EVOLUTION OF THE BRAIN: FROM BEHAVIOR TO CONSCIOUSNESS IN 3.4 BILLION YEARS

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ONCE LIFE BEGAN as single-cell organisms, evolution favored those able to seek nutrients and avoid risks. Receptors sensed the environment, memory traces were laid, and adaptive responses were made. Environmental stress, at times as dramatic as the collision of an asteroid, resulted in extinctions that favored small predators with dorsal nerve cords and cranially positioned brains. Myelination, and later thermoregulation, led to increasingly efficient neural processing. As somatosensory, visual, and auditory input increased, a neocortex developed containing both sensory and motor neural maps. Hominids, with their free hands, pushed cortical development further and began to make simple stone tools. Tools and increasing cognition allowed procurement of a richer diet that led to a smaller gut, thus freeing more energy for brain expansion. Multimodal association areas, initially developed for processing incoming sensory information, blossomed and began to provide the organism with an awareness of self and environment. Advancements in memory storage and retrieval gave the organism a sense of continuity through time. This developing consciousness eventually left visible traces, which today are dramatically evident on cave walls in France and Spain. We will take this journey from the single cell to human consciousness.

KEY WORDS: Brain, Consciousness, Evolution, Hominidae

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The human brain, at its best, is the origin of art, music, civilization, science, and technology. Although other advanced brains are present on Earth, including those of higher primates and cetaceans, ours is the only brain known to be capable of conceptualizing and developing complex technology projecting us beyond the environment into which we are born. Understanding how our brain evolved should shed light on the likelihood that other large-brained organisms capable of advanced technology have developed elsewhere in the universe.

The human brain developed on a terrestrial planet, and its evolution has depended on Earth's environment, changes in that environment over time, competition from other species, and intervening, sometimes catastrophic, events. If large-brained organisms exist on distant worlds, their brains will similarly reflect the conditions in which they evolved and the natural history of their planet.

Planet Earth originated approximately 4.5 billion years ago (bya) (31). Among the factors that favored the development of complex life are an atmosphere sufficient to protect life from radiation; water, the cradle of life on this planet; and land, essential to the development of terrestrially adapted nervous systems. Also important was a chaotic natural world, one with multiple niches and sufficient environmental stress to encourage evolution but not enough to stop the process. The evolutionary process that resulted in the human brain was lengthy (almost 4 billion years) and was dependent on the planet remaining geologically intact to enable single-cell organisms to evolve into conscious beings.

BEHAVIOR BEFORE BRAIN

The first single-cell organisms on Earth may have appeared as early as 3.8 to 3.9 bya (46). (This ancient age has recently been questioned [7].) Members of the kingdom Monera include the archaebacteria and eubacteria. These prokaryotes consist of cytoplasm and genetic material bounded by an external membrane. They lack a nucleus or membrane-bound organelles.

Early prokaryotes called cyanobacteria (blue-green algae) pioneered photosynthesis. They obtained energy from water and carbon dioxide and produced oxygen as a byproduct (60, p 66). Stromatolites, formed by successive generations of cyanobacteria, have been dated to 3.5 bya.

Escherichia coli, a coliform bacterium present in the human intestinal tract, resembles early flagellated bacteria thought to be living approximately 3.4 bya and serves as a model for understanding the behavior of organisms lacking neural struc-

tures (44). *E. coli* senses its environment through more than a dozen types of receptors embedded in its cell wall: transmembrane proteins that detect nutrients, such as sugar and amino acids, and toxins, such as heavy metal ions (2, p 4; 28). The bacterium chemically "processes" the information and then makes an integrated response. A signal is sent to the flagellar motors by chemical messengers and results in one of two possible actions: rotation of the flagellar motor in a clockwise or counterclockwise direction. When the environment is favorable, *E. coli* moves in a forward direction. In low nutrient concentrations or in the presence of toxins, the motors are reversed, and the bacteria momentarily tumble aimlessly (*Fig. 1*). This reorients the direction of *E. coli*, and once the organism resumes its forward motion, it begins making new environmental assessments.

By 2.7 bya, single-cell organisms containing a nucleus and membrane-bound organelles, such as mitochondria, began to appear. These eukaryotes may have evolved by the incorporation of other cells through the process of endosymbiosis: the fusion of two prokaryotes. As their internal structure became more complex, so did their behavior. New sensory receptors developed, including a primitive eye. The eukaryote *Halobacterium salinarium* contains a cell membrane receptor composed of a light-sensitive pigment similar to rhodopsin (2, p 7). This pigment is maximally sensitive to orange light and is used by *Halobacterium* to orient its swimming toward sunlight, from which it derives energy for photosynthesis. Thus, vision began as a system used to orient the organism to a source of light energy, the sun.

The eukaryote *Chlamydomonas* also uses the sensory input from light receptors to direct its movements. It possesses a simple eye at its anterior pole that senses blue-green light and is able to store short-term memories of different light intensities (2, p 7). This free-swimming algae changes direction by adjusting the movement of the two flagella also located at its leading end. Instead of the random running and tumbling movements of *E. coli*, *Chlamydomonas* continuously guides its movement in response the stimulus. The light intensity information is used to adjust the motions of its flagella, which bend like a swimmer's breaststroke to turn the organism toward the sun.

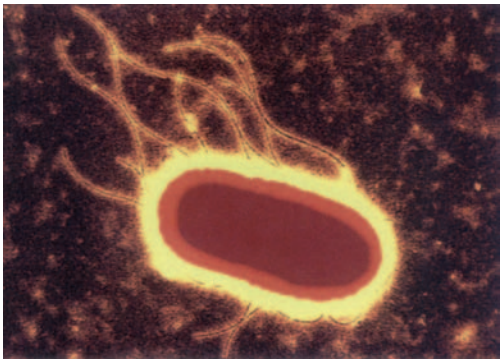

FIGURE 1. *Color-enhanced image showing* E. coli *with its flagella in tumble mode. After a brief moment,* E. coli*'s flagella rotate in a counterclockwise manner, gathering into a corkscrew-like bundle and again propelling the bacterium forward (*from, *Allman JM:* Evolving Brains. *New York, Scientific American Library, 2000 [2]).*

As single-cell organisms developed multiple motor effectors (flagella), a system was needed to signal them simultaneously. The *Paramecium* contains a series of flagella located all along its cell membrane and represents the next phase of behavioral evolution. Without coordinating the movement of its cilia, it cannot make adaptive responses. The problem is solved by depolarization. When a *Paramecium* strikes an object, voltage-gated calcium channels are activated and calcium enters the cell, depolarizing its membrane. This reverses the beating direction of the cilia in unison, and the *Paramecium* moves away from the impediment.

Thus, we see that single-cell organisms show increasingly complex behavior: receptors sense the environment, brief memory traces are stored, and signals from the receptors are integrated to produce adaptive responses. To respond appropriately to the multiple and constantly changing sensory signals, they act like hybrid computers: sensory information from multiple sources is processed in an analog manner; the response (to move or not to move) is all or none, or digital in nature.

MULTICELLULAR LIFE AND THE FIRST NERVOUS SYSTEMS

By 1.8 bya, unicellular organisms began to coalesce into multicellular life, the Metazoa. One of the first examples, still extant today, is the sponge. Its two cell layers, an ectoderm and an endoderm, are separated by an intervening mesoglea composed of a gelatinous matrix. The mesoglea contains scattered amebocytes but no nerves. The sponge is a tubular structure, with its cilia-lined endoderm facing a central cavity. Water, drawn through its open end, is filtered by the cilia for nutrients. These multicellular organisms evolved a system to coordinate responses to environmental stimuli. Studies on *Rhabdocalyptus dawsoni* are revealing the nature of their internal communication system (43, 56). When *R. dawsoni* is struck by an object, the mechanical stimulus causes a calcium influx that depolarizes the impacted cells. An electric current from these depolarized cells passes through the gelatinous mesoglea and depolarizes the sponge's endodermal cells, temporarily arresting cilia motion, thus stopping the influx of water. The transmission of this current through the mesoglea quickly sends a message to all the ciliated cells in the endoderm to change their behavior, and thus that of the organism. This coordinated response is performed in the absence of nerves.

The next crucial step in evolution is the origin of the neuron approximately 600 million years ago (mya). As reviewed by Raimundo Villegas and his associates at the 1999 Astrobiology conference, the first neurons appeared in the comb jellies, members of the phylum Ctenophora (56). These transparent, delicate animals are bilaterally symmetrical and consist of

ciliated plates arranged radially on their surface. A mouth (oral pole) is located under the leading end of the organism and a statocyst at the aboral pole. Comb jellies are active predators that feed on plankton, small crustaceans, fish eggs, and larvae. Unlike the sponge, which contains only amebocytes in the mesoglea, comb jellies have a new type of cell, the bipolar neuron. Within their mesoglea is found a network of fusiform bipolar neurons. The processes of these primitive neurons are not differentiated into dendrites or axons, and the neurons themselves are connected through bidirectional synapse-like junctions. The resulting neural network combines sensory, integrative, and motor functions without central control. A sensory organ located at the aboral end, the statolith, is used to control swimming. If water pressure from a wave causes a part of the comb jelly to tilt, the statolith increases pressure on balancer cilia on the side of the tilt. These balancer cilia activate the neural net, sending a signal to the cilia on the comb jelly's surface that causes them to beat more rapidly, thus correcting the swimming direction (49). Activation of the comb jelly's neural network occurs through a low-threshold calcium-dependent action potential for swimming and a higher-threshold sodium-dependent action potential for escape.

Thus, in the comb jellies, we find simple neurons, action potentials, sodium channels, neurosecretory granules, and simple synapses, the foundation of what Ramón y Cajal, millions of years later, called the Neuron Doctrine. The neural network allows selective communication with distant motor effectors, the surface cilia. The development of neurons transmitting an action potential to only certain areas of the organism, as seen in the comb jelly, created a capacity for more specific motor response and led to more advanced behavioral control and a survival advantage. It also allowed the development of larger and more complex organisms.

THE CAMBRIAN EXPLOSION AND CHORDATES

Beginning 545 mya, the oceans experienced "the greatest burst of animal evolution the planet has ever known" (23, p 120). In just 10 million years, the predecessors of most of the phyla alive today came into being. Known as the Cambrian Explosion, this burst was perhaps stimulated by increased oxygen in the seas and was driven by significant environmental stress. During the early Cambrian, the poles of the Earth shifted 90 degrees and caused radical climate oscillations, creating new environmental pressures and niches for evolution. Modern studies on the biomass present during this era, as measured by carbon-13, reveal a series of enormous fluctuations in the number of living organisms (2, pp 65–66).

Among the phyla developing during the Cambrian Explosion were the chordates, the immediate ancestors of the vertebrates. Chordates are named for their distinguishing feature, the notochord, a cartilaginous rod that serves as an anticompression device against which muscles work. Running parallel and dorsal to the notochord is a nerve cord. From the nerve cord run motor nerves that innervate segmental muscles (myomeres). Longitudinally differentiated, chordates contain gills and a mouth located at their leading end. These small predators had a highly developed sense of smell. The first known member of the chordate phylum, the *Pikaia*, has been found in the Burgess Shale of British Columbia (17, 23). The *Pikaia*, or similar animals, gave rise to all fishes, amphibians, reptiles, birds, and mammals.

Amphioxus, a living relative of the primitive chordates, is a free-swimming organism that lives by filtering microorganisms. At its leading end, the nerve cord of *Amphioxus* swells to a cerebral vesicle containing a few hundred neurons (60, p 125). Within the vesicle, or primitive brain, is a frontal eyespot that shares a common plan with the eye of vertebrates. Other features present in the *Amphioxus* cerebral vesicle evolved into structures present in all vertebrate brains. A dorsal lamellar body regulating daily activity cycles evolved into the parietal eyes of primitive vertebrates, and later, the pineal gland. A basal section of the cerebral vesicle containing neurosecretory cells and controlling physiological functions became the vertebrate hypothalamus. Olfactory receptors led to the development of olfactory tracts and a telencephalon for storing olfactory memories.

Gene duplication and diversification, fundamental mechanisms in the evolution of life, underlie brain evolution. An example is seen in the evolution of the visual system. "More than 500 million years ago the gene for the photoreceptor protein duplicated and the copies diverged in function" (2, p 67). One led to a rod-type photoreceptor for low-level light and the other to a cone-type photoreceptor for brighter light. The gene for the cone-type photoreceptor multiplied further into receptors sensitive to different portions of the color spectrum, thus allowing organisms to perceive a wider range of visual stimuli.

VERTEBRATES

Vertebrates, descendants of the chordates, appeared on Earth approximately 470 mya in the form of jawless fish (2, p 73; 18). Named for their vertebral skeleton, these creatures evolved a new brain structure, the telencephalon, located at the cranial end of the animal near the olfactory receptors. In the early vertebrates, the telencephalon processed olfactory information and stored olfactory "memories." This ability to sense, store, and respond to olfactory signals was essential for survival and greatly facilitated the pursuit of prey and elusion of other predators.

Jawless fish pursued higher-energy food sources (other animals) to meet the increasing energy requirements of their expanding brains. They evolved gills and specialized muscles of respiration to draw in oxygen that was delivered to the brain by single-chain hemoglobin. Visual information began to be mapped on the midbrain. The vestibular system and cerebellum continued to develop to stabilize the retinal image

while the animal was moving in pursuit of prey. Pharyngeal muscles emerged to facilitate prey capture.

The more clever the predator, the better it succeeded in finding nutrition, promoting further development of the energy-hungry brain. Thus, the evolution of jaws as instruments of predation was favored, and by 425 mya, jawed fish appeared. Their brains enlarged to control movements of the jaws and fins. A genetic duplication in hemoglobin resulted in four-chain hemoglobin, increasing oxygen delivery, particularly to the brain.

In addition to four-chain hemoglobin, jawed fish made a tremendous and unique evolutionary advance: the development of myelin. Present in all jawed vertebrates and their descendants, myelin forms a sheath surrounding the axon, much like insulation around a wire. Created by oligodendrocytes and Schwann cells, myelin is composed of protein and fat. A small gap, or node, exists between the sheaths created by the many oligodendrocytes supporting an axon. The axon potential, instead of running continuously along the fiber as in unmyelinated axons, jumps from node to node. This salutatory conduction greatly increased the velocity of the action potential and significantly reduced energy expenditure. The importance of this revolutionary breakthrough cannot be overemphasized.

There are two major groups on Earth that have highly developed sensory systems and large brains: the chordates and the cephalopods. Part of the Mollusc phylum, the cephalopods (the nautilus, squid, octopus, and cuttlefish) have never evolved myelin. In addition, they use hemocyanin, which has one-quarter of the oxygen-carrying capacity of hemoglobin. These two factors, the lack of myelinated axons and hemoglobin, hindered the evolution of the cephalopod nervous system, while the descendants of the jawed fish landed on the Moon.

AMPHIBIANS REACH LAND

The next landmark in brain evolution occurred 345 mya when amphibians crawled out of the water and began to live on land. Before that time, the brain had evolved in response to the marine environment, where olfaction was favored over vision, where efficient predators developed sleek forms, and where motor control of fins for directional motion and jaws for capturing and consuming prey were keys to survival.

Developing from jawed fish, amphibians used their fins to move from pool to pool in their coastal swamps. If their pool became dry, they had to move to an adjacent pool or die. As fins evolved into feet to better negotiate terrestrial surfaces, their oxygen supply systems further adapted to air, and amphibians spent increasing periods out of the water. The evolution of their brains became concentrated in traits favoring adaptation to conditions on dry land.

Land posed difficult challenges. The marked fluctuations in temperature between night and day had not been experienced in the relatively stable ocean. Because chemical reactions are temperature-dependent, the animals were sluggish during the colder nighttime. Among the animals experimenting with thermoregulation, the pelycosaur *Dimetrodon* (260 mya) used its dorsal fin as a solar collector. The early morning sun warmed blood circulating in the fin, enabling *Dimetrodon* to become active earlier in the day and thus be a more efficient predator: it could hunt without competition before other hunters were ready to prowl. The solar collector boosted the animal's metabolic rate and gave *Dimetrodon* a selective advantage over its more sluggish competitors.

A highly successful method of thermoregulation was pioneered by the Cynodonts (260 mya), the tetrapods that gave rise to mammals (14, 20). With their increasing brain size and the demands of thermoregulation, these mammal-like reptiles required greater energy. Differentiation of their teeth improved mastication and equipped them to obtain more energy from food. Development of a bony palate enabled them to breathe and swallow simultaneously, and sleeping in a curled-up position helped them conserve energy. Because their larger brains took more time to develop, an increasing portion of neural development occurred after birth, and infants became increasingly dependent on their parents for food and protection. This favored the development of mammary glands and nurturing behavior (*Fig. 2*).

THE PERMIAN-TRIASSIC EXTINCTION AND THE AGE OF DINOSAURS

By the end of the Permian period, the last of the Paleozoic era, there were three types of vertebrates adapting to land: reptiles, birds, and mammals. At first glance, it would seem that mammals, with their system of thermoregulation, would have the upper hand. However, approximately 250 mya, everything changed (30). A disaster struck, killing at least 90% of

FIGURE 2. *Drawing of a carnivorous cynodont the size of a small dog, Thrinaxodon, which lived in South Africa and Antarctica when the continents were joined. The mother protected her pups, whose larger brain required more time to develop (*from, *Czerkas SJ, Czerkas SA:* Dinosaurs: A Global View. *New York, Mallard Press, 1991 [14]).*

all species on Earth. Although the cause is unknown, recent evidence points to the impact of a 6- to 12-km-wide comet or asteroid. In southern China, Kaiho et al. (33) have found evidence of a "massive release of sulfur from the mantle to the ocean atmosphere system" (33, p 815). Together with findings of strontium isotope excursion, impact-metamorphosed grains, and a significant decrease in microfossils, the study suggests that a large extraterrestrial impact depleted the Earth's oxygen and caused acid rain and large-scale volcanism (33). Seismic studies in the shores of northwestern Australia have recently revealed supporting evidence of a sudden catastrophe: a possible impact crater approximately 200 km wide and approximately 250 million years old (5).

Thus ended the Permian period and began the Triassic period, the beginning of the Mesozoic era. The Permian–Triassic extinction, the most catastrophic to date, resulted in an Earth that favored reptiles. They evolved into multiple species, many growing to an enormous size, and dominated the Earth for almost 160 million years.

Mammals continued to slowly evolve, although they remained small. Advances in hearing, a chain of ossicles that could detect higher frequencies, allowed them to hear insects and communicate at frequencies beyond the sensory ability of their predators. The relative size of the forehead expanded, and a new, revolutionary structure, the neocortex, developed. Here, mammals processed and stored information about the structure of the environment (such as the location of food sources) in topographically organized maps. Cortical maps for motor control reflected the increasing capabilities of their limbs. Nursing mothers took increasing responsibility for their offspring. By 85 mya, near the end of the Cretaceous period, a new mammal began to evolve: the primate (55).

THE CRETACEOUS-TERTIARY EXTINCTION AND THE AGE OF MAMMALS

Sixty-five million years ago, the ruling order changed again. An asteroid approximately 10 km wide struck the Yucatan Peninsula and created an enormous 180-km-diameter crater, now known as Chicxulub (37, 38). The impact is suspected to have killed all animals larger than 25 kg, including all dinosaurs (57). Whether the impact-triggered extinctions were caused by a cloud of dust covering the earth and blocking photosynthesis or smoke from global fires is currently debated (39). Mammals, small thermoregulators accustomed to living in the dark, survived. Without the threat from dinosaurs, they rapidly evolved into a variety of species and are now the largest animals on Earth.

By 50 mya, *Smilodectes* showed all of the characteristics of fully developed primates: grasping hands, an enlarged brain, and a shorter snout secondary to the diminishing importance of smell among creatures living primarily in trees. As olfaction became less essential to nourishment and defense, visual acuity improved, stimulated by the need to identify fruits and insects. Movement of the eyes to a more frontal position increased visual field overlap and improved the primate's depth perception, important in judging the distance to a branch or insect (2, p 125). As the neural systems evolved to meet the needs of arboreal life, cortical sensory maps expanded to store the increasingly detailed sensory information. The motor maps also grew to control the increasingly refined motor movements.

These neuronal maps were the early foundations for the development of consciousness. Studies in apes have shown that premotor neurons that are active during movement are also active when the animal is observing the same movement in others (*Fig. 3*) (34). This evidence suggests that the cortex is creating an abstract representation of the motor task. Other structures of the brain continued to enlarge, including the cerebellum, which elaborated to coordinate the eye and limb movements of these rapidly moving predators.

ENTER THE HOMINIDS

Approximately 5 to 6 mya, a group of primates began to regularly ambulate on their lower limbs, creating a new family, the Hominidae. Intensive contemporary studies are constantly refining our sense of the hominid lineage as new fossils are discovered. Among the recent finds is a candidate for the earliest hominid, *Ardipithecus ramidus kadabba* (5.2–5.8 mya) (21, 27). Approximately the size of a modern chimpanzee, the position of the great toe shows that *A. ramidus kadabba* was bipedal. A skull has yet to be found, so no assessment of its brain size has been made thus far. An even older, though controversial, candidate (58), *Sahelanthropus tchadensis*, found in Chad in central Africa, dates to 6 to 7 mya (8).

Bipedalism was a major evolutionary advance. It freed the hands for carrying, intricate manipulations, and eventually toolmaking and use. By 3 to 4 mya, the hominid *Australopithe-*

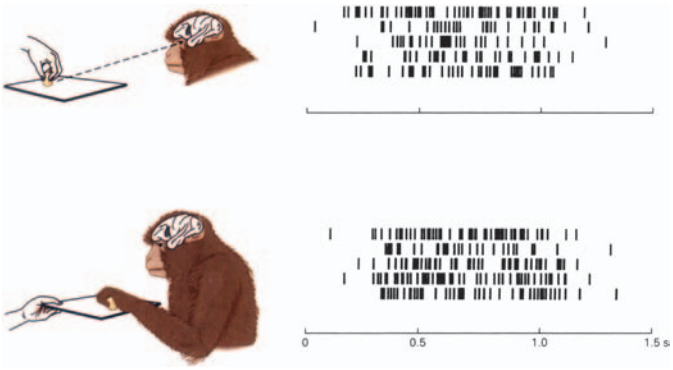

FIGURE 3. *Recordings from an individual neuron in the ventral premotor area of a primate showing a similar pattern of activity when the primate is observing someone pick up an object using a precision grip as when the primate picks up the object. This suggests that this so-called mirror neuron is involved in creating an abstract representation of the world as it relates to this action (*from, *Kandel ER, Schwartz JH, Jessell TM [eds]:* Principles of Neural Science. *New York, McGraw-Hill, 2000, ed 4 [34], reproduced with permission of McGraw-Hill Companies).*

cus afarensis appeared. Its brain size, 350 to 500 cm^3, was similar to that of the apes, and it had virtually no forehead. *A. afarensis* were primarily vegetarians and probably lived in social groups. There is no evidence that they made tools.

The 3.6-million-year-old footprints discovered at the Laetoli site in Tanzania by Mary Leakey in 1978 dramatically document hominid bipedalism (9; 19, pp 162–163; 26; 45, p 11). Fifty-four footprints of two individuals walking side by side, one larger than the other, possibly a male and a smaller female, were preserved for the ages in carbonatite ash after a volcanic eruption. The ash, moist from a recent rain, hardened like concrete. The footprints show the big toe to be in line with the other toes, unlike the ape foot, in which the big toe is set to the side (45, p 15). The pair seems to be unhurried, possibly moving to new territory after their environment was covered in ash. The female may have looked much like "Lucy," the *A. afarensis* found by Don Johanson in 1974 at the Hadar site in Ethiopia (32). Living 3.2 mya, Lucy's brain was approximately 415 cm^3.

By 2.3 to 3.5 mya, *Australopithecus africanus* shows a brain size of 420 to 500 cm^3. Raymond Dart discovered the first *A. africanus* fossil, the Taung child, in a quarry in South Africa in 1924 (*Fig. 4*) (19, pp 157–160). This remarkable specimen consists of a complete face, lower jaw, and an endocast of the brain. The frontal, temporal, parietal, and occipital lobes are well seen. The changing shape of the teeth and jaw and a flatter face than *A. afarensis* show that *A. africanus* had evolved a step closer to human form. The foramen magnum of *A. africanus* is located at the base of the skull, as in all hominids.

FIGURE 4. *Photograph of the skull of the 4-year-old Taung child, found in three pieces: the face with forehead, the lower jaw, and an almost complete endocast of the brain. The face is flatter and the teeth much smoother than those of the great apes. Raymond Dart was initially ridiculed for proposing the specimen as a link in the evolution of man (*from, *Flowers C:* A Science Odyssey: 100 Years of Discovery. *New York, William Morrow and Co., Inc., 1998 [19]).*

By 1.5 to 2.3 mya, the brain enlarged to approximately 700 cm^3 in *Homo habilis*, a size that allowed *H. habilis* to cross the "cerebral Rubicon": the manufacture of tools (45, p 11). The first evidence of toolmaking is stone flakes from 2.3 mya (40, 48), and possibly as early as 2.5 mya (50). Simple in form, these "Oldowan industry" tools are hand-sized rocks or cobbles from which flakes have been struck from one edge. Although crude, they allowed *H. habilis* to scavenge more effectively, thus increasing the caloric value of its diet and promoting further brain expansion.

When the brain enlarged to 850 cm^3 in *Homo erectus* (0.5–1.8 mya), we find a hominid with a long, low skull, a prominent browridge, fine thin body hair, and sweat glands (24, 54). Their Acheulian toolkit is evidence of their slowly growing intelligence. Sharp, multiply flaked stone tools in various shapes were used as hand axes, scrapers, and cleavers. The tools show that *H. erectus* could select the appropriate material, create a mental image of the intended result, maintain proper flaking angle, and control the movements of the striking arm and hand to create a razor-sharp tool.

This capacity for toolmaking gave *H. erectus* the ability to kill other large animals. Although high-calorie foods such as nuts and tubers remained important, *H. erectus* increasingly survived on scavenging. With more meat in their diet, they were able to travel beyond their vegetation sources and began a remarkable diaspora. Starting from eastern Africa, they spread to southern and northern Africa and eventually reached Asia (as far as Beijing), Indonesia, and Europe. (Some scientists believe that *Homo ergaster*, an ancestor of *H. erectus,* was the hominid that left Africa and later evolved to *H. erectus* [54].) Their brains gave them the ability to survive in climates and environments for which they were not initially adapted.

The next steps of hominid evolution remain mysterious, because the fossil record is meager. However, in 1978, at Atapuerca near Burgos in northern Spain, several fossil-rich sites were discovered that have been the subjects of intensive study since 1990 (1; 45, pp 118–143). At the Gran Dolina site, evidence has been found of a late wave of *H. erectus,* including a skull and bone and stone tools dating to 800,000 years ago (45, p 59). The investigators named this late *H. erectus* arrival to Europe *Homo antecessor.*

In West Sussex, England, at the site of an ancient shoreline, hand axes, carvers, and spearheads of a more recent hominid have been found (45, p 59). Animal bones at the site, including those of rhinoceroses (as large as 1.5 tons), hippopotamuses, and horses, show slashes made by these stone implements, clear evidence of the ability to hunt large animals and lay ambushes. Survival in this cold climate suggested that these hominids could make clothing, most likely from animal furs. Named *Homo heidelbergensis* from a jaw found near Heidelberg, they evolved approximately 500,000 ago (25). Finely crafted spears created by *H. heidelbergensis* 400,000 years ago have also been found near Heidelberg (45, p 127). Social

cooperation and communication must have been essential to reach this stage. Taken together, these capabilities show a hominid approaching the human. The brain of *H. heidelbergensis* was approximately 1100 cm^3, 250 cm^3 larger than that of *H. erectus* and just 250 cm^3 smaller than that of *Homo sapiens*.

Back in Spain, just a few hundred yards from Gran Dolina in Atapuerca, is a site called "La Sima de los Huesos" (1; 45, pp 133–143). Here, 300,000-year-old fossils show hominids that are tall like their *H. erectus* ancestors, but with heavy brow-ridges, prominent noses, no chins, and sturdy physiques, evidence that they were adapting to the colder climate. La Sima may be a burial site, suggesting concern for the dead and therefore some manner of spiritual consciousness. These *H. antecessor* seemed to be developing into the Neanderthal (*Homo neanderthalensis*), which began to appear approximately 250,000 years ago.

Between 130,000 and 200,000 years ago, a new hominid evolved in Africa: *H. sapiens* (4). This clever hominid, in a second diaspora, migrated out of Africa and reached Europe approximately 40,000 years ago, where it has become known as Cro-Magnon. Approximately 10,000 years after its arrival in Europe, Neanderthal suddenly disappeared. Paleoanthropologist Ian Tattersall of the American Museum of Natural History suggests that Neanderthal was driven to extinction by competition for resources or by direct conflict with *H. sapiens* (52, 53). In this view, *H. sapiens* replaced Neanderthal. Complex speech among *H. sapiens* may have been their survival advantage, although analysis of the hypoglossal canal suggests to some researchers that Neanderthal also possessed complex speech (35). Milford Wolpoff, an anthropologist at the University of Michigan in Ann Arbor, believes that Neanderthal disappeared by interbreeding with *H. sapiens* (13, 59). Recent analysis of mitochondrial deoxyribonucleic acid of both species favors the replacement model espoused by Tattersall (11, 41, 47).

THE HUMAN BRAIN, DIET, AND PARENTING

Thus, for the past 29,000 years, only one hominid brain, ours, has been present on Earth. With an average size of 1350 cm^3, our brain contains 100 billion neurons connected by an average of 1000 synapses per neuron (36). These neurons are supported by 10 times as many neuroglia, whose multiple roles include maintenance of ambience and homeostasis, guidance of embryonic neurons and processes, formation of the myelin sheath, and synthesis of neurotransmitters and trophic factors (34, p 397).

The evolution of large, complex brains created the need for an immense amount of energy. Although the human brain weighs just 2% of the total adult body weight, it requires 15% of cardiac output and metabolic budget when at rest. Easily digested, energy-rich foods permitted evolution of smaller stomachs, and the surplus energy was used to feed the expanding brain. A feedback loop was created that rewarded intellect. "We started to eat meat, got smarter, and thought of cleverer ways to obtain more meat, although learning to obtain other rich, but easily digestible foods, such as tubers, was probably also involved" (45, p 15). The development of fire, possibly discovered by *H. erectus*, turned "hard-to-digest carbohydrates into sweet, easy-to-absorb calories" (45, p 15). With better diets, hominids began to live longer, and the older members communicated the adaptive wisdom of accumulated experience and transmitted those cultural values that further promoted survival and mastery of the environment.

Large brains require a long time to mature, and hominid infants became increasingly dependent on their parents. Mothers had to meet their own energy requirements in addition to those of their infants and thus needed the support of the extended family.

SIGNS OF CONSCIOUSNESS

If the *H. sapiens* brain developed by 130,000 years ago, why did it take almost 100,000 years from its development to such visible signs of consciousness as art? Either cultural evolution and the passage of ideas took a long time, or earlier evidence of art and abstract thinking is no longer extant or is yet to be found. Recent discoveries point to the latter explanation. At the Blombos Cave in South Africa, two pieces of ochre containing a series of engraved crosshatched and horizontal lines have recently been discovered (29). Thermoluminescence dating shows the artifacts to be 77,000 years old. To the authors, the markings on the ochre suggest "arbitrary conventions unrelated to reality-based cognition" that were created with "symbolic intent" (29, p 1279).

By 35,000 years ago, unmistakable signs of consciousness became visible. Cro-Magnon began to paint on cave walls and carved statues. The Chauvet cave in France shows a beautiful and dramatic series of animals painted between 32,000 and 29,000 years ago (12, 22). These lifelike images, found deep in the cave, were painted from stored visual memory. A 30-cm ivory statuette from Johlenstein-Stadel in Germany, dated 30,000 to 32,000 years ago, shows the body of a man with the head of a lion, providing clear evidence of abstract thinking and of the ability to perceive and accurately recreate three-dimensional form (*Fig. 5*) (3, pp 100–101; 15). In France's Lascaux caves, an image painted 17,000 years ago shows the stick figure of a man wearing a bird mask near an eviscerated bison, both apparently lifeless (3, pp 178–179; 15). An image of a spear lies near the two figures. The Lascaux artist is apparently telling the story of a hunt. The painting suggests a well-developed capacity for narrative and graphic abstract thought. The multiple painted bisons on the wall and ceilings in the Altamira cave in Spain from 12,000 years ago show an artistic grace, use of color, and rhythm that would be recognized as high art in any age (*Fig. 6*) (6). Images of the human hand and reliefs of the human body clearly demonstrate self-awareness (3, p 124; 45, p 15).

The brains of these *H. sapiens* artists were composed of more than 1 trillion cells, but the numbers themselves did not gen-

erate consciousness. Consciousness and thought—the mind—are also products of the human brain's great order, complexity, and plasticity: a brain with centers for processing multiple types of sensory information and areas for well-coordinated movements of the eyes, face, mouth, tongue, and limbs, many in the form of topographically organized maps. The well-developed multimodal association areas of the brain "select and combine signals into an apparently seamless perception" (34, p 382). Although certain areas of the brain are important to specific elements of consciousness, such as the posterior parietal lobe in the hemineglect syndrome, consciousness is most likely an "emergent" property of the whole brain (34, p 397). This is best understood by considering the elements hydrogen and oxygen. It is unlikely that one could imagine two hydrogen atoms and one oxygen atom combining to create waterfalls, rain, oceans, and waves, phenomena that emerge from the combination of these simple elements. Such is likely the nature of consciousness. From a brain that evolved over millennia, the property of awareness of the self and the world eventually emerged.

FIGURE 5. *Photograph of a statuette, standing almost 1 foot tall, carved from mammoth ivory 30,000 years ago and found in Hohlenstein-Stadel, Germany. The feline face and human body are evidence of the artist's ability to think abstractly (*from, *Bahn PG, Vertut J:* Journey Through the Ice Age. *Berkeley, University of California Press, 1997 [3], reproduced courtesy of Ulm Museum, Ulm, Germany).*

FIGURE 6. *Photograph of a female bison, painted on the ceiling of the Cave of Altamira, Spain, 12,000 years ago, demonstrating the ability of its creator to retain the visual memory of a bison before painting it deep within a cave. The artist's refined artistic sensibility is evident and indicates the possession of a fully evolved* H. sapiens *brain (photograph by Antonio Beltrán © 1999,* from, *Beltrán A:* The Cave of Altamira. *New York, Harry N. Abrams, Inc., 1999 [6], reproduced courtesy of publisher).*

Three billion years of evolution suggest that the emergence of consciousness was adaptive; it enhanced the chances of survival and the likelihood that the organism would pass on its genes. As the volume and complexity of information coming into the brain increased and as the organism developed increasing capacity for multiple behaviors, responding in a stereotyped manner became increasingly difficult. The number of stereotyped responses needed to meet the changing circumstances would be enormous. Survival of the evolving hominid favored the creation of an internal representation of the world in which the self could navigate to assess the possible results of various actions. La Cerra and Bingham (42), in the *Origin of Minds*, call this structure the adaptive representational network: "individualized circuitries that generate behavioral solutions that precisely fit the specific environmental conditions, bioenergetic needs, personal experiences, and unique life history of the individual" (42, pp 186–187). These networks develop through learning and are based on memory.

Although memory by itself does not generate consciousness, without memory, "consciousness would be broken up into as many fragments as we have lived seconds" (51, p 1). The early unicellular organisms, much like the prokaryotes of today, lived in the eternal present, their chemical memories lasting not more than a few seconds. The dramatic expansion of memory over the past 3 billion years allowed *H. sapiens* to store experiences, thoughts, and emotions of practically a full lifetime. As stated by Cameron (10), "Intelligence may be the pride—the towering distinction of man; emotion gives color and force to his actions; but memory is the bastion of his being" (10, p 325).

This human consciousness and its capacity for cultural evolution have combined with intelligence to achieve the techno-

logically oriented societies in which we now live. Unfortunately, evolution has been uneven, and *H. sapiens* retains many aggressive traits that were initially adaptive in a hostile environment. Nevertheless, brain evolution has been the most outstanding of our physiological adaptations. The human brain is now able to query its own origins and even the origins of life and matter itself. As a species, we are poised to spread beyond the planet of our origin, our solar system, and possibly beyond. At the same time, we are listening for signals from other stars that may indicate the presence of other beings that share some element of what we call consciousness, an awareness of ourselves within an environment and a need to understand both (16).

SUMMARY

Throughout evolution, major advances in brain development have been made by small predators. Increasing sensory capabilities and motor skills were rewarded with survival; the smarter and more capable the organism, the more likely it was to survive. This cleverness came at the price of increased energy needs that were met by foraging or the pursuit of energy-rich game. An enlarging brain required a longer time to develop, and the organism needed increased maternal nurturing. Later, support from the father and from the extended family and community further enhanced the chances of survival. From the increasingly larger and more complex brain arose consciousness, the awareness of self and environment, a very recent phenomenon. "If the 4 billion years that life has been on Earth were a summer day, the past 200,000 years—which was the rise of anatomically modern humans, the origin of complex language, of art, religion, and trade, the dawn of agriculture, of cities, and all of written history—would fit into the flash of a firefly just before sundown" (60, p 71).

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COMMENTS

John Oró has always been a translator on behalf of neurosurgery. He led the organized efforts of neurosurgery with computer and technology applications, paving the road for the rest of us, many years ahead of the pack. In this review, he reaches into the literature on evolutionary biology and places the evolution of the nervous system and higher conscious behavior into a perspective of time line and complexity. The hypothesis of the review is neatly summarized in the final sentence of the article, quoting C. Zimmer.

The basic concepts in this review are not new, but they represent a novel synthesis for a neurosurgical readership. The scholarly literature is well referenced, and controversies are highlighted where appropriate, within the limits of length for this type of article. But the central thesis on the evolution and emergence of "higher consciousness" is somewhat problematic.

Much of the paleobiology literature is relatively speculative and based on the interpretation of a necessarily incomplete historical and evidentiary record. For example, the fossils of La Sima (Spain, 300,000 years ago) have been invoked as evidence of "concern for the dead," and yet the author claims that the first "visible signs of consciousness" did not emerge until much later, when art emerged in preserved caves: first, abstract art at Blombos Cave (South Africa, 77,000 years ago) and later, more dramatic and realistic art at Chauvet (France, 29,000 to 32,000 years ago). So who says that art alone defines consciousness rather than concern for the dead? What was our knowledge on the evolution of artistic ability until the very recent and serendipitous discoveries at Chauvet? And are we not more likely to discover evidence where it is best preserved and where we have the ability to look, whereas other evidence has most likely vanished and vast regions of the underdeveloped world undergo so much less excavation? What impact do these biases have on the story we develop in terms of when and where conscious behavior emerged?

These are not criticisms of this article but of the field as whole. Auguste Comte stratified the fields of science on the basis of their deterministic abilities (positivism). The field of evolutionary biology remains wonderful at explaining a retrospective record but very weak at predicting and very vulnerable to revisionism with emerging evidence. The foremost scientists of our era, such as Francis Crick, are devoting decades of their careers to attempting to define consciousness and understand its biological substrate. The field has challenged philosophers for centuries and has been of immense interest to neurosurgeons who try to preserve and restore consciousness at the bedside every day. Here, we read another teaser on consciousness for neurosurgeons to ponder, based on paleobiology and evolution therapy.

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I have always been an "ontogeny recapitulates phylogeny" kind of guy in my teleological attempts to understand development of the nervous system. Nonetheless, this interesting article takes a slightly different approach: understanding why the nervous system developed as it did by scientific review of its evolution from single-celled animals to humans. This may provide insight into how our brains work. But I would not count on it. Evolution depends on accidents: mutations. Over the past 3.5 billion years or so, organisms have been free to mutate and develop in millions of random ways within only a few natural constraints: requirements for a continuous source of energy, the need to excrete waste products of its own metabolism, and the need to repair itself when injured. And if a new species were to survive, it had to produce offspring that perpetuated the successful features of the new species. The result has been a dizzying array of mutations, solutions, and permutations for dealing with and

exploiting the natural environments found in water, land, and air. Nervous systems started out simply enough, and in this simplicity, they are understandable.

Single-celled organisms communicate with their neighbors by means of chemical messengers. To be successful, multicelled organisms required the development of specialized cells to communicate with each other and with cells that did something, such as move the organism away from predators and toward food. Nonetheless, these specialized cells still communicated by chemical messengers: neurotransmitters. As organisms became more complex, more cells specialized, and their nervous systems developed a corresponding level of complexity. Transmission of an action potential down a long cell body requires more energy to support, for example, the sodium-potassium pump mechanisms to maintain the membrane potentials necessary for additional action potentials. So organisms became even more mobile to find and ingest the required nutrients. As this article describes, more mobility required an even more complex nervous system to coordinate effective movement. All of this seems reasonable, logical, and comprehensible. It conforms to basic natural laws and simple logic. But try to understand the inner workings of a modern digital computer in the context of a simple natural law such as "current flows in the path of least resistance."

Fast-forward 3.5 billion years; the complexity of the nervous system has grown to cosmic proportions. Those trillion or so neurons can surely direct simple hunting and gathering, excreting, moving, and reproducing as easily as the modern computer can run a spreadsheet. However, my point is that there is so much untapped capacity, and those trillion or so neurons have to complicate the simple tasks of keeping the organism alive by thinking about such matters as being able to afford that Lexus, picking out the right tie, writing articles for *Neurosurgery*, getting the kids into Harvard, enjoying Mozart, and pondering the fact of absurdity as we praise God and develop progressively more sophisticated and ingenious ways of blowing each other up. Dr. Oró's metaphoric flash of the firefly in the summer's day of cosmic time may end in a flash measured in megatons.

The world may revert to animals that were here before us and may outlive us, organisms that adapt to but do not alter their environment in ways that disturb the balance of nature's delicate ecosystems. This may be what does us in, eventually. Personally, as a champion of long-term survival, I vote for the lowly cockroach. They have derived superior survival skills that allow them to move, eat, breathe, excrete, and have little cockroaches. They have changed very little in 400 million years, so what they're doing must be working for them. And one of the major factors in cockroach survival may be the fact that they do not "think."

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This is an ambitious article that discusses in a systematic way the contributions of neurophysiology to evolutionary changes in the nervous system that ultimately resulted in the human brain. The analysis would have been enhanced significantly by a correlation of these neurophysiological changes with alterations in molecular genetics, and at some point perhaps this sort of correlation will become possible. This is a scholarly and thought-provoking analysis of a subject that fascinates all of us.

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