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Evolutionary Origins of Your Right and Left Brain

The division of labor by the two cerebral hemispheres—once thought to be uniquely human—predates us by half a billion years. Speech, right-handedness, facial recognition and the processing of spatial relations can be traced to brain asymmetries in early vertebrates

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The left hemisphere of the human brain controls language, arguably our greatest mental attribute. It also controls the remarkable dexterity of the human right hand. The right hemisphere is dominant in the control of, among other things, our sense of how objects interrelate in space. Forty years ago the broad scientific consensus held that, in addition to language, right-handedness and the specialization of just one side of the brain for processing spatial relations occur in humans alone. Other animals, it was thought, have no hemispheric specializations of any kind.

Those beliefs fit well with the view that people have a special evolutionary status. Biologists and behavioral scientists generally agreed that right-handedness evolved in our hominid ancestors as they learned to build and use tools, about 2.5 million years ago. Right-handedness was also thought to underlie speech. Perhaps, as the story went, the left hemisphere simply added sign language to its repertoire of skilled manual actions and then converted it to speech. Or perhaps the left brain's capacity for controlling manual action extended to controlling the vocal apparatus for speech. In either case, speech and language evolved from a relatively recent manual talent for toolmaking. The right hemisphere, meanwhile, was thought to have evolved by default into a center for processing spatial relations, after the left hemisphere became specialized for handedness.

In the past few decades, however, studies of many other animals have shown that their two brain hemispheres also have distinctive roles. Despite those findings, prevailing wisdom continues to hold that people are different. Many investigators still think the recently discovered specializations of the two brain hemispheres in nonhumans are unrelated to the human ones; the hemispheric specializations of humans began with humans.

Here we present evidence for a radically different hypothesis that is gaining support, particularly among biologists. The specialization of each hemisphere in the human brain, we argue, was already present in its basic form when vertebrates emerged about 500 million years ago. We suggest that the more recent specializations of the brain hemispheres, including those of humans, evolved from the original ones by the Darwinian process of descent with modification. (In that process, capabilities relevant to ancient traits are changed or co-opted in the service of other developing traits.) Our hypothesis holds that the left hemisphere of the vertebrate brain was originally specialized for the control of well-established patterns of behavior under ordinary and familiar circumstances. In contrast, the right hemisphere, the primary seat of emotional arousal, was at first specialized for detecting and responding to unexpected stimuli in the environment.

In early vertebrates such a division of labor probably got its start when one or the other hemisphere developed a tendency to take control in particular circumstances. From that simple beginning, we propose, the right hemisphere took primary control in potentially dangerous circumstances that called for a rapid reaction from the animal—detecting a predator nearby, for instance. Otherwise, control passed to the left hemisphere. In other words, the left hemisphere became the seat of self-motivated behavior, sometimes called top-down control. (We stress that self-motivated behavior need not be innate; in fact, it is often learned.) The right hemisphere became the seat of environmentally motivated behavior, or bottom-up control. The processing that directs more specialized behaviors—language, toolmaking, spatial interrelations, facial recognition, and the like—evolved from those two basic controls.

The Left Hemisphere

Most of the evidence that supports our hypothesis does not come from direct observation of the brain but rather from observations of behavior that favors one or the other side of the body. In the vertebrate nervous system the connections cross between body and brain—to a large degree, nerves to and from one side of the body are linked to the opposite-side hemisphere of the brain.

Evidence for the first part of our hypothesis—that the vertebrate left hemisphere specializes in controlling routine, internally directed behaviors—has been building for some time. One routine behavior with a rightward bias across many vertebrates is feeding. Fishes, reptiles and toads, for instance, tend to strike at prey on their right side under the guidance of their right eye and left hemisphere. In a variety of bird species—chickens, pigeons, quails and stilts—the right eye is the primary guide for various kinds of food pecking and prey capture. In one instance, such a lateralized feeding preference has apparently led to a lateralized bias in the animal's external anatomy. The beak of the New Zealand wry-billed plover slopes to the right; that way, the plover's right eye can guide the beak as the bird seeks food under small river stones.

As for mammals, the feeding behavior of humpback whales is a spectacular example of a lateral feeding preference. Phillip J. Clapham, now at the Alaska Fisheries Science Center in Seattle, and his colleagues discovered that 60 out of 75 whales had abrasions only on the right jaw; the other 15 whales had abrasions only on the left jaw. The findings were clear evidence that whales favor one side of the jaw for food gathering and that "right-jawedness" is by far the norm.

In short, in all vertebrate classes—fishes, reptiles, amphibians, birds and mammals—animals tend to retain what was probably an ancestral bias toward the use of the right side in the routine activity of feeding.

Origins of Right-Handedness

What do these findings say about the alleged uniqueness of human right-handedness? Evidence for a right-side bias in birds and whales is intriguing, but it hardly makes a convincing argument against the old belief that right-handedness in humans had no evolutionary precursors. Yet more than a dozen recent studies have now demonstrated a right-handed bias among other primates, our closest evolutionary relatives—clearly suggesting that human right-handedness descended from that of earlier primates. The right-hand preference shows itself in monkeys (baboons, *Cebus* monkeys and rhesus macaques) as well as in apes, particularly in chimpanzees.

Many of the studies of apes have been done by William D. Hopkins of the Yerkes National Primate Research Center in Atlanta and his colleagues. Hopkins's group observed right-hand preferences particularly in tasks that involved either coordinating both hands or reaching for food too high to grab without standing upright. For example, experimenters placed honey (a favorite food) inside a short length of plastic pipe and gave the pipe to one of the apes. To get the honey, the ape had to pick up the pipe in one hand and scrape out the honey with one finger of the opposite hand. By a ratio of 2 to 1, the apes preferred to scrape honey out with a finger of the right hand. Similarly, in the reaching experiments, the apes usually grabbed the food they wanted with the right hand.

The Yerkes findings also suggest to us that as early primates evolved to undertake harder and more elaborate tasks for finding food, their handedness preferences became stronger, too. The reason, we suspect, is that performing ever more complex tasks made it increasingly necessary for the control signals from the brain to pass as directly as possible to the more skilled hand. Since the most direct route from the left hemisphere—the hemisphere specialized for routine tasks—to the body follows the body-crossing pathways of the peripheral nerves, the right hand increasingly became the preferred hand among nonhuman primates for performing elaborate, albeit routine, tasks.

Communication and the Left Brain

The evolutionary descent of human right-handed dexterity via the modification of ancient feeding behavior in ancestral higher primates now seems very likely. But could feeding behavior also have given rise to the left-brain specialization for language? Actually we do not mean to suggest that this development was direct. Rather we argue that the "language brain" emerged from an intermediate and somewhat less primitive specialization of the left hemisphere—namely, its specialization for routine communication, both vocal and nonvocal. But contrary to long-held beliefs among students of human prehistory, neither of those communicative capabilities first arose with humans; they, too, are descended from hemispheric specializations that first appeared in animals that lived long before our species emerged.

In birds, for instance, studies have shown that the left hemisphere controls singing. In sea lions, dogs and monkeys, the left hemisphere controls the perception of calls by other members of the same species. One of us (Rogers), in collaboration with Michelle A. Hook-Costigan, now at Texas A&M University, observed that common marmosets open the right side of their mouths wider than the left side when making friendly calls to other marmosets. People also generally open the right side of their mouths to a greater extent than the left when they speak—the result of greater activation of the right side of the face by the left hemisphere.

Little is universal in nature, though, and in some animals a vocal response to highly emotional circumstances has also been linked to the left brain, not—as one might expect—to the right. When a male frog is clasped from behind and held by a rival male, for instance, the left hemisphere seems to control the vocal responses of the first frog. The left hemisphere in mice controls the reception of distress calls from infant mice, and in gerbils it controls the production of calls during copulation. But those animals may be exceptions. In humans and monkeys—and perhaps in most other animals—the right brain takes control in highly emotional vocalizing; the left brain sticks to the routine.

Nonvocal communication in humans has evolutionary antecedents as well. Not only do chimpanzees tend to be right-handed when they manipulate objects, but they also favor the right hand for communicative gestures. Gorillas, too, tend to incorporate the right hand into complex communications that also involve the head and the mouth. Adrien Meguerditchian and Jacques Vauclair, both at the University of Provence in France, have even observed a right-handed bias for one manual communication (patting the ground) in baboons.

The evolutionary significance of all this becomes clear as soon as one notes that humans also tend to make communicative gestures with the right hand. The lateralized behavior we share with baboons suggests that right-handed communications arose with the first appearance of the monkeylike ancestor we share with baboons. That creature emerged perhaps 40 million years ago—well before hominids began to evolve.

Evolution of Speech

A fundamental question remains: Just how could any of the behaviors already controlled by the left brain—feeding, vocalizing, communicating with the right hand—have been modified to become speech—one of the most momentous steps in the history of life on earth?

One of us (MacNeilage) has hypothesized that it required the evolution of the syllable, the basic organizational unit underlying a stream of speech in time. The typical syllable is a rhythmic alternation between consonants and vowels. (Consonants are the sounds created when the vocal tract is momentarily closed or almost closed; vowels are the sounds created by resonance with the shape of the vocal tract as air flows relatively freely out through the open mouth.) The syllable may have evolved as a by-product of the alternate raising (consonant) and lowering (vowel) of the mandible, a behavior already well established for chewing, sucking and licking. A series of these mouth cycles, produced as lip smacks, may have begun to serve among early humans as communication signals, just as they do to this day among many other primates.

Somewhat later the vocalizing capabilities of the larynx could have paired with the communicative lip smacks to form spoken syllables. Syllables were perhaps first used to symbolize individual concepts, thus forming words. Subsequently, the ability to form sentences (language) presumably evolved when early humans combined the two kinds of words that carry the main meaning of sentences: those for objects (nouns) and those for actions (verbs).

The Right Hemisphere

What about the second half of our hypothesis? How strong is the evidence that, early in vertebrate evolution, the right hemisphere specialized in detecting and responding to unexpected stimuli? In what ways has that underlying specialization evolved and been transformed?

One set of findings that lend strong support to our hypothesis comes from studies of the reactions to predators by various animals. After all, few events in ancient vertebrate environments could have been more unexpected and emotion-laden than the surprise appearance of a deadly predator. Sure enough, fishes, amphibians, birds and mammals all react with greater avoidance to predators seen in the left side of their visual field (right side of the brain) than in their right visual field.

Evidence that the same hemispheric specialization for reactions holds for humans comes from brain-imaging studies. In a summary of those studies, Michael D. Fox and his colleagues at Washington University in St. Louis conclude that humans possess an “attentional system” in the right hemisphere that is particularly sensitive to unexpected and “behaviorally relevant stimuli”—or in other words, the kind of stimuli that say, in effect, Danger ahead! The existence of such an attentional system helps to make sense of an otherwise inexplicable human propensity: in the laboratory, even right-handed people respond more quickly to unexpected stimuli with their left hand (right hemisphere) than with their right hand.

Even in nonthreatening circumstances, many vertebrates keep a watchful left eye on any visible predators. This early right-hemisphere specialization for wariness in the presence of predators also extends in many animals to aggressive behavior. Toads, chameleons, chicks and baboons are more likely to attack members of their own species to their left than to their right.

In humans the relatively primitive avoidance and wariness behaviors that manifest right-hemisphere attentiveness in nonhuman animals have morphed into a variety of negative emotions. Nineteenth-century physicians noticed that patients complained more often of hysterical limb paralyses on the left side than on the right. There is some evidence for right-hemisphere control of emotional cries and shouts in humans—in striking contrast with the emotionally neutral vocalizations controlled by the left hemisphere. People are more likely to become depressed after damage to the left hemisphere than to the right. And in states of chronic depression the right hemisphere is more active than the left.

Recognizing Others

Along with the sudden appearance of a predator, the most salient environmental changes to which early vertebrates had to react quickly were encounters with others of their own species. In fishes and birds the right hemisphere recognizes social companions and monitors social behavior that might require an immediate reaction. Hence, the role of the right hemisphere in face perception must have descended from abilities of relatively early vertebrates to recognize the visual appearance of other individuals of their species.

For example, only some species of fishes—among the earliest evolving vertebrates—may be able to recognize individual fish, but birds in general do show a right-hemisphere capacity to recognize individual birds. Keith M. Kendrick of the Babraham Institute in Cambridge, England, has shown that sheep can recognize the faces of other sheep (and of people) from memory and that the right hemisphere is preferentially involved. Charles R. Hamilton and Betty A. Vermeire, both at Texas A&M, have observed similar behavior in monkeys.

In humans neuroscientists have recently recognized that the right hemisphere specializes in face recognition. Prosopagnosia, a neurological disorder that impairs that ability, is more often a result of damage to the right hemisphere than to the left. Extending face recognition to what seems another level, both monkeys and humans interpret emotional facial expressions more accurately with the right hemisphere than with the left. We think that this ability is part of an ancient evolutionary capacity of the right hemisphere for determining identity or familiarity—for judging whether a present stimulus, for instance, has been seen or encountered before.

Global and Local

We have argued for a basic distinction between the role of the left hemisphere in normal action and the role of the right hemisphere in unusual circumstances. But investigators have highlighted additional dichotomies of hemispheric function as well. In humans the right hemisphere “takes in the whole scene,” attending to the global aspects of its environment rather than focusing on a limited number of features. That capacity gives it substantial advantages in analyzing spatial relations. Memories stored by the right hemisphere tend to be organized and recalled as overall patterns rather than as a series of single items. In contrast, the left hemisphere tends to focus on local aspects of its environment.

Striking evidence for the global-local dichotomy in humans has been brought to light by a task invented by David Navon of the University of Haifa in Israel. Brain-damaged patients are asked to copy a picture in which 20 or so small copies of the uppercase letter A have all been arranged to form the shape of a large capital H. Patients with damage to the left hemisphere often make a simple line drawing of the H with no small A letters included; patients with damage to the right hemisphere scatter small A letters unsystematically all over the page.

A similar dichotomy has been detected in chickens, suggesting its relatively early evolution. Richard J. Andrew of the University of Sussex in England and one of us (Vallortigara) have discovered that, as in humans, the domestic chick pays special attention to broad spatial relations with its right hemisphere. Moreover, chicks with the right eye covered, hence receiving input only to the right hemisphere, show interest in a wide range of stimuli, suggesting they are attending to their global environment. Chicks that can attend only with the left hemisphere (left eye covered) focus only on specific, local landmark features.

Why Do Hemispheres Specialize?

Why have vertebrates favored the segregation of certain functions in one or the other half of the brain? To assess an incoming stimulus, an organism must carry out two kinds of analyses simultaneously. It must estimate the overall novelty of the stimulus and take decisive emergency action if needed (right hemisphere). And it must determine whether the stimulus fits some familiar category, so as to make whatever well-established response, if any, is called for (left hemisphere).

To detect novelty, the organism must attend to features that mark an experience as unique. Spatial perception calls for virtually that same kind of “nose for novelty,” because almost any standpoint an animal adopts results in a new configuration of stimuli. That is the function of the right hemisphere. In contrast, to categorize an experience, the organism must recognize which of its features are recurring, while ignoring or discarding its unique or idiosyncratic ones. The result is selective attention, one of the brain’s most important capabilities. That is the function of the left hemisphere.

Perhaps, then, those hemispheric specializations initially evolved because collectively they do a more efficient job of processing both kinds of information at the same time than a brain without such specialized systems. To test this idea, we had to compare the abilities of animals having lateralized brains with animals of the same species having nonlateralized brains. If our idea was correct, those with lateralized brains would be able to perform parallel functions of the left and right hemisphere more efficiently than those with nonlateralized brains.

Fortunately, one of us (Rogers) had already shown that by exposing the embryo of a domestic chick to light or to dark before hatching, she could manipulate the development of hemispheric specialization for certain functions. Just before hatching, the chick embryo’s head is naturally turned so that the left eye is covered by the body and only the right eye can be stimulated by light passing through the egg shell. The light triggers some of the hemispheric specializations for visual processing to develop. By incubating eggs in the dark, Rogers could prevent the specializations from developing. In particular, she found, the dark treatment prevents the left hemisphere from developing its normal superior ability to sort food grains from small pebbles, and it also prevents the right hemisphere from being more responsive than the left to predators.

Rogers and Vallortigara, in collaboration with Paolo Zucca of the University of Teramo in Italy, tested both kinds of chicks on a dual task: the chicks had to find food grains scattered among pebbles while they monitored for the appearance of a model predator overhead. The chicks incubated in light could perform both tasks simultaneously; those incubated in the dark could not—thereby confirming that a lateralized brain is a more efficient processor.

Social “Symmetry Breaking”

Enabling separate and parallel processing to take place in the two hemispheres may increase brain efficiency, but it does not explain why, within a species, one or the other specialization tends to predominate. Why, in most animals, is the left eye (and the right hemisphere) better suited than the right eye (and the left hemisphere) for vigilance against predation? What makes the predominance of one kind of handedness more likely than a symmetric, 50–50 mixture of both?

From an evolutionary standpoint a “broken” symmetry, in which populations are made up mainly of left types or mainly of right types, could be disadvantageous because the behavior of individuals would be more predictable to predators. Predators could learn to approach on the prey’s less vigilant side, thereby reducing the chance of being detected. The uneven proportion of left- and right-type individuals in many populations thus indicates that the imbalance must be so valuable that it persists despite the increased vulnerability to predators. Rogers and Vallortigara have suggested that, among social animals, the advantage of conformity may lie in knowing what to expect from others of one's own species.

Together with Stefano Ghirlanda of the Universities of Stockholm in Sweden and of Bologna in Italy, Vallortigara recently showed mathematically that populations dominated by left-type or by right-type individuals can indeed arise spontaneously if such a population has
frequency-dependent costs and benefits. The mathematical theory of games often shows that the best course of action for an individual may depend on what most other members of its own group decide to do. Applying game theory, Ghirlanda and Vallortigara demonstrated that left- or right-type behavior can evolve in a population under social selection pressures—that is, when asymmetrical individuals must coordinate with others of their species. For example, one would expect schooling fish to have evolved mostly uniform turning preferences, the better to remain together as a school. Solitary fish, in contrast, would probably vary randomly in their turning preferences, because they have little need to swim together. This is in fact the case.

With the realization that the asymmetrical brain is not specific to humans, new questions about a number of higher human functions arise: What are the relative roles of the left and right hemispheres in having self-awareness, consciousness, empathy or the capacity to have flashes of insight? Little is known about those issues. But the findings we have detailed suggest that these functions—like the other human phenomena discussed here—will be best understood in terms of the descent with modification of prehuman capabilities.

Did the Syllable Evolve from Chewing?
According to one of the authors (MacNeilage), the origin of human speech may be traceable to the evolution of the syllable—typically an alternation between consonant and vowel. In the word "mama," for instance, each syllable begins with the consonant sound [m] and ends with the vowel sound [a]. As the cutaway diagrams show, the [m] sound is made by temporarily raising the jaw, or lower mandible, and stopping the flow of air from the lungs by closing the lips (below left). To make the following vowel sound [a], the jaw drops and air flows freely through the vocal tract (below right). MacNeilage has thus proposed that the making of syllabic utterances is an evolutionary modification of routine chewing behavior, which first evolved in mammals 200 million years ago.

A Lateralized Brain Is More Efficient
One of the authors (Rogers) discovered that if she exposed chick embryos to light or to dark before they hatched, she could control whether the two halves of the chick brains developed their specializations for visual processing—that is, whether the chicks hatched with weakly or strongly lateralized brains. Rogers and another one of the authors (Vallortigara), with Paolo Zucca of the University of Teramo in Italy, then compared normal, strongly lateralized chicks with weakly lateralized chicks on two tasks. One task was to sort food grains from small pebbles (usually a job for the left hemisphere); the other task was to respond to a model of a predator (a cutout in the shape of a hawk) that was passed over the chicks (usually a task for the right hemisphere). The weakly lateralized chicks had no trouble learning to tell grains from pebbles when no model hawk was present. But when the hawk "flew" overhead, they frequently failed to detect it, and they were much slower than normal chicks in learning to peck at grains instead of pebbles. In short, without the lateral specializations of their brain, the chicks could not attend to two tasks simultaneously.

Note: This article was originally printed with the title, "Origins of the Left and Right Brain."

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