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Neuroanatomy, Comparative

The history of comparative neuroanatomical studies, as they apply to physical anthropology, can be conveniently divided into three broad, though somewhat arbitrary, periods of development: (1) the Premodern, which embraces much of the nineteenth century and the early twentieth century; (2) the Early Modern, which spans the period from the 1920s to the early post–World War II years; and (3) the Modern, from the 1950s to the present.

Premodern Period: ca. 1800–early 1900s

During the first half of the nineteenth century, there was a mounting interest in comparative neurocranial studies. This interest had its origins in the developing concept of organization and the emergence of a functional approach to comparative anatomy at the close of the eighteenth century. The views expressed by the British anatomist William Lawrence (1783–1867) in his *Lectures* (1819) mirror this conceptual shift in the early 1800s. In marked contrast to savants of the 1700s, Lawrence and his contemporaries subscribed to the view that intelligence was inextricably linked with cerebral complexity and the level of somatic organization. Like others, Lawrence was struck by the prodigious development of the human cerebral hemispheres and convolutions compared to all other mammals. Based on his own observations and those of other investigators, Lawrence felt justified in formulating a simple hierarchy of intelligence and cerebral organization beginning with the European brain on through the "lower" human races to the anthropoid apes. At the same time, other investigators, such as German physician Franz Gall (1758–1828) (1810) and his disciple Johann Spurzheim (1766–1832), were forging a relationship between brain structure and behavior, promoting the idea that human intelligence was grounded in innate faculties located in specific organs of the brain, and that these centers had an external influence that was manifest in corresponding locations on the external cranium. Although the school of phrenology had initially gathered considerable support, by the early 1840s the scientific validity of its teachings had been discredited (cf. Flourens 1842), bringing a general retreat from the concept of localization. This latter idea, however, was not completely abandoned; it was resuscitated, thirty years later, by the French surgeon-anthropologist Paul Broca (1824–1880), when he presented evidence suggesting that articulate speech in humans was controlled by a local region in the left cerebral hemisphere (*vide infra*).

Another early pioneer was the Heidelberg anatomist Friedrich Tiedemann (1781–1861), who through his comparative studies endeavored to quantify and thereby understand more clearly the apparent relationship between the size of the cerebrum and intelligence (cf. Tiedemann 1836). His work, along with that of others, such as the Dutch anatomist-zoologist Willem Vrolik (1801–1863), corroborated the earlier observation of the English anatomist Thomas Willis (1621–1675) that the human brain was, indeed, more asymmetrical than that of any other primate species. These later works also confirmed what the British anatomist Edward Tyson (1650–1708) had observed at the end of the seventeenth century—that the neuroanatomical differences between humans and the anthropoid apes are essentially quantitative rather than qualitative ones. However, it was only with the careful work of Louis Pierre Gratiolet (1815–1865) and François Leuret (1797–1851) in the 1840s and 1850s that realistic illustrations of the convolutions of human and other primate brains emerged (e.g., Gratiolet 1854).

A major event in the mid-nineteenth century was the arrival of the Darwinian synthesis and the resulting reinstatement of Linnaean classification. At the close of the eighteenth century, the German anatomist Johann Friedrich Blumenbach (1752–1840) had presented a compelling case for the separation of human beings (Bimana) from the nonhuman primates (Quadrumana) on the ordinal level (cf. Bendyshe 1865). Blumen-

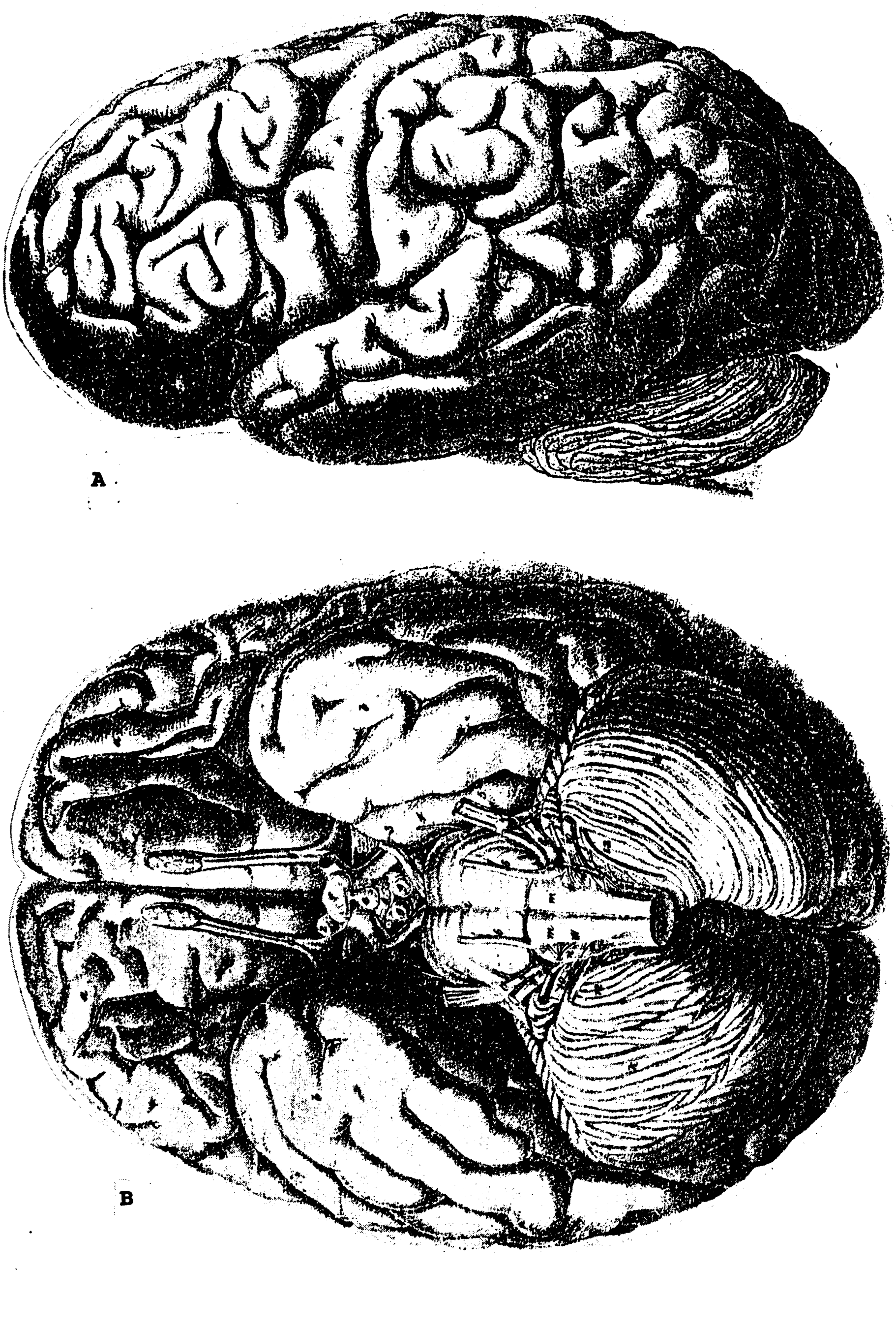

Fig. 1. Drawings of a male Negro brain: A lateral view; B: inferior view. From Tiedemann (1836).

bach's scheme was widely adopted by naturalists during the first half of the nineteenth century, and just prior to the publication of Charles Darwin's (1809–1882) *On the Origin of Species* (1859), the British anatomist Richard Owen (1804–1892) endeavored to push Blumenbach's scheme to its extreme limits. Building on the long-held conviction that the corpus callosum was the "great characteristic" of the mammalian brain, Owen argued not only that mammalia could be differentiated according to the size and conformity of their brains, but also that it was possible, from this perspective, to justify the separation of humans from the anthropoid apes into a subclass of their own (cf. Owen 1857, 1859). Specifically, he contended that the human brain was distinguished by the presence of three unique structures: the posterior lobe of the cerebrum, the hippocampus minor, and the posterior cornu of the lateral ventricle. These characters, as well as Owen's general synthesis, were immediately challenged by the British zoologist Thomas Henry Huxley (1825–1895), who in a series of publications in the early 1860s (culminating with his influential text *Evidence as to Man's Place in Nature* in 1863) not only demonstrated that there was no taxonomic characteristic of ordinal importance to separate humans from the nonhuman primates, but also promoted the Darwinian thesis, which he viewed as an agenda for future research. Indeed, Huxley's work immediately inspired several British anatomists to dissect primate brains to establish the validity of the case against Owen. For example, John Marshall (1818–1891) studied the chimpanzee (1861) and George Rolleston (1829–1881) the orangutan (e.g., 1861), while William Henry Flower (1831–1899) examined the brains of various other primates (e.g., 1861, 1863).

Although the research of the second half of the nineteenth century might simply be dismissed as a consolidation of the Huxley-Darwin viewpoint, this simplification does obscure the development of new techniques to study and preserve neuroanatomical structures, as well as the steady increase in more-detailed neuroanatomical studies. Most prominent in this growing community were German researchers, including, among others, Alexander Ecker (1816–1887) (1873), Theodor Bischoff (1807–1882) (1867), N. Rüdinger (1832–1898) (1882), J.H.F. Kohlbrügge (b. 1865) (cf. 1897), Wilhelm Waldeyer (1836–1921) (1891), and Carl Wernicke (1848–1905) (*vide infra*). Similar research was also conducted in France by such workers as Théophile Chudziński (1840–1897) (1878–1882), and in Italy by Giovanni Mingazzini (1859–1929) (cf. Mingazzini 1928). The studies were carried into the first decades of the twentieth century. (For bibliographic details of this burgeoning literature, see Connolly 1950.)

From a strictly anthropological perspective, the work of Paul Broca during the third quarter of the nineteenth century is of particular interest. During the 1860s, he made a very specific case for the dominance of the left hemisphere in language (Broca 1863, 1865). It is interesting to note that a similar idea had been proposed by the French physician Gustave Dax in the 1830s (it was later published in 1865)—but from all indications Broca was not aware of this earlier work (cf. Finger 1994). Broca's (and Dax's) argument was subsequently supported by a number of workers, but in particular by Wernicke in his monograph *Der Aphasische Symtomencomplex*, published in 1874.

Given Broca's interest in neuroanatomy, it is not surprising that his Société d'Anthropologie de Paris, founded in 1859, became an important forum for the discussion of racial differences in brain weight and organization. Initially, Broca was of the opinion that there was a connection between brain size and intelligence; he had argued that educated people had bigger brains than the noneducated, and he had criticized Tiedemann for having preconceived views about the equality of brain size in all human races. However, as more comparative data became available on living and fossil populations during the early 1870s, Broca modified these views—though he still believed that racial groups like the Hottentots and the Australian Aborigines were innately inferior because of their comparatively smaller brain capacities. (Further historical details on this issue can be found in Finger 1994.)

In addition to these debates on the truth or fiction of the racial inequality of brain size, the end of the nineteenth century introduced the controversy of the lunate sulcus (simian sulcus, *affenspalte*) and its disposition in apes and humans. The German anatomist Nicholaus Rüdinger was the first to apply this term to a fissure in the human brain in 1882. Among those who initially questioned this observation were the Dublin anatomist John Cunningham (1850–1909) and the Swedish anatomist-anthropologist Magnus Gustaf Retzius (1842–1919). While Cunningham (1892) was plainly skeptical of it being a homologous structure, Retzius (1896) believed the sulcus was a transitory feature rather than a homologue. This controversy was essentially resolved by the Australian anatomist-anthropologist Grafton Elliot Smith (1871–1937). From gross dissections of numerous monkey and ape brains, Smith showed that the stripes of Gennari (named after the Italian anatomist Francesco Gennari [1750–1797] by the German anatomist Heinrich Obersteiner [1847–1922]) characterized the primary visual striate cortex (later known as "area 17 of Brodmann"), which was bounded anteriorly by a deep crescentic (hence "lunate") sulcus. This feature, he contended, was shared by most primates, including humans (cf. Smith 1903, 1904). Among humans, however, the lunate, when and if present, was always in a more posterior position than in apes, signifying that there was a reduction of the relative size of striate cortex and a relative increase in parietal association cortex in humans (cf. Connolly 1950 for an excellent discussion of this structure, along with a review of the similarities and differences between humans and other primates, as well as racial differences in *Homo sapiens*). Although there were some notable workers, such as the American neurologist Frederick Tilney (1870–1951) (1928), who continued to doubt that humans had a homologue of the *Affenspalte*, the vast majority accepted Smith's argument. In the meantime, Smith was so intent in advancing his case for the primacy of the brain in human evolution that he "saw" the lunate sulcus in the endocasts of fossils such as the now infamous and bogus Piltdown remains (Smith 1913), and much later he studied the endocranial cast of "Rhodesian Man" (1928) (cf. Fig. 3).

The study of the brain endocast of the La Chapelle-aux-Saints Neandertal fossil conducted by the French workers Marcellin Boule (1861–1942) and Raoul Anthony (1874–1941) in 1911 was guided by a similar expectation—and these workers also claimed that the La Chapelle brain manifested a primitive disposition of the lunate sulcus (cf. Boule & Anthony 1911). These studies, and in particular Smith's views on the Piltdown endocast, met with a hostile reaction from the Belfast anatomist Johnson Symington (1851–1924) (1916), who vigorously attacked these claims as "highly speculative and fallacious"—arguing that such identifications based simply on endocast material were almost impossible to confirm. Although the lunate sulcus remains a contentious neocortical landmark, the issue is no longer whether it exists but rather *when* it was in a fully human posterior position—by the time of *Australopithecus* or by the time of early *Homo*? An early posterior migration would indicate that brain evolution was quite early in fossil hominids and preceded the great increase in brain size, thus making the brain one of the first organs, rather than the last, to evolve in human evolution (Holloway 1985).

Early-Modern Period: 1920s–1950

The early-modern period is characterized by the increasing number of research publications that manifest a continuing emphasis on comparative racial neuroantomy, as well as an increase in paleoneuroanatomical studies. Research in the latter category was fed primarily by the mounting tempo of hominid fossil discoveries in Asia, Africa, and Europe. Following in the wake of the Dutch physician Eugène Dubois' (1858–1940) 1924 study of the endocast of the Javan *Pithecanthropus erectus* calvaria he had found at the close of the nineteenth century was a series of studies on the hominid crania (i.e., *Sinanthropus* = *Homo erectus*) recovered from the Zhoukoudian site in China in the late 1920s and early 1930s. The Canadian anatomist Davidson Black (1884–1934), who had been largely responsible for these discoveries described the endocast remains of *Sinanthropus pekinensis* in 1933; while the Dutch neuroanatomist C.U. Ariëns Kappers (1877–1946) wrote several papers on both the Chinese and the Javanese pithecanthropine endocasts (Ariëns Kappers 1933; Ariëns Kappers & Bouman 1939). Similarly, the German anatomist-anthropologist Franz Weidenreich (1873–1948), who succeeded Black at Zhoukoudian in the mid-1930s, also made several important contributions to the study of human brain evolution between 1936 and 1947, particularly with regard to *Sinanthropus*.

During this same time period, several new European and African hominid fossils received attention. In France, for example, the details of Anthony's earlier study of the La Quina endocast were published as a part of the French paleoanthropologist Henri Martin's (1864–1936) memoir on *L'homme fossile de La Quina* (cf. Anthony 1923), while in England, Wilfrid Edward Le Gros Clark (1895–1971) described the endocranial cast of the Swanscombe remains (cf. Hinton et al. 1938). The most significant and clearly the most controversial find of the period was the infantile australopithecine skull found in 1924 at Taung in South Africa, which was described by the anatomist Raymond A. Dart (1893–

1988) at the University of the Witwatersrand, Johannesburg. Dart had studied for a while under Grafton Elliot Smith at Manchester University in England and had been influenced by him. In the description of this new hominid genus (which he named), published in 1925, Dart argued that the Taung child showed some modern features in its natural brain endocast. As this and his later work indicate, Dart was a champion of the concept of reorganization in the human brain—an issue that remains controversial. Dart's assessment of the Taung specimen was vigorously resisted. During the 1930s and 1940s, however, adult representatives of this early hominid were found at other South African sites, which led to the publication of the important monograph in 1946 by Robert Broom (1866–1951) and G.W.H. Schepers on *The South African Fossil Ape-Men: The Australopithecinae*, in which Schepers, an anatomist from the University of the Witwatersrand, contributed sections on

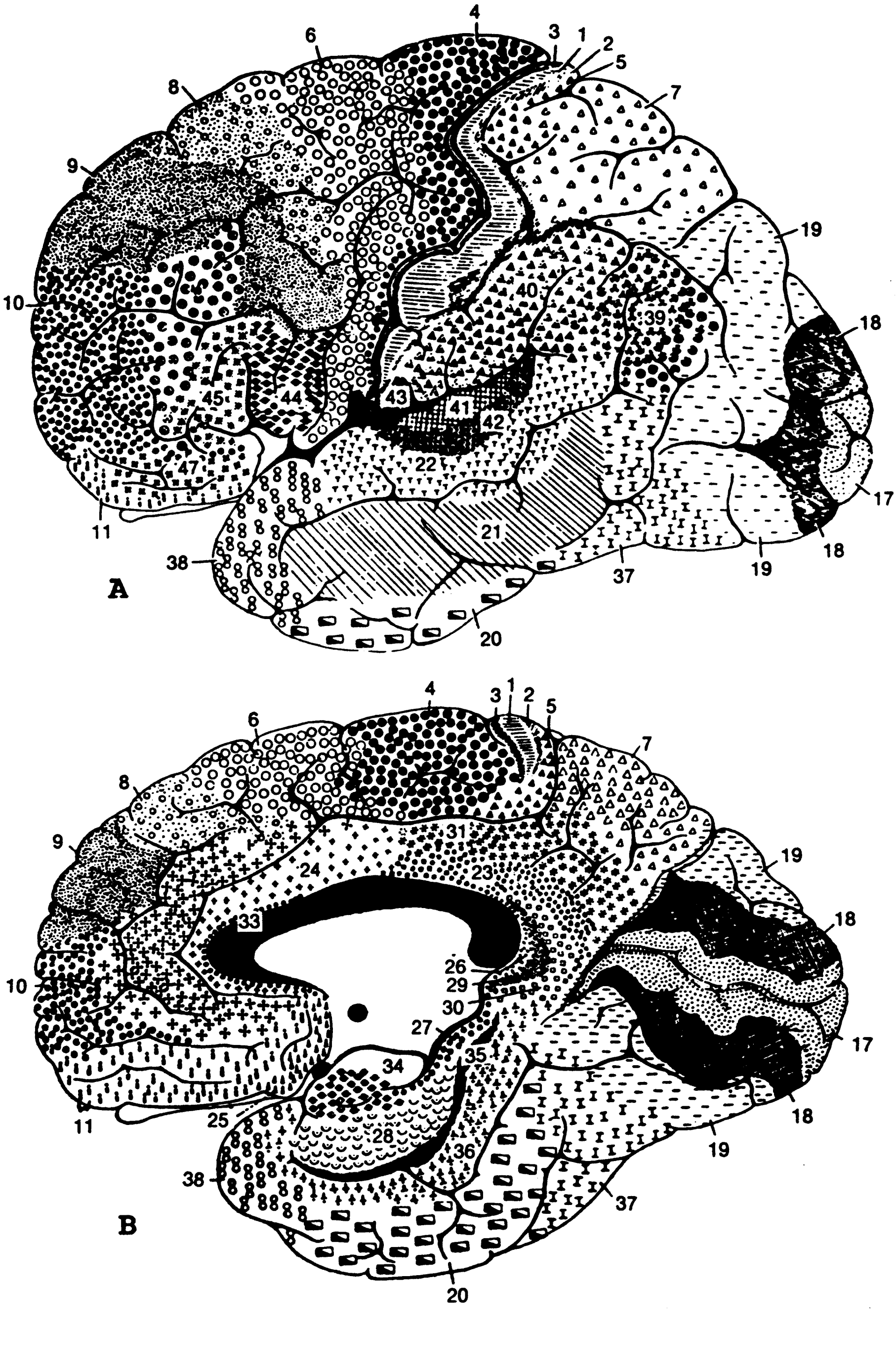

Fig. 2. Brodmann's cytoarchitectural map of the brain. The various areas are labeled with different symbols and identified further by figures. (A) is a lateral view of left hemisphere, and (B) is a medial view of right hemisphere.

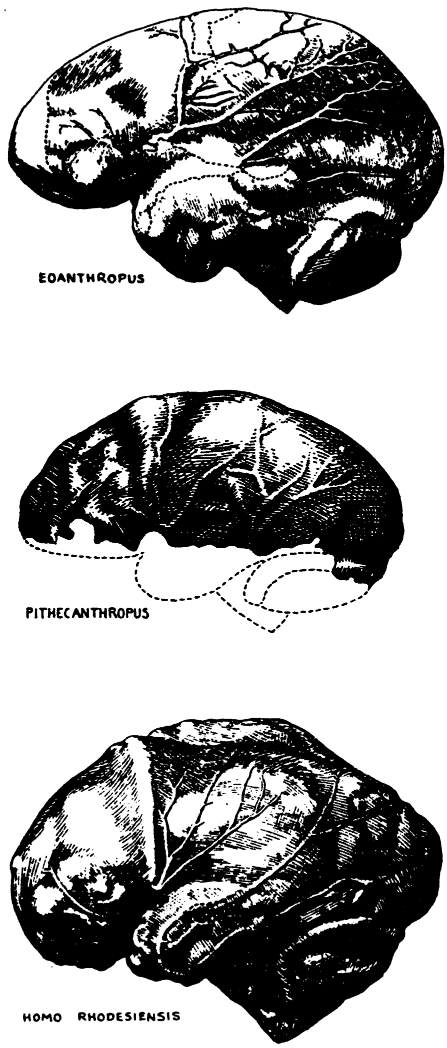

Fig. 3. Endocranial casts studied by Grafton Elliot Smith. From his collection of essays on The Evolution of Man *(1927).*

the natural brain endocasts recovered mostly from Sterkfontein (cf. Broom & Schepers 1946: 155–272). Their opinion was similar to that of Dart's that the brain endocasts were from animals more advanced than apes—an opinion that found a more secure foothold in the anthropological community when Clark endorsed it in an article published in the *Journal of Anatomy* in 1947 (cf. Holloway 1985 for a review of this matter).

Racial studies of the human brain were numerous during this time period, and the reader is directed to the excellent bibliography provided by C.J. Connolly (1950) and S. Finger (1994). These studies tend to stress morphological variations that were present or absent in various races and whether some of these patterns were more primitive than others. Reading this literature in the light of modern knowledge is a curious experience. Many of the published descriptions suggest that variation does exist and that it is patterned differently in various geographical areas. Since World War II, the comparative study of morphological and possibly racial neurophysiological variability has been replaced exclusively with concerns and debates regarding either the size of the brain in the sexes and various races or the encephalization quotients applied to our fossil ancestors (*vide infra*).

Building on the foundations laid earlier by the Spanish neurohistologist Santiago Ramón y Cajal (1852–1934), the German neurologist Korbinian Brodmann (1868–1918) (1909) found that areas of the cerebral cortex were distinguished by differences in the arrangement of their six cellular layers, which allowed him to subdivide the human cerebral hemisphere into more than forty discrete areas, the so-called Brodmann areas (see Fig. 2). His numerical system is still used today. It is interesting to note in passing that during this same time period, Smith was able to produce a cortical map based only on gross dissection with a scalpel and magnifying glass (1907).

During the 1930s, detailed cortical maps of human brains were developed—most notably by the American neurosurgeon Wilder G. Penfield (1891–1976) and his coworkers and the German neuroanatomist Gerhardt von Bonin (1890–1979). Important data on the cerebral cortex for nonhuman primates were also gathered at this time—for the gorilla (Fulton 1938), the chimpanzee (Mingazzini 1928; Kreht 1936), the orangutan (Kreht 1936), *Ateles* (Fulton & Dusser de Barenne 1933), and *Macaca* (Dusser de Barenne & McCulloch 1938). These studies remain important contributions to the understanding of primate variation in cytoarchitectonic cortical studies, which, in concert with C.N. Woolsey's major work on neurophysiology (cf. Woolsey 1958), paved the way for the modern finer-grained understanding of these elements.

During this period, Ariëns Kappers produced two major texts on comparative neuroanatomy, one in 1929 and the other in 1936 (in collaboration with G.C. Huber and E.C. Crosby). These works have since become "bibles" for physical anthropologists and zoologists alike. Several other valuable sources were produced during this time, including Frederick Tilney's two-volume work *The Brain from Ape to Man* (1928) and C.J. Connolly's *The External Morphology of the Primate Brain* (1950). The latter work is extraordinarily valuable not only for its bibliography but also for its breadth and erudition. Another excellent source is the seldom mentioned doctoral dissertation of P. Hirschler, entitled *Anthropoid and Human Endocranial Casts,* which was published in Amsterdam in 1942.

Modern Period: 1950s–1990s

The growth of neuroscience since the late 1950s has been astonishing—indeed, advances have been so rapid that keeping up with the literature has become an increasingly difficult task. Furthermore, without a firm foundation in molecular biology, the nonspecialist will find it difficult to even read the titles of published papers. New techniques such as MRI (magnetic resonance imaging) and PET (positron emission tomography) have added and will continue to add radically to our knowledge regarding where in the brain particular cognitive tasks take place, and their actual process in real time. These studies have already had important impacts on our understanding of motor and receptive aspects of language behavior and the relationship to such traditionally-thought-of regions of the brain as Broca's and Wernicke's areas. In general, the findings indicate that far more of the cortex and subcortex are involved in both simple and complex cognitive tasks. The growing sophistication with which cytoarchitecture of the cortex is now studied, and the complex cortical maps thus far developed for a number of primate species, are producing a tremendous amount of data that will lead to some critical needs for synthesis between the more or less standard areas of the neurosciences, such as neuroanatomy, cell biology, neurophysiology, and neurochemistry, and the newer foci, such as neuroimmunopsychology, neuroimmunoendocrinology, and neurogenetics. However, it should be noted that all of these trends are essentially molecular in nature and, as such, provide no handles with which to deal with the hard fossil evidence regarding the brain. Similarly, these studies have yielded no greater understanding of racial variation or simple within-species variation in humans.

Since the 1960s, there has been a trend among investigators with a direct interest in brain evolution toward the study of brain size and allometry. Although the concepts of scaling and/or allometry extend back into the nineteenth century (e.g., Dareste 1862; Baillarger 1872; Snell 1892; Dubois 1897); and the early twentieth century (Lapique 1912; Count 1947), it was not until the late 1960s and early 1970s that allometry took hold. This trend can be traced in large part to the influence of the American zoologist Harry Jerison and his former student Stephen Jay Gould. Jerison's writings (e.g., Jerison 1963, 1973) and particularly Gould's (1977), which integrated brain–body relationships within an evolutionary framework, have become a driving force in the thinking of many physical anthropologists and zoologists. The arguments have unfortunately taken the force of law, as in Jerison's works and many others. The value of the allometric approach is not that it provides answers to how the brain and behavior coevolved; it is rather that allometric relationships show that there are clearly genetic constraints operating, around which different species vary. Constraint vs. genetic law is a distinction seldom appreciated (cf. Holloway 1979). The American functional morphologist Leonard Radinsky (1937–?1986), who was a major contributing force to the development of paleoneurology during the 1960s and 1970s, was also an open but critical spirit regarding the importance of allometry. He believed that while this approach would offer no solutions to the question of brain organization, it nevertheless could not be ignored (cf. Radinsky 1974).

In addition to a preoccupation with problems of scaling, other quantitative viewpoints have arisen that have taken on a curious life of their own. Two such concepts, "extra cortical neurons" (N_c's) and "encephalization quotients" (E.Q.'s) are popular in physical anthropology into the 1990s. The "Extra Cortical Neurons" concept was developed by Jerison (1963) as a way of quantifying the number of neurons beyond those necessary to operate basic vegetative functions related to body size. Jerison assumed that animals such as shrews had a cortex devoted exclusively to vegetative functioning, and, by using them as a basal standard, he devised an equation based on a double exponentiation of body weight and one of brain weight for other animals. This was based on the assumption that brain–body scaling in mammals was 0.66. With this equation, it became possible to calculate the "extra number of cortical neurons" by simply inserting an animal's brain and body weights into the equation. Despite criticisms leveled at this concept (e.g. Holloway 1966, 1974, 1979), it has remained influential (cf. Tobias 1971, 1987). What is not generally taken into account is that in most mammals' brains, the cerebral cortex is anything but homogeneous. Different cortical regions have very different neural densities, and, at least in primates, there have been some major changes in the distribution of different cytoarchitectural patterns in the cerebral cortex (Holloway 1968).

The whole question of what is "extra" functionally, in the cortex and the corresponding animal behavior, is, to say the least, a thorny one. The upshot is that this has led to undue speculation regarding the number of "extra" cortical neurons in australopithecines vs. habilines based on unknown quantities of brain and body weights that have to be estimated without any final empirical checks.

The E.Q.'s concept, also devised by Jerison (1973), has been championed by many physical anthropologists. This quotient is derived by dividing an animal's actual brain weight by a "basal" allometric equation derived from some set of animal brain and body weights, in which the animal's actual body weight is placed in the equation. Many investigators have introduced their own equations, depending on their perception of what basal animal group is the most appropriate. These are then calculated for fossil hominoids after speculating on their body weights. But what is seldom appreciated is that these E.Q's are entirely relative to the equation chosen, leading to a "relativity" of relative brain weights (cf. Holloway & Post 1982).

Another area of modern concentration has been asymmetries in the brain, particularly the cerebral cortex. As noted earlier, concern with this problem can be traced to the work of Willis in the seventeenth century. Cunningham (1892) had demonstrated asymmetries in the height of the sylvian fissure in a number of primate species' brains. Work along these lines has been carried out by the American anatomist Marjorie LeMay and her colleagues (cf. LeMay 1976; LeMay et al. 1982), as well as the American physical anthropologists Ralph Holloway (Holloway & DeLacoste-Lareymondie 1982; Holloway 1975, 1976, 1983a, b, c; Heilbroner & Holloway 1989) and Dean Falk (e.g., 1978, 1980a, 1980b). It was LeMay's earlier study of the relationship between cerebral petalias and handedness that led Holloway and DeLacoste-Lareymondie (1982) to study the brain endocast collection of both hominids and pongids, and to observe that only hominids had the combined torque-like pattern of a left-occipital petalia combined with a right lateral frontal one. Previously, neuroanatomists had reported brain asymmetries in nonhuman primates (e.g., Yeni-Komshian & Benson 1976), but these were in anatomical structures seldom available in brain endocasts.

A central issue to almost all paleoneuroanatomical studies is the question, When in the evolutionary process did specific reductions or modifications occur? Since the late 1970s, considerable ink has been consumed in a debate regarding the lunate sulcus and its position relative to the occipital pole in the australopithecines. One view is that the shift occurred in early australopithecine times (cf. Holloway 1975, 1983a, 1983b, 1983c; Holloway & Kimbel 1986); the opposing view favors a primitive ape-like retention in australopithecines and a human organization in *Homo habilis* (cf. Falk 1987). This debate, however, like so many others in paleoanthropology, will be resolved only by more fossil discoveries or by other independent assessments of the actual measurements on chimpanzee and australopithecine brain endocasts.

Finally, neuroscientific studies regarding human variation both ethnically and between the sexes have been relatively rare in the latter part of the twentieth century. The overall perception is that differences between the races or sexes with regard to either brain size or organization are not of any scientific value, and, as such, research along those lines has been discouraged. In 1992, however, the journal *Nature* carried a limited exchange between J. Phillipe Rushton and his detractors regarding apparent brain-size differences between "Asians, Blacks, and Whites" (e.g., *Nature* 358:532, 1992). Unfortunately, the fundamental issue of what these differences mean with regard to either behavioral variation or human evolution and adaptation was not addressed. Indeed, these and related questions remain as elusive and unanswered as they were two hundred years ago.

The question of differences in absolute and relative brain weights between females and males is still bandied about, usually with great inaccuracy. Since the 1970s, however, evidence has emerged for minor differences—though of questionable significance—in cognitive behavior between females and males. Similarly, much controversy surrounds issues such as organizational differences between male and female brains. Studies have shown that females have relatively larger corpora callosi compared to males (cf. Holloway et al. 1994 for a review of these questions). There has also been a growing acceptance of the proposition that perhaps males' and females' brains do differ in a number of ways beyond the anterior nucleus of the hypothalamus. Research in the 1990s has been directed to brain differences in gay males and females compared to heterosexuals (cf. Levay 1991, 1993), and with regard to chromosomal evidence as well (Hamer 1994). If these trends can be maintained with judicious and open studies to verify or refute previous studies, neuroscience and anthropology will have close connections. However, if sexual rhetoric wins out, it will ultimately be a loss for all.

Despite the enormous volume of research in primate neuroanatomy during this "modern" period, anthropologists are still unable to provide satisfactory explanations for the qualitative changes that occurred during primate evolution. While this prevailing situation can be blamed in part on the availability of evidence, it is also clear that the profession has, contrary to expectations, failed to muster a concerted research effort in this direction.

Given the central role that the brain has played in human evolution (and surely much of antecedent primate evolution as well), the subject of comparative neuroscience should be a central part of the training of physical anthropologists, but it is not. A careful glance at all of the textbooks devoted to physical anthropology since the Harvard physical anthropologist Earnest A. Hooton's *Up from the Ape* (1946) will quickly show that the brain seldom commands more than a page or two of textual description, and even less for the problems surrounding its evolution (beyond size, with allometry being only a recent concern for such authors) and how the subject might be studied. If nothing else, this might at least equip the physical anthropologist of the twenty-first century to comprehend the anticipated advances in this crucial and exciting field of scientific inquiry.

Ralph L. Holloway

See also Anthony, Raoul; Australopithecines; Black, Davidson; Blumenbach, Johann Friedrich; Broca, Paul (Pierre); Broom, Robert; Chapelle-aux-Saints, La; Chudziński, Théophile (Teofil); Clark, (Sir) Wilfred Edward Le Gros; Dart, Raymond A(rthur); Darwin, Charles Robert; Evolutionary Theory; Flower, (Sir) William Henry; Germany; Gratiolet, Louis Pierre; Huxley, Thomas Henry; Mingazzini, Giovanni; Owen, (Sir) Richard; Paleoanthropology Theory; Phrenology; Piltdown; Retzius, Magnus Gustaf; Smith, (Sir) Grafton Elliot; Taung (formerly Taungs); Tyson, Edward; Weidenreich, Franz

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New World Primate Studies

The living nonhuman primates of the Western Hemisphere (Central and South America), commonly known as New World primates, platyrrhine monkeys, or ceboid monkeys, first became known to inhabitants of the Eastern Hemisphere in the early sixteenth century as a result of reports of early European explorers. In his now classic tenth edition of *Systema naturae* (1758) the Swedish naturalist Carolus Linnaeus (1707–1778) included all monkeys (both Old and New World) in the same genus, *Simia*; however, he recognized seven species of Neotropical monkeys: *Callithrix jacchus*, *Saguinus midas*, *S. oedipus*, *Ateles paniscus*, *Cebus apella*, *C. capucinus*, and *Saimiri sciureus*. By the twelfth edition (1766), he added five additional species. The French naturalist Etienne Geoffroy Saint-Hilaire (1772–1844) was the first to recognize the distinctive nature of the "platyrrhine" (broad) nose of the New World monkeys (cf. Geoffroy Saint-Hilaire 1812). Collectors in the nineteenth century, especially the German naturalist Alexander von Humboldt (1769–1859), added greatly to the knowledge of these primates. The most recent genus described was *Callimico* (Goeldi's monkey) by the British mammologist M.R. Oldfield Thomas (1858–1921) in 1904. New species continue to be found, however, including two in 1992. The evolutionary history of the New World primates is poorly known; however, it is certain they radiated in South America and did not spread to Central America until the "Great Faunal Interchange" of the Pliocene. Fossils are also known from Caribbean Islands.

For the purpose of description, the history of primate field studies in the New World is divided into four phases.

The Carpenter Era: 1931–1937

The first analytical census of any nonhuman primate population was conducted by Clarence Raymond Carpenter (1905–1975) in the early 1930s, working on a postdoctoral fellowship under the psychologist Robert M. Yerkes (1876–1956) at Yale University. At that time, the only previous scientific attempts at studying primates in the wild were by Harold C. Bingham (1888–1958) and Henry Nissen (1901–1958), two other students sent to Africa by Yerkes in 1929 and 1930, respectively. Beginning on Christmas day 1931, Carpenter inaugurated the first field investigation of a Neotropical primate, *Alouatta palliata*, the howler monkey on Barro Colorado Island (BCI). BCI is a 15 km² island created by the flooding of the Chagres River to form Lake Gatun during the building of the Panama Canal. The island became a research reserve of the Smithsonian Institution, Washington, D.C., in 1923.

Over a period of about a year and a half, Carpenter spent about eight months of intensive observation on BCI; in addition, he ob-