Right-Left Asymmetries in the Brain

Structural differences between the hemispheres may underlie cerebral dominance.

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The concept of cerebral dominance (*1*) for certain human abilities was rapidly accepted after Paul Broca's demonstration in 1861 that lesions producing language disorders were nearly always located in the left hemisphere (*2*). In the past 25 years, the interest in unilateral prepotency for certain cerebral functions has grown rapidly, and now many behaviors are thought to be subserved by one or the other side (*3*). Language, handedness, musical talents, visuospatial abilities, attention, and emotion all appear to be activities in which dominance effects are prominent.

Summary. Structural asymmetries between the hemispheres are found in the human brain. Asymmetries in the auditory regions and in the Sylvian fissures are present even in the fetus. The Sylvian asymmetries may have existed in Neanderthal man and are found consistently in some apes. They may relate to right-left differences in function. Thus, the striking auditory asymmetries could underlie language lateralization. The asymmetries in the frontal and occipital lobes and the lateral ventricles are correlated with hand preference. Anatomical asymmetries may help to explain the range of human talents, recovery from acquired disorders of language function, certain childhood learning disabilities, some dementing illnesses of middle life, and the evidence for behavioral lateralization in nonhuman primates.

Despite the major importance of cerebral dominance in human biology, its underlying mechanisms remained obscure for many years. The possibility that anatomical asymmetry is partly or totally responsible for it appeared early (*4*), and many investigators searched for differences in the structure of the two hemispheres. More than 100 years after the search had begun, von Bonin reviewed these investigations and concluded that whatever anatomical asymmetries of the hemispheres had been discovered were not impressive enough in their magnitude to account for the remarkable functional differences (*5*). It was generally assumed that dominance reflected either subtle anatomical differences or physiological asymmetries without an obvious structural substrate. Some even believed it depended solely on learning (*6*).

Within the last 10 years, however, there has been a marked change. It is now well accepted that the human brain contains regions that are typically different in size on the two sides. These differences are often of considerable magnitude. Many of the asymmetries are easily observed with the naked eye in postmortem specimens, and others are found in human living patients by means of radiological methods, including the newer, noninvasive computerized tomographic techniques. In this article we will review the evidence for cortical asymmetries and their relationship to handedness and language. In addition, we will present new evidence to show the relationship of these asymmetries to differences in the extent of cytoarchitectonic areas (*7*) on the two sides. Furthermore, we will point out the evidence for the presence of similar asymmetries in the ancestors of modern man and in the higher nonhuman primates; we will allude briefly to their presence in nonmammalian forms. Finally, we will summarize some of the possible implications of these studies for differences between the right- and left-handed, recovery from brain lesions, developmental disorders of childhood, degenerative dementing illnesses of middle life, and the possibility of pharmacological differences between the hemispheres.

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Asymmetries in Cortical Areas

The best-defined asymmetries in the gross configuration of the human cerebral cortex occur on the upper surface of the temporal lobe. Heschl, in his original description of the anterior transverse gyrus, noted certain asymmetries in cortical folding (*8*). Pfeifer described asymmetries in the planum temporale (*9*), the cortical area lying between Heschl's gyrus and the posterior margin of the Sylvian fossa (Fig. 1). He did not provide any data on the frequency of these asymmetries, and von Bonin regarded his evidence as weak (*5*). Geschwind and Levitsky (*10*), however, in a study of this region in 100 adult brains, confirmed the presence of asymmetries in the planum readily visible with the naked eye and tabulated their frequency. They found that the planum was larger on the left side in 65 percent of the brains, approximately equal in 24 percent, and larger on the right in 11 percent (χ^2 test, $P < .001$). These findings have since been confirmed in several studies (*11–14*). Wada was the first to show that the planum asymmetry is present in the fetus and the newborn (*12*), and Chi, Dooling, and Gilles (*14*) have shown that it can be observed as early as week 31 of gestation.

Geschwind and Levitsky (*10*) found that the left planum averaged 3.6 ± 1.0 centimeters in length while the right averaged 2.7 ± 1.2 cm (χ^2 test, $P < .001$). The left planum is thus nearly 1 cm longer than the right and is on the average one-third larger in area. In the most striking cases it is five or more times larger than the right planum. Wada *et al.* (*13*) claim, in fact, that in some cases the right planum is absent.

Pfeifer (*9*) also noted that besides Heschl's gyrus there may be additional transverse gyri on the superior temporal plane, and that multiple transverse gyri were seen more commonly on the right side. This has been confirmed in both the adult (*15*) and in the fetus (*14*).

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Cytoarchitectonic Asymmetries

The gross asymmetries on the upper surface of the temporal lobe described in the preceding section are potentially of major significance in that, as has been known since 1874 (*16*), damage in the posterior and superior part of the temporal lobe on the left side leads to distinctive disturbances of language function. It would therefore be tempting to argue that the observed gross anatomical asymmetries represent the structural substrate for cerebral dominance for language. However, certain objections to this view could be raised. It is conceivable that the gross asymmetries observed merely result from differences in the pattern of folding of the cortex on the two sides. It is therefore essential to study the extent of cytoarchitectonic areas (*7*). The cortex can be divided into a large number of regions of distinctive cellular architecture, often with equally distinctive physiological characteristics (*17*). It is reasonable to assume that most asymmetries of functional significance would be reflected in cytoarchitectonic regions of differing sizes on the two sides. Economo and Horn (*18*) first attempted to test this hypothesis in 1930 by studying the extent of cytoarchitectonic areas on the superior temporal plane; they reported asymmetries corresponding to the differences in the size of the planum. They failed, however, to measure the size of those parts of the cytoarchitectonic areas that extended beyond the limits of the planum or into the depths of the sulci within the planum itself. More recently, Galaburda and Sanides (*19*) have mapped the full extent of the several cytoarchitectonic areas contained within the planum and including the portions extending beyond its limits in three serially sectioned brains from the Yakovlev collection (*20*). The major difference between the two sides of the brain is the greater extent of the temporoparietal cortex (area Tpt) on the left side (Fig. 2 and Table 1) (*21*). The volume of this area on the left side of this brain was approximately seven times larger than on the right side.

Asymmetry in the Crossing of the Pyramidal Tracts

After Yakovlev and Rakic had reported on asymmetries in the patterns of decussation of the pyramids in the medulla of newborn and fetal human brains (*22*), Kertesz and Geschwind studied 158 adult medullas and found similar asymmetries (*23*). The decussation of the left pyramid was rostral to that of the right pyramid in 82 percent of the cases. Since the rostrally crossing fibers in both pyramids usually go to the arm and hand areas in the spinal cord (*23*), an attempt was made to correlate the pattern of decussation with the handedness of the individual. Of the four purely left-handed and three partly left-handed subjects in this series, five showed the common pattern, that is, a more rostral decussation of the left pyramid. Only one showed a preferential crossing of the right pyramid. Because of the small number of non-right-handed subjects in their study, however, the possibility that the reverse pattern of decussation of the pyramids or a more even crossing are more common in the left-handed could not be adequately assessed.

A statement about the relative sizes of the left and right pyramidal tracts should be added. Work by Flechsig during the last century showed that in 40 percent of specimens an asymmetric number of fibers cross from one side to the other (*24*). Asymmetries in the size of the tracts below the decussation result from these asymmetries in degree of crossing.

Table 1. Relative volumes (in planimetric units) of auditory cytoarchitectonic areas measured on one brain. Three types of cortex are distinguished: KA or primary receptive area; pa A or association cortex (with subdivisions r, e, i, and c); and Tpt (*22*) or temporoparietal cortex. Some of the subdivisions are larger on the right side, but the most striking asymmetry is in Tpt, which is more than seven times greater on the left side.

Area	Right side		Left side	
KA	140		114	
pa Ar	53	447	50	366
pa Ac	50		106	
pa Ai	193		102	
pa Ae	151		108	
Tpt	35		254	

Radiological Asymmetries

The ability to demonstrate asymmetries in living subjects by radiological techniques, particularly by computerized axial tomography (*25*), has increased the pace of data collection on the relation between anatomy and cerebral dominance, since large numbers of subjects can be studied without risk. Figure 3 demonstrates in one of these tomograms a striking asymmetry in the planum temporale (PT); the left planum is larger, as it is in the majority of the right-handed. Because of technical difficulties, however, the planum cannot be visualized by this method in a large number of cases. LeMay has demonstrated other asymmetries in computerized scans that are readily seen and measured. The most striking are the pres-

Table 2. Distribution of hemispheric asymmetries seen by computerized axial tomograms of brain (*30*). Values represent proportions of brains in each group.

Group	Frontal lobe				Occipital lobe			
	N	Left wider	Equal	Right wider	*N*	Left wider	Equal	Right wider
Right-handed	174	0.09	0.21	0.70	158	0.64	0.2	0.16
Left-handed	49	0.2	0.4	0.4	50	0.1	0.3	0.5

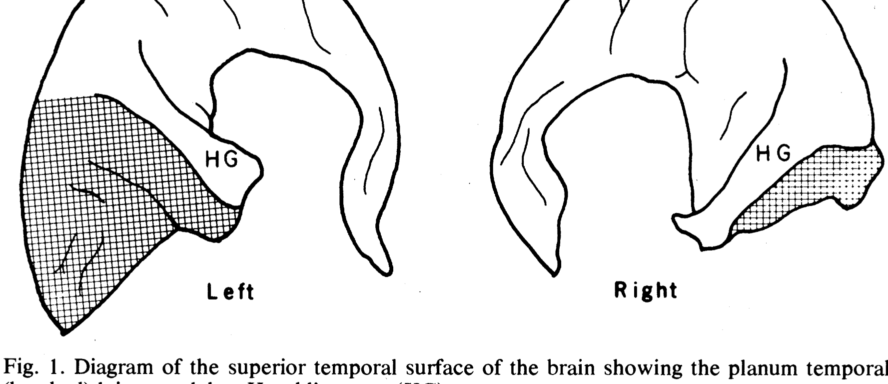


Fig. 1. Diagram of the superior temporal surface of the brain showing the planum temporale (hatched) lying caudal to Heschl's gyrus (*HG*).

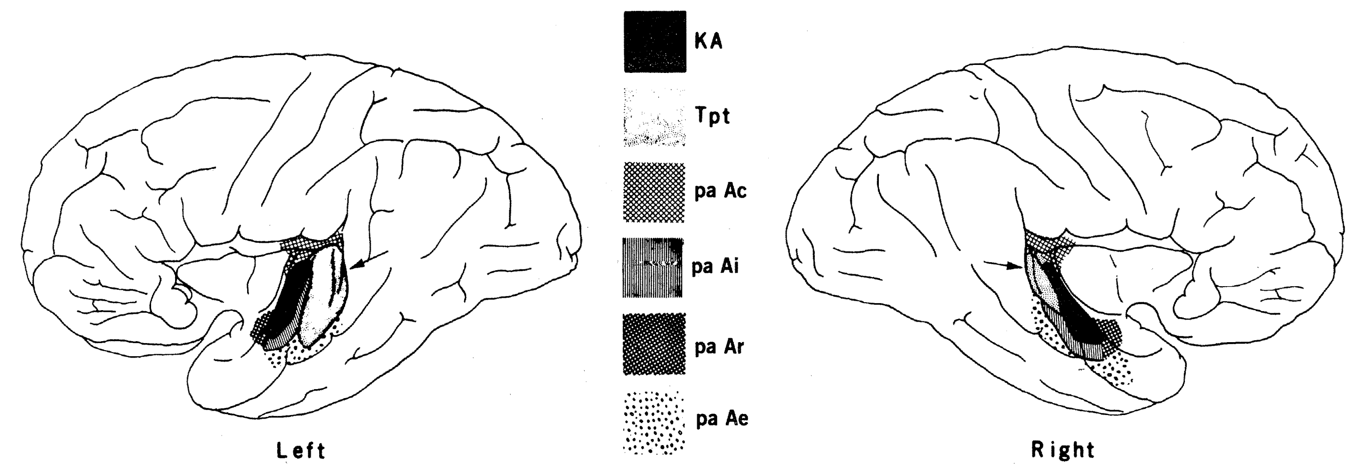


Fig. 2. Diagram of cytoarchitectonic areas of the human auditory cortex in one brain. Note the marked left-right asymmetry of Tpt (arrows), an area related to language function.

ence of a wider left occipital lobe and a wider right frontal lobe (*26*). Figure 4 shows this characteristic configuration and Table 2 summarizes its distribution among right- and left-handed subjects. In the right-handed, a wider left occipital lobe is nearly four times more common than a wider right. Also in the right-handed, a wider right frontal lobe is nearly nine times more common than a wider left. In the left-handed, the differences are much less striking.

The hemispheric asymmetries of a wider left occipital lobe and right frontal lobe often produce changes in the appearance of the skull. These changes have been used by LeMay to study asymmetries in fossil remains as well as in routine radiographs of the skull. The larger lobes may produce a smooth indentation in the inner and outer tables of the skull, an effect known as petalia. Thus, paralleling the hemispheric asymmetries, left occipital petalia and right frontal petalia are more common, especially in the skulls of right-handed individuals (*26*).

Asymmetries in the size of the left and right lateral ventricles can also be demonstrated by computerized techniques as well as by injecting air into the ventricles during pneumoencephalography and ventriculography (air studies). Ventricular asymmetry has been correlated with handedness. McRae *et al*. (*27*) showed in air studies that, in right-handed subjects, the left occipital horn of the lateral ventricles is longer than its mate in 60 percent of cases (Fig. 4), and the right occipital horn is longer in 10 percent. Only 38 percent of the left-handed and ambidextrous individuals had a longer left occipital horn, while 31 percent had a longer right one.

An asymmetry in the length and configuration of the Sylvian (lateral) fissures, which was noted by early investigators on autopsy specimens (*28*), can also be demonstrated by cerebral angiography. By this technique the blood vessels are rendered radio-opaque with an iodinated compound and can thereby be visualized as they emerge at the level of the Sylvian fissure on their way to supply the cerebral convexities. In this manner the configuration of the fissures is outlined. In an angiographic study, LeMay and Culebras found that the left Sylvian fissure was longer and more horizontally placed than the right fissure in both adult and fetal brains (Table 3) (*29*).

Asymmetries from the Fossil Record and in Nonhuman Species

LeMay and Culebras (*29*) found that the impressions of the Sylvian fissures in the La Chapelle-aux-Saints Neanderthal skull (*30*) appear to show a long horizontally placed left fissure, and a shorter, upwardly curved right fissure, as in the brain of most modern right-handed persons (*29, 31*). A similar pattern is suggested by the endocast of Peking man (*Sinanthropus pekinensis*) (*32*). The cast of Pithecanthropus I (*33*) shows right occipital petalia, while that of Pithecanthropus II shows the more common pattern of left occipital petalia found in modern man. Smith suggested in the early part of the century that occipital asymmetries were associated with handedness. He speculated that Pithecanthropus I had been left-handed (*34*). More recently LeMay and her colleagues have shown support for this notion in their radiological studies on living humans (*29, 31*), and McRae *et al*. have found a similar correlation of handedness with the size of the occipital horns of the lateral ventricles (*27*).

The great apes manifest certain brain asymmetries that are similar to those found in modern humans (*35*). Asymmetries in the configuration of Sylvian fissures which are common in the great apes, show the same pattern seen in humans, that is, the right Sylvian fissure is angled up more sharply than the left. Among the apes, the most striking Sylvian asymmetries in angulation are seen in the orangutan, which can show differences in the height of the posterior end of the fissures of more than 5 millimeters. The Sylvian asymmetries are least marked in the gorilla. Sylvian asymmetries in the brains of lesser apes and monkeys are not at all striking. Although 17 of 28 great apes showed significant Sylvian asymmetries (height difference > 3 mm), only 3 of 41 New World monkeys, Old World monkeys, and lesser apes showed them. Yeni-Komshian and Benson (*36*) found a longer left Sylvian fissure in 20 of 25 chimpanzees.

In nonhuman primates, left occipital petalia is also seen. In six of nine chimpanzee brains, the left occipital lobe was larger than the right one, as is common in humans (*26*). Among all of the great apes, however, right occipital petalia is seen more commonly (*35*). Because handedness cannot be determined in these animals with certainty, there is no available correlation of occipital lobe asymmetry and handedness. However, a gorilla known as John Daniels II, thought by LeGros Clark after years of observation to be right-handed was found after death to have a larger left occipital lobe (*37*). Structural asymmetries in the auditory region of the cortex such as those found in the planum temporale and its cytoarchitectonic areas in humans have not been described in nonhuman primates. Recent findings of left hemispheric preponderance in the mediation of certain auditory-dependent activities in monkeys (38), however, suggest the importance of further neuroanatomical research in lower animals.

Structural asymmetries in the nervous systems of nonmammalian species have also been recorded, although their functional significance is not understood. Of these the most consistent are differences in the epithalamus and habenula of some fishes and amphibians. Typically the habenular nucleus on one side is larger and more lobulated (39). In contrast, functional lateral asymmetries have been reported for which structural differences are not known. The most striking example is illustrated by lesion experiments on chaffinches and canaries, which show that bird song is abolished by left-sided neural lesions but not by right-sided ones (40).

Findings of pharmacological asymmetry may help to uncover the functional correlates of some structural asymmetries. In rats, injecting certain neuroactive substances into the blood produces unidirectional running in circles (41). A higher concentration of dopamine is found in the hemisphere opposite the favored direction of rotation (41). The asymmetry in rotation exerted by a substance delivered equally to both sides of the brain can be inferred to reflect asymmetry in the sensitivity to the neuroactive substance, which is probably related to an asymmetry in the number of receptor sites. A difference in the size of the subcortical gray masses containing these receptors has not yet been reported but deserves investigation. It is not unreasonable to wonder whether the great differences in size of certain cortical areas may not lead to pharmacological asymmetries in humans.

Significance of the Asymmetries

The ultimate aim of the search for anatomical asymmetries is the better understanding of human higher cerebral functions. A strong tendency for hand preference is typically human and is probably related to the higher cerebral functions. McRae *et al.* (27) and LeMay (26) have shown interesting correlations with handedness. As pointed out by LeMay and Geschwind (35), a general pattern appears to emerge from the data (Table 2): (i) brains without a particular asymmetry are more common in the left-handed; (ii) the left-handed are more likely than the right-handed to show the reverse asymmetry, but the extent of the asymmetry is less striking; and (iii) in some cases the asymmetry is in the same direction in the left-handed as in the right-handed, but, again, it is less striking in magnitude. The data, even at this early stage of collection, are compatible with many findings suggesting that the effects of functional dominance are less striking in the left-handed (42).

Table 3. Distribution of asymmetries of the Sylvian fissures seen by carotid angiography (25). Values represent proportions of brains in each group.

Group	*N*	Right higher	Equal	Left higher
Right-handed	106	0.67	0.25	0.08
Left-handed	28	0.2	0.7	0.1

Several other generalities may be induced from the data: (i) asymmetries seem to be distributed along a continuum, that is, the region which is larger on one side may vary from being only slightly larger to, at times, being many times larger; (ii) asymmetries appear to be inborn, since they are present in the fetus; and (iii) according to Wada *et al.* (13) and Heschl (8), there may be sex differences in the distribution and extent of the asymmetries.

Although specific information about the relationship of anatomical asymmetries to function is lacking, it is possible to speculate on the basis of available data. It is conceivable but unlikely that such striking asymmetries are of no functional importance. It is possible that the functions of areas usually found to be larger on the right side of the brain are different from those of areas which are generally larger on the left. For instance, a larger left planum temporale might indicate a significant degree of verbal ability, while a larger right planum might signify a high degree of musical potential.

An alternative speculation is that homologous areas have similar functions; and a larger area on one side would indicate that that side is dominant for a function. This hypothesis runs into difficulties. Out of 100 aphasics, fewer

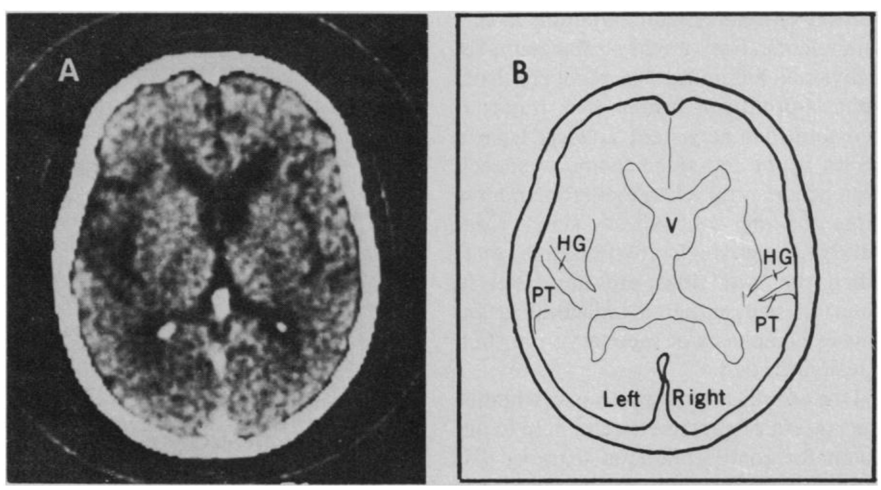
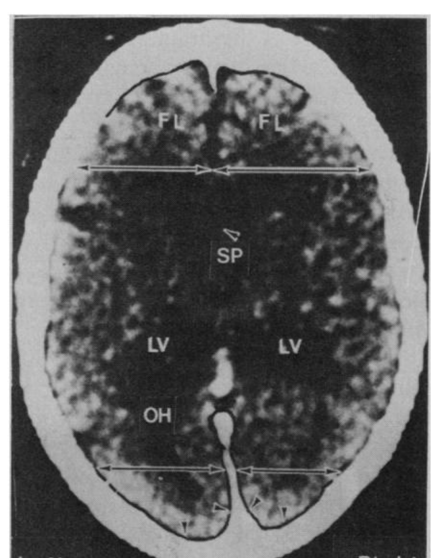


Fig. 3 (above). (A) Computerized axial tomogram of a brain showing asymmetry of the planum temporale. (B) Diagram made from (A) outlining the asymmetry of the planum temporale (*PT*). Heschl's gyrus (*HG*) is well seen as is the ventricular system (*V*). Fig. 4 (right). Computerized axial tomogram of a brain showing the usual pattern of hemispheric asymmetry. Note the wider right frontal lobe (*FL*, upper arrows), the wider left occipital lobe (lower arrows), and the more prominent left occipital horn (*OH*) of the lateral ventricles (*LV*). The septum pellucidum (*SP*) denotes the midline. Note also the left occipital pole distorting the midline and protruding into the right side, a common situation (lower arrowheads). Some asymmetries have been highlighted with India ink for greater clarity.



than four will have lesions on the right side (*43*), yet in 11 percent of cases studied by Geschwind and Levitsky (*10*), the right planum temporale was larger. This discrepancy might disappear if one had measures of the sizes of cytoarchitectonic areas rather than only the observations of gross asymmetries. If the cytoarchitectonic extent of the various primary and association auditory cortices on the two sides were compared, the asymmetry might be even more strongly lateralized to the left side. Alternatively, it is possible that right-sided cerebral dominance for speech is more common than is generally thought.

The presence of asymmetries in other species opens the possibilities for research on areas homologous to those in humans. Such research may help to bridge the wide gap between studies of human and nonhuman cerebral function.

Since there are great individual differences in the extent of asymmetries, it will be important to investigate whether these correlate with individual differences in function. One obvious question is whether the extent of asymmetries correlates with variations in certain talents. They might also account for individual differences in recovery from aphasia-producing lesions (*44*). It is conceivable that persistent aphasia from a lesion in the left-sided temporal speech area occurs only when the left planum is large and the right is very small. Conversely, one might hypothesize that, when the two sides are more nearly equal in size, either a unilateral lesion causes no aphasia or recovery from such a lesion is good.

One would also wish to ask whether the pattern of asymmetry can help to account for some childhood learning disorders. Is it possible that in some children the brains contain areas that are small on both sides? In the Yakovlev collection there is the brain of a man diagnosed as having developmental dyslexia. Both his father and a male sibling had similar difficulties with reading. Preliminary study appears to indicate that the planum temporale on the two sides is smaller than in normal brains (*45*). It is possible that this difference in size will be reflected in the size of cytoarchitectonic auditory areas on the two sides.

When Pick's disease, a degenerative illness of middle life that causes dementia, produces asymmetric atrophy, as it does in some cases, the right frontal lobe and the left occipital-parietal area are primarily affected (*46*). Although the relationship of this finding to the finding of volumetric preponderance of these regions in the majority of right-handed individuals is not known, the cytoarchitectonic areas that are larger on one side may be the same areas that are vulnerable to the etiologic agent which causes Pick's disease; furthermore, possible chemical differences on the two sides might account for this lateralized vulnerability. The finding of asymmetry may thus point the way to research in this and other disease states.

References and Notes

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7. Cytoarchitectonics refers to the study of the arrangement and morphology of cells which serve to delineate distinct areas. Early cytoarchitectonic maps of the human cerebral cortex still in use include those of K. Brodmann [*Vergleichende Lokalisationslehre der Grosshirnrinde* (Barth, Leipzig, 1909)] and of C. von Economo and G. N. Koskinas [*Die Cytoarchitektonik der Hirnrinde des Erwachsenen Menschen* (Springer-Verlag, Berlin, 1952)].
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21. Area Tpt is a clearly definable cytoarchitectonic area which has both parietal and temporal features. The structure is seen in both the human and the rhesus monkey. In the monkey it appears to be a subdivision of the parasylvian aspect of Brodmann's parietal area 7, and in the human it is physically separated from area 7 by Brodmann's parietal areas 39 and 40, from which it can be easily distinguished on cytoarchitectonic grounds. In the human, Tpt corresponds closely to temporal area TA_1 of Economo and Koskinas, an area which from pathological studies appears to be affected in cases of Wernicke's aphasia [D. Pandya and F. Sanides, *Z. Anat. Entwicklungsgesch.* **139**, 127 (1973); C. von Economo and G. N. Koskinas, *Die Cytoarchitektonik der Hirnrinde des Erwachsenen Menschen* (Springer-Verlag, Berlin, 1925); J. E. Bogen and G. M. Bogen, in *Origins and Evolution of Language and Speech*, S. R. Harnad, H. D. Steklis, J. Lancaster, Eds. (New York Academy of Sciences, New York, 1976), p. 834].
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47. We thank Professor F. Sanides for his valuable guidance in the cytoarchitectonic work. Supported in part by NIH grant NINCDS06209 to the Boston University Aphasia Research Center, a biomedical support research grant of the Beth Israel Hospital, Boston, Mass., and NSF grant BNS 77-05674 to the Beth Israel Hospital, Boston, Mass.