The Argument from Animals to Humans in Cognitive Neuroscience

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ABSTRACT Neuroscientists make inferences about the human brain by studying nonhuman species, an enterprise that depends on assumptions about the nature of evolution. Traditionally, many neuroscientists have supposed that all mammals possess variants of the same brain which differ only in size and degree of elaboration. Under this model, the brains of nonhuman species can be treated as simplified versions or models of the human brain. However, there is evidence that mammalian cerebral organization is much more variable than is commonly acknowledged. The diversity of mammalian brain organization implies that neuroscientists can make better inferences about human brain organization by comparing multiple species chosen based on their evolutionary relationships to humans, than by studying individual “model” or “representative” species. The existence of neural diversity also suggests that nonhuman species have evolved cognitive specializations that are absent in humans.

During the past two decades, neuroscientists have developed a host of new techniques for studying the organization of the nervous system at a level of detail and precision scarcely imaginable by earlier generations of researchers. However, many of the most useful and informative techniques, including those used to trace neural connections, require invasive or terminal procedures. For this reason, they are used to study nonhuman species almost exclusively, and provide no direct information about the human nervous system. As a result, much of what neuroscientists believe to be true about the human brain, particularly about its connectional and areal organization, is based on inference or extrapolation from studies of other species.

From an evolutionary standpoint, it is reasonable to expect that we can learn much about humans by studying other species, especially closely related species. After all, humans share a long history of common ancestry with other primates and with mammals generally. Evolution necessarily entails change, however, and change poses a problem for those who would extrapolate findings from one species to another. Neuroscientists rarely confront this challenge directly. It is entirely commonplace to read reports of studies of a single primate species, usually the rhesus macaque, that purport to be studies of “the monkey” or “the primate.” This practice discourages critical evaluation of evolutionary differences. Furthermore, since humans are primates, it tempts one to conclude that what is true of “the primate” will also be true of humans. The problem is that, strictly speaking, there is no such thing as “the primate” or “the monkey.” Rather, there are approximately 200 living species of primates (Fleagle, 1988; Nowak, 1991), representing several distinct phyletic groups: prosimians, New World monkeys, Old World monkeys, and hominoids (apes and humans). Unless evolution has produced very few changes in neural organization, we have no prior grounds to conclude that what is true of any single primate species—rhesus macaque, squirrel monkey, owl monkey, or whatever—is true of primates generally, or of humans in particular.

Furthermore, if it is the case that evolution has produced so few differences between the brains of humans and other primates that we can comfortably ignore them, why should we suppose there is anything unusual about primates? Perhaps the features of cerebral organization found in humans evolved early in mammalian history. If so, the choice of species to be studied becomes largely a matter of cost and convenience, and it would be difficult to defend the study of anything other than rats. Indeed, Kolb and colleagues have vиг...
orously defended the status of rats as "representative" mammals, and regard rat cortex as a good model system for understanding the structure and function of the human cortex, even the higher-order association regions (Kolb and Tees, 1990; Kolb and Whishaw, 1990). People who study primates may scoff at this, but if one accepts that evolution produced important differences between rodents and primates, one must acknowledge that it could have produced important differences between rhesus macaques and humans as well.

The purpose of this chapter is to consider how ideas about evolution affect the practice of neuroscience. First, I will contrast the modern conception of evolution, which embraces both similarities and differences, with the traditional view adopted by many neuroscientists, which emphasizes similarity and continuity. Next, I will review some of the evidence for phyletic differences in mammalian cerebral organization. I will then propose procedures for making inferences about human neural organization from the study of animals that are grounded in modern evolutionary principles, and thus do not rely on the traditional (and unwarranted) assumption that all primates or all mammals possess, in a fundamental sense, the same brain. Finally, I will consider how the evolutionary model advocated here can provide new perspectives on human cognition and its relationship to other varieties of animal cognition.

**The evolutionary tradition in neuroscience**

To illustrate the potential pitfalls involved in making inferences about the human brain from studies of macaques or other putative model species, imagine trying to make inferences about the nonneural characteristics of humans by studying macaques (Fleagle, 1988;Richard, 1985). To be sure, we would get some things right. Humans, like macaques, have eyes set together in the front of the face rather than on the sides of the head, have dexterous hands with opposable thumbs and digits tipped with nails instead of claws, and live in complex societies. Unfortunately, we would also make many mistakes. For example, we would conclude that humans walk on all fours, have a tail, and possess a thick coat of fur. We would infer that humans possess a pouch of tissue in the cheek, where food can be hidden from higher-ranking individuals (figure 81.1). Furthermore, we would conclude that human social groups are centered on a stable core of closely related adult females, with males leaving their natal groups when they reach puberty. Besides leading us to ascribe erroneous characteristics to humans, the study of macaques would provide us no information about the unique evolutionary specializations of humans: bipedalism, functional hairlessness, unique hand muscles, a new layer of fatty tissue, and language, among others (Aiello and Dean, 1990; Napier, 1993).

![Figure 81.1](image.png)

A rhesus monkey (*Macaca mulatta*), marked for identification as part of a field study, showing cheek pouches distended with food. Check pouches are evolutionary specializations of the Old World monkey subfamily Cercopithecinae, to which macaques belong. (Courtesy of A. Richard)
Other Mammals
(3500+ living species)

Whales, Rodents,
Carnivores,
Hoofed mammals,
Elephants, etc.

Prosimians

Lemurs, Lorises,
& Galagos
(46 species)

Bats

Tree Shrews

Tarsiers
(4 species)

New World
Monkeys
(64 species)

Apes &
Humans
(14 species)

Ancestral mammals
claws, non-divergent
big toe, nocturnal
insectivorous

Origin of
Primates

Last common ancestor of living primates
convergent orbits,
nails, divergent big toe,
frugivorous & insectivorous

Anthropoids

Macaques and other
Old World Monkeys
(94 species)

“sisterhood,”
cheek pouch

opposable
thumb

gregarious social organization

diurnal, fovea,
loss of tapetum lucidum

FIGURE 81.2 An evolutionary tree, showing the relationship
of primates to other mammals, and the relationships among
primates. The origins of evolutionary specializations distinctive
of different groups, inferred from comparative and palaeontological
studies, are mapped onto the tree diagram. So, for example,
the origin of primates was marked by the evolution of convergent
orbits and the modification of claws into

In extrapolating from macaques to humans, why
would we get some features right and others wrong?
The answer lies in the geometry of evolution. Evolution
is like a branching tree (figure 81.2). Every species is a
composite of characteristics that evolved at different
points in its ancestry; closely related species share more
features, distant relatives fewer features. Macaques and
humans share a long history of common ancestry. This
is reflected in the characteristics they have in common,
which are the characteristics we correctly attribute to
humans based on the study of macaques. However, the
macaque and human lineages separated about 25 million
years ago, and since that time each has evolved its
own unique features: the cheek pouch and “sisterhood”
social organization in the case of macaques, bipedalism
and language in the case of humans. It is

nails, among other changes. The features are shared by later
primates. Humans and macaques differ due to evolutionary
events that occurred subsequent to the divergence of their
respective lineages (marked with horizontal and vertical
bars, respectively). The number of species of primates and
other mammals is derived from Nowak (1991).

features such as these, the evolutionary specializations
of particular taxonomic groups, that confound attempts
to make extrapolations from one group to another. When we consider a particular feature of macaque
neural organization, how are we to know whether
this is a feature present in humans rather than some
unique product of macaque evolution? How can we tell
whether we are studying the neural analogues of the
opposable thumb and frontotied orbits, rather than
something akin to a cheek pouch? And how can we ever
hope to understand what is distinctive about the
human brain by studying macaques?

Given the diversifying nature of phyletic change, it is
difficult to imagine a modern evolutionary biologist
endorsing the use of macaques (much less rats or cats)
as model humans. Why are neuroscientists not trou-
bled by this procedure? The answer seems to be that neuroscientists, for the most part, do not view brain evolution as treelike. There is a tradition in neuroscience and psychology that holds that the important events in brain evolution involved mainly progressive increases in the size and “differentiation” of the brain and its components, without fundamental changes in basic structures and functions (in mammals, at least). That is to say, the pattern of brain evolution has been likened to a unitary scale or ladder rather than to a branching tree.

The view that evolution is like a scale is certainly not unique to neuroscientists: this was the predominant view of evolution among biologists from Darwin’s era until well into this century, and it remains the predominant view in our culture at large. Nevertheless, modern evolutionary biologists are inclined to view the phylogenetic scale as a relic of the nineteenth century, with its emphasis on the march of Progress and the inevitable ascent of Man (Richards, 1987, 1992). Faced with the fact that lineages tend to evolve distinctive specializations, and unable to document a unitary, progressive trend in the history of life, evolutionary biologists consider the branching tree a more suitable metaphor for evolution than the scale (Gould, 1989; Williams, 1966, 1992).

In continuing to embrace the phylogenetic scale, therefore, the neurobehavioral sciences are out of step with modern evolutionary biology (Hodos and Campbell, 1969; Kaas, 1987; Povinelli, 1993; Preuss, 1993). How are we to understand this adherence to an otherwise discredited idea? Without question, the scale holds particular appeal for students of the brain and cognition. The scale ranks animals from lower to higher, and few of us would question the placement of humans at the top, at least with regard to cognition. Yet even as it affirms the special status of humans, the scale metaphor suggests a unity among animal brains, and so provides a rationale for extrapolating from animals to humans. For the scale permits change only within very narrow limits: Along the scale, change is strictly cumulative, so that brains may become improved, added to, and enlarged, but they do not diverge. Thus, lower forms can serve as simplified models of higher forms. The appeal of the phylogenetic scale may also reflect the fact that neurobiology has deep roots in a particular anatomical doctrine closely linked to the phylogenetic scale. According to this doctrine, known as typological or idealistic morphology, the member species of each major taxonomic group are regarded as manifestations or elaborations of an ideal, inherent form or archetype (Richards, 1992). Under this theory, the goal of comparative anatomy was to glimpse the common archetype through the haze of variations, the different expressions of the archetype presented by actual organisms.

Typological morphology was the dominant anatomical doctrine of the eighteenth and nineteenth centuries, predating the theory of evolution. The idea that differences between related species are not fundamental—that variations represent different expressions of a shared type—was held by many early evolutionists, including Darwin. This is evident in Darwin’s insistence that humans possess no structures that are not also present in other animals, and by his emphasis on continuity between living forms in both physical and mental characteristics (Darwin, 1871, chap. 1). For example, in the Descent of Man, Darwin asserted that “the difference in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind” (Darwin, 1871, 105). The only uniquely human characteristic he acknowledged (grudgingly, it seems) is language. For Darwin, human evolution was largely a process of improving upon faculties present in other animals, rather than adding new ones (Povinelli, 1993; Preuss, 1993; Richards, 1987).

Evolutionary biologists today take a different view of the evolutionary process: The changes organisms undergo in evolution represent departures or deviations from an ancestral condition, rather than different expressions of a common type (e.g., Williams, 1992). Yet, neurobiologists embraced Darwin’s narrow doctrine of evolution, along with its typological foundations, early in the development of their discipline; and the influence of typological morphology continues to this day. For example, Cajal (1904) maintained that structures corresponding to the higher-order cortical areas of humans are present in other mammals, although smaller than in humans. Later, Elliot Smith (1924) and his student Le Gros Clark (1959), both central figures in the development of primate neuroanatomy, acknowledged that the number of cortical areas increased in evolution. However, they rationalized these changes as improvements or refinements of common brain structures rather than as the evolution of new structures. Ebbesson’s (1980) idea that brain evolution is largely a matter of “parcellation”—the progressive segregation of elements originally mixed in one structure into mul-

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tiple daughter structures—also belongs within this tradition: The brain is enlarged, and the parts rearranged, but nothing new appears.

Recently, Kolb and his colleagues have developed a framework for thinking about brain evolution and its relevance to animal models of human neuropsychology (Kolb and Whishaw, 1983, 1990; Kolb and Tees, 1990). Their approach is very much in the traditional vein, in that they acknowledge that mammalian species differ in brain size and in the number of cortical areas while denying that such differences are fundamental or qualitative. They specifically deny that evolution has produced new connective or functional systems: the major features of cortical organization are present throughout the class Mammalia and are therefore said to be “class common.” They conclude, “There is no strong evidence for unique brain-behavior relations in any species within the class Mammalia, including Homo sapiens” (Kolb and Whishaw, 1990, 110). From this perspective, it follows that the rat can serve as a “representative mammal” for the purposes of generalizing from animals to humans, even regarding such functionally higher-order regions as prefrontal and parietal cortex (Kolb and Tees, 1990).

The diversity of cortical structure

I now turn to the evidence for variation in neural organization among mammals, focusing on the cortex and related structures. The fact of variation is not at issue: No one suggests that all mammalian brains are exactly the same. What is at issue is the nature of variation. Is it the case, as many neuroscientists have supposed, that brains vary only by degrees from a common mammalian type, such that the study of a few species would lead to an accurate picture of all other species, including humans? Or is there evidence of more substantial differences? A review of the literature suggests that mammalian brains display a number of remarkable variations, at several levels of organization. (For further discussion of neural diversity, see Kaas, 1987; Kaas and Preuss, 1993; and Preuss, 1993.)

Histology Ever since techniques were first developed to stain nerve cell bodies, biologists have been struck by the distinctive, laminated appearance of neocortex. Figure 81.3A presents a Nissl-stained section through the primary visual area (V1, area 17) of an owl monkey. The laminated appearance of the cortex reflects in part the segregation of cell types into different strata, for example, the concentration of small, granular cells in layer IV and of larger, pyramidal cells in layers III and V. (Six main layers are usually distinguished in neocortex.) Lamination is developed to an extreme degree in the visual cortex of anthropoid primates, but similar (if less vivid) patterns can be discerned in cortical areas in almost all mammals that have been examined (Brodmann, 1909). But there is at least one outstanding departure from this pattern among mammals—the cortex of cetaceans (whales and dolphins). Figure 81.3B shows a Nissl-stained section through the visual cortex of a bottlenose dolphin. Clearly, this is cortex with a difference. Layer I is enormously thick in these animals, compared to the other layers. No granular layer IV can be distinguished in adult dolphins, although granule cells are present in other cortical layers. Moreover, Golgi studies indicate that the pyramidal cells of dolphin visual cortex include a variety of unusual morphologies (Garey, Winkelman, and Brauer, 1985; Glezer, Jacobs, and Morgane, 1988). These characteristics are found throughout the cortical mantle of cetaceans that have been studied to date. Some workers believe that the distinctive characteristics of cetaceans represent the retention of a primitive stage in the evolution of mammalian cortex (Glezer, Jacobs, and Morgane, 1988), while others believe they constitute evolutionary specializations (Johnson, 1988; Preuss, 1993). In either case, the unusual character of cetacean cortex is very interesting, in view of the reputedly high intelligence of these animals: If cetaceans are indeed intelligent in a manner recognizable to humans, their intelligence rests on a very different neural foundation than does ours.

Cetaceans pose a challenge for the view that there is a “basic uniformity in structure of the neocortex” across mammals (Rockel, Hiorns, and Powell, 1980). Although cetaceans are probably an extreme case, there is evidence of more subtle variations in the laminar and cellular organization of cortex between mammalian species and between cortical areas in the same species (Beaulieu and Collonier, 1989; Beaulieu, 1993).

Connectivity Although it is now widely accepted that the number of cortical areas differs among mammalian groups, it is not as commonly recognized that the connectional and functional relationships between areas also vary. Even the relationship between primary
sensory areas and secondary areas may change. For example, inactivation of V1 by cooling or lesion in anthropoid primates produces functional deactivation of the immediately adjoining visual area, V2, and other extrastriate visual areas (Rocha-Miranda et al., 1975; Schiller and Malpeli, 1977; Kaas and Krubitzer, 1992). Inactivation of V1 in cats has a less profound effect on the visually driven activity of neurons in extrastriate visual areas (e.g., Sherk, 1978; Guido, Tong, and Spear, 1991), presumably because in cats (unlike in primates), there are significant projections from the lateral geniculate nucleus to visual areas beyond V1 (Rosenquist, 1985). A similar evolutionary "rewiring" of thalamocortical and corticocortical connections in the somatosensory system of primates has also been documented (Garraghty et al., 1991).

The cortical connections of rats and primates appear to differ in several respects. For example, the primary motor area (M1) of rats is connected with orbital cortex (Reep, Goodwin, and Corwin, 1990; Paperma and Malach, 1991); despite intensive study of M1 in nonhuman primates, no orbital connections have been reported (e.g., Stepniewska, Preuss, and Kaas, 1993). The rat primary visual area (V1) also differs from that of primates and carnivores, having direct projections to medial limbic and possibly frontal cortex (Vogt and Miller, 1983; Reep, Goodwin, and Corwin, 1990; Paperma and Malach, 1991); visual-limbic connections have also been described in tree shrews (Sesma, Casagrande, and Kaas, 1984).

The carnivore literature provides two interesting examples of species differences. In rats and macaques, it
is well established that the amygdala sends strong pro-
jections to the thalamic mediodorsal nucleus (MD),
specifically to its medial part (Krettek and Price, 1977;
Russchen, Amaral, and Price, 1987), which projects in
turn to medial frontal and orbitofrontal cortex. How-
ever, studies with comparable techniques indicate that
the amygdala does not project significantly to MD in
cats (Krettek and Price, 1977; Velayos and Reinoso-
Suárez, 1985). In cats, as in primates, there is a region
of cortex anterior to the somatic motor region from
which eye movements can be elicited by electrical stim-
ulation; this is usually called the frontal eye field, al-
though this region is actually composed of multiple areas
in both primates and cats (Schlag and Schlag-
While it is tempting to view this as a case of class-
common organization, the connectional evidence sug-
gests otherwise. In nonhuman primates, the frontal
oculomotor areas receive their main cortical inputs
from parietal and temporal areas located at the fringe
of the extrastriate visual region (Huerta, Krubitzer,
and Kaas, 1987). In cats, by contrast, the main input
to frontal oculomotor cortex arises from cortex near the
insula, at a distance from the main extrastriate zone, a
region that includes the anterior ectosylvian visual ar-
a (EVA) (Nakai, Tamai, and Miyashita, 1987; Olson
and Graybiel, 1987). EVA is unlike any visual area
known in primates, being separated from the rest of the
extrastriate visual cortex by intervening territories of
auditory and somatosensory cortex, and having un-
usual receptive field properties (Olson and Graybiel,
1987; Mucke et al., 1982). It seems likely that EVA is
a cat area that has no homologue in primates. So,
although both primates and carnivores possess frontal
oculomotor cortex, they differ with respect to the ma-
jor cortical connections of the region. This suggests
that one or more of the frontal oculomotor fields of
primates and carnivores are the products of convergent
evolution and are therefore not homologous. There is
evidence of other differences in frontal lobe organiza-
tion between primates and nonprimates (Preuss and

**MODULAR AND LAMINAR ORGANIZATION** In cortical
areas, the terminal fields of input fibers and the cells of
origin of outputs are typically segregated in different
laminae, and are sometimes also segregated into re-
peating “columns” or “modules” oriented orthogon-
ally to the laminae. These patterns of segregation vary
across mammalian groups. The best-known examples
of modular segregation are the ocular dominance col-
umns of primary visual cortex. In most mammals,
dense projections from the lateral geniculate nucleus of
the thalamus terminate in layers III and IV of cortical
area V1; these projections relay visual information
from the left and right eyes to V1 on each side of the
brain. In some primate species, inputs from the left and
right eye are segregated into alternating bands within
layers III and IV, known as ocular dominance col-
umns. The degree of segregation varies considerably
among primates, however, and some New World mon-
keys exhibit virtually no segregation at all (reviewed
by Florence, Conley, and Casagrande, 1986). Ocular
dominance columns are absent in other mammals that
have been examined, with the exception of carnivores
(reviewed by Casagrande and Kaas, in press). Ocular
dominance columns probably evolved independently
(convergently) in primates and carnivores. One reason
for concluding this is that carnivores, which possess
columns, are distantly related to primates, whereas tree
shrews, which are thought to be closely related to pri-
mates (Novacek, 1992), lack columns (Hubel, 1975).
However, tree shrews offer an interesting twist to the
ocular dominance story. Although they lack ocular
dominance columns, inputs from each eye are differen-
tially distributed within layers III and IV of the pri-
mary visual area. Specifically, inputs from both eyes
converge in the upper and lower tiers of layer IV, but
inputs from the contralateral eye have additional ter-
ninations in the middle tier of layer IV and in layer
III (Hubel, 1975). This laminar arrangement of ocular
inputs is unique among mammals studied to date.

Area V1 of primates exhibits another form of modu-
lar organization. As shown in figure 81.4, sections cut
parallel to the cortical surface and stained for the meta-
bolic enzyme cytochrome oxidase (CO), exhibit a regu-
ar pattern of darkly stained spots, termed “puffs” or
“blobs.” CO blobs have been described in at least sev-
genera of anthropoid primates (including *Homo*)
as well as in a number of prosimians, but have not
been clearly demonstrated in any nonprimate mammal
(Horton, 1984; Kaas and Preuss, 1993; Preuss, Beck,
and Kaas, 1993; Casagrande and Kaas, in press). These
results are consistent with the suggestion of
Horton (1984) that CO blobs are an evolutionary spe-
cialization of primate V1. CO blobs are thought to
constitute a specialized processing channel within the visual cortex, a point I will consider in a later section.

**Neurochemical Distribution** It is axiomatic among cell biologists that macromolecular pathways and systems have been highly conserved during the evolution of eukaryotic organisms. This conservatism is reflected in the presence of a common set of neurotransmitter, neuromodulator, and receptor molecules across a spectrum of invertebrate and vertebrate groups. Nevertheless, there are phyletic differences even at this level of organization, particularly with regard to the biochemi-
cal phenotypes of specific classes of neurons and the distribution of specific transmitter- and modulator-containing axons within the cortex.

One of the best-studied examples is the differential distribution of dopamine (DA)-containing axons in the frontal cortex of rats and macaques (Berger, Gaspar, and Verney, 1991; Berger, 1992). Dopaminergic neurons, with cell bodies located in the substantia nigra and ventral tegmental area of the midbrain, send strong projections to the frontal cortex, where they appear to modulate the responses of target neurons to other afferents. In rats, DA-containing fibers are concentrated in the medial frontal and orbitofrontal regions, with relatively weak projections to the primary motor cortex (M1) and supplementary motor area. Macaques and humans also have DA projections to medial and orbital cortex, but in addition exhibit very dense DA innervation of M1 and the supplementary motor area, with fibers distributed across all layers of cortex (see also Williams and Goldman-Rakic, 1993). In rat motor cortex, by contrast, DA-containing fibers are essentially restricted to layers V and VI. In rats, furthermore, the DA-containing fibers of frontal cortex also contain neurotensin, whereas in macaques, rats, DA and neurotensin are localized in different fibers, which project to different laminae (Berger, Gaspar, and Verney, 1991).

To take another example, there is now good evidence that rats possess a population of intrinsic neurons in cerebral cortex that contain acetylcholine (ACh); these have been identified using several different antibodies raised against choline acetyltransferase, the synthetic enzyme that is a definitive marker for ACh (Houser et al., 1985). Studies employing similar techniques provide no evidence of ACh-containing cortical neurons in macaques (Lewis, 1991), humans (Mesulam and Geula, 1991), or cats (Kimura et al., 1981).

From nonhumans to humans

The diversity of mammalian neurological organization cannot be denied or dismissed as trivial. We need to consider how the fact of diversity affects the practice of neuroscience. If we cannot simply extrapolate results from nonhumans to humans, how are we to advance our understanding of the human brain?

We can, of course, carry out more intensive studies of human beings, as suggested by Crick and Jones (1993). The problem, as Crick and Jones recognize, is that the techniques currently available for studying the connectional organization of the human brain are markedly inferior to those available for studying nonhumans. Certainly, innovations that improve our ability to study the human brain directly are only to be welcomed. For the immediate future, however, our methods for studying animals will remain superior to our methods for studying people. A second approach, to be advocated here, seeks to improve the inferences we make about humans from animal studies. One major goal of this approach is to determine those features of nonhuman neurological organization that are likely to be present in humans, as determined through a program of comparative research, guided by our understanding of evolutionary relationships. This approach promises fruitful interactions with more direct studies of human organization. Another goal of this approach is to understand in what respects the brains of species differ from each other, and how and why those differences evolved. Of particular interest and importance are those characteristics that distinguish humans from other animals.

The manner in which comparative studies can yield inferences about humans, and the potential for interaction between human and animal studies, are illustrated by recent investigations of extrastriate visual cortex (see also Kaas, 1993). This region has been extensively studied in Old World monkeys, mainly macaques, which have been taken as models for human organization. Crick and Jones (1993) have criticized this approach, arguing that macaque studies can provide only a working hypothesis about human organization, about which we have little direct knowledge. Humans and macaques presumably differ in ways we cannot determine at present. This is a reasonable expectation on evolutionary grounds, but it must be recognized that our knowledge of visual organization in nonhuman primates is not restricted to Old World monkeys: New World monkeys and prosimians have been studied in detail as well. One can identify a number of visual areas, based on similarities in architectonics, location, connections, and physiological properties, that are present in species belonging to each of these major primate groups (reviewed by Kaas, 1993; Krubitzer and Kaas, 1993; Preuss, Beck, and Kaas, 1993). As shown in figure 81.5A, the shared areas include the primary visual area (V1), second visual area (V2), dorsolateral area (DL; also known as V4), middle temporal area (MT; also known as V5), and the dorsome-
Figure 81.5. The organization of extrastriate visual cortex in humans and nonhuman primates. (A) Visual areas shared by nonhuman primates. Studies of prosimians, New World monkeys, and Old World monkeys have made it possible to identify a set of visual areas common to these groups, depicted in the figure at the top. In addition to the primary visual cortex (V1; striate cortex), the common areas include the second visual area (V2), dorsomedial area (DM), dorsolateral area (DL; and known as V4), middle temporal area (MT; also known as V5), and the area of the fundus of the superior temporal sulcus (FST). There is also evidence for multiple divisions of posterior parietal (PP) and inferotemporal (IT) cortex in these groups. Given the similarities among prosimians, New World monkeys, and Old World monkeys, it is likely that these visual areas were present in the last common ancestor of the living primates (LCA1), as indicated in the tree diagram at the bottom. The phylogenetic distribution of visual areas also implies that these areas were present in the last common ancestor of apes, humans, and Old World monkeys (LCA2). (B) The organization of visual cortex in humans, based on recent architectonic and in vivo imaging studies (modified from Kaas, 1992). The area denoted as MT in humans is very densely myelinated and is responsive to moving stimuli, as is MT in other primates. The location of human DL (V4) is controversial. Zeki et al. (1991) have identified a region of cortex on the ventromedial surface of the occipital lobe that is metabolically active while subjects view colored stimuli; they regard this as the homologue of DL (V4) of nonhuman primates, an area they consider to be the color-processing area. By contrast, Kaas (1992) suggests that in humans DL (V4) should be located the lateral surface of the occipital lobe, between V2 and MT, as it is in all other primates examined.

dial area (DM). There is also evidence that all major primate groups possess posterior parietal and inferotemporal cortex, although much remains to be learned about the organization of these regions, especially in New World monkeys and prosimians. While there are doubtless additional visual areas, these are the areas which, based on current evidence, appear to be shared by the major primate groups and thus are likely to have been present in ancestral primates.

The fact that we can identify a common pattern of extrastriate organization, shared across a wide variety of nonhuman primates, suggests that human extrastriate cortex is organized in similar fashion. This organization may have been modified during human evolu-
tion, but the common pattern of primate organization —inferred from studies using multiple techniques and diverse species—provides a solid foundation from which to pursue human investigations. Efforts are currently being made to identify homologues of extrastriate areas in humans, using evidence from architectonics, location, and function (Kaas, 1992). For example, there is good evidence that humans possess a homologue of MT, located anteriorly to V1 and V2 in the lateral occipitotemporal region (figure 81.5B), as one would expect based on comparative studies (Clarke and Miklossy, 1990; Zeki et al., 1991). By contrast, the location of area V4 is controversial. Zeki and colleagues (1991) argue that this area is located in the inferior and medial part of the occipital lobe, because they regard V4 as the cortical color center, and the inferomedial region is activated metabolically when subjects view colored stimuli. In response, Kaas (1992) has noted that if Zeki and colleagues are correct, human V4 differs in its location from that of all other primates studied. In nonhuman primates, V4 or DL is located on the lateral surface, between area MT and the foveal representation of V2. While it is possible that evolution has “relocated” V4 in humans, the spatial arrangement of anatomical structures tends to be highly conserved in evolution (Darwin, 1859), a principle illustrated nicely by the stability of extrastriate organization across nonhuman primates. The comparative evidence thus suggests that the cortical region activated by colored stimuli in the study by Zeki and colleagues (1991) corresponds to some visual area other than V4, or perhaps to a limited portion of V4.

It is common to hear neuroscientists assert that they are not really interested in comparative issues; what they care about is function. Yet a comparative perspective can provide unique insights on function. Consider the cytochrome oxidase–rich “blobs” in the primary visual area of primates (figure 81.4). Physiological investigations in Old World and New World monkeys have shown that blobs contain a higher proportion of color-opponent cells than surrounding cortex (Livingstone and Hubel, 1984). Blobs have thus come to be regarded as components of a specialized color-processing “channel” within the visual system—as indeed they may be, in diurnal primates such as macaques and squirrel monkeys (figure 81.4A). However, the comparative evidence puts the relationship between blobs and color vision in a different light (as it were). In addition to diurnal primates, which have well-developed color vision, CO blobs are present in such nocturnal primates as galagos (figure 81.4B), lorises, and owl monkeys (Horton, 1984; Livingstone and Hubel, 1984; Preuss, Beck, and Kaas, 1993), in which color vision is not well developed. What is more, because nocturnality is probably the ancestral condition for primates (Fleagle, 1988), it is likely that blobs originally evolved in animals with poor color vision. For this reason, researchers have considered other possible functions of blobs. Along with color-opponent cells, blobs contain broadband, brightness-selective cells (Livingstone and Hubel, 1984), prompting the suggestion that in primates generally, blobs constitute part of a perceptual brightness constancy system (Allman and Zucker, 1990). Furthermore, Allman and Zucker propose that when diurnal primates evolved, the brightness constancy system was modified to accommodate color-specific brightness differences. That is, they propose that evolution constructed primate color vision using structures that originally subserved other aspects of vision.

The foregoing example illustrates an important evolutionary principle. Evolution is a tinkerer, building new structures and systems by modifying existing structures, rather than by designing them from scratch (Simpson, 1967; Jacob, 1982). If we ask, Why is this system constructed in this way? we must consider not only what the system does but also where it came from. And that is a question about evolution, to be addressed through comparative studies.

It is because evolution adapts old structures to new ends that we may find studies of nonhuman species helpful in understanding the structural basis of even uniquely human functions. Consider the case of language. It has long been argued that the ventral premotor area (PMV) of nonhuman primates resembles Broca’s area in cytoarchitecture and location (e.g., Bonin, 1944; figure 81.6). Recent studies provide additional evidence that Broca’s area and PMV are homologous. Connectional and microstimulation studies in nonhuman primates indicate that PMV represents forelimb and orofacial movements (Preuss, 1993; Stepniewska, Preuss, and Kaas, 1993). Metabolic and surface stimulation studies in humans suggest that Broca’s area also represents nonlinguistic forelimb and orofacial movements (Fox et al., 1988; see also Roland et al., 1980; Uematsu et al., 1992). Results such as these have
led Fox and colleagues (1988) to suggest that Broca's area is a general premotor area without specific linguistic functions. Alternatively, it might be the case that Broca's area has both linguistic and somatic motor functions, and that evolution constructed the neural systems of language in part by "recruiting" existing motor areas, as Bonin (1944) suggested. The latter hypothesis suggests why language can be conveyed as naturally and fully with manual signs as with speech (Klima and Bellugi, 1979).

The foregoing examples demonstrate how we can make reasonable inferences about the structure of the human brain by comparing the neural organization of animals closely related to humans. This procedure does not require that the animals we compare be alike in all features of organization, merely that they possess some features in common by virtue of shared ancestry.

Studies of nonhuman primates are of particular relevance for identifying likely features of human organization, for these are the animals with which humans share the longest period of common descent.

The matter of inferring human brain structure represents only one aspect of comparative neuroscience, a specific aspect that is best addressed by studying animals closely related to humans. There are other neurobiological issues of a more general nature, though still pertinent to understanding humans, for which different comparative strategies are appropriate. For example, if we want to know why information processing in the human visual system is compartmentalized into blobs and columns, it is useful to consider the range of circumstances under which compartments develop and the structural and functional consequences of compartmentalized processing. Such an inquiry properly

Figure 81.6 The location of the ventral premotor area (PMV) in nonhuman primates compared to that of Brodmann's area 44 (the posterior part of Broca's area) in humans. PMV has been identified in prosimians, New World monkeys, and Old World monkeys, as a discrete region that represents forelimb and orofacial movements and is located immediately anterior to the inferior part of primary motor cortex (M1) (Preuss, 1993). Brodmann's area 44 occupies the same location with respect to M1 in humans. Recent metabolic and stimulation studies in humans suggest that Broca's area is involved in the control of forelimb and orofacial movements.
extends to whatever species and systems exhibit compartmentalization, from the barrel fields of rat somatosensory cortex (Kaas, Merzenich, and Killackey, 1983) to the optic tectum of three-eyed frogs, with its artificially induced visual columns (Constantine-Paton, 1982).

A diversity of minds

Providing the basis for making inferences about humans from the study of other species is just one way that evolutionary ideas can inform cognitive neuroscience. Indeed, if we accept the modern metaphor of evolution as a branching tree, and if we accept that neural organization varies among mammals, we are led to a new and challenging conception of the relationship between human minds and animal minds, one that is fundamentally different from that suggested by the scale metaphor. Under the older view of life represented by the phylogenetic scale, humans stand at the zenith of a continuum of mental development, and other beings are ranked according to a human standard. The modern conception of evolution as a branching tree removes this standard, so that nonhuman species are seen not as steps on the ladder to humanity but as alternative outcomes of the evolutionary process. Under this view, the human mind represents not the highest expression of a common animal mind, but rather one mind among many.

What are the consequences of acknowledging a diversity of minds? For one thing, it suggests new questions about the human brain and cognition. If the human mind is one evolutionary outcome among many, we must ask: Why this outcome and not some other? What specific cognitive capacities were selected for in human evolution? How were the components of neural and cognitive systems present in our primate ancestors modified to produce new systems in humans? Questions like these make little sense under the phylogenetic scale, in which the emergence of the human mind is the almost inevitable outcome of a general process of improvement. And these are fundamental questions about human nature rarely asked by neuroscientists.

To view evolution as treelike is to raise new questions about other animals as well. We should expect that nonhuman species are in some respects truly different from humans, with neural systems and functional capacities that humans lack. Understanding what other animals are like, when they are not like humans, is perhaps the most profound and intriguing challenge faced by cognitive neuroscientists.

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