

Second Edition

# Cognitive Neuroscience

THE BIOLOGY OF  
THE MIND



MICHAEL S. GAZZANIGA  
RICHARD B. IVRY  
GEORGE R. MANGUN



## 14

# Evolutionary Perspectives

In the early 1990s, Giacomo Rizzolatti and his colleagues at the University of Parma studied how single cells in the prefrontal cortex of a monkey respond when the animal moves its hand to grasp an object, in fact, a nice juicy grape. Research has shown that the area they were testing may be homologous to Broca's area in humans, which you may recall from Chapter 9 is identified with language. The researchers found that these cells fire when the monkey grasps the grape with its hand. They do not fire when the monkey sees the grape or is *about* to grasp the grape, but only when it grasps it. Now comes the ingenious part. Rizzolatti showed that the neurons also fire when the monkey observes a human experimenter reaching out to grasp the grape! These "mirror neurons" respond to both the monkey's actions and the actions of others. Rizzolatti suggested that these neurons play a role in "understanding motor events." His view is that the mirror neurons may help the monkey understand another individual's motor actions by mapping the same meaning it associates with its own action onto its observations of the other individual's action.

Is this the ancestral beginnings of what has been called the "theory of mind" module (see Chapter 16)? This system that humans possess allows them to have a theory about another organism's intentions. These mirror neurons are recognizing a movement in another and mapping it to the monkey's own movement. So the meaning of the observed action is matched with that of a self-action. Although the monkey's neurons operate in a system without language, the fact that the mirror neurons are in an area that is considered homologous to Broca's speech area in humans could indicate that these neurons may be the ones that have evolved in humans and allow us to make an assumption about another's intentions. In short, mirror neurons, or what is called a *preadaptation*, may be the beginnings of a neural system that sustains a more complex function in a higher animal.

The fascinating experiments of Rizzolatti raise the questions, How did we get here? Why are our brains the way they are? What do we have in common with other

animals? What makes us unique? What can we learn from existing animals about our origins? What does evolutionary theory have to say about the nature of human cognition?

Neuroscience and cognitive science are beginning to incorporate the facts and theories of comparative anatomists and evolutionary biologists to address these questions. We will start this chapter by reviewing the history of this approach. We then will learn the basic terminology and concepts used by comparative neuroanatomists to illuminate how examining the brains of existing animals can teach us about our evolutionary roots. This enterprise is a tricky one because the structure of animal bodies and brains can vary dramatically, and trying to deduce similar features of brain organization and unique features is difficult. Therefore, we must learn the strategy that comparative neuroscientists use to avoid the pitfalls of applying conclusions from the brain of one species to that of another.



In the second half of the chapter we will show how evolutionary theory is important for understanding learning and cognition. The mind is a collection of old adaptations designed to solve problems that our prehis-

toric ancestors faced, and newly developed features that take shape via activity-dependent mechanisms. Appreciation of the roots of our mental behavior is essential in exploring current cognitive capabilities and limitations,

## EVOLUTION OF THE BRAIN

The brain is a compromise, and therefore the functions that it generates are absolutely imperfect, although relatively optimal. This statement may be bothersome to some of you, possibly because it implies that we humans must be imperfect. This notion, and our long history of struggles to prove just the opposite, has a dramatic impact on our current thinking about the mind, the brain, and the complex behaviors it generates. In addition, the notion goes against what can only be considered a history of dogma regarding two major tenets of human design that shaped the direction of science in earlier times and often form the basis of modern theory. The first is that humans are the pinnacle of life or the center of the cosmos, and the second is that the mind or soul is somehow distinct from the body. The former idea affects how we view humans, and the human brain compared to the brains of other animals. We tend to view evolution as linear, with humans at the top and other animals as degraded forms of ourselves. Therefore, we view brain evolution as additive rather than in the nonlinear fashion in which it should be regarded. For example, complex brains like those of humans are not simply monkey brains or chimpanzee brains with a few new parts added, such as Broca's area and prefrontal cortex. Rather, the human brain is a unique amalgamation of evolutionary old areas and new areas that have been modified in predictable ways through expansion or reduction of existing parts, formation of new connections, and adaptations for new environmental demands. The latter notion, that there is some unique aspect of the human condition that is different from the condition of other animals, affects how we compare animal brains with human brains, and the conclusions we reach regarding cortical evolution in mammals.

Before we can actually talk about the nuts and bolts of evolution and its impact on our thinking about the brain and cognition, it is necessary to discuss the history of evolutionary thought. History shapes our current understanding of the brain and our beliefs about how things work. Indeed, as already noted, two very old ideas are embedded in our culture

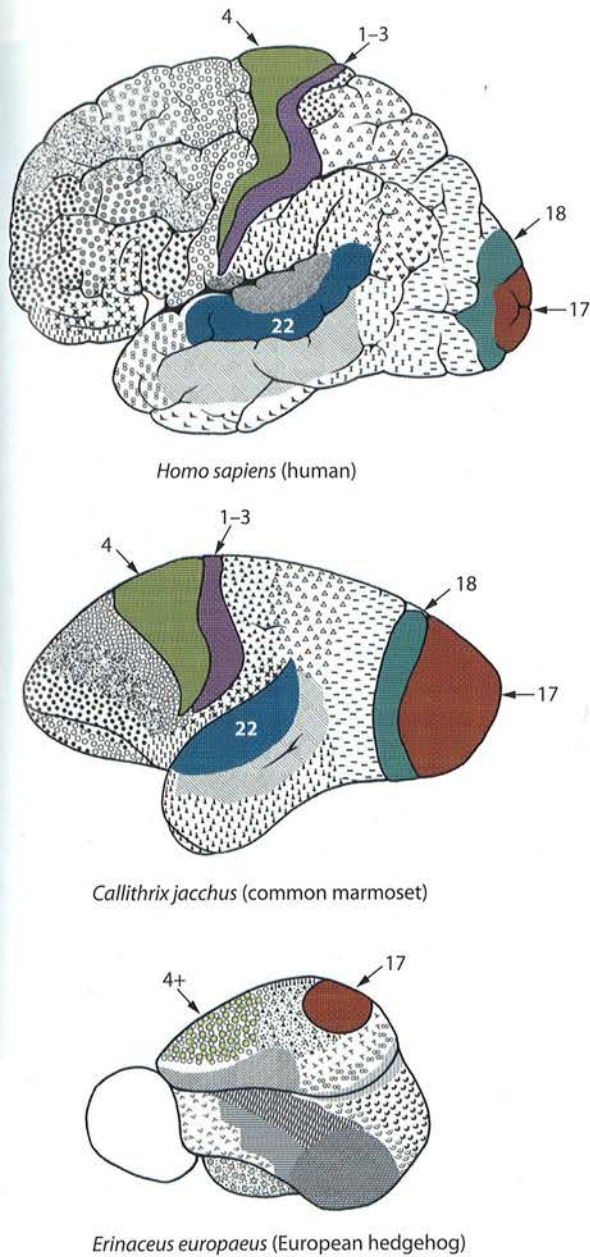
and form the basis of our current thinking on issues regarding cognition and the evolution of the nervous system.

### The Historical Underpinning of Contemporary Evolutionary Neurobiology

Probably the most significant event in the biological sciences during the nineteenth century was the discovery by Charles Darwin (1859) and Alfred Russell Wallace that **natural selection** was the vehicle of evolution. The basic observations were that individuals within a population vary, and that changes in individuals arise via natural selection of these variants. The trait or characteristic that is selected for has no absolute value, but its value is measured by how well it contributes to the individual's fitness within a particular environment. The details of this theory deserve a more in-depth discussion and are dealt with later. Here, we only wish to underscore the historical importance of this discovery, and its impact on modern evolutionary biology.

A number of twentieth-century scientists contributed to our understanding of the brain and its evolution. Investigators early in this century, such as Korbinian Brodmann (1909), utilized the technique of Franz Nissl to distinguish the architecture of the cerebral cortex in humans from that in other mammals. Most of us know Brodmann for his cytoarchitectonic descriptions of the human brain. Although he made a number of errors regarding the divisions of the cerebral cortex, an illustration of the divisions of the human brain likely exists in every textbook on the brain that has ever been printed. Perhaps his most important contribution was his cross-species comparisons of the cytoarchitecture of the cerebral cortex (Figure 14.1). He observed that some cytoarchitectonic areas of the brain, such as area 17, could be found in all species examined. The ubiquity of these fields across phyla suggested that they must be inherited from a common ancestor. He proposed that these cytoarchitectonic areas had different functions, although there was no direct evidence for this hypothesis. We now know that area 17 corresponds to the primary visual area





**Figure 14.1** Cytoarchitectonic divisions of the human, marmoset, and hedgehog neocortex as described by Brodmann (1909). The different patterns of black and white stipple denote separate regions of the neocortex that have different architectonic appearances. Some cortical areas, such as areas 17 and 4, were present in all animals investigated, suggesting that these regions are homologous. Other regions, such as area 22, were present only in primates.

in all mammals. Contemporaries of Brodmann such as Joseph Shaw Bolton, George Elliot Smith, and Constantin von Economo devoted much time to parceling the human cerebral cortex into separate divisions based on cytoarchitecture. These early investigators established a

common view of the functional organization of the human brain that still persists today.

This view, outlined by Jon Kaas (Merzenich and Kaas, 1980), is that sensory input is relayed from subcortical structures to primary receiving areas of the neocortex (such as V1). These primary areas send this sensory information to secondary sensory or “psychic” cortex in which more complex perceptual functions are performed. This information is finally relayed to multimodal “association areas” for higher-order processing. This traditional view, with the caveat that humans possess more association cortex than any other mammal, still dominates neuroscience. However, as Kaas (1999) pointed out, a dramatic revision of this view is necessary as most of the neocortex is sensory or motor rather than associative in nature.

Major events occurring in other disciplines in the middle of the twentieth century were to have a tremendous impact on neuroscience in general and evolutionary neurobiology in particular. James Watson, Francis Crick, and Maurice Wilkins discovered the molecular structure of deoxyribonucleic acid (DNA), the “double helix,” and its significance for information transfer in living organisms. Their discovery that life could be reduced to this very basic unit of organization, which continually replicates itself, rocked the world. On the heels of this discovery, a quiet revolution was brewing. From the 1950s through the 1970s Konrad Lorenz, Niko Tinbergen, and Karl Von Frisch, all of whom shared the Nobel Prize in medicine (physiology) in 1973, led the fields of **ethology**, the study of animal behavior, and its counterpart, **neuroethology**, the study of the neurobiology of animal behavior. Lorenz and Tinbergen contributed to the fields in two fundamental ways. They focused attention on the innate aspects of behavior, and they provided empirical data from animal studies that allowed behavior to be understood from a more biological perspective.

Probably the most famous study of Tinbergen and Lorenz (see Tinbergen, 1957) was that on the egg-rolling response in greylag geese. When the brooding goose notices that an egg has rolled outside of the nest, a very stereotypic behavior ensues. First, the goose fixates on the misplaced egg and then rises and extends her neck to touch the egg. She then places her bill over the egg and carefully rolls it back into the nest. Tinbergen and Lorenz at first believed that the goose was thoughtfully performing a behavior to return a lost egg to the nest. However, when these scientists removed the egg once the goose had initiated the behavior, the goose continued with the behavior despite the absence of the egg. Thus, this behavior has an initial releaser (the sight of the egg out of the



## MILESTONES IN COGNITIVE NEUROSCIENCE

**An Interview with Steven Pinker, Ph.D.** Steven Pinker is a professor of brain and cognitive science at MIT. He has worked on problems in vision, attention, development of language, and evolution.

**Authors:** Why is it important for students of the mind to understand the principles of evolution?

**SP:** The brain is a highly organized, nonrandom system, and it can't be understood without knowing the forces that gave rise to that organization. We know the brain did not fall out of the sky; like other parts of the body, its functional complexity—the fact that it can do interesting things like see, think, and act—is a product of evolutionary forces, particularly natural selection.

**Authors:** OK, let's get down and dirty. Suppose a student is interested in the problem of memory or attention or even morality. These issues can be studied without mentioning natural selection. How does natural selection inform them about their chosen topic?

**SP:** These issues cannot be understood without natural selection. Natural selection is the rationale for reverse-engineering the brain—figuring out what it was designed to accomplish. Why do we remember recent and frequent items best? Is it some inherent property of the stickiness and softness of neural tissue? Or could evolution have built a brain that remembers everything equally well, but steps in that direction were selected against? When you compare the computer information

retrieval system at the library, which spills hundreds of useless titles in your lap, to a human expert, who homes in on the five or six most appropriate ones, you appreciate that human memory might be close to optimal in trading off the likelihood of finding needed information against the costs in time of considering unneeded information. Since organisms operate in real time, this is not a trivial trade-off. John Anderson has shown that retrieving frequent and recent items is the optimal strategy for any information access system, so the explanation for the human case is quite likely to be that the brain is specially organized to be frequency- and recency-sensitive because of the selective advantages it brought, not that calcium channels or whatever make it inevitable. As for morality, the necessity of evolutionary thinking is even stronger. Evolutionary game theory has made very strong predictions of what kinds of algorithms have to be in the mind of an organism that can engage in moral behavior. Many commonsense notions prevalent among academics (e.g., that morality evolved for group cohesion, or that there is an instinct for aggression) are literally unevolvable.

**Authors:** Unevolvable? Come at that point one more time.

nest) that triggers it, and then an innate, highly stereotypic pattern that they termed a *fixed action pattern*. A fixed action pattern, once initiated, continues through to completion, independent of feedback.

Ethologists and neuroethologists stressed the importance of invoking evolutionary theory to understand animal behavior. Unfortunately, while evolutionary theory was used to understand animal behavior, it was still excluded from explanations of human behavior. Indeed, at this point, sociology and psychology were all but devoid of any theory that incorporated evolutionary principles, as Hodos and Campbell (1969) pointed out.

In the early 1970s, E.O. Wilson sought to “reformulate the foundations of the social sciences” and “biologize” them, and in essence contracted a marriage between zoology and population biology. He invoked evolutionary theory to explain social phenomena, and in 1975 promoted the new field of **sociobiology**, which

he defined as the systematic study of the biological basis of all social behavior. Sociobiology allowed for a logical explanation of animal behavior that at first glance seemed counter to natural selection. For instance, highly social insects, such as ants, have cooperative care for the young and a reproductive division of labor, with a number of sterile individuals working on the behalf of fecund nest mates. A lack of reproduction by all individuals in the colony seemed at odds with what was known about evolution and natural selection. However, others described the reproductive benefits of colonial life by examining the relatedness of individuals within the colony, and the high net contribution to their reproductive fitness that such lifestyles allow (i.e., the propagation of their genes into future generations).

Wilson (1975) observed that “. . . in evolutionary time the individual organism counts for almost nothing. In a Darwinist sense the organism does not live for itself. Its



**SP:** One might think a group of indiscriminate altruists, all helping each other out, would do better than a group of selfish creatures who refuse to sacrifice for the benefit of all. But the problem is getting the altruistic group to begin with. A mutant with a tendency toward selfishness would enjoy all the benefits of his altruistic buddies without paying the costs. Nothing could stop it from proliferating through the group, given that individuals reproduce faster than whole groups. As for aggression, again the text of other organisms has to be taken into account. A bully mutant would do fine at first, but after a bunch of generations everyone will be a bully, and the advantage is gone. It's not that altruism and aggression can't evolve; it's just that they can evolve only in conjunction with information-processing mechanisms that strategically assess how and when to deploy them.

**Authors:** Finally, with the new awareness of the importance of evolutionary thinking for understanding mental processes, how might experiments be executed in the future? If, for example, one hypothesized that human memory systems were built to aid in finding food sources scattered about a home base, might one reject using word-pair associates as a way of understanding human memory? Instead wouldn't one want to study the efficiency of memory with and without a lot of spatial cues?

**SP:** Certainly, it would do everyone good to pay more attention to the ecological validity of the stimu-

lus materials and the task used in experiments. It also is important to think of the brain as a family of systems engineered to solve the kinds of problems the organism faced in its evolutionary history (e.g., foraging, mating, language or other forms of communication, etc.) rather than hoping to explain intelligence exclusively with very crude general mechanisms like forming associative bonds. And attention to phylogeny and speciation would correct the lamentable tendency to treat all animals as half-baked humans we can cut up, rather than as cohesively functioning species that are well adapted to their own niches.

But ultimately, evolutionary thinking isn't a specific theory that one goes out and tests like a hypothesis about shape recognition. A cognitive neuroscientist should understand evolution for the same reason a biologist should understand chemistry, or a chemist should understand physics. The chemist doesn't ask, "How will knowing physics help me to design my next experiment?" He or she had better know physics because everything done in chemistry ultimately has to make sense in the light of physics. Similarly, cognitive science and neuroscience are studying the products of specific causal processes (natural selection and other evolutionary forces) and ultimately nothing in those fields makes sense—no explanation, no experiment, no choice of an organism to study—until it is made consistent with what we know about those processes.

primary function is not even to reproduce other organisms; it reproduces genes, and it serves as their temporary carrier." This idea represented a large shift in paradigm from traditional psychology, sociology, and ethology, and constituted a virtual revolution in perspective. The contributions of Maynard Smith, William Hamilton, Robert Trivers, and David Barrash, along with many others scientists, helped shape the field of sociobiology in its infancy in the late 1970s and 1980s. In 1976, the highly popular book *The Selfish Gene*, by Richard Dawkins, drew attention to the field and put the gene at the center of importance. Dawkins's contention was that life is simply about the replication of genes and the propagation of "good" genes into the future.

Since its introduction, sociobiology has undergone a rebirth and has been strongly embraced by psychology and sociology. Modern proponents of the newly evolved field of **evolutionary psychology** are Steven Pinker (see

An Interview with Steven Pinker, Ph.D.), Leda Cosmides, and John Tooby, who use an evolutionary framework to explain cognitive behavior. Evolutionary psychologists have painted a picture different from that portrayed by sociobiologists. They do not believe all behaviors are driven by genetic mechanisms. Rather they believe the brain has built into it adaptations that are of a more general nature. These adaptations are a set of rules that govern behavior. However, since there are an infinite number of environments, the rules can be applied differently, resulting in an infinite number of behaviors. This view is quite different from that of traditional sociobiologists; it allows for a more objective, biologically compatible view of human behavior compared with traditional psychology-based interpretations.

Cosmides and Tooby (1995) stated their case in terms of answering the question, What are our brains built for?



Understanding the neural organization of the brain depends on understanding the functional organization of its cognitive devices. The brain originally came into existence, and accumulated its particular set of design features only because these features functionally contributed to the organism's propagation. This contribution, that is, the evolutionary function of the brain, is obviously the adaptive regulation of behavior and physiology on the basis of information derived from the body and from the environment. The brain performs no significant mechanical, metabolic, or chemical service for the organism; its function is purely informational, computational, and regulatory in nature. Because the function of the brain is informational in nature, its precise functional organization can be described accurately only in a language that is capable of expressing its informational functions, that is, in cognitive terms, rather than in cellular, anatomical, or chemical terms. Cognitive investigations are not some soft, optional activity that goes on only until the real neural analysis can be performed. Instead, the mapping of the computational adaptations of the brain is an unavoidable and indispensable step in the neuroscience research enterprise....

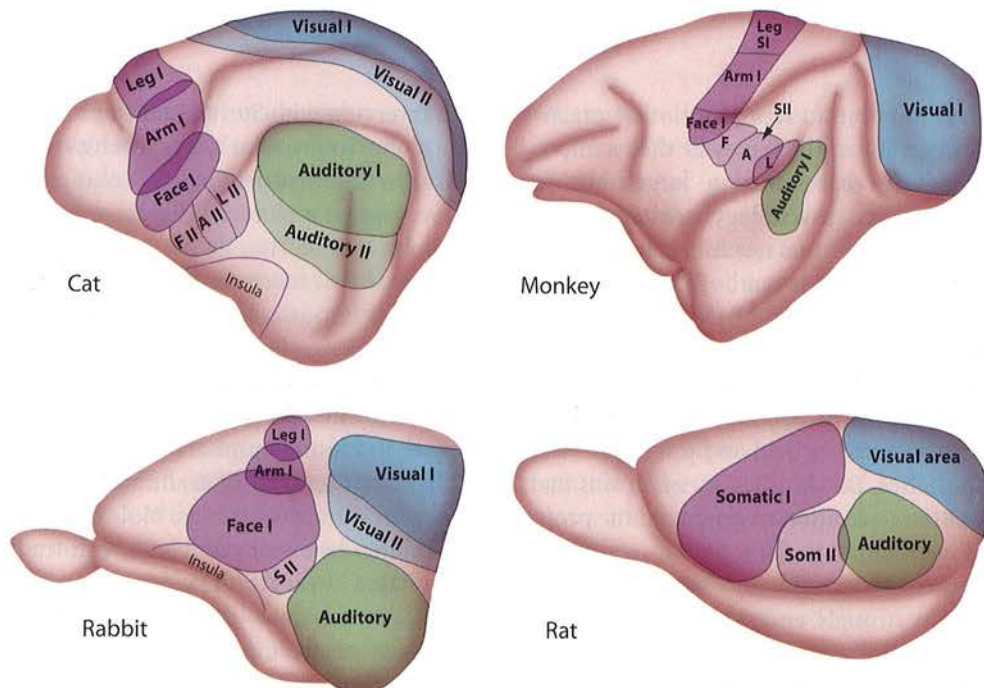
We shall return to these ideas after considering how current neurobiologists approach studying the brain from a comparative perspective.

### Modern Evolutionary Neurobiology: Assumptions and Aims

Modern evolutionary neurobiology or **comparative neuroscience** (Bullock, 1984a), while not incompatible with sociobiology, evolutionary psychology, or neuroethology, differs from these disciplines in that it is more brain centered and systems oriented. Further, while it has an appreciation of the fundamental role of genes in evolution, it also has an appreciation of the complex interaction between genes and the environment in the construction of a nervous system. Comparative neuroscience probably began with Brodmann (1909) and his demonstration that mammals have neocortical areas in common, despite very distant phylogenetic relationships. Unfortunately, evolutionary neurobiology was put on the back burner for some 40 years.

Around the middle of the twentieth century, Clinton Woolsey (1952, 1958) and colleagues used electrophysiological recording techniques to subdivide the neocortex into functional subdivisions in a variety of mammals (Figure 14.2). His work empirically demonstrated what Brodmann only proposed: that the separate architectonic areas of the neocortex were indeed related to different functions.

**Figure 14.2** Functional subdivisions of the neocortex as described by Woolsey and colleagues (1952, 1958) in the middle of the twentieth century. Evoked potentials in response to mechanical stimulation of the sensory surface were used to determine the number and topographic organization of different sensory neocortical areas in a variety of mammals. Some areas, such as the primary visual area (V1), somatosensory area (S1), and auditory area (A1), were in all the mammals they investigated, suggesting descent from a common ancestor. Additional sensory areas, such as S2 and V2, also were present in most of the mammals investigated.





Charles Judson Herrick, a contemporary of Woolsey, also advanced the field of comparative neuroanatomy. As a result of his numerous cross-species comparisons of neural structures, he reached profound conclusions regarding how complexity is achieved in the nervous system. After examining the connections of the brain in a variety of species, he proposed that a slight increase in the connectivity of homologous structures could effectively increase the processing capacity of the brain exponentially. Herrick (1963) proposed that “during a few minutes of intense cortical activity the number of interneuronic connections actually made (counting also those that are activated more than once in different associational patterns) may well be as great as the total number of atoms in the solar system. Certainly not all anatomically present connections of nervous elements are ever used, but the *potentialities* of diversity of cortical associational combinations are practically unlimited and the personal experience of the individual is probably an important factor in determining which of these possibilities will be actually realized.”

From the 1960s through the 1980s, Irving Diamond, influenced by George Bishop and Le Gros Clark in the 1950s, focused his research on the evolution of the mammalian brain and the use of the comparative approach to understand the brain, particularly the evolution of thalamocortical relationships. He was a pioneer in the use of modern neuroanatomical techniques and trained a number of contemporary comparative neuroscientists, including Jon Kaas.

Kaas, a graduate student of Diamond's and a postdoctoral student of Woolsey's, elegantly applied the comparative approach to understanding brain organization and evolution. He has combined the techniques used in each of his mentors' laboratories to examine the functional and anatomical organization of the neocortex in mammals. Using multiunit electrophysiological recording techniques, along with examinations of cortical architecture and connections, Kaas has studied species ranging from tenrecs (small insectivores from Madagascar) to lorises (small primates found in Southeast Asia) to humans, and has become the leading figure in the evolutionary neurobiology of the mammalian brain.

Kaas has advanced our understanding by challenging the traditional view that primate neocortex, particularly human neocortex, is composed predominately of “association areas.” Association cortex was defined by default as cortex that was not sensory, and presumably was involved in high-level perceptual and cognitive processing. His work in primates over the past several decades has demonstrated that almost all of the neocortex is sensory and motor in nature, and that complex brains evolve not by simply expanding association cortex, but by increasing the number of

sensory and motor areas and the interconnections between them. As Kaas (1997) himself put it, “The validity of a comparative approach depends on the basic premise that theories of brain organization applied to any given species, say humans, should be compatible with evidence and theories of brain organization for other species, with the evidence and theories for closely related species being most relevant.”

Scientists who compare brains of animals to deduce how brains are constructed in evolution use a variety of names to identify themselves, including *comparative neuroanatomists*, *physiological psychologists*, *evolutionary neurobiologists*, and *comparative neuroscientists*. However, all modern comparative studies are undertaken to address several aims based on a few underlying assumptions. The first assumption is that *all behavior in all animals is generated by the nervous system*. This definition of behavior is not limited to sensory, perceptual, and motor behaviors but includes cognitive behaviors and even those that are difficult to define and measure, such as consciousness. The second assumption is that *brains evolve, and therefore behaviors evolve*. Thus, behavior cannot be completely understood without an evolutionary perspective. The final assumption is that *we can understand the process of the evolution of the brain and the behavior it generates by examining the products of the process, the products of the process being extant (existing) animals*.

Theodore Bullock (1984a) has led the field of comparative neurobiology for nearly half a century. As he put it, “Long before the human species appeared, the pinnacle and greatest achievement of evolution was already the brain—as it had been before mammals appeared, before land vertebrates, before vertebrates. From this point of view, everything else in the multicellular animal world was evolved to maintain and reproduce nervous systems—that is, to mediate behavior, to cause animals to *do* things. Animals with simple and primitive or no nervous system have been champions at surviving, reproducing, and distributing themselves, but they have limited behavioral repertoires. The essence of evolution is the production and replication of diversity—and more than anything else, diversity in behavior.”

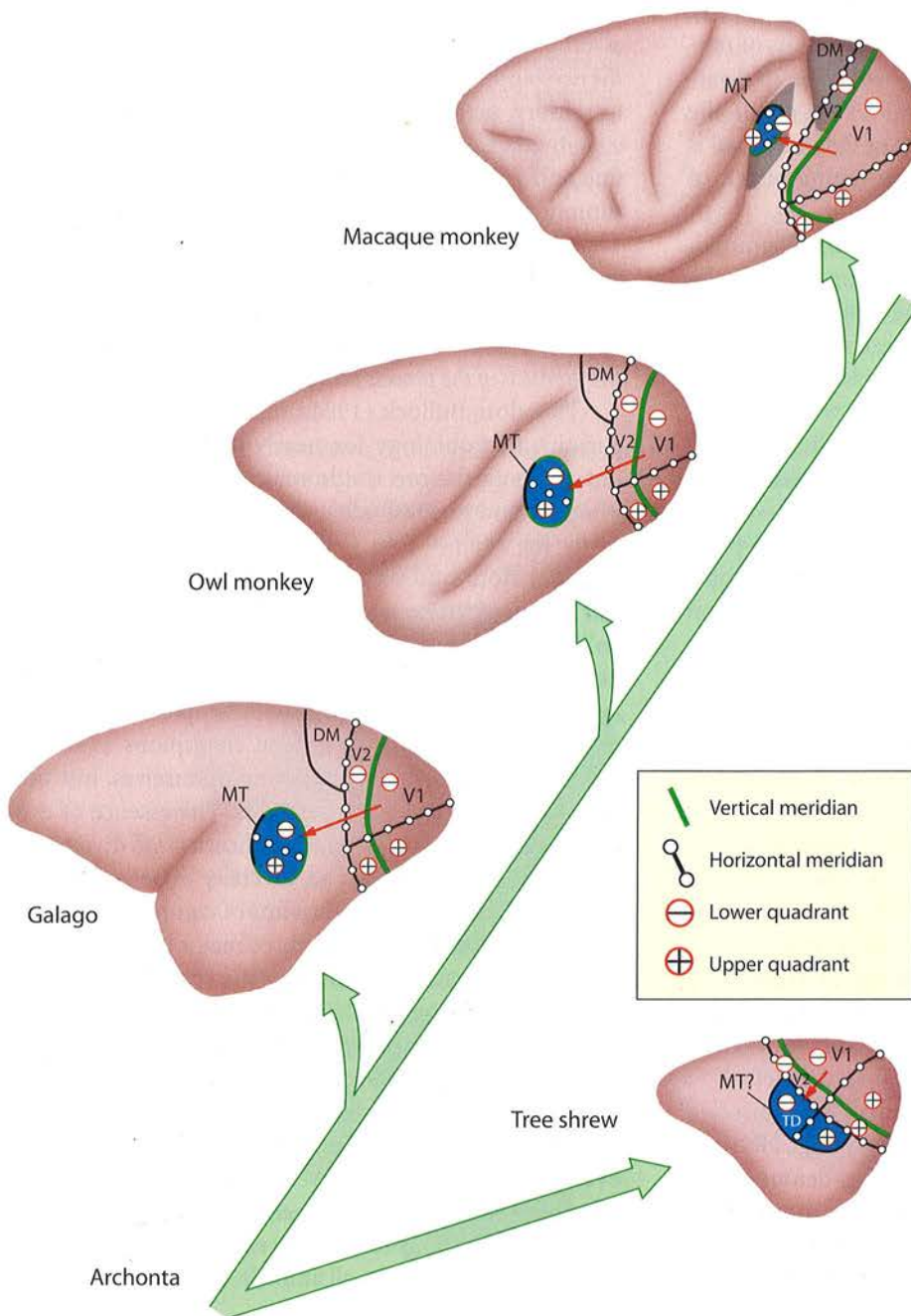
Bullock describes well the aims of comparative neuroscience, and lists them under three major headings: roots, rules, and relevance. By phylogenetic *roots*, he means the evolutionary history of the brain and behavior. How are brains similar and different? What has evolution produced? He describes the *rules* of change as the mechanisms that give rise to changes in the nervous systems in the course of evolution. Are there constraints under which evolving nervous systems develop? Finally, the *relevance* of our observations refers to the general principles of organization and functions that can be extrapolated from a particular animal studied to all animals, including humans.



The choice of animal that researchers use for their experiments depends on their aim. For instance, if they are interested in how sodium channels work in neurons, the squid is an excellent choice because it contains axons that are large and easily accessible. Further, because sodium channels evolved very early in animal evolution, and their basic contribution to the action potential has not changed, findings in the squid are relevant to human neurons.

If researchers are interested in when the middle temporal (MT) visual area, an area linked to motion perception in primates, first appeared (i.e., the roots of MT),

then their choice of animals should include representatives of early primate lineages such as lemurs, galagos, and lorises, as well as other archontans such as tree shrews (Figure 14.3). Tree shrews (squirrel-like mammals) belong to a family of mammals termed Tupaiidae, whose ancestors are believed by many to form an early branch of the primate lineage. Lemurs form a unique family of primates and exist only on the island of Madagascar off the southeastern coast of Africa. Galagos and lorises are members of another primate family (Lorisidae) and are found in Africa and Southeast Asia. The ancestor of these



**Figure 14.3** A comparative analysis can be used to determine when area MT (blue) evolved in primates. The visuotopic organization and relative location of MT are similar in prosimians (galagos), New World monkeys (owl monkeys), and Old World monkeys (macaque monkeys). In addition, the architectonic appearance of area MT and the presence of direct connections from the primary visual area add further support to the hypothesis that area MT is homologous in all of these primates. An out-group analysis of a more distantly related group (tree shrews) indicates that some features of an MT-like area are present in the area labeled TD. However, further evidence needs to be gathered to determine if TD is homologous to MT in primates. Without this evidence, it appears that area MT evolved some time before the emergence of prosimians, but after the radiation of early archontans such as tree shrews. Shaded gray areas indicate cortex that resides in fissures.



primates diverged very early in primate evolution, and extant species are believed to represent, at least to some extent, the primate ancestor.

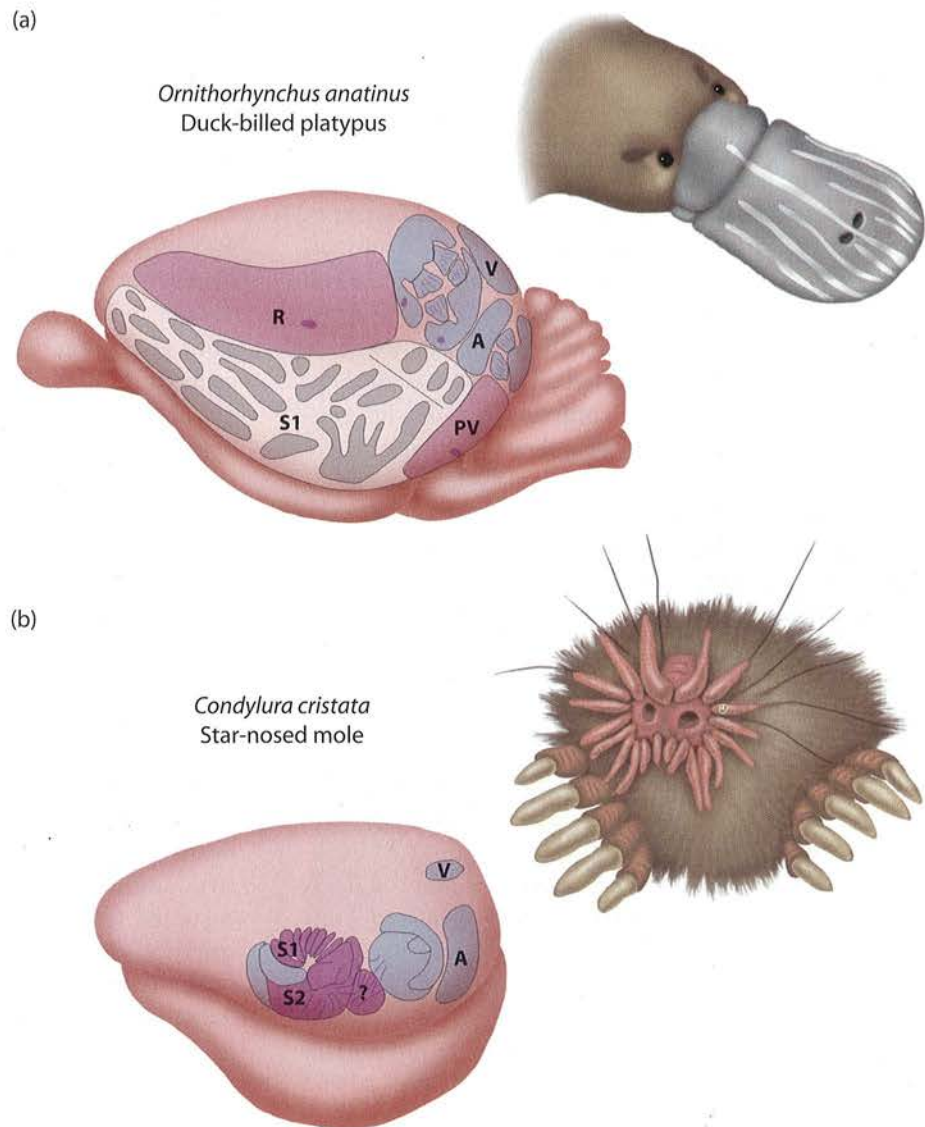
Kaas has addressed the question of when area MT arose in primate evolution. He has examined primates from different infraorders, including Lorisiformes (primates that include galagos and lorises), New World monkeys (South American monkeys such as squirrel monkeys and marmosets), and Old World monkeys (African and Asian monkeys such as macaque monkeys and talapoin monkeys), and has determined that all of these primates have an area MT. Although there have been no studies on lemurs, his examination of tree shrews demonstrated a V1 projection zone that shares some features of MT. However, a distinct MT, like that in primates, does not appear to be present. Thus, he concluded that MT may have had some primitive underpinning early in primate evolu-

tion, but probably arose after the Tupaiidae radiation and some time before the emergence of Lorisiformes.

If researchers are interested in the rules of change for specialized peripheral structures and the behaviors associated with these structures, they might use a variety of highly specialized mammals such as the duck-billed platypus (Krubitzer et al., 1995; Krubitzer, 1998) or the star-nosed mole (Catania et al., 1993; Catania and Kaas, 1995) to determine how the somatosensory and motor cortex is modified in relation to specialization, and if the changes take a similar form. For instance, the duck-billed platypus has a specialized bill, and approximately 80% of its nervous system is devoted to processing inputs from the bill. Likewise, the star-nosed mole has an extraordinary specialization of the nose, and like the platypus, a large portion of its nervous system is devoted to processing inputs from the nose (Figure 14.4). This neural magnification of

**Figure 14.4** Some mammals are highly derived (have extreme specializations of some body part, behavior, or piece of neural tissue).

(a) The bill of the platypus contains both mechanosensory (gray) and electrosensory (white) receptors arranged in stripes. In the primary somatosensory area (S1), neurons are aggregated in groups of mechanosensory (gray) and electrosensory (white) inputs. The magnification of the representation of the bill in the neocortex is extreme, assuming about 75% of the entire neocortex. (b) Specializations of the face, including the nose of the star-nosed mole, have evolved independently in a number of lineages. The nose of this mole has evolved a number of movable appendages used for exploration, prey capture, and feeding. An independent magnification of the representation of this highly derived nose is found in the primary (S1) and secondary (S2) somatosensory areas in the neocortex. These examples illustrate that the types of modifications to the neocortex are highly constrained. (a) Adapted from Krubitzer (2000). (b) Adapted from Catania et al. (1993) and Catania and Kaas (1995).





specialized body parts arose independently in these mammals and is a feature of modifications shared by a number of mammals. Because the neural specialization looks remarkably similar, it seems likely that its nervous system implements certain rules when it is generating representations of specialized body parts. Thus, studying the neural organization and connections in these mammals may provide some insight into what these rules are.

## FIRST PRINCIPLES

Charles Darwin (1859) is a powerful and pervasive figure in modern biology. His theory of evolution via natural selection is one that everyone believes they understand. After all, isn't the idea of natural selection that only the fittest survive? Doesn't it have something to do with our evolution from lower animals? It turns out that when most people are asked about the significance of evolution, a hodgepodge of ideas bubble up, unstructured and diffuse. If we are to thoroughly understand its importance, and how we can apply this evolutionary perspective to our theories of cognition, we must learn a few basic principles of the evolutionary theory (Williams, 1966).

The concept of evolution was appreciated well before Darwin's time. Early scientists noted that animals had a number of parts in common and therefore all animals must be related. In other words, there must be a common ancestor. Early scientists further reasoned that if God had indeed created all animals simultaneously, and if all animals are complete, why do some animals have features or parts that they apparently do not use? However, while speculation regarding evolution was rife, the vehicle by which it proceeded was not appreciated. In the mid-1800s, both Charles Darwin and Alfred Russell Wallace hit upon this vehicle. Three observations led to Darwin's theory of evolution by natural selection. The first was that individuals within a population of animals vary, the second was that some of this variation is **heritable**, and the third was that not all individuals within a population survive. How this variability was generated was not appreciated until Gregor Johann Mendel's (1822–1884) principles of heredity were rediscovered in the early twentieth century. Evolution proceeds by differential reproductive success, by the natural selection of some **traits** or characteristics over others. The traits or characteristics that are selected for endow some benefit. It should be noted that there is no absolute value given to any trait selected for (i.e., big brains with many parts are not absolutely better).

Now that we have an overview of the theoretical basis of an evolutionary perspective, we need to delve more deeply into evolution via natural selection, the terms associated with the field of evolutionary neurobiology, and the use of the comparative approach to formulate hypotheses and make valid inferences regarding the human condition.

Natural selection acts on the variations of the phenotype within the population. The **phenotype** is an observable trait, or set of characteristics of an organism. A phenotype can refer to a morphological structure, like the hand, foot, leg, heart, or kidney, as well as a neural structure, such as the lateral geniculate nucleus, the superior colliculus, the neocortex, or a cortical field within the neocortex. We also can describe neural properties as having a particular phenotype, such as the on/off responses of ganglion cells in the retina, and behaviors as being phenotypic, such as the caching of food by squirrels. A **genotype** refers to the genetic composition of an organism. Any particular phenotype is the result of the genotype (which is not directly observed) as well as environmental or activity-dependent mechanisms (see Chapter 15).

The measure of evolutionary success in terms of some gene, trait, or behavior being represented in future generations is a measure of its **fitness**. An **adaptation** is a characteristic of a living thing that contributes to its fitness. Thus, it is a process by which a species adjusts to environmental change, or a feature of an organism that is suited to the environment. For example, the hand in primates is an adaptation of the distal forelimb used for tactile exploration and active reaching. This same (i.e., homologous—see below) structure has been adapted in bats for flying, in dolphins for swimming, and in moles for digging. The acquisition of adaptations through natural selection is the heart of the evolutionary process. This applies to morphological structures, behaviors, and the underlying nervous system that generates them.

A related term is exaptation, first coined by Stephen Jay Gould of Harvard University. **Exaptation** refers to a structure that serves a particular function but then is co-opted for some other, very different function. For instance, the lateral line in aquatic anamniotes (e.g., jawless vertebrates, cartilaginous fish, amphibians) contains hair cell-like receptors used for electroreception (the ability to detect changes in electrical current) or mechanoreception (the ability to detect mechanical



## MILESTONES IN COGNITIVE NEUROSCIENCE

## Darwin's Big Idea

Charles Darwin was a genius by any measure. He provided humankind with the key idea about our origins, the idea of natural selection. He was the first one who brought together extensive data that the idea of natural selection had sustaining value in understanding human origins. He summarized his idea in two long sentences, as recently recounted by Daniel Dennett in his fascinating book, *Darwin's Dangerous Idea* (1995). Here is that idea:

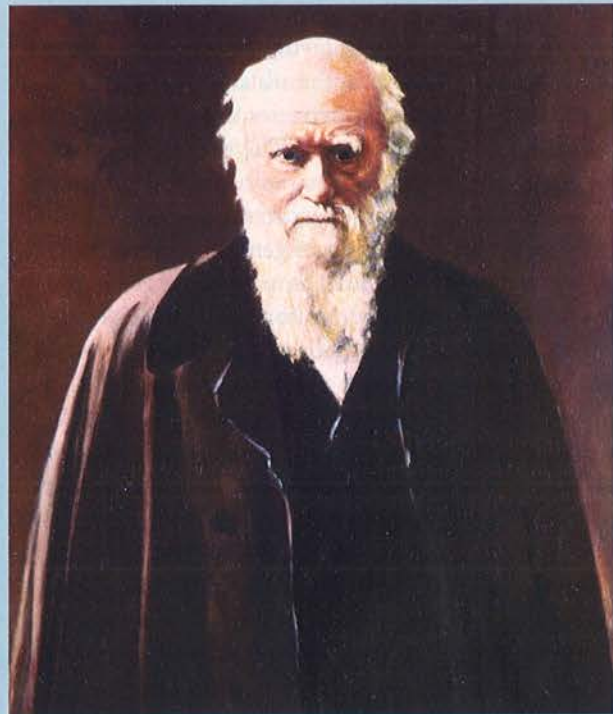
If during the long course of ages and under varying conditions of life, organic beings vary at all in the several parts of their organization, and I think this cannot be disputed; if thereby, owing to the high geometric powers of increase of each species, at some age, season, or year, a severe struggle for life, and this certainly cannot be disputed; then considering the infinite complexity of the relations of all organic beings to each other and to their conditions of existence, causing an infinite diversity in structure, constitution, and habits, to be advantageous to them, I think it would be a most extraordinary fact if, no variation ever had occurred useful to each being's own welfare, in the same way as so many variations have occurred useful to man. But if variations useful to any organic being do occur, assuredly individuals thus characterized will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance they will tend to produce offspring similarly characterized. This principle of preservation, I have called, for the sake of brevity, Natural Selection.

Now, while Darwin could have used an editor, he did condense the most powerful idea in biology into two sentences. And yet, as Dennett pointed out in his book, his brilliant idea was not born from whole cloth. In his *Dialogues*, the great philosopher David Hume had three characters carry out a fictional debate about whether the world exists as a result of a design; that is, any complex entity must have a designer and in this case it is God. Cleanthes, the Greek philosopher, had previously defended the Argument for Design:

Look round the world: Contemplate the whole and every part of it: You will find it to be nothing but one great machine, subdivided into an infinite number of lesser machines, which again admit of subdivisions to a degree beyond what human senses and faculties can

trace and explain. All these various machines, and even their most minute parts, are adjusted to each other with an accuracy which ravished into admiration all men who have ever contemplated them. The curious adapting of means to ends, throughout all nature, resembles, exactly, though it much exceeds, the productions of human contrivance, of human design, thought, wisdom, and intelligence. Since therefore the effects resemble each other, we are led to infer, by all the rules of analogy, that the causes also resemble, and that the Author of Nature is somewhat similar to the mind of man, though possessed of much larger faculties, proportioned to the grandeur of the work which he has executed. By this argument a posteriori, and by this argument alone, do we prove at once the existence of a Deity and his similarity to human mind and intelligence.

Translate "Deity" to "Natural Selection" and a tangible mechanism has been articulated, which was Darwin's genius. And yet, the idea was in the air 80 years before he wrote about it.



Charles Darwin



displacement of some structure, e.g., hair follicle, skin, and cilia of hair cells). In mammals, the inner ear is an exaptation of the lateral line. The hair cells in the inner ear of mammals are involved in transducing air pressure changes (sound) into neural activity via hydraulic and mechanosensory mechanisms.

The heritable part of the natural selection equation is the gene. **Genes** are composed of a complex organic molecule termed *deoxyribonucleic acid* or DNA, and have alternative forms called **alleles**. For instance, if two alleles for a gene responsible for height exist in the population (A for tall and a for short), the phenotype will include one of three allelic combinations (AA, aa, or Aa). *Homozygous* refers to the occurrence of identical alleles at one or more genetic loci (e.g., AA or aa), while *heterozygous* refers to the occurrence of different alleles at one or more genetic loci (Aa). From an evolutionary perspective, over time different alleles compete with each other for space on the chromosome. A **chromosome** is a structure composed of nucleic acids and proteins within the nucleus of a cell, which contains the genetic material (DNA) of an organism. Selection is the ultimate process of the differential reproductive success of alternative alleles.

At this point it is useful to introduce two terms regarding genes, and ultimately the characteristics or functions that they generate. The first is genetic specificity. **Genetic specificity** means that one gene is responsible for a single function or behavior. For instance, a single gene encodes the egg-laying peptide prohormone of molluscs such as aplysia, the sea slug (Geraerts et al., 1994). Thus, a very specific behavior, egg-laying, appears to be encoded by a single gene. The general idea in sociobiology that complex behaviors such as altruism, aggression, and even some aspects of cognition are controlled by a gene, or a set of genes directly responsible for that behavior, at least in part, subscribes to genetic specificity. While this notion is attractive and has gained much notoriety because of its simplicity, most consider genetic specificity to be the exception to the rule, rather than a common occurrence. The second concept is **genetic pleiotropy**, or one gene that has many functions. From a developmental perspective, one gene can participate in the generation of a number of different events and can be expressed differentially at various times for different purposes.

For example, one might ask why diseases like Alzheimer's or even schizophrenia survive in the population. Alzheimer's disease appears late in life, and accumulating evidence indicates that this disease is mediated genetically. Why would such genes be selected for? The likely answer to this question is that their selection is

due to genetic pleiotropy. The genes responsible for unleashing the neuropathological state of this disease are selected for because they play some positive role early in life. That the same gene has detrimental effects later in life is irrelevant in evolutionary terms, because its negative effects occur well after the age of reproduction. Even the genes for schizophrenia, which has a wide distribution throughout the species, most likely have a positive role as well as the relatively negative effect in the environment in which they currently are expressed.

Because of genetic pleiotropy, structures, or components of structures, functions, and behaviors get carried along in evolution as a package of positive, negative, and neutral events. The assignment of a trait as negative or positive depends on the environment in which it is expressed. This is why the brain is a compromise. It is a well-adapted structure, yet it consists of a combination of positive, negative, and neutral characteristics, with the net effect based on the particular environment in which it finds itself. Should the environment change, the value or fitness of the package (although genetically static) can change dramatically and lead to eventual genetic changes, speciation, or extinction.

The problem for neuroscientists is to decipher whether a structure, receptor type, connection, neural property, or behavior under investigation is functionally significant to the organism in the environment to which it is adapted, or whether it is an epiphenomenon of evolution. *Epiphenomenon* refers to a secondary symptom or effect, occurring with but not necessarily the cause or result of a phenomenon or event. Thus, the characteristic or feature we observe, or are studying, may be a by-product of selection for something quite different. For example, ocular dominance columns (ODCs) are the result of correlated activity within each eye and uncorrelated activity between the two eyes during development (see Chapter 5). Thus, ODCs are an epiphenomenon of development. Indeed, this system in cats and monkeys has been used extensively as a model to study the role of correlated activity in wiring the nervous system (i.e., rules). While the current organization in primate brains, which include ODCs, is functionally optimal, such an arrangement is not a requisite for stereopsis, for instance.

Another example is consciousness. Has the actual behavior that we term *consciousness* been selected for in evolution, or is it an epiphenomenon of the neural circuitry of a brain that evolved to solve complex sensory problems? Although consciousness indeed may be a by-product of complexly organized brains, it does not mean that, as a characteristic itself, it cannot ultimately be selected for. Thus, what was initially an epiphenomenon can become highly adaptive in a particular environ-



ment. This is where the story becomes extremely convoluted, and why evolution is likened to a tinkerer (see Jacob, below). If the above example is true, then in order to select for something like consciousness, it is necessary to select for all the bits and pieces of the original system that generated this characteristic. While there may be more than one method to neurally achieve the conscious experience, in terms of evolution it is tied to the expansion of our sensory systems and all the individual components selected for over generations.

From an evolutionary perspective complex behaviors are very difficult to study. The genetic contribution to some complex phenomenon like consciousness is rarely straightforward. As François Jacob (1977) noted, "Natural selection has no analogy with any aspect of human behavior. However, if one wanted to play with a comparison, one would have to say that natural selection does not work as an engineer works. It works like a tinkerer—a tinkerer who does not know exactly what he is going to produce but uses whatever he finds around him whether it be pieces of string, fragments of wood, or old cardboards; in short it works like a tinkerer who uses everything at his disposal to produce some kind of workable object . . . The tinkerer gives his material unexpected functions to produce a new object . . . Tinkerers who tackle the same problem are likely to end up with different solutions."

As noted earlier, because of genetic pleiotropy, what we observe, while functionally optimal, may not be the best or only method of accomplishing a particular task (such as ODCs). For example, the method of cell-cell communication that has evolved in animal nervous systems, the action potential, is only one of a number of possible ways in which cells can communicate. Indeed, synaptic transmission, with its highly intricate molecular mechanisms, is a superb example of evolutionary tinkering.

Our nervous system then, and that of any animal that we study, is a snapshot in evolutionary time of a very fluid process, and is composed of a number of adaptations for previous environments, exaptations, and epiphenomenal characteristics that may or may not be functionally important and ultimately selected for themselves.

## Evolutionary Mechanisms

How is phenotypic variability achieved within a population? A number of epigenetic, or activity-dependent factors contribute to the phenotype, but we will deal with these in Chapter 15 when we examine development and plasticity. We know that genes are ultimately responsible for evolutionary changes in the phenotype, and that phe-

notypic variability is achieved by genetic mechanisms. The first mechanism is mutation. **Mutation** refers to a sudden change in the genetic structure of an organism that affects the development of the organism. Mutations are rare and can have a positive, negative, or neutral effect on the organism. Recent work on mutant and transgenic mice demonstrates well the mixed effects that a mutation can have on the phenotype. For instance, molecular neurobiologists have begun to use mutant mice to "genetically lesion" a molecule, brain area, or connection pathway, in an effort to understand the genetic contribution to the generation and maintenance of the phenotype.

Unfortunately, there are several problems with this marvelous new tool. The first is that a large percentage of mutants die very early in development. The second, related problem is that the "genetic lesion" of the characteristic under study is never really specific. Thus, the mutants, if they are viable, have a plethora of other phenotypic changes (both peripheral and central) associated with the lesion. Both problems are due to genetic pleiotropy. In the first instance of nonviable offspring, the mice generally do not die from the targeted characteristic that was genetically lesioned (e.g., loss of thalamo-cortical connections), but from other effects such as kidney failure, respiratory abnormalities, or cardiac dysfunction. The point is that the single gene controls not only the characteristic in question but also a number of other functions. This is why mutations are relatively rare, and genetic change across species is small. Indeed, modern DNA sequencing techniques indicate that humans are very closely related to chimpanzees, and our genetic relationship to something as simply organized as a sea anemone is relatively close considering the rather large phenotypic differences in the two species.

Despite the very close genetic relationship we share with other primates, and even other animals, there is a remarkable degree of phenotypic variability in both external morphology and organization of the brain and behaviors. This indicates that (1) phenotypic change via genetic change is difficult to accomplish, (2) a slight change to the genotype can account for very large changes in the phenotype, and (3) there must be a relatively large epigenetic component that contributes to phenotypic variability.

Another genetic mechanism that increases phenotypic variability is recombination. Genetic **recombination** refers to a change in the array of alleles of existing genes. Here, the combination of existing alleles on a chromosome, rather than the frequency of any given allele in a population, is changed. Factors that affect the frequency of any given allele within a population



include genetic flow and genetic isolation. *Genetic flow* refers to individuals within the same species migrating into particular populations and interbreeding with its members. *Genetic isolation* is usually the result of geographic discontinuity. A population of individuals of

the same species can become isolated due to shifts in landmasses or water, and ultimately are unable to mate with others outside of the geographically isolated population. Genetic isolation may be an important factor in speciation.

## THE COMPARATIVE APPROACH

Neuroscientists who work on animals other than humans in order to discover the basic principles of neural organization that can be applied to humans are comparative neurobiologists. While you may actually be more interested in studying the human brain directly, the tools currently available are limited. For example, functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) are only indirect measures of neural activity. While magnetoencephalography (MEG) and electroencephalography (EEG) allow us to appreciate the latency of processing of some stimulus with varying degrees of localization specificity, we can only infer connectivity and the hierarchy of networks involved in some given behavior. Unfortunately, directly examining neural activity, connections, neurotransmitter distribution, or the molecular mechanisms that mitigate information transfer sometimes cannot be done adequately or at all in humans. Therefore, we must rely on studies of other animals to provide insight into a number of aspects of organization and function of the human brain. For these reasons, understanding the theory behind the comparative approach is critical.

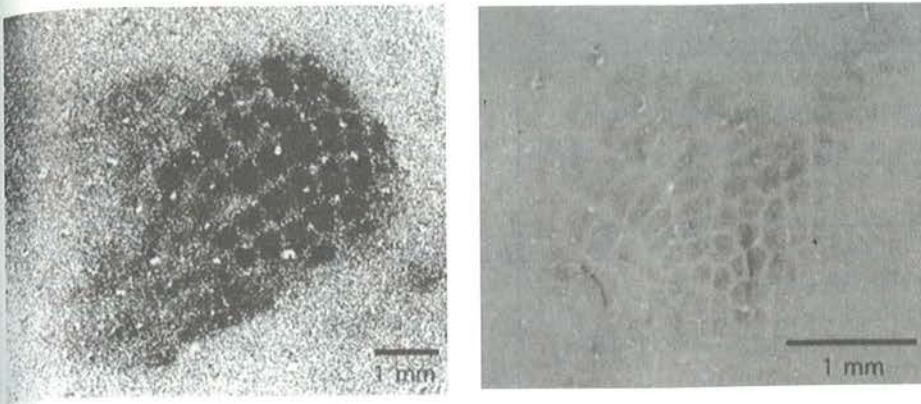
When one truly embraces an evolutionary perspective for solving problems in neuroscience, the strength of the comparative approach is unquestionable. What we cannot test directly, we can infer with varying degrees of accuracy, our extrapolations can be more precise, and our hypotheses can be biologically compatible.

Perhaps the best place to start is with the most ill-used word in the field of neuroscience, homology. **Homology** simply refers to a structure, behavior, or gene that has been retained from a common ancestor. Homology is a relative term. That is, some structure in one species is homologous to some structure in another species. The hand of a monkey and the hand of a human are homologous. The wing of a bat and the hand of a human are also homologous because both structures have the same evolutionary descent. *Homology* is also used to refer to structures in the brain. For instance, area MT in the macaque monkey is homologous to area MT in the owl monkey and galago (see Figure 14.3).

It is important to keep in mind that homologous structures do not necessarily have the same function (i.e., they are not always analogous). For example, V1 in humans is homologous to V1 in monkeys, and because of similarities in organization it is likely to be analogous in humans and monkeys. V1 in humans and other primates and V1 in the duck-billed platypus are also homologous. However, the internal organization and connections of V1 in each species vary dramatically. Thus, while V1 is homologous in both groups, it is unlikely to be analogous. A homologous structure may or may not look the same (homoplaseous). For example, although the wing of a bat and the hand of a monkey are homologous, the wing of a bat is considered to be a derived feature that has been co-opted for different functions (an exaptation). Thus, the two appendages look quite different and serve very different functions. A *derived trait* is one that is specialized and limited to a particular group or species. Examples of derived features include the bill of a duck-billed platypus, the flipper of a dolphin, and the nose of the star-nosed mole. We also can examine derived features of the nervous system. For example, the primary somatosensory cortex of murine rodents (mice and rats) contains a highly derived feature called *barrel fields*, which are related to whiskers. A **plesiomorphic** trait is one that is a general feature of some group or lineage. For instance, area MT is a general feature of primates.

**Homoplasy** refers to structures that look the same but do not necessarily have a common ancestry. For instance, the wing of a bat and the wing of a fly are homoplaseous and analogous but not homologous. This also holds true for features of the brain. A barrel field has been identified in the primary somatosensory area of murine rodents (Woolsey et al., 1975) and in some marsupials such as possums (Weller, 1993). The barrel fields in each group are considered to be homoplaseous but not homologous (Figure 14.5). The remarkable similarity in appearance of the barrel fields in these very distantly related mammals (approximately 125 million years of independent evolution) indicates that the rules governing neocortex development and evolution are





**Figure 14.5** The barrel cortex in the primary somatosensory area (S1) in the brush-tailed possum (**left**) and the mouse (**right**) as demonstrated with Nissl stains and cytochrome oxidase stains, respectively. The barrel cortex represents the mystacial vibrissae in these mammals. Despite over 100 million years of independent evolution, the neural organization of this peripheral specialization looks remarkably similar. (a) Adapted from Weller (1993).

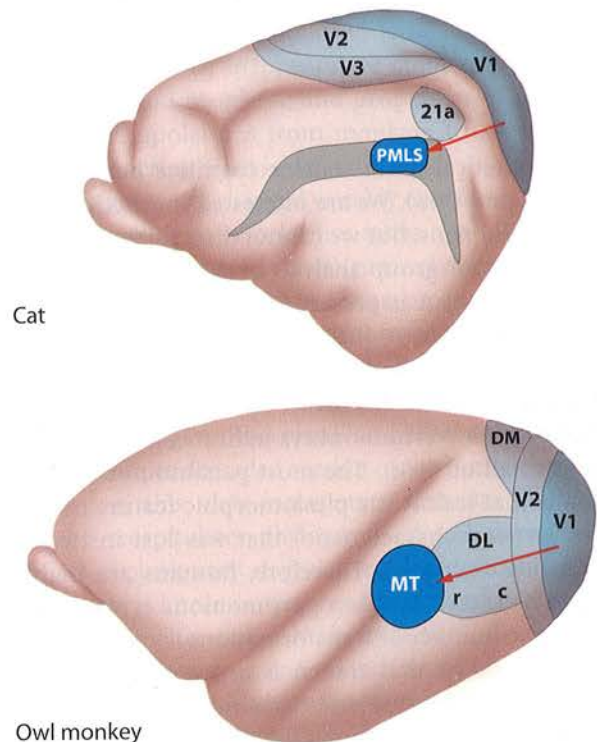
very highly constrained. Likewise, visual motion areas have been identified in other mammals as homoplasious and analogous to MT; an example is the posteromedial lateral suprasylvian (PMLS) area in cats (Figure 14.6). The question of whether these fields in cats and monkeys are homologous is still contentious. The implication that similarities can arise independently in different lineages (**convergent evolution**) is a sign of the limited and rigid rules by which brains evolve.

To determine whether features of the brain are homologous, homoplasious, or analogous, an **out-group comparison** is done. An out-group comparison defines phylogenetic relationships among animals (Figure 14.7). Basically, close sister groups of a species are examined to determine if they possess the structure in question. The probability that close sister groups will have the characteristic in question is higher than for a distantly related species. For instance, the middle temporal visual area (area MT) was first identified in owl monkeys. The question that arose after its discovery was: Is this a derived feature of owl monkey brains, or is this a general feature of primate brains, including humans? Decades of research on a number of sister groups (such as New World monkeys, Old World monkeys, and prosimians) indicate that MT is indeed a general feature of most, if not all, of the primate brains studied, and is likely to be a feature of human brains as well. This hypothesis recently was tested using fMRI in humans and was proved correct. MT is also homoplasious in all primates because it looks the same across species. The question of whether MT is analogous across primates is not certain. However, because the connections of MT appear similar across primates, and neurons in area MT have similar response properties, the most parsimonious conclusion is that MT has the same function in all primates.

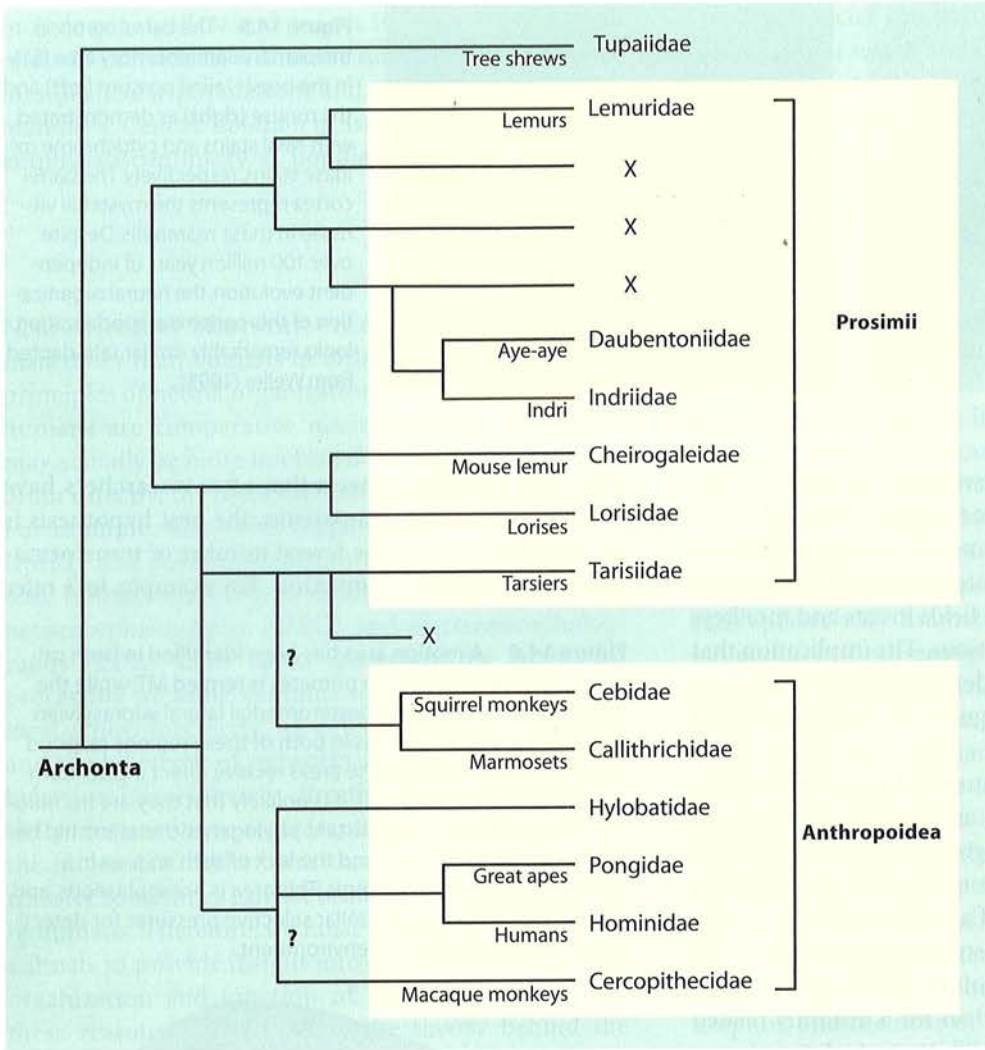
When researchers use the comparative approach, the **principle of parsimony** is applied to arrive at the most accurate inference regarding the unknown condi-

tion. This principle asserts that after researchers have done an out-group comparison, the best hypothesis is the one that requires the fewest number of transformations to explain a phenomenon. For example, let's refer

**Figure 14.6** A motion area has been identified in both primates and cats. The area in primates is termed MT, while the area in cats is termed the posteromedial lateral suprasylvian (PMLS) area. While neurons in both of these regions respond to moving stimuli, and these areas receive direct inputs from the primary visual area (V1), it is unlikely that they are homologous because of the very distant phylogenetic relationship between cats and primates, and the lack of such an area in a number of intervening groups. This area is homoplasious, and likely emerged owing to similar selective pressures for detecting moving objects in the environment.







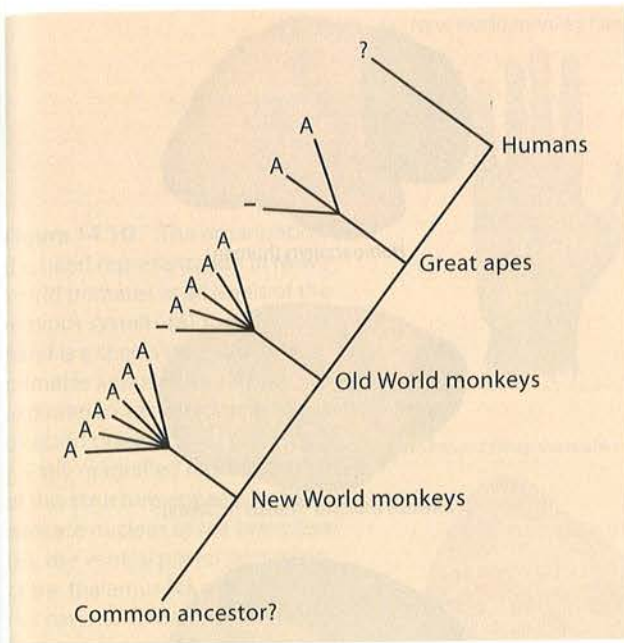
**Figure 14.7** A simplified diagram of the phylogenetic relationships between extant primates. Archonta is the grand order to which the order of primates belong. Primates are divided into two suborders, Prosimii and Anthropoidea. Each suborder is divided into several families (e.g., Lorisidae and Tarsiidae for Prosimii, and Hominidae and Cercopithecidae for Anthropoidea). The common names of some representatives, or groups are found just to the left of the family names. Although no dates are given, and some of the details of the relationships are still in dispute, this diagram gives a general overview of relationships and is used in comparative analysis. Tupaiidae diverged early in the archontan line and is not considered to be a primate, but its neocortex does possess some primate-like features. Adapted from Eisenberg (1984), Walker (1964), and Grzimek (1990).

to a hypothetical brain trait or cognitive behavior as trait A (Figure 14.8). We are interested in whether trait A exists in humans, but we cannot directly test for it in humans. An out-group analysis of three great apes indicates that trait A is present in two of these animals but not the other. A further analysis of Old World monkeys indicates that trait A is present in four of the five species examined. Finally, an examination of six species of New World monkeys indicates that trait A is present in all of them. The most parsimonious explanation is that trait A is a plesiomorphic feature of primates (general characteristic) that was lost in two of the species examined. Therefore, humans are highly likely to have trait A. A less parsimonious explanation, because the number of transformations is considerably greater, would be that trait A is not a plesiomorphic feature of primates but has arisen independently in six New World monkeys, four Old World monkeys, and

two great apes. Based on this explanation, trait A is not likely to be present in humans.

Let's apply the principles of parsimony to the previous example of area MT. We have concluded that MT is a general feature of all primates that looks the same and is likely to have a similar function. Is the motion area identified in cats (PMLS) homologous to MT in primates? This question has been vigorously contested. An out-group comparison, which includes representatives of all of the major mammalian radiations, indicates that MT is not present in rodents, ungulates, or other carnivores. The most parsimonious explanation is that a motion area evolved independently in primates and cats. MT and PMLS are homoplaseous and may be analogous but are not homologous. Does this mean that it is not worthwhile to study the motion area in cats? Absolutely not. It is not a simple coincidence that an area that has a number of similar features of organization arose inde-





**Figure 14.8** An example of how an out-group analysis can be used to make inferences about the unknown condition (e.g., the common ancestor, or an extant group that cannot be studied, such as humans). Great apes are relatively closely related to humans, while Old World and New World monkeys are less closely related. If we are interested in whether some brain characteristic (A) exists in humans, we can do an out-group comparison to make a fairly accurate inference about humans, even though we cannot study them directly. For instance, if two of three great apes, four of five Old World monkeys, and six of six New World monkeys examined possess feature A, then the most parsimonious conclusion is that the common ancestor of these primates possessed this feature, and that it was lost in one group of Old World monkeys and one group of great apes.

pendently in two distinct lineages. The implication here is that while the roots of the motion area are different, the rules of how the brain constructs a motion area in evolution must be highly constrained. Homoplasy allows us to examine the rules of how brains can change over time, and the limitations inherent in constructing nervous systems.

### The Scale of Nature Revisited

In 1969, Hodos and Campbell wrote the following: “The concept that all living animals can be arranged along a continuous ‘phylogenetic scale’ with man at the top is inconsistent with contemporary views of animal evolution. Nevertheless, this arbitrary hierarchy continues to influence researchers in the field of animal behavior [neurophysiology, neuroanatomy, neuroscience and cognitive

neuroscience] who seek to make inferences about the evolutionary development of a particular type of behavior. . . . The widespread failure of comparative psychologists [and most neuroscientists] to take into account the zoological model of animal evolution when selecting animals for study and when interpreting behavioral similarities and differences has greatly hampered the development of generalizations with any predictive value.”

Despite the advances that we have made in understanding the brain, we still find it hard to move away from a human-centered or anthropocentric view of life, the brain, and the behavior it generates. We all have some internal ranking of animals on a continuous dimension of low, intermediate, and higher levels. Generally this ranking puts insects as the least important and progresses in importance or value from fish, to reptiles, birds, small rodent-like mammals, cats, dogs, monkeys, apes, and finally humans. This general thinking is reflected in our everyday life, our value system or moral codes, and our political system. For instance, we would feel much worse if we ran over a dog with our car than if we stepped on a bug. We eat tuna that has been caught without endangering dolphins. Animal welfare activists generally do not target scientists who work on sea slugs, but do target those who work on cats and monkeys. We feel it critical to save whales from extinction, but include few, if any insects on the list of species to save from extinction. In short, our very socialization does not allow us to be objective about the biology of our behavior, our own nervous system, or that of other animals. It affects the choice of animals we study; promotes the use of inappropriate comparisons between rats, cats, and monkeys; and propels us to make erroneous extrapolations from monkeys to humans without considering what is derived.

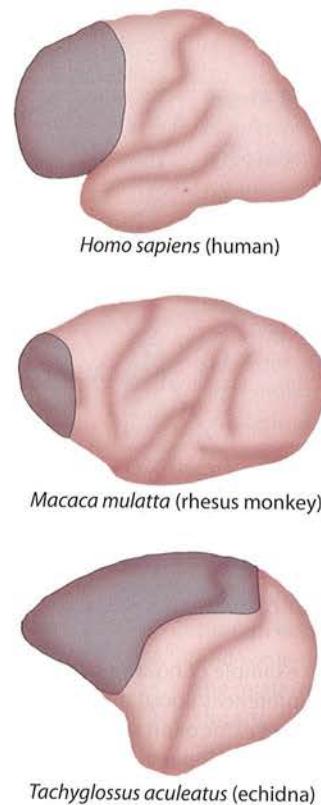
Lineages have changed variably over time. Thus, some animals reflect more primitive states (less changed), and others more advanced states (more changed). The latter condition is not due to a linear process across extant groups but has been achieved, often independently, in a number of different lineages (e.g., dolphins, apes, and humans). Unfortunately, most scientists still view human brains as being “most evolved” and other animal brains as some lesser or degraded version of the human brain. Not only does this view incorporate elements of the “ontogeny recapitulates phylogeny” (developmental stages reflect evolutionary stages) theory, but it suggests that evolution is linear or simply additive, and promotes the idea that “higher-order” brain areas that subserve behaviors such as language, cognition, and even consciousness should be distinguishable as some part that was added on to “lower animal” brains.



The following two examples of brain areas that are considered higher-order areas in humans are reinterpreted from an evolutionary perspective. We can use a comparative analysis of other mammal brains to make inferences about the roots and rules of “higher-order” areas. The first example is prefrontal cortex. We view this region as the hallmark of human brain evolution and consider it to have been added on to human brains during the course of human evolution. A comparative or evolutionary perspective suggests that the prefrontal cortex actually arose from a very old system, the olfactory system, and has been modified in the human lineage with the expansion of sensory cortex, to which it is interconnected via multisynaptic pathways. All mammals have some retained (homologous) orbitofrontal pathways that are similar to those described in nonhuman primates and presumably humans as well. For instance, all mammals that have been investigated have connections between the pyriform cortex and orbitofrontal cortex, and both the pyriform cortex and orbitofrontal cortex are densely interconnected with the amygdala. In addition, orbitofrontal cortex receives indirect inputs from higher-order sensory cortex in primates (Kupfermann, 1991). In humans, orbitofrontal cortex may have expanded to become prefrontal cortex (which consists of several divisions), and this expansion likely was tied to the expansion of sensory neocortex. Although there may be some overlapping functions of orbitofrontal cortex mediated by homologous neural pathways among mammals, this region of cortex has been co-opted for more varied functions in the human brain.

Interestingly, other mammals, such as echidnas, have independently “added on” a large prefrontal cortex (Figure 14.9). However, in this species we do not automatically liken this expansion to increased intelligence or a “more evolved” state. Echidnas are monotremes, mammals whose ancestor diverged very early in mammalian evolution (some 200 million years ago). These egg-laying mammals are thought to represent a primitive form of mammals (not to be confused with being a primitive form of the common ancestor), and they possess a fairly limited behavioral repertoire compared to that of humans. It is only our anthropocentric view that compels us to equate this expansion with a more highly evolved intellect. Although there is clearly a tie between evolution of the prefrontal cortex and complex human abilities, its presence is not the hallmark of advanced neocortical evolution.

Another example is Broca’s area. Broca’s area generally is considered to be an added-on language area of the human cortex. An evolutionary perspective provides an alternative view of Broca’s area. We know from a number



**Figure 14.9** The location and extent of “prefrontal” cortex (gray) in three different species. The brains have been scaled to approximately the same size. The proportion of the entire neocortex that the prefrontal cortex assumes in humans is larger than the proportion in other primates such as macaque monkeys. In other species, such as the spiny anteater or the echidna, an expanded prefrontal cortex (relatively larger than that in humans) has evolved independently. The pressure that drove this expansion is likely to be quite different in humans and echidnas, and therefore the prefrontal cortex in each group is not analogous.

of experiments on sensory and motor cortex in a variety of mammals that morphological and behavioral specializations are associated with cortical specialization. Such specializations usually take the form of enlargement or modularization of the cortical area representing the specialized portion of the sensory epithelium or muscle group (Figure 14.10).

For instance, the duck-billed platypus has evolved a bill with a unique distribution of mechanosensory (touch) receptors interfaced with a novel type of sensory receptor called *electroreceptors*. Specialized motor programs have evolved in the platypus in which oscillatory movements of the bill are used to help localize and identify prey. The representation of the bill along the entire neuroaxis has been modified, particularly in the neocortex. This modification takes the form of an enlargement in the amount of neural



(a) New World monkey hand



(b) Owl monkey cuneate nucleus (brainstem)

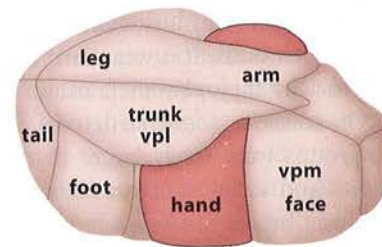


**Figure 14.10** The organization of the hand representation in New World primates at all levels of the nervous system. **(a)** The glabrous hand is a specialized structure in primates adapted for tactile exploration, recognition, and goal-directed grasping and reaching. A greatly magnified representation of this structure appears in the cuneate nucleus of the brainstem **(b)**, the ventral posterior nucleus of the thalamus **(c)**, and the anterior parietal somatosensory areas of the neocortex **(d)**. The red indicates the amount of each of these nuclei and fields associated with the specialized representation. (b) Adapted from Florence and Kaas (1995). (c) Adapted from Kaas et al. (1984). (d) Adapted from Merzenich et al. (1978).

(d) Owl monkey somatosensory cortex



(c) Squirrel monkey ventral posterior nucleus (thalamus)



space devoted to the specialized structure and its receptors, as well as specialized motor programs that generate foraging behaviors associated with the bill.

Other examples of neural specializations that reflect morphological specializations abound. For instance, the glabrous hand of most primates and the raccoon shows a similar magnification of representation along the entire neuroaxis, as does the nose of the star-nosed mole. All of these neural specializations have arisen independently, although all reside in the primary somatosensory area and appear to follow the same rules of specialization. Thus, while all mammals have a primary somatosensory area (S1), only in the platypus cortex has the bill representation been modified to such a large extent. In the star-nosed mole, the nose representation has been modified in a similar fashion, and in the raccoon and some primates the hand representation has been modified similarly.

In humans, if we view the changes in the density and distribution of receptors for the tongue, lips, and teeth, and the physical changes to the structure of the larynx and the motor programs associated with it, in the manner in which we view other mammal specializations, then we would view Broca's area quite differently. We would not view this region of the brain as an area that

has been added on in humans, but as a region that is present in most mammals, and certainly in all primates, but is highly derived in humans. The derived state in humans is a magnification of the cortical representation of the face and oral structures in the premotor cortex (PM), as well as M1 and S1, as a consequence of, or in conjunction with, changes in the periphery. Like in other species with sensory and motor specializations, changes in the connections and the motor programs direct the use of these structures (e.g., nose in star-nosed mole is used for exploration; platypus bill for oscillation; hand in primate, for reaching and grasping). In the case of Broca's area, interconnections with specialized auditory regions of the brain (such as Wernicke's area) have formed. Thus, while all mammals have an M1, and certainly all primates have a PM, only in humans have the motor and sensory representations of oral and facial structures been modified in such a manner.

A comparative analysis suggests that the most parsimonious and biologically compatible explanation is that the modification to the human brain known as Broca's area has homologous counterparts in other primates, and certainly follows highly restricted rules of cortical field modification. However, the formation of new patterns of connections, and the clear behavioral differences



this region of cortex generates, indicate that it is not analogous. Interestingly, Broca himself appreciated that there were two alternative explanations for areas in the brain involved in articulate language (see Greenblatt, 1984). The first (which he favored) was that they are part of the human intellectual function. The second explanation was that they are part of cerebral functions that have to do with motion or the motor system.

## ADAPTATION AND THE BRAIN

Evolutionists interested in human behavior think that the modern human brain was adapted to deal with the world as it was in Pleistocene hunter-gatherer societies 100,000 years ago. This period was picked because of the slowness of new adaptations. Our auditory system, for instance, is not adapted to sensory events such as loud rock and roll music. This is why hard-rock musicians and their audiences wear earplugs, raising the question as to why they play their music that loud to begin with. Or consider social structures. In hunter-gatherer times, groups were rarely larger than fifty. With today's vast cities and social structures like government bureaucracies, our brains are severely challenged to cope. So, when we think about the functions of the modern brain and what it does and does not do well, we should take into account what the early hunter-gatherers had to solve.

This proposal takes a novel tack in the study of decision making. W.T. Wang (1996) argues that mechanisms for decision making evolved in a particular social context. In particular, he focuses on the idea that for most of our evolutionary history, humans lived in small groups. As such, he proposes that our decision-making capacities are tailored for such contexts and that there may well be differences in how we make decisions in different social contexts. This idea is intriguing. There has been a movement toward bringing evolutionary thinking into the mainstream of cognitive psychology. Wang's experiments to date have focused on the framing effect. In a framing experiment, people are presented with two choices regarding some risky situation, such as which of two treatments should be applied to combat a potential medical disaster. In the classic demonstration by Tversky and Kahneman (1988) of the framing effect, the treatments are posed in either a positive or a negative light (e.g., treatments to save lives or treatments to minimize death). The basic finding here is that risk-taking behavior differs in these two situations. When the treatment is framed in a positive manner, people tend to choose sure bets; when it is framed in a negative manner, people tend to choose more probabilistic options. The framing effect is one demon-

If we throw out the "scale of nature" and invoke the history of change (roots) and the proposed mechanisms (rules) that generate these changes over time in other mammals, we can allow for richer and more varied hypotheses regarding particular cognitive behaviors. These hypotheses will be more objective, less anthropocentric, and more compatible with evolutionary neurobiology.

stration of human irrationality, or more specifically, that a purely cost-benefit analysis will not be sufficient to account for human decision making.

This example illustrates well that in a number of respects our behaviors are adapted for a simpler life, the life of the Stone Age human. Back then we had to be ready to defend ourselves, detect cheaters, read other people's facial expressions, forage, avoid incest, recognize kin, and read other people's minds and their intentions. Our mind does not instinctively share common goals with others. Have you ever been to a meeting that sets policies? It takes luck, persuasion, and brute force to get a group of independently minded people to agree on anything.

According to evolutionary thinking, these special capacities grow from separate and individual adaptations. The cognitive system that evolved is not a unified system that can work by applying special solutions to individual problems. This fundamental point is at the heart of the evolutionary perspective, and concurs with a vast amount of neuropsychological research. Localized brain lesions can lead to a loss of some capacity, say, facial recognition, but local brain lesions also can have a maddening, mild effect on specific functions. This latter truth most likely reflects the observer's inability to present the right challenge to the patient. That is, the patient probably does possess deficits, but the examiner's tests are either incorrect or not sensitive enough to detect the disorder. Alternatively, the failure to find a deficit may mean that devices built into the brain for other functions can solve other challenges. Just as a screwdriver can loosen screws, it can also open paint cans.

The adaptations built into our brains are the physical, or neural, structural devices we should try to understand when trying to figure out how the brain works. As already pointed out, an important rule to remember, one commonly overlooked, is to focus on the adaptation, not on the ancillary events associated with the adaptation. Bones are an adaptation, but their whiteness is a by-product, or epiphenomenon, of the calcium that gives bones their strength. Calcium was available in the



environment and was used to build the bones' rigid structure. If we want to study bones and how they came to be, it would be a mistake to delve into the fact that they are white. We should simply distinguish between what are proximate factors versus ultimate ones when we consider why something evolved. *Proximate factors* are those at hand, and part of a structure. But their presence may not be why the structure evolved.

### Adaptations at Multiple Brain Levels

It is easy to see how adaptations gradually developed in primates; they occurred with primary sensorial systems like our visual and auditory systems. Furthermore, we have adaptations for more complex behaviors like our capacity to have a theory of mind about someone else. We look at another human and quickly theorize about their intentions toward us and how we should respond. At these levels evolutionary processes operate—and deserve comment.

At the simpler level of understanding vision, today's researcher may have insights that are consonant with the realities of the Pleistocene landscape. After all, the physical world of light and object has not changed all that much. Our visual system is built to take a two-dimensional retinal image and turn it into a real-world representation of the visual scene. David Marr of MIT first articulated the true problems associated with understanding how vision must work. As Marr (1982) put it, "Trying to understand perception by studying only neurons is like trying to understand bird flight by studying only feathers: It just cannot be done. To understand bird flight, we have to understand aerodynamics; only then do the structure of feathers and the different shapes of birds' wings make sense."

Marr is widely recognized as a genius, and the field was devastated when he died a young man. He was pursuing a computational analysis of what he was interested in understanding. In general terms, he liked three levels of description for any information-processing device, whether it be a cash register or a brain. In brief, he based his ideas on the following logic: First, information-processing devices are designed to solve problems. Second, they solve problems by virtue of their structure. And, third, they explain a device's structure when one knows what problem it was designed to solve and why it was designed for that problem and not another one.

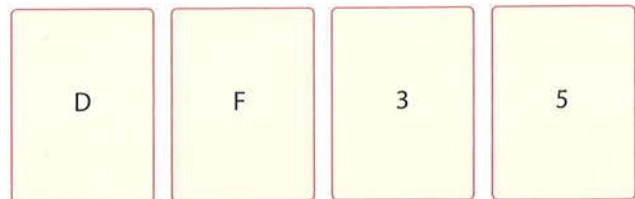
These issues were partly illuminated when researchers in artificial intelligence tried to build a device that could analyze a visual scene just as a human does. Marr first realized that the evolutionary function of vision is scene analysis: The brain must reconstruct a

model of real-world conditions from a two-dimensional visual array—the information on the retina.

The first discovery was that scene analysis is far more complicated than had been imagined. A simple object sitting on the horizon in the morning light looks completely different when the sun reaches high noon and then falls over the opposite horizon. An intricately specialized system must have been built into the primary visual system to allow for this natural progression and enable us to see the object as constant. Second, investigators discovered that our visual system apprehends far more information about a scene than can any artifact. It has many adaptations built in for this, all specific to vision. Finally—and this is the tricky part—our evolved visual system must have a cognitive, built-in component that has deduced that objects in the world have regularities which allow for the proper computations. This built-in component is what developmentalists mean by biologically prepared implicit knowledge in infants and children.

As we move up the scale to more complex adaptations like those associated with problem solving, social exchange, and the like, the insights we might gain by looking around us in our present world are probably not as helpful. Most studies do not take into account the sorts of ways that Stone Age humans dealt with social problems. In many of today's attempts to understand human rational processes, subjects are presented with artificial thought problems developed in the laboratory. Yet our brains are adapted only for real-world problems. For instance, many logic tests on issues of social exchange stump college sophomores because they are posed in the abstract. Does their failure mean that sophomores are illogical? No, because when the same logic problem is based on a real-life story about obtaining beer or food, their logic systems work just fine.

Leda Cosmides (1984) worked out a telling example of this fact. She built on a test first developed by Peter Wason, who showed how poorly-educated people can perform a simple logical task. Try it yourself: Each card has a number on one side and a letter on the other. Examine the following four cards:



The task is simple. You are to determine if the following rule has any exceptions: If a card has a D on one side, it has a 3 on the other side. Which cards do you



## HOW THE BRAIN WORKS

## Lessons from a Frog

Wonderful examples illustrate how evolutionary theory has led to great insights into brain function. Perhaps the most famous example is the work of Jerome Lettvin, one of the fathers of modern neuroscience and an extremely lively intellect. In 1959 he wrote a famous paper with colleagues, titled “What the Frog’s Eye Tells the Frog’s Brain.” Lettvin broke with his predecessors and asked questions about the visual system based on his understanding of how a frog views the world.

Prior to Lettvin’s work, the eye was regarded as an organ that translated an image into electrical impulses, and then the brain sorted out and interpreted this retinal information. The great American physiologist, H.K. Hartline, gave support to this idea in 1938 by studying the retina with simple points of light and dark. Using these abstract stimuli, Hartline and his colleagues con-

cluded that the frog’s retina passed on to the brain information about the tone of various objects. They concluded that the retina’s ganglion cells had but one function, and that was it.

Lettvin changed this interpretation. While recording from the frog’s ganglion cells and stimulating the frog’s visual system with bugs, twigs, and other ecologically relevant material, he and his colleagues discovered several types of ganglion cells—five, to be exact. In simple terms, Lettvin showed how much information is weeded out by biological systems like the retina. Evolution has seen to it that the frog’s brain does not detect things about the visual environment that it does not need in order to function and survive. Hence, the male frog’s brain does not spend energy on noticing the actor Melanie Griffith, but does detect the movement of female frogs.

**Table 14.1** Types of Detectors

1. *Sustained-edge detectors* (SEDS): These showed the greatest response when a small, moving edge entered and remained in their receptive field. Immobile or long edges did not evoke a response.
2. *Convex-edge detectors* (CEDs): These were stimulated mainly by small, dark objects with a convex outline like beetles and other bugs.
3. *Moving-edge detectors* (MEDs): These were most responsive to edges moving in and out of their receptive fields.
4. *Dimming detectors* (DDs): These responded most to decreases in light intensity, such as a shadow cast suddenly over the frog.
5. *Light-intensity detectors* (LIDs): These cells’ responses were inversely proportional to light intensity, being most responsive in dim light.

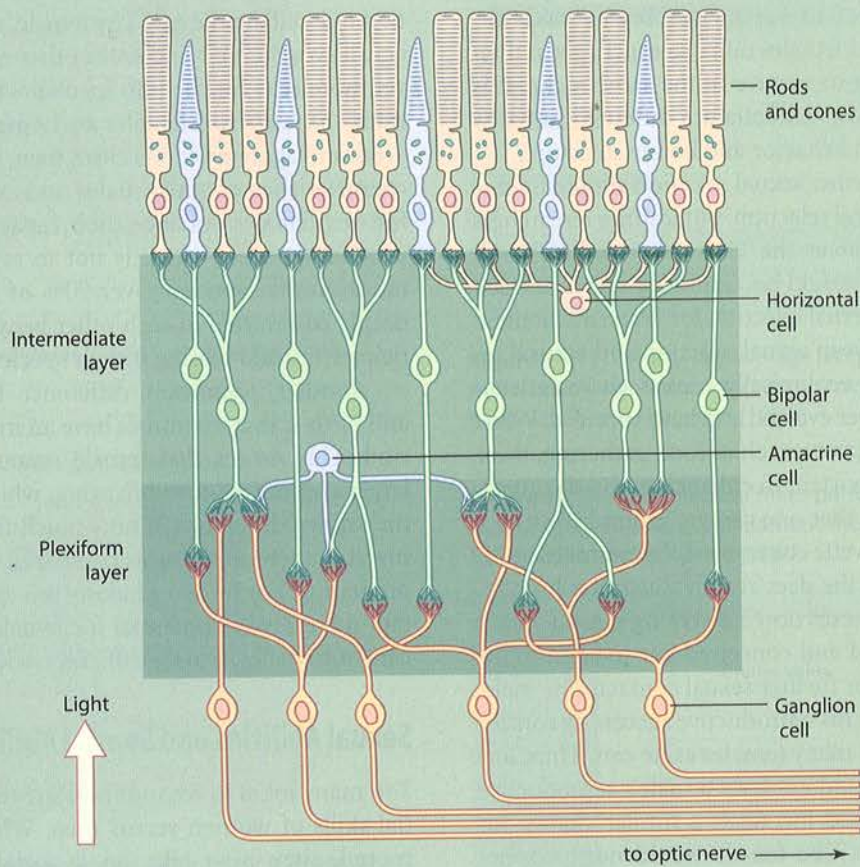
need to turn over to discover if this is true? Feel your mind rattling? But now consider the following problem: You are a bouncer at a bar and your job is to make sure no one under 21 drinks beer at the bar. The cards below have information about age on one side and what the patron is drinking on the other. Again, which cards do you need to turn over?

Beer	Soda	25	17
------	------	----	----

The mind springs to action on this task. It is obviously the first and last card, just like in the more abstract example earlier. Why? Cosmides and Tooby (1992) maintained that we have a built-in cheater detector system that has been a necessary part of our brains ever since we as a species began to exist in social groups. The moment survival becomes conditional on what a group does, as opposed to what an individual does, there must be a way to make sure the collective idea works as it is supposed to. In other words, we have the beginnings of a social contract.

The argument here is that social exchange can be expressed by a conditional statement such as, If you take the benefit, then you must pay the cost. For example, if you play on the hotel’s golf course, then you must be a guest at the hotel. A cheater is someone who takes a ben-





The cells of a frog's retina. The ganglion cells are toward the front of the frog's eye, as compared to the photoreceptors, which are farthest away from the source of light but through which light must travel before processing in the ganglion cells takes place.

efit without paying the cost. People are quite good at detecting potential violations of these kinds of conditional rules (i.e., catching potential cheaters), whereas they cannot detect potential violations of purely descriptive rules. An example of the latter being, If a man wears a tuxedo, then he must wear a bow tie. In studies of undergraduates in the United States and Germany, 75% to 90% of people reason correctly about social exchange, compared with only 4% to 25% of people reasoning correctly about abstract or descriptive rules. Detecting potential cheaters is an important evolutionary problem—those who could not detect cheaters got ripped off more often, and did not end up as our ancestors.

This intriguing new work has built on the insight of Robert Trivers (1971). Many years ago Trivers, now at

Rutgers University, showed that the elements of social exchange are based on the evolution of reciprocal altruism. Reciprocity amounts to roughly equal amounts of give and take in social relationships. The associated cognitive, psychological, and emotional systems allow us to develop and maintain friendships with nonkin. Kids implicitly recognize the reciprocal nature of friendships, and socially reject kids who do not reciprocate.

Social exchanges and titrating of reciprocity give rise to many emotions. Indeed, Trivers argued that many emotional reactions regulate social exchange. If we give more than we take in a social relationship, we get angry; if we take more than we give, we feel guilty. Guilt motivates returning the favor, while anger motivates us to break off relationships with people who cheat, who do not reciprocate.



## Sexual Selection and Evolutionary Pressures on Behavior

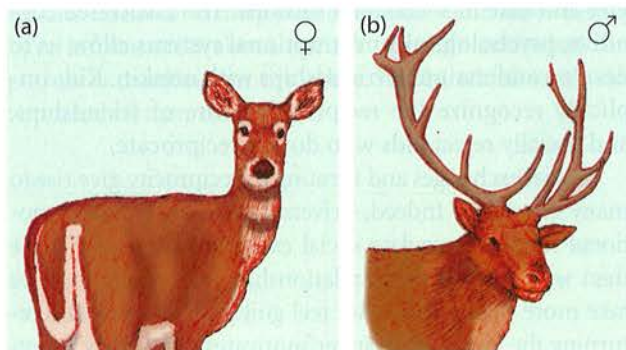
Sex has realities that are at once clear and puzzling. Darwin knew natural selection was at work, but he was bothered by why males and females differ so much, given their mutual goal of trying to survive in the same niche. It is easy to understand why genitalia are different, but why such big differences in behavior and bodily structure?

Some dispute whether sexual selection should be distinguished from natural selection, but leading researchers such as Steven Gaulin at the University of Pittsburgh (1995) argued that it should be. Gaulin, who has puzzled over the problem of sexual selection for years, maintained that a distinction between sexual selection and natural selection explains how ecologically useless characteristics such as antlers on a deer evolved and have survived. While not necessary for functions such as food gathering, these characteristics are important in enhancing sexual contact. An analogy would be that one can get around town in a Honda, but a red Corvette conveys a different message.

The sexual life of the deer readily illustrates how selection starts the two sexes down diverging paths. Once a female deer has mated and conceived her maximum litter, she has no need for further sexual contact. The male, though, can maximize his reproductive success by continuing to impregnate as many females as he can. Thus, any somatic event that would enhance a male's reproductive fitness would be selected for, while a similar change for the female would not. The female would not gain, because her reproductive limit has been met (Figure 14.11).

This pattern for mammals has exceptions, and it is the exceptions that bring strength to the idea that sexual selection is distinct from natural selection. First, male

**Figure 14.11** The typical morphology of (a) a female doe that invests her energy into raising her offspring and that of (b) a polygamous male elk with its large investment of energy into the massive set of antlers, which aid his ability to attract mates and fight off competitors.



mammals have small and many sex cells, whereas females have large cells. In other animals, the quickly reproducing sex is the female, and the male stays home with the young. In some shorebirds, the male stays in the nest to incubate the egg. The female, right after laying the egg, leaves the nest and seeks other males, so she can lay yet more eggs for them to incubate. In this turnabout of roles, the fast-sexed females are larger, more brightly colored, and aggressive. It is clear, then, that the flamboyant characteristics of most males and of the less common fast-sex females enhance their capacity for a higher reproductive rate—which is not to say that there are no monogamous species. Over 90% of foxes and birds are deeply committed to each other because both must participate in child rearing if their species is to survive.

Another significant difference between mammals and birds is that mammals have an internal gestation period. This means that female mammals are making a larger commitment to offspring, which may underscore the known difference in how much the male and female invest in their offspring as compared with spending time on mating. For birds and many fish species, external gestation creates the potential for females to force parental care onto males, a more difficult trick with mammals.

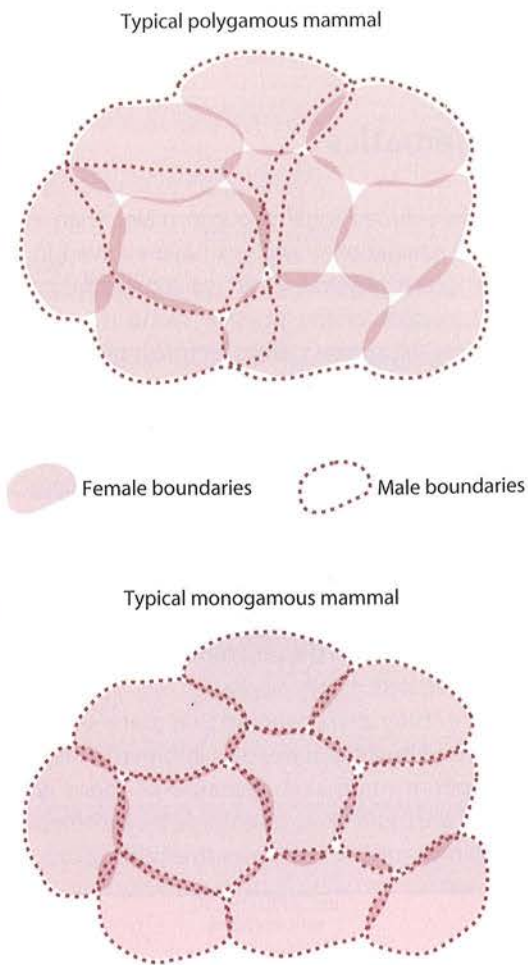
## Sexual Abilities and Spatial Abilities

Too many jokes to recount here are made about the spatial skills of women versus men. While once good-humored, they now take on a social significance that becomes lost in current social values. Still, some facts are intriguing. Spatial abilities do vary according to sex—and they do so because of selective pressures. These spatial skills differ in humans and animals of all kinds, which suggests that brains manage spatial skills differently in males and females.

Natural selection sees to it that males and females have basic navigational skills. Both meet the same challenges for reward and risk in food gathering and other life-perpetuating activities. Where sexual selection might start to mold differences is when males of a species are polygamous. Here the males might need better spatial skills to find available females for sex and yet return home. This phenomenon pertains to polygamous rather than monogamous mammals (Figure 14.12).

In trying to test the hypothesis that polygamous males would have greater spatial skills as compared to females, we run into a problem: Over 95% of mammalian species are polygamous. In fact, verifiable sex differences in spatial skills have been discovered in rats, mice, and people. To truly test the hypothesis, we would



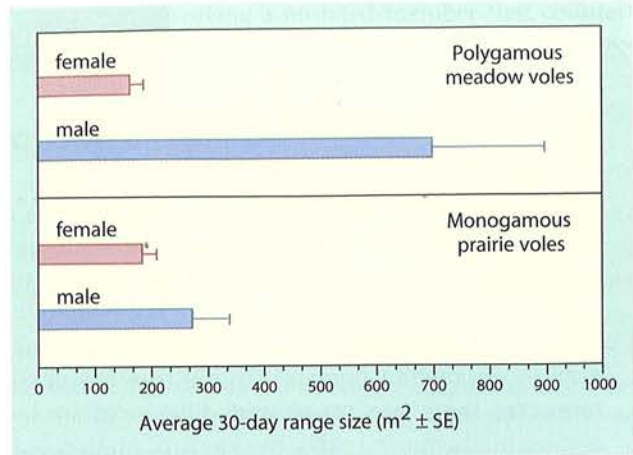


**Figure 14.12** Typical home-range patterns for polygamous versus monogamous mammals. For many polygamous species, male home ranges overlap with numerous, smaller female ranges. Females and males in monogamous species where parenting by both sexes is necessary for the raising of young tend to have smaller, isomorphic home ranges.

need a species with monogamous and polygamous strains, to evaluate each group's spatial skills.

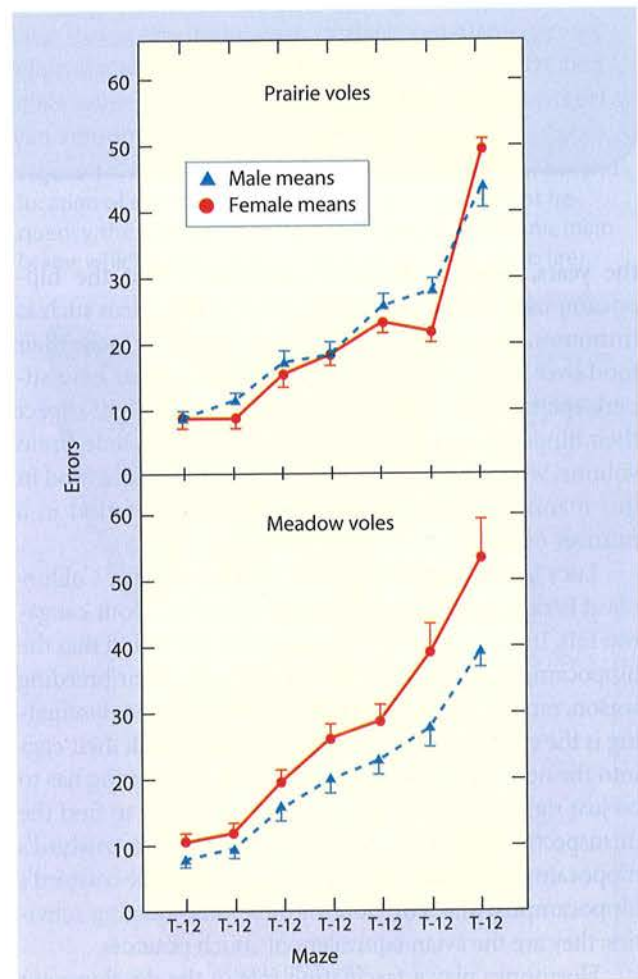
Studies of wild voles have elucidated these issues. These rodents were chosen because we have a myriad of well-developed spatial tests for them. Yet the sizes of the ranges of the two monogamous pine and prairie voles did not differ (Figure 14.13). At the same time, the free-wheeling, polygamous meadow vole demonstrated huge differences in range sizes between females and males. Gaulin and his colleagues confirmed these spatial skills by testing the same species in a laboratory. Males with larger range sizes had better spatial skills (Figure 14.14).

With the spatial abilities of the two sexes clearly demonstrated, researchers became eager to establish whether brain structures for spatial abilities varied. Over



**Figure 14.13** Thirty-day average range area of monogamous prairie voles and polygamous meadow voles. Adapted from Gaulin and Fitzgerald (1989).

**Figure 14.14** Symmetrical maze performance by monogamous prairie voles and polygamous meadow voles. Adapted from Gaulin and Fitzgerald (1989).





## HOW THE BRAIN WORKS

## Sexual Selection and Mathematics

**T**he perennial topic of sex-related differences in mathematical abilities has been exhaustively studied by David Geary at Columbia University (1995). He observed that there are no sex-related differences in biological primary mathematical skills, even in nonhuman primates. This is true for all cultures. Yet there are sex-related differences in secondary mathematical skills, the kinds of math taught in schools in the industrialized world. Males consistently outperform females in word and geometry problems. Geary suggested that this capacity builds on the sort of male superiority in spatial skills seen in many species, such as the ones described in this chapter. In short, it is a secondary benefit to males, arising out of the sexual selection process we have described.

Geary went on to show that sex hormones, which are the proximate mechanisms associated with sexual selection, appear to indirectly influence mathematical ability. He argued that sexual selection resulted in greater elaboration of the neurocognitive systems that support navigation

in three-dimensional space in males than in females. These navigational systems have evolved in the three-dimensional physical world, so some information about the structure of the physical world is built into these systems. It appears that features of Euclidean geometry are a mathematical representation of the organization of the physical world; thus, an implicit understanding of aspects of geometry is built into the spatial system. Males do better in geometry than do females because evolution has provided males with more built-in knowledge of geometry. These same spatial skills can solve other types of math problems, such as word problems, because solving word problems is much easier if important information in the problems is diagrammed or spatially represented.

This same study also observed that many sex differences are found in social styles and interests; these play into the superior math skills. Because of these differences, males are more likely to engage in mathematical problems, which further enhances their ability.

the years, many investigators discovered that the hippocampus is crucial to spatial memory tasks. Birds such as titmouses, nuthatches, and loud-mouth jays all cache their food over a large spatial area. Because they must have superb spatial skills to retrieve their food, one might expect their hippocampus to be larger, corrected for whole-brain volume, when compared to birds that do not store food in this manner. This is exactly what researchers found in a number of species such as the vole (Figure 14.15).

Lucy Jacobs and colleagues at the University of California at Berkeley (1990) asked similar questions about kangaroo rats. In two species of kangaroo rats, she found that the hippocampus is larger in males that, during their breeding season, range more widely than do females. Just as fascinating is the cowbird, a species whose females sneak their eggs into the nests of other species. The cowbird's timing has to be just right, and she has to search a wide area to find the unsuspecting host nest. Sure enough, a female cowbird's hippocampus is much larger compared to a male cowbird's hippocampus. Males do none of these wide-ranging activities; they are the avian equivalent of couch potatoes.

Hormones play a fascinating role in the development of spatial abilities (Dawson et al., 1973). Investigators

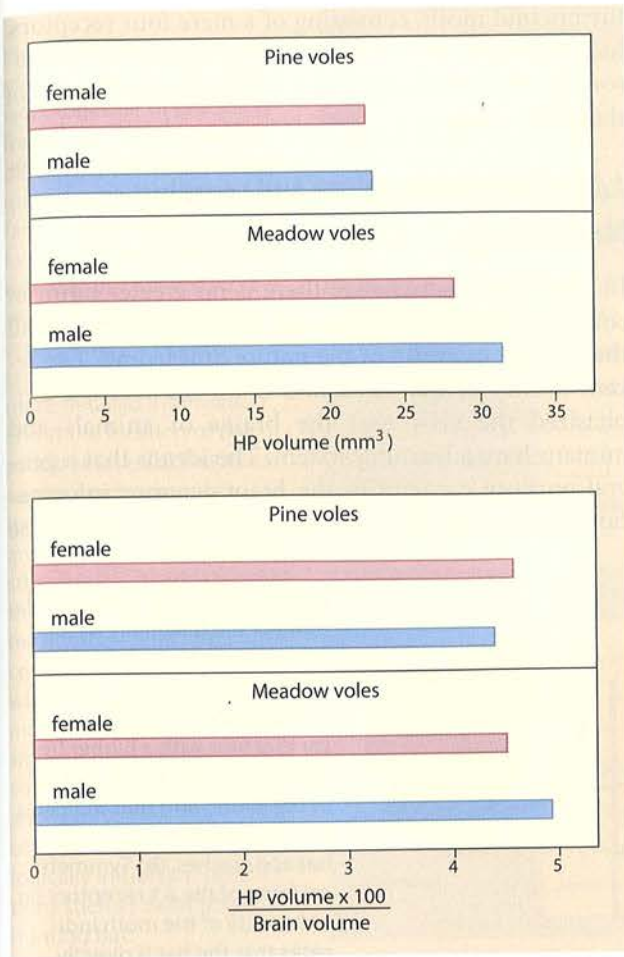
showed that sex-typical patterns of maze performance can be reversed by the early administration of appropriate hormones. How, we might ask, can hormones affect the genetic blueprint for sex differences such as spatial skills?

The expression of sexual differences involves ontogenetic forces, which are the forces at work during an organism's development—in this case, in the fetal stage. The true genetic differences between males and females are slight, and they are expressed by factors such as the local hormone environment. For example, in humans who have Turner's syndrome, a neuroendocrine genetic disorder, the gonads remain undifferentiated. As a result, a phenotypic female who was deprived of androgen and estrogen during development has spatial abilities significantly below her verbal skills. The same is true for males who experience low androgen levels during development, such as in Klinefelter's syndrome, another genetically based neuroendocrine disorder. They too exhibit depressed spatial skills.

### Evolution and Physiology

By now, it should be clear that natural selection is crucial in shaping each species's brain (Gazzaniga, 1992). Special





**Figure 14.15** Comparison of hippocampal volume for monogamous pine voles and polygamous meadow voles. Adapted from Jacobs et al. (1990).

devices built into each brain enhance the species's capacity to reproduce and to promulgate itself; the devices vary tremendously, as each species has different niches and predators. Since no two species utilize the exact same kind of resources, and since no two species have the exact same predators, each species also has special isolating reproduction mechanisms. This is important to understand, as each species has unique traits to pass on, and thus sensory receptors and brain decoders in each species are rather idiosyncratic. This recurring theme is a fundamental one for students of the nervous system. Even though nerve cells may share similarities, and nervous systems may be universally composed of certain nerve cells, each nervous system varies from one species to another in ecologically appropriate ways (Bullock, 1993).

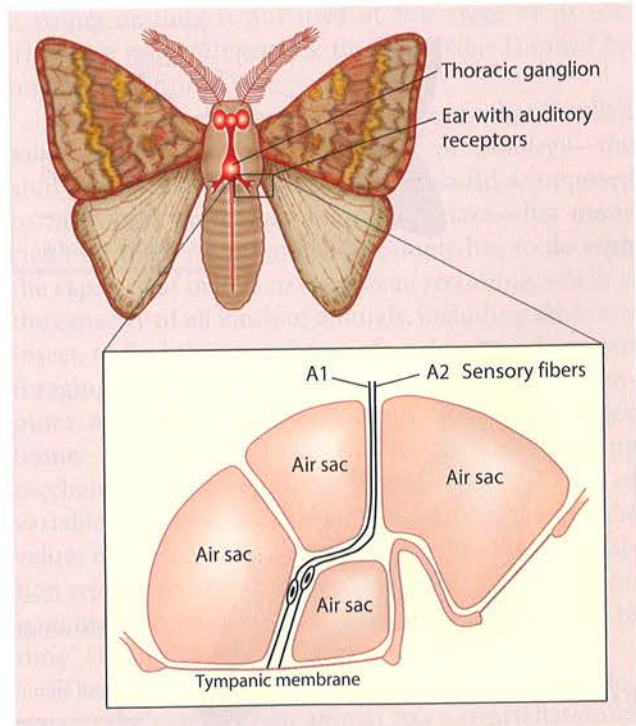
There is a wonderful example of how biological structures coevolve, each trying to adapt to meet its own needs. In a predator-prey relation, as the predator develops an edge by evolving toward better fitness, the prey

responds by evolving a mutated member that counters the new predator's skill and subsequently enhances reproduction—much as the bat and the moth it eats.

As contrasted with the visual system we predominantly use to navigate, bats maneuver through their environments by emitting high-frequency sound waves and detecting their weak echoes off surfaces. The bat's nervous system has evolved sophisticated adaptations that enable the bat to be sensitive to these weak echoes. As a bat approaches an object like a moth, it emits more sound waves to gain exact information on the object's direction and distance. Because of their mode of transportation, flying insects give more clues to the bat. As an insect moves its wings for flight, rhythmic reflections of the bat's sound waves striking the upper and lower surfaces of the insect's wings return to the bat. The bat uses these to distinguish between moths and tree leaves. With such an accurate detection system, it is hard to believe bats' prey could stand a chance of survival.

But prey such as the noctuid moth have evolved antipredator adaptations to prevent them from becoming the next meal of a strong hunter like the bat. The noctuid moth has two ears, each with only two receptors, the A1 and A2 receptors, with which to perceive an approaching bat (Figure 14.16). The A1

**Figure 14.16** The noctuid moth's (*Agrotis ypsilaeon*) ear, and location of receptors. When sounds are of a sufficient frequency, the auditory receptors stimulate the tympanic membrane, which in turn induces the auditory neurons to fire.



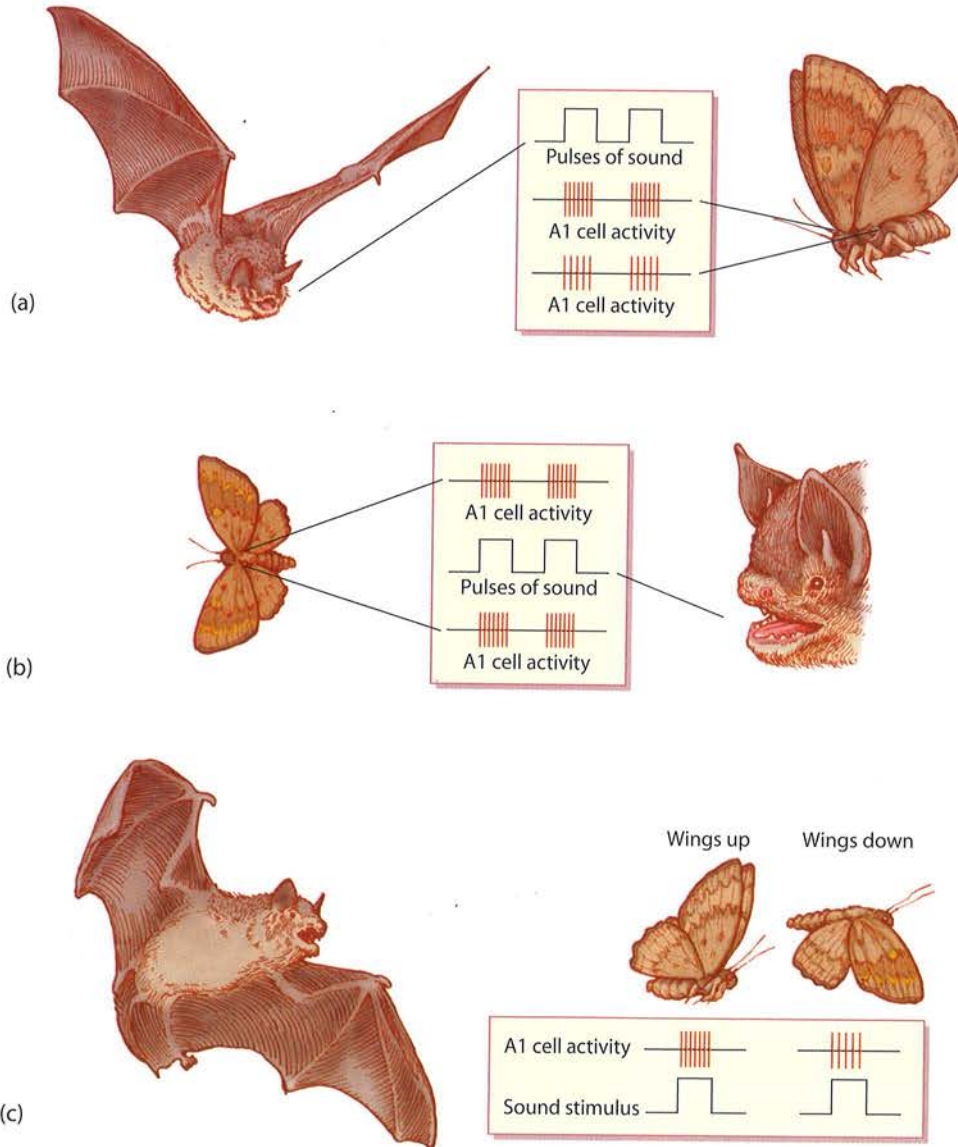


receptor responds to low-intensity sounds such as the ones from a bat 3 to 30 m (10 to 100 feet) away. The moth's ears work as ours do to locate a sound source; the moth relies on its knowledge that whichever receptor is closer to the sound will be activated slightly before the receptor that is farther from it. In this way, the moth can tell if the bat is to its left or right. Because the beating of the moth's wings makes small interruptions in the reception of the bat's signal, the moth can determine whether the bat is above or below it (Figure 14.17). If the bat approaches within 3 m (10 feet), the moth's A2 receptors, which are sensitive to high-intensity sounds, start firing, and the moth responds by beating its wings irregularly, thereby throwing off the bat's detection strategy and prompting the moth to dive for safety (Figure 14.18). This simplistic system of

the noctuid moth, consisting of a mere four receptors, has coevolved with the bat's more sophisticated sensory system. The result is a balanced coexistence of these two species.

### Adaptive Specializations and Learning Mechanisms

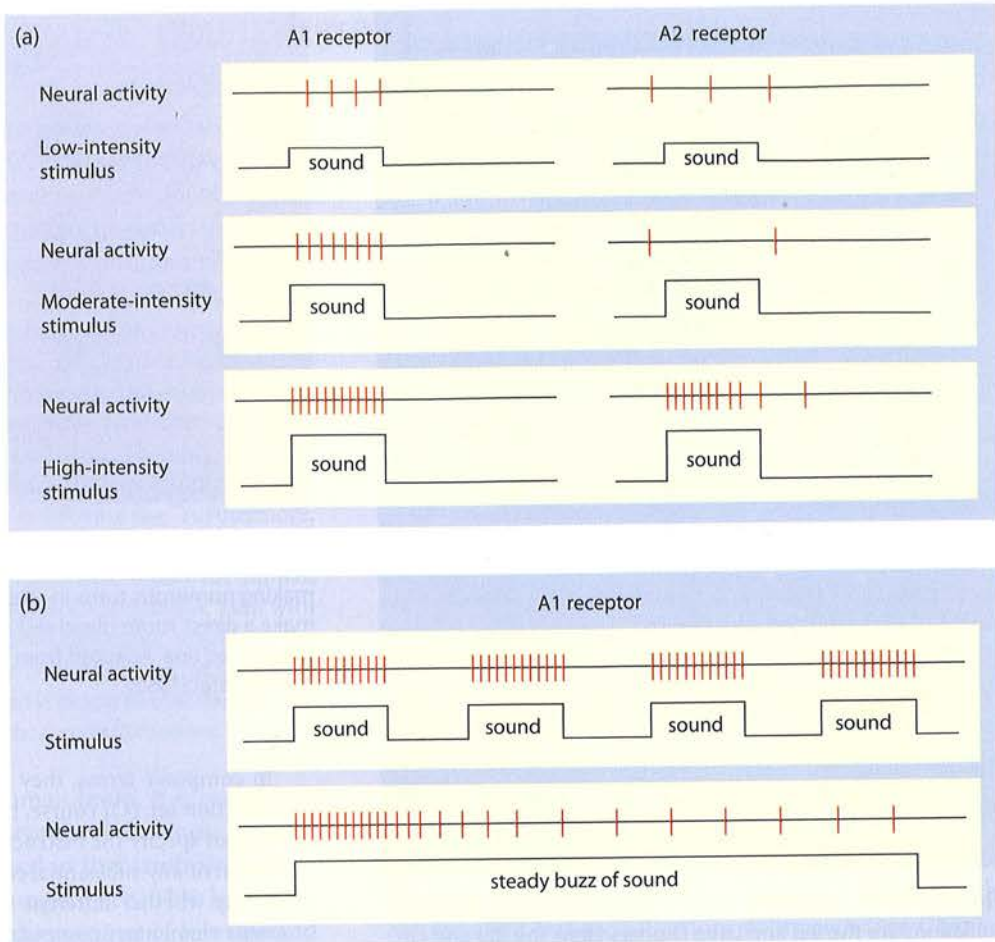
In cognitive neuroscience there is no greater point of contact between evolutionary theory and the mind than on the question of the nature of learning. The recent history of the mind and brain sciences has emphasized the view that the brains of animals and humans have a learning system. The idea is that a general-purpose capacity in the brain acquires information during any and all kinds of learning tasks. The



**Figure 14.17** (a) Differential firing of the bilaterally located A1 receptors indicates from which direction, left or right, a bat is approaching. The receptor that fires with a higher frequency is closer to the source of the sound and thus indicates the direction from which the bat approaches. (b) Symmetrical firing of the A1 receptors on either side of the moth indicates that the bat is directly behind the moth. (c) The interruption of the bat's sounds due to the location of the moth's beating wings indicates whether the bat approaches from above or below.



**Figure 14.18** (a) The simplistic A1 and A2 receptors work together to process information about sounds of different intensities and frequencies. When the bat is farther away, sounds of lower intensity affect the A1 receptor but not the A2 receptor. As the intensity increases, the A2 receptor starts firing to give the moth more detailed information about the location of the sound source. (b) The A1 receptor reacts strongly to high-frequency sounds that are detected in pulses. If the stimulus is a steady sound of the same frequency and intensity, the A1 receptor will cease firing after a short while. This prevents the moth from being overly sensitive to persistent, irrelevant sounds in its environment, and reserves the functioning of these receptors for ecologically important situations such as detecting a hunting bat.



idea of simple associationism was prevalent and, in early American experimental hands, became known as *stimulus response* or *SR psychology*. With the right reinforcement contingencies and the right brain state, learning could proceed with ease.

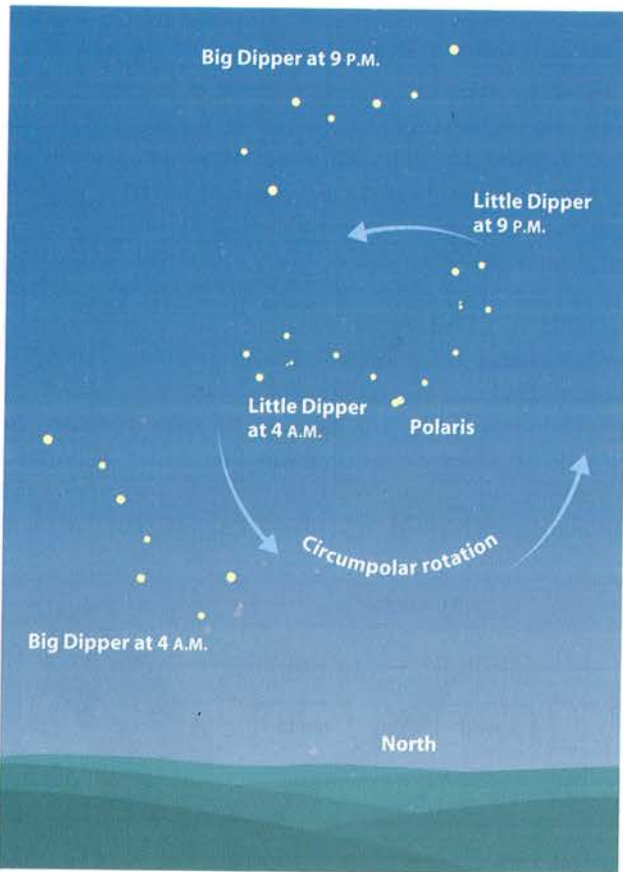
This dominant view has changed over the past few years. Leading the charge has been Randy Gallistel (1995) at the University of California, Los Angeles. He argued for the idea that there are many learning mechanisms, each computationally specialized for solving problems. He took the strong view that the association formation mechanisms so ubiquitously touted by psychologists are not even responsible for classic and instrumental conditioning. To support his ideas, Gallistel recounted how migratory thrushes must learn the center of rotation of the night sky when they are mere nestlings. This knowledge, gained as a young bird, is called upon only when they grow up and use their knowledge of the night sky's celestial pole to maintain their southerly route during their first migratory flight (Figure 14.19). A simple associationism could never explain this behavioral capacity. The knowledge gained as

a young nestling is not used at this stage of its life. There are no contingencies; the knowledge is called on only at a later time.

We have no shortage of examples of what is called *nonassociative learning*. The field of *ethology*—the study of animal behavior in the real world as opposed to the world of the laboratory rat maze—has many rich examples. An often-cited example has to do with the capacity of insects to learn *dead reckoning*, which is the capacity of all kinds of animals, including the lowly insect, to find their way home after they have been out foraging. When the ant leaves its home base, it computes and stores information on how to get back home. As Gallistel (1995) put it, “Like all learning mechanisms, it computes and stores the value(s) of variables. In this case, the mechanisms compute the values of the variables that represent the animal's position relative to its nest or home base. The computation is equivalent to integrating velocity with respect to time” (Figure 14.20).

These sorts of examples have led several ethologists to the view that an animal has a constellation of

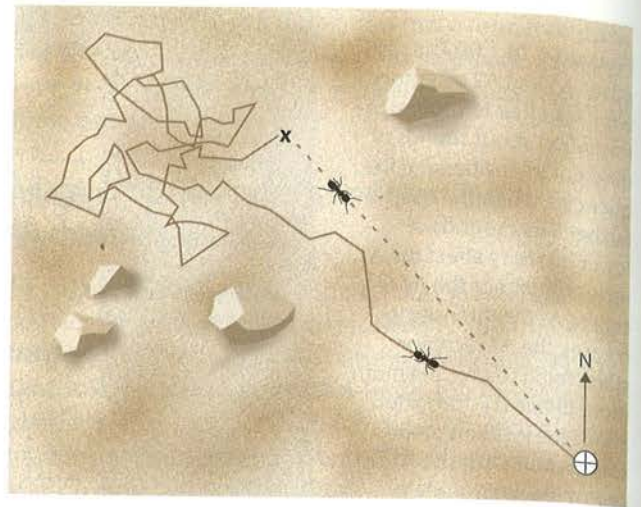




**Figure 14.19** Two of the most prominent circumpolar constellations are the Big and Little Dippers. Here, the Big and Little Dippers are seen as they would appear at 9:00 P.M. and 4:00 A.M. from temperate latitudes in the northern hemisphere in the spring. Migratory birds learn the directions North and South by observing the rotation of the circumpolar stars around the celestial pole (near Polaris now). Adapted from Gallistel (1995).

specialized learning mechanisms. The learning capacity exhibited in one situation works only in that situation and no other. Peter Marler (1991) at University of California at Davis and others called these examples of *problem-specific learning mechanisms*. The importance of this to issues in cognitive neuroscience is that when we are trying to understand how the brain enables learning, we must realize that there may be several mechanisms, not just one. We saw in Chapter 11 another example of this: the idea that the cerebellum is essential for representing the temporal relation between a tone and a forthcoming air puff in order to respond at the right time.

Gallistel argued that although there are many different learning mechanisms, there may still be some commonalities. The basic computational operations may be the same. As he put it:



**Figure 14.20** A foraging ant's path. The solid line represents the outward, searching journey until food was found at X. After making numerous turns in all directions, the ant is able to make a direct route (dead reckoning) home, as designated by the dashed line. Adapted from Harkness and Maroudas (1985) and Gallistel (1995).

In computer terms, they may all use the same basic instruction set. (Of course, they may not. At a time when we cannot specify the instruction set underlying any computation of any substantial complexity, we are in no position to say whether different complex computations use the same elementary computational operations.)

The other thing that all learning mechanisms must do is store and retrieve the values of variables. The bird has to store values that represent the center of rotation of the night sky and retrieve them when it determines what orientation to adopt with respect to whatever constellation of circumpolar stars it can see at the moment. The foraging bee must store the distance and direction of the food source and retrieve that information when it gives the dance that transmits the values to other foragers. The dead-reckoning mechanism must store the values that represent the animal's current position and then add to them whenever the animal moves, because dead reckoning amounts to keeping a running sum of displacements.

As we ascend into the human brain, we can see from an evolutionary perspective how humans must possess special devices for learning. William James stated that the human has more instincts than animals, not fewer. It is in this setting that Noam Chomsky and Steven Pinker argued for the view that there is a special learning module for human language. It has specific features and capacities, and most likely a definite neural organization. In short, the work on animals, where specialized systems are easily identified, raises provocative notions about the human brain's organization and cognitive powers.



## EVOLUTIONARY INSIGHTS INTO HUMAN BRAIN ORGANIZATION

A major assumption in neuroscience is being challenged: the idea that a larger brain with more cells is responsible for the greater computational capacity of the human being. Consider Passingham's (1982) main conclusion to his fascinating book, *The Human Primate*:

Simple changes in the genetic control of growth can have far-reaching effects on form. The human brain differs from the chimpanzee brain in its extreme development of cortical structures, in particular the cerebellar cortex and the association areas of the neocortex. The proportions of these areas are predictable from rules governing the construction of primate brains of differing size. Furthermore, there appears to be a uniformity in the number and type of cells used in building neocortical areas; the human brain follows the general pattern for mammals. Even with two speech areas we believe we can detect regions in the monkey brain that are alike in cellular organization. The evolution of the human brain is characterized more by expansion of areas than by radical reconstructions.

The uniqueness of the human brain, it is commonly believed, can be traced to its large size. It has more neurons and more cortical columns, and in that truth lies (somewhere) the secret to human experience. This is entirely consistent with many other observations of humans and animals. The disproportionately large representation of some sensory and motor regions of the cortex in animals and humans is well established. The recognized correlation between the large inferior colliculus for echo-locating bats and dolphins, and the enlarged optic lobes for visual fish is well known. In short, the idea that a larger brain structure reflects an increase in function is ubiquitous.

Even Charles Darwin promoted the idea that big brains explained the uniqueness of the human condition. In *The Descent of Man and Selection in Relation to Sex* (1871), he wrote that there is no fundamental difference in the mental faculties of humans and the higher mammals. He went on to add that the difference in mind between humans and the higher animals, great as it is, is certainly one of degree and not of kind. He did not want to be part of any thinking that there may be critical qualitative differences between the subhuman primate and humans. Darwin left the actual anatomy to his colleague Thomas Henry Huxley. At that time, Richard Owen, another anatomist, maintained that there was a special structure in the human brain, the hippocampus minor. Yet Huxley proved that this structure was also found in other primates, thereby undercutting the idea that the human brain was qualitatively different from the primate brain. So here we had Darwin, the

genius who articulated natural selection and diversity, arguing for a straight-line evolution between primates and humans. Organisms, the product of selection pressures, displayed rich diversity in the evolution of species. But when it came to brain and mind, Darwin thought the human brain to be a blown-up monkey brain, a nervous system that had a monotonic relation to its closest ancestor.

Nonetheless, a lot of evidence shows that the human brain's unique capacities do not rely on cell number so much as the appearance of specialized circuits. That the human brain has more cells does not explain greater capacities. Evolutionary perspectives would find the human brain adapted to its own biological niche, and one would predict differences in brain organization from other animals. After millions of years of natural selection, we have accumulated circuits that enable us to carry out specific aspects of human cognition. In short, just as comparative neurobiologists have demonstrated the presence of specialized circuitry in lower animals that reflect adaptations to niches, similar demonstrations can be made in humans.

Let's look at more evidence for specialized circuits. Consider the human brain's two halves, left and right. We know the left cortex is specialized for language and speech, and the right has specializations of its own (see Chapter 10). Each half is the same size and has roughly the same number of nerve cells. The cortices are connected by the corpus callosum. The total, linked cortical mass contributes to our unique human intelligence. What would happen to intelligence if the halves were disconnected, leaving the left operating independently of the right and vice versa? Would split-brain patients lose half of their cognitive capacity because the left, talking hemisphere would now operate with only half of the total brain cortex?

A cardinal feature of split-brain research is that after cerebral hemispheres are disconnected, the patient's verbal IQ remains intact, and the problem-solving capacity of the left hemisphere, such as hypothesis formation, remains unchanged. While there can be deficits in recall capacity and in other performance measures, the total capacity for problem solving remains unaffected. Isolating essentially half of the cortex from the dominant left hemisphere, then, causes no major change in cognitive functions. Following surgery, the integrated 1200- to 1300-gm brain becomes two isolated 600- to 650-gm brains, each about the size of a chimpanzee's brain. The capacity of the left half remains unchanged from its preoperative level, while the largely disconnected, equally-sized right hemisphere is seriously hampered from performing tasks. Although the



largely isolated right hemisphere remains superior to the isolated left hemisphere for things like recognizing upright faces, attentional skills, and perhaps emotions, it is poor at problem solving and many other mental activities. A brain system (the right hemisphere) with roughly the same number of neurons as one that easily cognates (the left hemisphere) is incapable of higher-order cognition—strong evidence that cortical cell numbers do not fully account for human intelligence.

Perhaps the most influential and dominant idea that more cortical area means higher-level function came from Norman Geschwind and Walter Levitsky (1968). Over the past 30 years, their report that the left hemisphere has a larger planum temporale solidified the belief that more brain area meant higher-level function. They concluded their classic paper by stating, “Our data show that this area is significantly larger on the left side, and the differences observed are easily of sufficient magnitude to be compatible with the known functional asymmetries.” In other words, the belief was that the greater brain area in this language zone was responsible for language.

Because this classic finding makes a strong case for a relation between cortical area and function, the issue of whether the left planum temporale is larger than the right planum has been re-examined. With three-dimensional reconstructions of normal brains provided by magnetic resonance imaging, the posterior temporal region was carefully measured using the same methods Geschwind used; approximately the same percentage of brains had apparent asymmetry, with the left side being larger. But this measurement is not a true three-dimensional reconstruction since it does not take into account the natural curvature of the cortical surface from one coronal slice to another (see Figure 10.4). When a true three-dimensional reconstruction algorithm is applied to this region, its cortical surface area is not reliably asymmetrical. In a sample of ten brains, as many had a larger cortical surface area in the right as in the left hemisphere.

Many lines of anatomical and physiological research suggest that cortical areas within a species contain variable proportions of morphologically and neurochemically defined cell types. For example, primary and secondary visual, somatosensory, and auditory cortices express varying distributions of specific nerve fibers, and the density of certain nerve cells, called *chandelier cells*, differs between prefrontal and visual cortical regions (Lewis and Lund, 1990).

Cortical connectivity varies among species, which may reflect the organism’s niche. The squirrel monkey and bush baby have differing connections of the interblob region in their visual cortices. In the bush baby, layer IIIB nonblobs receive input from lamina IV alpha, while in the squirrel monkey this layer receives input from lamina IV beta. The effect is altered inputs to lam-

ina IIIB from magnocellular pathways in the bush baby, and altered inputs to parvocellular pathways in the squirrel monkey (Lachica et al., 1993).

Blob regions in these two species are connected almost identically. The significance of the species’ difference in the nonblob regions of visual cortex is likely related to their activity patterns (Livingstone and Hubel, 1984): Bush babies are nocturnal and squirrel monkeys are diurnal. Bush baby layer IIIB receives input from layer IV alpha (the magnocellular stream), while squirrel monkey layer IIIB receives input from layer IV beta (the parvocellular stream).

Fascinating clues have emerged from work on human brain tissue. For example, the physiological properties of dendritic spines in the human might differ from those in other animals. Gordon Shepherd and his colleagues (1989) at Yale University studied presumed normal cortical tissue removed from epileptic patients. Comparing the membrane and synaptic properties of human and rodent dentate granule cells, they noticed important variations. First, humans had less spike-frequency adaptation in comparison with rodents; second, feedback was inhibited in human tissue, while rodent tissue showed feedforward and feedback inhibition—consistent with Shepherd’s neuronal modeling. This work suggests that by simply adding a few calcium channels to the dendritic spine, vastly complex computational capacities can result in the spines and lead to more information-processing capability. These suggestive study results are exciting, and may point to new ways of thinking about variations in neuronal physiology among species (Williamson et al., 1993).

Nonhuman primate and human visual systems also have different organizational properties. When comparing, for example, the anterior commissure between humans and other primates, it is easy to see how the species differ in neural organization. The anterior commissure is one of the neural connections between the two halves of the brain. It is the smaller of the two cortical connections, second in size to the huge corpus callosum. When this structure is left intact but the corpus callosum is sectioned, visual information easily transfers in monkeys but not in humans. Thus, species vary considerably in how they transfer visual information between hemispheres.

What is more, lesions to the human primary visual cortex render patients blind, whereas monkeys with similar lesions are capable of residual vision. When residual vision is discovered in a human, as with blindsight, it likely reflects incomplete damage to the primary visual cortex. When a monkey has residual vision, it reflects capacities of other secondary visual system processes.

Examples abound of system-level variations between primates and other lower animals, but less attention is paid to those between nonhuman primates and humans. Yet the preceding observations elucidate major differences



in anatomical organization, even though the monkey's visual system and the human's visual system have virtually identical sensory capacities. Careful psychophysical measurement of acuity, color, and other parameters reveals identical sensitivities. In addition, at the level of anatomical processes, both have approximately 1.2 million retinal ganglion cells. Even though the gray matter volume of the primary visual cortex in humans is three times larger than it is in the *Macaca mulatta* and five times larger than that in owl monkeys, this cortical area has the same number of cells in rhesus monkeys and humans.

In grasping the differences between monkey and human behavior, one has to consider the variations between the neuronal organization of each visual system. Can these differences be understood in relation to the connectivity of major processing areas or to the level of synaptic function? We do not know.

Arguing about similarities between species has been criticized by many. Take the problem of intelligence. It is naive anthropomorphism to apply the concept of human intelligence to the behavior of animals. It is simply a fact that each species has developed behavioral capabilities that are advantageous to its own survival, and that each member of that species possesses these capacities. There have been many attempts to raise the intelligence of a rat by selective breeding. All have failed. A rat that might run a maze better turns out to be lousy at discrimination learning. Our human brains are larger because they have more devices for solving problems, and the devices are shared by all members of the species. It is not likely that the variations seen in our own species's capacity to solve problems will vary with brain size; recent direct measures have shown there is no correlation.

Even though brain size cannot explain the unique capacities of the human, Noam Chomsky (1957) favored the view that, although language is deeply biological in nature, it is not a product of natural selection. Chomsky left open the possibility that language is the result, the concomitant, of massive interactions of millions of neurons. So, in the heart of the great Chomsky, the one who argued deeply for the biological basis of language, there lingers the idea that bigger is better.

Steven Pinker (1997a) challenged this bit of backsliding by Chomsky. Cranking up his unusually insightful and lively style, Pinker chided his colleague: "If Chomsky maintains that grammar shows signs of complex design, but is skeptical that natural selection manufactured it, what alternative does he have in mind? What he repeatedly mentions is physical law. Just as the flying fish is compelled to return to the water and calcium-filled bones are compelled to be white, human brains might, for all we know, be compelled to contain circuits for Universal Grammar."

Chomsky wrote (see Pinker, 1994):

These skills [e.g., learning a grammar] may well have arisen as a concomitant of structural properties of the brain that developed for other reasons. Suppose that there was selection for bigger brains, more cortical surface, hemispheric specialization for analytic processing, or many other structural properties that can be imagined. The brain that evolved might well have all sorts of special properties that are not individually selected; there would be no miracle in this—only the normal workings of evolution. We have no idea, at present, how physical laws apply when 10<sup>10</sup> neurons are placed in an object the size of a basketball, under the special conditions that arose during human evolution. We may have no idea—just as we do not know how physical laws apply under the special conditions of hurricanes sweeping through junkyards—but it seems unlikely that an undiscovered corollary of the laws of physics causes human-size and -shaped brains to develop the circuitry for Universal Grammar.

Neuroscientists have had a hard time accepting the view that big brains may be a by-product of other processes for establishing the uniqueness of each species's nervous system. Yet biologists have known for years how specialized circuits define differences between fish and reptile, reptile and mammal, snail and octopus, worm and jellyfish. It is only logical that this information would help to define the neural processes supporting unique human capacities, especially language, and that big brains (corrected for body size) may get bigger because they collect more specialized circuits.

## SUMMARY

The lesson of this chapter is simple: Complex capacities like language and social behavior are not constructs that arise out of our brain simply because it is bigger than a chimpanzee's brain. No, these capacities reflect specialized devices that natural selection built into our brains through blind trial and error. Mutations create variations in capacities. If the variations produce a

slightly unique state of affairs that helps our brains make better decisions about enhancing reproductive success, the new capacities will survive. Variations that further enhance the capacity in question will also survive. An eye was not built in a day. It started as something that worked a little bit, which was better than something that did not work at all. As it evolved, the visual



system became the finely tuned device it is now. So, too, with language and other mental abilities. The positive-feedback mechanism of natural selection, not experience, builds complexity into organisms.

The structure of animal bodies and brains can vary dramatically, and trying to deduce similar features of brain organization and unique features is difficult. Therefore, the strategy comparative neuroscientists use is crucial. Bullock proposed three main aims for comparative neuroscience: roots, rules, and relevance. Roots refer to the evolutionary history of the brain and behavior. How are brains similar and different? What has evolution produced? Rules of

change are the mechanisms that give rise to changes in the nervous systems in the course of evolution. Are there constraints under which evolving nervous systems develop? Relevance refers to the general principles of organization and functions that can be extrapolated from a particular animal studied to all animals, including humans.

Finally, a multitude of commonalities connect all species and lend strength to much of biological research. At the same time, species exhibit crucial differences, such as those reviewed here, and human brain research has uncovered unique aspects of human behavior that may be supported by specialized neural circuitry.

### KEY TERMS

adaptation	exaptation	homology	plesiomorphic
alleles	fitness	homoplasy	principle of parsimony
chromosome	genes	mutation	recombination
comparative neuroscience	genetic pleiotropy	natural selection	sociobiology
convergent evolution	genetic specificity	neuroethology	traits
ethology	genotype	out-group comparison	
evolutionary psychology	heritable	phenotype	

### THOUGHT QUESTIONS

1. A hypothetical cortical area, DE, has been newly discovered in macaque monkeys. The investigators who first described it hypothesize that it is involved in tactile object discrimination and propose that it might be present in humans as well. How can they test this hypothesis without performing experiments using fMRI or PET?
2. What are the three major aims of comparative neuroscience? Briefly explain each.
3. Why is the study of convergent evolution of brain structures or fields important?
4. An area MT has been described in humans. This re-

- gion does not reside at the tip of the superior temporal sulcus as it does in all other primates that have been investigated. Further, the cortical architecture (how it looks in neural tissue that has been histologically processed) is quite different from that in other primates. Although it becomes active in response to moving stimuli, so do a number of other areas of human neocortex. Is this field homologous to the area MT described in other primates? Why or why not?
5. Should one look for a genetic explanation for all behaviors? Explain your answer.

### SUGGESTED READINGS

- BULLOCK, T.H. (1984). Comparative neuroscience holds promise for a quiet revolution. *Science* 225:473–478.
- JACOB, F. (1977). Evolution and tinkering. *Science* 196:1161–1166.
- MERZENICH, M.M., and KAAS, J.H. (1980). *Principles of Organization of Sensory-Perceptual Systems of Mam-*

- mals*. New York: Academic Press.
- PINKER, S. (1997). *How the Mind Works*. New York: W.W. Norton.
- WILSON, E.O. (1975). *Sociobiology, The New Synthesis*. Cambridge, MA: Belknap Press of Harvard University Press.