

We are used to thinking of humans as occupying the sole pinnacle of evolutionary intelligence. That's where we're wrong

By Paul Patton

e were talking about politics. My housemate, an English professor, opined that certain politicians were thinking with their reptilian brains when they threatened military action against Iran. Many people believe that a com-

ponent of the human brain inherited from reptilian ancestors is responsible for our species' aggression, ritual behaviors and territoriality.

One of the most common misconceptions about brain evolution is that it represents a linear process culminating in the amazing cognitive powers of humans, with the brains of other modern species representing previous stages. Such ideas have even influenced the thinking of neuroscientists and psychologists who compare the brains of different species used in biomedical research.

Many Minds

Over the past 30 years, however, research in comparative neuroanatomy clearly has shown that complex brains—and sophisticated cognition—have evolved from simpler brains multiple times independently in separate lineages, or evolutionarily related groups: in mollusks such as octopuses, squid and cuttlefish; in bony fishes such as goldfish and, separately again, in cartilaginous fishes such as sharks and manta rays; and in reptiles and birds. Nonmammals have demonstrated advanced abilities such as learning by copying the behavior of others, finding their way in complicated spatial environments, manufacturing and using tools, and even conducting mental time travel (remembering specific past episodes or anticipating unique future events). Collectively, these findings are helping scientists to understand how intelligence can arise—and to appreciate the many forms it can take.

The Tree of Life

To understand why a new view of the evolution of brains and minds is only now coming to full fruition, it is useful to review historical notions. Medieval naturalists placed living things along a linear scale called the great chain of beings, or *scala naturae*. This hierarchical sequence ranked creatures such as worms and slugs as lowly and humans as the highest of earthly beings. In the late 1800s the enormous mass of evidence contained in Charles Darwin's masterwork, *On the Origin of Species*, convinced most of his scientific contemporaries that evolution was a reality. Darwin explained that modern species were related by physical descent and saw the relations among species as resembling the diverging branches of a family genealogical tree. Few, however, fully grasped the revolutionary im-



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plications of this tree of life—in which modern species represent the tips of the branches and inner branches represent past species, forming junctions where two lineages branch from a common ancestor.

So when comparative neuroanatomy first blossomed at the end of the 19th century, most researchers interpreted its findings in terms of the old linear scale. They believed modern invertebrates (animals without backbones), fish, amphibians, reptiles, birds, mammals and humans to be living representatives of successive evolutionary steps toward a more complex brain, with new brain components added at each step. Given the relative lack of interest in comparative neuroanatomy during the mid-20th century, these ideas persisted unchallenged for decades. The traditional ideas about sequential brain evolution appeared, for example, in the late neuroscientist and psychiatrist Paul D. MacLean's triune brain model, formulated in the 1960s. Mac-Lean's model promoted the belief that the human brain

FAST FACTS Brains of the Species

Despite cartoons you may have seen showing a straight line of fish emerging on land to become primates and then humans, evolution is not so linear. The brains of other animals are not merely previous stages that led directly to human intelligence.

2>>> Instead—as is the case with many traits—complex brains and sophisticated cognition have arisen multiple times in independent lineages of animals during the earth's evolutionary history.

3>>> With this new understanding comes a new appreciation for intelligence in its many forms. So-called lower animals, such as fish, reptiles and birds, display a startling array of cognitive capabilities. Goldfish, for instance, have shown they can negotiate watery mazes similar to the way rats do in intelligence tests in the lab. contains a "reptilian complex" inherited from reptilian ancestors.

Beginning in the 1980s, the field of comparative neuroanatomy experienced a renaissance. In the intervening decades evolutionary biologists had learned a great deal about vertebrate evolutionary history, and they developed new and effective methods of applying Darwin's concept of the tree of life to analyze and interpret their findings. It is now apparent that a simple linear hierarchy cannot adequately account for the evolution of brains or of intelligence. The oldest known multicellular animal fossils are about 700 million years old. By the Cambrian period, about 520 million years ago, the animal kingdom had branched into about 35 major groups, or phyla, each with its own distinctive body plan. As a separate branch of the tree of life, each lineage continued to evolve and diversify independently of the others. Complex brains evolved independently in multiple phyla, notably among the cephalopod mollusks of the phylum Mollusca and, of course, among various groups of vertebrates. Vertebrate evolution has likewise involved repeated branching, with complex brains evolving from simpler brains independently along numerous branches.

Alien Minds

Cephalopod mollusks, a group that includes octopuses, squid and cuttlefish, have evolved the most sophisticated nervous system of all invertebrates—and their cognitive abilities reflect that complexity. The brain of an octopus contains an estimated 170 million neurons, a number comparable to that of the brains of some vertebrates. In relation to body size, this brain is as large as that of some birds. Having evolved independently in another phylum, the structure of the octopus's brain looks utterly alien as compared with the more familiar brains of vertebrates. The exquisitely sensitive and flexible tentacles of the octopus contain as many neurons as its brain does, and severed tentacles remain capable of coordinated movements.

Behavioral studies show that octopuses can distinguish and classify objects based on size and shape, much as rats do. They can learn to navigate simple mazes and to solve problems, such as removing a tasty food item from a sealed container. In 1992 two Italian neuroscientists, Graziano Fiorito of the Dohrn Zoological Station in Naples and Pietro Scotto, then at the University of Reggio Calabria in Catanzaro, published surprising evidence that an octopus can learn to accomplish a task by watching another octopus perform it. They trained octopuses to choose between a red ball and a white ball. If the octopus opted for the correct ball, it got a piece of fish as reward. If it selected incorrectly, it received a mild electric shock as punishment. Once the training was completed, the investigators let an untrained octopus watch a trained animal perform the task from behind a glass barrier. The untrained animals did monitor the trained animals, as indicated by movements of their head and eyes. When allowed to select between the two balls themselves, the observer octopuses then made correct choices, which they could only have learned by watching. The ability to learn by studying others has been regarded as closely related to conceptual thought.

Undersea Smarts

Unlike the octopus, bony fishes and their cartilaginous cousins are fellow vertebrates and seafaring members of our own phylum, Chordata. Research in the past few years has shown that these animals display some cognitive abilities once thought unique to mammals. In a series of studies starting in 1994, a team of investigators at the University of Seville in Spain tested the spatial smarts of goldfish, a familiar bony fish. The goldfish swam through watery versions of mazes such as those traditionally used to test similar cognitive skills in rats. They showed many of the same basic spatial abilities that rodents do, including the ability to use distant visual cues to find a particular place, even when the surrounding maze has been reoriented.

The forebrains of fishes endow them with these abilities. The forebrains of most vertebrates also directly receive and process smell information. Early comparative neuroanatomists, guided by their belief in a linear evolutionary scale, thought the forebrains of "primitive" fishes and amphibians were olfactory centers that did little else. We now know that, as in mammals, the forebrains of fishes and amphibians receive the full panoply of sensory information. The main modern group of bony fishes, the teleosts, first ap<complex-block>

peared about 200 million years ago, well after vertebrates ancestral to humans had emerged onto land, further proof of the independent development of their intelligence. In body-relative terms, the brains of these fishes are often comparable in size to those of landdwelling reptiles. In the old phylogenetic scale, fish were considered "lower" than reptiles.

Cartilaginous fishes constitute a separate lineage from bony fishes, and their defining trait is a skeleton consisting of cartilage. Modern examples of this group

-P.P.

Evolutionary Missteps

P aul D. MacLean's widely popularized triune model of the vertebrate brain from the 1960s held that human brains were the culmination of linear evolution progressing from simpler animals. Drawing on the work of pioneering comparative neuroanatomist Ludwig Edinger, MacLean proffered four sequential steps: a "neural chassis" corresponding to the brains of fish and amphibians; a reptilian complex, consisting of the basal ganglia, which were held to dominate the brains of reptiles and birds; a paleomammalian component, consisting of the brain's limbic system, which supposedly emerged with the origin of mammals and which was responsible for emotional behavior; and finally a neomammalian component, consisting of the neocortex, the site of higher cognitive functions. These ideas are still very much alive in popular culture and even within psychology.

Neomammalian

Paleomammalian

(limbic system)

Reptilian

Minds through Time >



Medieval naturalists rank living things along a linear scale called the great chain of beings, or scala naturae. Creatures such as worms and **slugs** are considered lowly and humans the highest of earthly beings.

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Improvements to the

microscope and tech-

past species, forming

1940s to 1950

niques for staining to render neurons visible under the microscope make comparative neuroanatomy feasible, but most biologists retain aspects of the hierarchical scala naturae in their thinking.

Konrad Lorenz, Nikolaas Tinbergen and Karl von Frisch found the field of ethology, the scientific study of innate animal behaviors. Tinbergen and Lorenz study egg-rolling behavior in the **greylag goose** and conclude nonmammals are instinctdriven automatons. In contrast, von Frisch discovers that **worker bees**--communicate the loca-tion of nectar sources to their nest mates via a "dance language"—the



In 300 million years of separate evolution, two groups evolved sophisticated abilities based on different forebrain plans.

include sharks, skates and rays. Though once regarded as primitive, some members of this lineage have evolved the largest brains in relation to their bodies of any nonmammalian aquatic vertebrate. In 2005 neuroethologists Vera Schluessel and Horst Bleckmann, both at the University of Bonn in Germany, repeated some of the Spanish group's spatial tests on the freshwater stingray. It exhibited place-finding abilities akin to those found in goldfish.

By performing tests on goldfish after parts of their forebrain had been destroyed, the Spanish team showed in a study published in 2006 that the spatial abilities of goldfish derive from a part of the roof, or pallium, of the forebrain that may correspond to the hippocampus in mammals. Together these new studies indicate that the common ancestor of cartilaginous fishes, bony fishes and land vertebrates may already have possessed a hippocampuslike structure and the spatial cognitive abilities it confers. The hippocampus, which is also involved in processing emotions, is the main pallial component of the limbic system; in MacLean's triune brain scheme, it was supposed to have originated with mammals. A variety of other limbic system structures are now known to exist in nonmammals.

Birds and Reptiles

When a lineage of bony fishes left the seas for land about 365 million years ago, it eventually gave rise to all the four-limbed land vertebrates alive today—and two major types of brain organizational plans. These vertebrates branched into two main groups. The first group, the synapsids, appeared 320 million years ago and eventually evolved into modern mammals, whereas the second, the sauropsids, appeared 10 million years later and evolved into modern birds and reptiles (as well as the extinct dinosaurs). In their 300 million years of separate brain evolution, some members of each of the two groups have evolved quite sophisticated cognitive abilities based on very different forebrain organizational plans.

This difference in forebrain organization initially caused confusion among comparative neuroanatomists. When seen in cross section, each hemisphere of the vertebrate forebrain consists of a mass of neural tissue surrounding a central fluid-filled cavity called the ventricle. The forebrains of reptiles and birds include a prominent mass of neural tissue that bulges into this ventricle, in some cases largely obliterating it. Early comparative neuroanatomists mistook this bulge for a part of the basal ganglia, a structure in the floor of the forebrain. They concluded that the forebrains of reptiles and birds were dominated by the basal ganglia and possessed only a rudimentary pallium. The pallium is the structure that has elaborated into the cerebral cortex in mammals. Pioneering behavioral studies reinforced the interpretation suggested by the apparent-





1960s to 1970s

first hint of higher cognition outside mammals.

Paul D. MacLean's **triune brain model**, which specifies "primitive" complexes in the human brain inherited from animal ancestors, still reflects traditional ideas about sequential evolution nearly 100 years after Darwin [see box on page 75]. Though among neuroscientists, MacLean's ideas were popularized by Carl Sagan's 1977 Pulitzer Prizewinning best seller, *The Dragons of Eden.* R. Glenn Northcutt, then

never widely accepted

at the University of Michigan at Ann Arbor, and others introduce **modern cladistic analysis** into com1990s to present

parative neuroanatomy. Cladistic analysis determines evolutionary relations by comparing structures across related species using objective quantitative principles grounded in Darwin's concept of the tree of life. It soon becomes apparent that complex brains have evolved from simple brains, not once but many times independently, along different evolutionary lineages.

Cognitive ethologists show that **sophisticated cognition** has arisen independently in multiple groups of animals, representing different instances of the evolution of complex brains and different branches of the tree of life.

ly rudimentary pallium. "The bird, its brain dominated by its basal nuclei, is essentially a highly complex mechanism with little learning capacity," concluded comparative anatomist Alfred Romer in 1955. As it turns out, these seemingly consistent neuroanatomical and behavioral findings were both mistaken.

A series of comparative neuroanatomical studies in the 1960s, beginning with the work of Harvey J. Karten, now at the University of California, San Diego, has conclusively shown that the bulging mass of neural tissue in sauropsid forebrains, now known as the dorsal ventricular ridge (DVR), is not a part of the basal ganglia. It is instead a part of the pallium and appears to be the sauropsid counterpart of the mammalian neocortex. In mammals the neocortex is the largest part of the pallium and is involved in sophisticated cognitive abilities such as executive planning, learning and memory, reasoning, fine-motor control and perception; in humans it accounts for language. The basal ganglia in fact make up no larger part of the forebrain in sauropsids than they do in mammals. Mammals have nothing like the DVR. Neuroanatomical terminology for birds was revised to reflect this new awareness only in 2002.

The neocortex of mammals and the DVR of reptiles and birds are dramatically different in structure. The former is an extended thin sheet of tissue, with nerve cells organized into layers and with different territories of the sheet essentially performing different functions. The latter is a bulk mass of neural tissue structured into a series of clusters of nerve cells, or nuclei, with nuclei specialized for various functions. Despite these structural differences, the neocortex and DVR share similar connections to other parts of the brain as well as apparently similar cognitive functions. For example, there is now evidence that a part of the DVR in birds, called the nidopallium caudolaterale, may be involved in planning and executive control of behavior, much like the frontal lobes of the neocortex in mammals. In its internal structure and connections with other brain parts, the DVR in reptiles is generally simpler than that in birds. Despite their common forebrain plan, birds typically have much larger forebrains in relation to their bodies than reptiles do.

Far from being "birdbrains," our feathered friends have displayed clever behaviors. Among birds, the largest forebrains are those of parrots and corvids (a group that includes crows, jays, ravens and jackdaws). Relative to body size, the brain of a parrot is as large as that of a chimpanzee, although, in absolute terms, it is about the size of a walnut. In recent years researchers have documented stunning cognitive abilities in these two groups of birds.

In the wild, for example, New Caledonian crows manufacture two types of simple tools to gain access to otherwise unobtainable foods. They trim and sculpt twigs to fashion hook tools to poke out insect larvae from holes in trees. And they make probes for finding insects under leaf detritus by stripping off pieces of the barbed pandanus leaves to sharpen them to a point. Psychologists Gavin Hunt and Russell Gray, both at

(The Author)

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the University of Auckland in New Zealand, reported in 2003 that New Caledonian crows' tools have some features that appear more sophisticated than those of chimpanzees. The crows can craft a diverse variety of tools, modified by innovation from a common design. They can add cumulative improvements to their tools and can teach other members of their group to copy good designs faithfully.

Nicola S. Clayton, now at the University of Cambridge, has demonstrated, in a series of papers beginning in 1998, striking cognitive abilities in the Florida scrub jay, another type of corvid. These birds stash food in hundreds of different hidden caches dispersed over a wide area. They can remember the locations of all their hoards and retrieve food from them at a later time. Nonperishable foods, such as seeds, may remain in storage for months on end. Perishable foods, such as grubs and worms, must be retrieved just hours or days later.

Clayton and her students were able to use this naturally occurring behavior to show that Florida scrub jays can recall specific episodes in their past. The birds were provided with perishable worms and nonperishable nuts, which they cached in the individual compartments of sand-filled ice cube trays. They cached in different trays on different days and were then denied access to the trays for a specified period. If the birds could not access the trays for a short time, they should have tried to retrieve the worms, which are their preferred food, from the appropriate compartments of the appropriate trays. On the other hand, if the birds were denied access to the trays for a longer time, the worms no longer would have been fresh, and the jays should have tried to retrieve the nuts. To solve this problem, the birds needed to recall what they cached, where they cached it and when they did so. The birds successfully performed this complex task. Such an ability has yet to be demonstrated in a nonhuman mammal.

Even more amazingly, Clayton showed that the birds can anticipate unique future events. She allowed jays to observe others of their kind cache food and then permitted them to pilfer the caches. Later these birds cached their own food, either alone or in the presence of another jay. Birds that had acted as thieves took great precautions to conceal their food-caching activities when in the presence of another jay. Although the jays had experienced food theft only in the role of thief, they nonetheless were able to imagine themselves in the role of victim. The ability to recall specific episodes in the past and to predict future occurrences is known as mental time travel [see "Intelligence Evolved," by Ursula Dicke and Gerhard Roth; SCIENTIFIC AMERICAN MIND, August/September 2008]. Before Clayton's work, this cognitive ability was thought to be unique to humans.

Perhaps most stunning, an African gray parrot named Alex became famous for his ability to name 50 different objects. Alex learned the labels for seven colors and five shapes. In 1996 psychologist Irene M. Pepperberg, then at the University of Arizona, reported that Alex could classify objects by color and shape. Alex could ask for objects by name using phrases such as "want banana." Alex even learned number labels from one to six and seemed to grasp the concept of zero, as evidenced by an appropriate use of "none." A host of control experiments showed that Alex's feats were genuinely cognitive and not the result of simple conditioned learning. Similar cognitive abilities had never been demonstrated outside humans and their closest primate relatives [see "Bird Brains? Hardly," by Christine Scholtyssek; SCIENTIFIC AMERICAN MIND, April/May 2006].

Although scientists have yet to discover birdlike cognitive abilities in reptiles, the view of them as instinct-driven automatons appears likewise to have been misconceived. Reptiles are the victims of biased intelligence tests. Mammals, with their high and constant body temperatures, must incessantly seek food to fuel their energy-costly metabolism. They can thus easily be induced to perform all manner of learning tasks for a food reward. Reptiles lack a comparably powerful demand for food and often perform poorly when it is offered as a reward. They are now known to exhibit a variety of forms of simple learning when provided with species-appropriate rewards, such as the warmth of a sun lamp. Experiments with spatial mazes, for example, have demonstrated that turtles possess spatial skills similar to those described for fishes earlier, including the ability to find a particular place based on distant visual cues, despite rotational displacement of a maze.

Scientists still do not have answers for a great many questions about animal intelligence and its evolution. A major problem involves the identification of speciesappropriate tests of cognition. Clayton's demonstration of mental time travel in Florida scrub jays exploit-

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ed a naturally occurring behavior of that species. We will not know whether this knack is an unusual quirk of scrub jays and other food-caching birds or a widespread capacity until behaviorally appropriate tasks are identified for other species. The cognitive facilities demonstrated for birds, mammals and cephalopod mollusks depend on very different nervous systems. What allows them all to serve similar cognitive functions? Our understanding of intelligence and the brain in nonmammals is still in its infancy.

In recent decades scientists have cast aside a linear, sequential view of brain evolution in which the human brain incorporates components resembling the brains of modern fishes, amphibians, reptiles and birds and have adopted a new view of divergently branching brain and mind evolution. Substantial cognitive abilities have evolved multiple times, based on differing neural substrates—including the mental agility that enables us humans to decipher brain evolution and its meaning. M

(Further Reading)

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