by modern mammals. The reptilian brain in reptiles and higher vertebrates controls the crude, vital body functions. Skills needed to survive on land, such as movement and balance, are controlled by the cerebellum; the five senses and the ability to move voluntarily have also complexified. Vital functions controlled by the brain stem and reticular formation make up the main function of the reptilian brain; however, from the level of the amphibians, the cerebrum and olfactory lobes have nearly doubled in size. New brain additions and skills were added on top of the old ones; this was the mode of brain elaboration.

Reptiles have a “variety of sense organs that can detect danger or potential prey” (Biggs 840). These sense organs have developed in many reptilian species independently of others. Rattlesnakes have heat-sensitive pits below their eyes that enable them to detect prey in total darkness. The snake can tell the exact distance and direction in which to strike because the pits are paired. Also in snakes, Jacobson’s organ is a pitlike chemoreceptive sense organ in the roof of the mouth. The long, flexible tongue picks up airborne molecules and transfers them to the Jacobson’s organ for chemical analysis. In reptiles, the ability to associate has increased in complexity from amphibians and fish. Obviously, a small, quick-moving heat signature would represent food to a snake, possibly a mouse. The Jacobson’s organ allows snakes to “picture” their environment from the subtle chemicals in the air. The snake could then quickly learn to associate the scent of a cat or other predator with danger.

V. The Evolution of the Mammalian Brain

However, the second greatest advancement of vertebrate neural evolution was already under way. From the development of the notochord into the brain and spinal cord, the next phase was an exponential expansion and complexification of the mammalian cerebrum. This expansion led to the formation of consciousness and intelligence--two unique properties of *Homo sapiens*--brought about only by the development of the cerebral cortex.

In the evolution from reptiles to mammals, numerous changes occurred in the nervous system that are related in large measure to the increased activity and flexibility of mammalian responses. The major change in the brain is the evolution of a neopallium (early cortex) in the cerebral hemispheres to which sensory impulses are projected. The neopallium “first appears in reptiles, and enlarges considerably in the evolution to mammals” (Dillon 206). It pushed the original olfactory lobes apart and comes to form the greater part of the cerebrum. When it enlarged, it gradually assumed the dominant integrating role. Another important change is the great enlargement of the cerebellum. This is correlated with the increased complexity of muscular movement, an increased projection of sensory data to this region, and an interconnection of cerebral hemispheres and cerebellum. Here, the cerebellum becomes divided into hemispheres as the cerebrum.

Other changes in the mammalian brain tend to be related to the increased importance of the neopallium and the cerebellum. The thalamus enlarges as it becomes an important pathway and relay station between the cerebrum and other parts of the CNS. Important centers develop in the midbrain and metencephalon, the red nucleus and pons, respectively, for the interconnection of the cerebellum and cerebrum. Larger and more numerous fiber tracts, both afferent and efferent, evolve in the mesencephalon and rhombencephalon since the cerebrum, cerebellum, and the other brain areas have more influence over the body that they did in lower vertebrates.

VI. The Evolution of the Human Brain

The most evolved vertebrate organism is man, representing the finished product of nearly 500 million years of neural evolution. From the invertebrate sponge, which has "only seven specialized cells that form its brain," and only three hundred neurons for its entire body, the human brain is the apex of brain elaboration (Suzuki). Mammals inherited the crude reptilian brain but evolved the mammalian brain, resulting from a progressive, unrelenting expansion of the cerebrum in proportion to the mesencephalon and rhombencephalon. Crude, vital brain parts were moved inside and dwarfed by the cerebrum. The cerebrum in consecutively higher vertebrates expands anteriorly and laterally, even posteriorly to depress the cerebellum and lower brain regions. The animal with the most brain convolutions, caused by brain growth within the tight confines of the skull, is man--the cerebrum has evolved to such a great size.

During one of the more recent Ice Ages, the neural formation that separates man from other vertebrates evolved. The cerebral cortex probably evolved first in mammoths to respond to the extreme environmental conditions of the time. The brain's intelligence was tested, and the cortex, a unique conscious processing center, was first created. The cortex, arising from the primitive mammalian neopallium, sped up mammalian adaptation. In the evolution from quadrupedal mammals to bipedal humans, the brain stem has gradually shifted from horizontal with the cerebrum to a nearly vertical position through the foramen magnum.

DNA is often used to compare the similarities and differences of animal species. The closest relative of man is *Pan troglodytes*, the chimpanzee, but it still has a one-percent difference. Besides certain proteins, the majority of that one percent comes from the enlarged cerebral cortex. There can be little doubt that the frontal region has undergone numerous changes, as well as the greatest proportionate growth to other brain areas. The size increase is apparent when comparing the relative positions of the central sulcus between man and other close primates. The central sulcus, a cortical landmark, is located anterior to the middle of the cerebrum in the chimpanzee; in man, it lies distinctly posterior to the midpoint, at least at its dorsal end.

The first human brain weighed less than a pound. *Homo habilis* made tools, and the brain became half a pound heavier. *Homo erectus* discovered the use of fire and hunting a million years ago, and the brain size doubled. One hundred years ago, the brain of *Homo sapiens* was three pounds, four times larger, and three times heavier. This logarithmic increase resulted from the migration of two-thirds of all neurons into the cortex.

VII. The Development and Complexification of the Human Cerebral Cortex

The cortex filters the outside world; it is the human thinking cap, allowing higher functions. A section of cortex less than the size of a pinhead contains more than 33,000 neurons. One neuron in the human brain has 50,000 other neurons synapsing with it; one hundred billion neurons times 50,000 connections is enough to produce the human power of consciousness and intellect. Trillions of neural networks can create thoughts without outside stimuli, leading to complex functions as calculation, memory, and dreaming. In the cortical convolutions, the surface is organized into columns, thousands each a millimeter wide and less than a quarter of an inch thick. These columns organize the pathways for information and evolved because of increased information storage. Although the visual cortex responsible for vision appears to have grown smaller from that of the chimpanzee, it has grown toward the base of the brain and the cortical vision-associated area has dramatically grown.

Since the inner brain of all higher vertebrates predates even the time of the early amphibians, the brain stem, basal ganglia, and the limbic system are the same as in other vertebrates; however, the human limbic system controls both vital functions and emotion. It is the cerebrum alone which creates humanity, and because of the cerebral cortex's pliability and responsive flexibility, the environment can physically change the brain. The human brain is dynamic, constantly shaping and reshaping itself with the help of genes and the environment. Neural connections, as in other higher vertebrates, are the basis for all neural activities; however, the act of forming maps and connections of neurons correlating with specific cerebral functions is unique to man.

VIII. The Outcome of Vertebrate Brain Evolution

The evolution of the vertebrate brain has been a tedious but progressive process. Directed by the pressures of natural selection and the environment, the vertebrate brain has developed to its greatest potential for only one purpose--to allow the organism to adapt and survive better in its environment. The increasing stimuli handled by the vertebrate brain through the millennia has become responsible for the ultimate product of evolution, the human brain, gifted with the conscious ability to understand the means of its own evolution. Through the elaboration of more sophisticated sensory mechanisms and the differentiation of the nerve network into central and peripheral systems, the brain can assess and respond better to its environment. Through the differentiation of afferent and efferent nerve fibers and the increased complexity of association, the brain can make responses to previously learned situations. However, without the elaboration of the vertebrate brain from seven specialized ancient neurons, the greatest milestones in the evolution of life on Earth could not have been achieved.

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