Early Theory and Research on Hemispheric Specialization

by Lauren Julius Harris

Abstract

This article provides an account of early theory and research on hemispheric specialization. It begins by tracing theory and research on localization of function that set the stage for the discovery of hemispheric specialization. After that, it describes the studies of Paul Broca, John Hughlings-Jackson, and others on hemisphere specialization and reviews some of the proposed explanations for the phenomenon. It then turns to the study of hemispheric specialization and mental illness, and it ends by identifying some of the linkages between theory and research from the past and the present.

Key words: Hemispheric specialization, laterality, history.

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In Paris in 1865, at a meeting of the *Société Anthropologié de Paris,* the physician and surgeon Paul Broca famously declared: "Nous parlons avec l'hémisphère gauche"—"We speak with the left hemisphere." In London in 1874, the neurologist John Hughlings-Jackson proposed a complementary role for the right hemisphere: Just as the left is specialized for speech, so the right is specialized for visual-spatial functions, or, as Hughlings-Jackson put it, for the recognition of "objects, places, persons, &c."

These were the first public statements of what, over the past 20 years or so, has become perhaps the most familiar of scientific principles about the human nervous system—that the left and right hemispheres play different roles in mental functioning. E.D. Hirsch (1987) implied that it is a core fact every American needs to know to be culturally literate. I infer this from the appearance of "asymmetry" and "cerebral cortex" in his list of "What literate Americans know." But if literate Americans, not to mention all literate people, know or should know about hemispheric specialization, they may not appreciate something about it that is quite remarkable. Compared to other paired organs that lie on either side of the body midline—the lungs, kidneys, gonads, and so on—only the neocortical hemispheres have different functions so far as we know.[1] This means that injury to or even loss of a lung, kidney, or gonad need not exact a great cost to our well-being, whereas injury to a cerebral hemisphere can be devastating—to speech and other language functions when it is the left hemisphere, to visuo-spatial perception as well as other nonlinguistic functions when it is the right.

Broca did more in 1865 than declare a fundamental principle about speech and the left hemisphere: He immediately inspired a torrent of new research by physicians who drew from the same well of clinical material as he had used, and after that by investigators from other disciplines. The same level of attention to the right hemisphere came much later. Today, both hemispheres, as well as the connections between them, receive intense scrutiny from investigators representing a range of disciplines from basic and clinical neuroscience, psychology, psychiatry, anthropology, and linguistics, among others. The articles in this issue of *Schizophrenia Bulletin* reflect some of the fruits of this new research, especially as it applies to the study of mental illness.

With so much that is new, it is easy to lose sight of the old and of the threads linking present and past. Dr. Gur, therefore, has invited me to recount some of the main themes and representative studies of the past. Although my account had to be very selective, for most parts of the story comprehensive histories exist and many of them are

[1]Evidence also points to functional differences between the left and right lobes of the thalamus and, perhaps, the basal ganglia, of the same general type as are found in the neocortical hemispheres. The point is that lateral specialization seems to emerge only as we reach the "highest" levels of the neuroaxis.

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cited in the text. (All translations are my own unless noted otherwise.) I begin with the era of theory and research on localization of function that set the stage for the discovery of hemispheric specialization. I then turn to the studies by Broca, Hughlings-Jackson, and others that first documented hemisphere differences, review some of the ways these differences were explained, and describe the views of certain critics of the time. After that, I show how theory and research on hemispheric specialization were applied to the study of mental illness. Finally, I identify some of the links between present and past.

Setting the Stage for the Discovery of Hemispheric Specialization

Organology and Phrenology. In the half-century before Broca's time, the neuropsychological theory commanding the greatest attention was phrenology, or organology. The latter term was used by the theory's creator, the anatomist and physician Franz Joseph Gall.[2] The theory was built on four principles. First, it was localizationist: Gall identified 27 "faculties," "talents," or "powers" of mind comprising two categories; namely, *intellectual,* which ran the gamut from "sense of number," "places and space," and "people" to wisdom and metaphysical depth of thought, to speech and verbal memory; and *moral,* which encompassed the passions, or feelings and affections, such as love of offspring, friendship, courage, and destructiveness.

Second, in contrast to many earlier investigators who saw the cerebral cortex as merely a crust or rind, with no specific functions, Gall gave it pride of place by siting each faculty in a distinct region, or cortical organ, with the intellectual faculties in front, the passions in back, and one faculty, amativeness, in the cerebellum. In locating all faculties, intellectual as well as emotional, in the brain, Gall broke with still another convention, namely the view that located only intellectual, or cognitive, functions in the brain and relegated the passions to the viscera (heart, stomach, intestines). This was the position of Gall's great contemporary, Marie François Xavier Bichat (1805/1809).

Third, Gall assumed that organ size varied with the strength of the corresponding faculty so, for example, the organs of language should be large in the linguistically gifted and small in the linguistically deficient.

Finally, Gall posited that faculty strengths and weaknesses are expressed as protuberances and depressions on the cortical surface as well as on the overlying skull. In this way, a person's psychological profile—strengths and weaknesses alike—could be mapped through examination of the brain or skull.

Gall was not the first localizationist. Thomas Willis (1681/1965), Georgius (Jirí) Procháska (1784), and Emanuel Swedenborg (1740–1741), among others, had come before. Unlike Gall, however, they considered only domain-general faculties such as perception, reasoning, and memory, faculties that may be said to vary in *how* information is processed, not in *what* information is processed. Gall's faculties were domain-specific, varying in what, not how. (I am adopting the terms and distinctions used by Fodor 1983; see also Marshall 1980, and Heeschen 1994.) The distinction is critical because Gall regarded only the domain-specific faculties to be localizable.

Gall used a variety of methods to build his organological map. His primary method was to examine the skulls of people "with very one-sided talents" (Heeschen 1994, p. 7), either lacking a certain faculty or having it in abundance.[3] Thus, in the case of speech and verbal memory, he looked for and claimed to find cranial prominences in the region of the orbital frontal gyri in orators and writers and depressions in the same region in a lunatic unable to articulate words (see Spurzheim 1833). He also studied a few individuals with what he called "accidental mutilations" of their brains. One was a young soldier, Édouard de Rampan, who had been injured by a fencing foil that penetrated just below his left eye into the region that, in Gall's system, contained the organ of verbal memory. Gall (1835) found him to be mute but otherwise mentally unimpaired: "Nothing is lost in him but the faculty of speaking" (vol. V, p. 23; see also Riese 1947; Stookey 1954, pp. 563–564). Such cases provided clinico-pathological evidence of the same kind as would be used by later investigators, including Broca himself.

Phrenology was widely praised and just as widely condemned, both within and outside the medical-scientific community (Young 1970; Cooter 1984; Harris 1997). Antilocalizationists inveighed against the often wild overstatements, the reliance on anecdote and uncontrolled clinical reports, and the large and seemingly arbitrary choice of faculties. The American anatomist Thomas Sewall (1837, Lecture II) also pointed to certain anatomical facts incompatible with phrenological principles. For example, he argued that "the frontal sinuses and temporal muscles alone" put the majority of organs "beyond the reach of observation" (Lecture II, p. 51). The experimen-

[2] Gall's original works are available in French and English translation (e.g., Gall and Spurzheim 1810; Gall 1819, 1835). There also are many scholarly accounts of phrenology and the phrenological movement, for example, Bentley (1916), Ackerknecht and Vallois (1956), Krech (1962), Critchley (1965), Lanteri-Laura (1970), Young (1970), Cooter (1984), Clarke and Jacyna (1987), and Finger (1994).

[3] In 1802, Gall was said to possess over 300 skulls and 120 casts of skulls of persons with known characteristics (Möbius 1905, cited in Bentley 1916, p. 104; Ackerknecht and Vallois 1956).

tal physiologist Marie Jean Pierre Flourens (1824, 1846) showed that extensive portions of cortex could be removed without loss of function and that, as more tissue is removed, all faculties weaken together and die out gradually. To Flourens, that meant that all faculties are coextensive rather than discrete so that, although different sense organs might have separate, localized projection areas, the functional value of the localization depended on the cerebral cortex as a whole.

Gall and his supporters fired back. They noted that most of Flourens' experimental subjects were pigeons, chickens, and frogs—animals with meager neocortex compared to man; that, instead of studying domain-specific faculties, many of which, according to Gall, were common to animals and man, Flourens studied only domain-general faculties, such as perception and movement, which Gall had stipulated were not localizable; and finally, that instead of ablating discrete regions, Flourens removed the cortex by successive layers, a method, Gall (1835) complained, that "mutilates all the organs at once, weakens them all, extirpates them all at the same time" (vol. VI, pp. 165–166).

These were fair retorts. Ultimately, however, what drew many to phrenology were the positive things they felt it offered: simplicity, grandness of scale, and the promise of understanding the self. Finally, for many physicians, prominently Jean-Baptiste Bouillaud (1825, 1839–1840) and Jacques Étienne Belhomme (1848) in France, and Samuel Jackson (1828), Henry Dickson (1830), and Daniel Drake (1834) in the United States (see Freemon 1991), their own clinical experiences made phrenology credible. Like Gall, they had seen patients who had lost their speech following "accidental mutilations" of the anterior lobes, which convinced them that the brain center that presides over the faculty of speech—what Bouillaud (1825) called the "legislative organ of speech [*organe législateur de la parole*]"—was in the anterior lobes, just as Gall said. Of course, not all clinical evidence was so clear. The French physician Gabriel Andral (1843) reported cases of speech loss associated with softening of the brain, but of no region in particular, which led him to opine "that the efforts . . . to assign to certain parts of the brain the faculty of articulating and arranging language, are, at least, premature" (p. 240; translated by D. Spillan). Still, the antilocalizationist landscape was changing. At least for speech and language, the possibility of cortical localization was beginning to be taken seriously.

The Brain as a Double Organ: Localization Without Lateralization. So far, I have said nothing about lateralization, or hemispheric specialization. The reason is that in the early 19th century, it played no role in the debate between cortical localizationists and antilocalizationists, largely because of Xavier Bichat (1805/1809). Bichat observed that all parts of the brain that are in pairs "resemble each other on every side," and, from this feature, declared what came to be known as the law of symmetry: "two parts essentially alike in their structure, cannot be different in their mode of acting" (translation by T. Watkins, pp. 8, 14). Gall took the same line. He acknowledged that "the nervous systems of the spinal marrow, of the organs of sense, and of the brain, are double, or in pairs" (1835, vol. II, p. 164; English translation by W. Lewis) but, seeing no differences between the two sides, envisioned his 27 cortical organs as duplicate sets, 1 in each hemisphere. Being symmetrical in structure, the cerebral hemispheres must be symmetrical in function as well.

In this law of symmetry, Gall (1835) saw an important implication: If one hemisphere is injured, all normal functions could go on as before, supported by the other hemisphere:

> Just as when one of the optic nerves or one of the eyes is destroyed, we continue to see with the other eye, so when one of the hemispheres of the brain, or one of the brains, has become incapable of executing its functions, the other hemisphere or the other brain may continue to perform those belonging to itself; in other words, the functions may be disturbed or suspended on one side, and remain perfect on the other. [vol. II, p. 164; see also Gall and Spurzheim 1810, vol. I]

Clinical evidence seemed to bear this out. Speaking of a patient who had been hemiplegic for many years, with severe wasting on the diseased side, Gall (1835) said, "I did not observe that he had lost any of his intellectual faculties" (vol. II, p. 165). Of course, in certain patients, such as Édouard de Rampan, unilateral injuries did cause the loss of a faculty, but Gall supposed that in these cases, normal function depended on the hemispheres' acting together in symmetry, or balance, which the lesion had disrupted. A theory that explained so much was, in the end, a theory that explained too little.

Objections to the View That the Cerebral Hemispheres Are Symmetrical. Bichat's and Gall's views on the structural symmetry of the cerebral hemispheres were widely but not universally endorsed. The physician and anatomist Felix Vicq d'Azyr (1786), the experimental physiologist François Magendie (1827), and the surgeon Joseph-François Malgaigne (1859) were among those who remarked on the asymmetrical appearance of the hemispheres. Magendie said they "never exhibit the same arrangement in their circumvolutions" (footnote, p. 21).

But did asymmetry in structure mean asymmetry in function? Only Malgaigne spoke to this point, and his answer was yes: "[I]f the phrenological organs are situated in these convolutions, the necessary conclusion will be that these organs are not the same in the two hemispheres" (p. 371). Nonetheless, the judgment that prevailed was Bichat's and Gall's, not Malgaigne's, so that the principle of a structurally and functionally symmetrical nervous system remained the consensus view in French medicine and physiology. So entrenched was this view that it may have dissuaded others from making a case for hemispheric specialization from the evidence at hand.

One possible victim was Bouillaud. In his 1825 report, Bouillaud listed 29 individuals with anterior-lobe lesions. When Benton (1984) checked the report, he determined that 25 individuals had unilateral lesions, 11 in the left hemisphere and 14 in the right, and that 8 (73%) of the left-side group were aphasic compared to only 4 (25%) of the right. If Bouillaud fell victim to conventional wisdom, it was only in the sense that he failed to compare his left- and right-side cases or chose not to comment on the difference.

The physician Marc Dax, in an article written in 1836, actually proposed that the left hemisphere was the speaking side, based on his observation that aphasic patients more often have right than left hemiplegia. Dax prepared his article for a meeting of the Montpellier Medical Society but, evidently, never delivered it, and it remained unknown and unheralded until his son, Gustave, published it in 1865 along with his own report on the same subject (M. Dax 1865, G. Dax 1865).[4]

The Law of Symmetry and the Problem of Handedness

To Bichat's principle that two parts essentially alike in their structure cannot differ in their mode of acting, there was at least one exception: the human hands. Alike in structure, they differed in action, one hand normally leading in acts of strength and skill, the other serving in support. It was also common knowledge that right-handedness was the modal form. As the English physician Sir Thomas Browne (1646) said, "[A]lmost all Nations have used this [right] hand and ascribed a preheminence thereto" (p. 86).

By the early 1800s, the reasons for handedness had long been the subject of debate. Many supposed the explanation to lie in blood supply. Magendie (1827) was among those to point out that "the nourishing artery of the right arm," meaning the right subclavian artery, "is larger than that of the left" (p. 33). This was taken to mean that more blood flowed to the right arm than the left, making most people right-handed. When measurements occasionally favored the left subclavian, left-handedness was the presumed result (for a review, see Harris 1980).

Bichat (1805/1809) understandably had a different view. He acknowledged that the right subclavian's "slight excess of diameter" could "influence limb use" (p. 22) but called this inconsequential compared to the symmetry of the limbs themselves, which showed "perfect equality of volume, number of fibers and nerves" (pp. 22, 24). It followed that "this discordance [between the left and right sides] is seldom or never in Nature, but is the manifest consequence of our social habits" (p. 22), especially the use of the right hand for writing. Bichat even explained why the right hand was favored: it was because of the direction of writing. Being left to right, it required use of the right hand, "which is better adapted than the left to the formation of letters in this direction" (p. 22).

The Discovery of Left-Hemispheric Specialization for Speech

Paul Broca and Messieurs Leborgne, Lelong, et al. As I said, when Broca arrived on the scene, Flourens' views to the contrary notwithstanding, the landscape of opinion was opening to the possibility of cerebral localization. Broca (1861*d*) was among those to endorse the idea. Although doubting the feasibility of "constructing a detailed system of localization" like Gall's, he credited Gall with the "incontestable merit of proclaiming the great principle of cerebral localization" (p. 191) and called it "the point of departure of all the discoveries of our era on the physiology of the brain" (p. 191). Like Gall and Bouillaud, Broca was interested only in localization, not lateralization. This becomes clear in the reports on his first aphasic[5] patient, M. Leborgne.

The cirumstances that brought Leborgne and Broca together have been described many times (e.g., Bernard 1885) chapter 7; Schiller 1979, chapter 10). In 1840, at the age of 30, Leborgne, a last maker, lost his speech under unknown circumstances. He was admitted to the Bicêtre, a hospital on the outskirts of Paris, where, beginning in 1845, Broca was posted in the hospital's surgical service. At the Bicêtre, Leborgne became known as

[4]For a translation of the manuscript by Marc Dax, see Joynt and Benton (1964). For accounts of the case, see Critchley (1964), Cubelli and Montagna (1994), and Finger and Roe (1996).

[5]"Aphemia," rather than "aphasia," was Broca's term. The choice led to a debate between Broca (1864) and Armand Trousseau (1864), clinical professor at the Hôtel Dieu Hospital in Paris (see Stookey 1954; Ryalls 1984). Trousseau's choice was "aphasia," the term that has prevailed, so I use it in references to Broca's work.

"Tan" because to all questions, "tan, tan" was his only reply. In 1850, he developed hemiplegia, initially of the right arm, then the right leg. On April 12, 1861, he was first seen by Broca for treatment of gangrene of the leg, but evidently it was too late and Tan died on April 17. During this period, members of the *Société Anthropologique de Paris* were engaged in a spirited debate about localization of function, and Broca, recognizing the potential significance of the case, demonstrated Leborgne's brain at a meeting of the Society on April 18. The brain showed extensive softening throughout the left frontal lobe, with the focus, in Broca's estimation, in F3, the third convolution, corresponding to the triangular and opercular parts of the inferior frontal gyrus.

Because, as I said, Broca was interested only in localization, not lateralization, of function, his reports about Leborgne emphasized only the lesion's frontal, not its left-side, location (Broca 1861*a*, 1861*b*, 1861*c*). It was the same for his second aphasic patient, the 84-year-old M. Lelong (Broca 1861*b*). But as evidence for frontal localization continued to mount, so did Broca's attention to trends in the data that Bouillaud (1825) had failed to note on his own, namely, signs that the localization was to a particular side. By 1863, Broca could list eight cases of aphasia associated with F3, and "the most remarkable thing [*chose bien remarquable*]" was that, in all cases, the lesion was on the left (p. 202). Still, Broca said that he dared not draw any conclusions but instead would await more evidence [*j'attends de nouveaux faits*] (p. 202). Finally, in 1865, with more evidence in hand, Broca declared, "We speak with the left hemisphere."

What Did Broca Think Was the Underlying Deficit in Aphasia? Leborgne, Lelong, and the other aphasic patients had lost their speech, but what exactly did Broca think that meant? What was the primary deficit? To find out, we must digress briefly to consider the state of theory and evidence on another issue—the motor excitability of the cerebral cortex. In the 1860s, the cerebral cortex had not yet been shown to be excitable. No one, that is, had distinguished between an anterior cortical region projecting motor impulses and a posterior "sensory" region, with the central sulcus as the dividing line. That revelation would come only later, in the 1870s, first in conjectures from clinical evidence by the anatomist and psychiatrist Theodor Meynert (1870) and by Hughlings-Jackson (1873; see Papez 1970), and then in demonstrations on dogs and monkeys by Fritsch and Hitzig (1870/1960) and by Ferrier (1873, 1876). Before then, the consensus was that the cortex was "inexcitable," purely for mental acts, and that the "motor" centers lay below in the corpus striatum and other basal ganglia (see Jeannerod 1983, especially chapter 4; Neuburger 1981, chapter 9). In 1864, Hughlings-Jackson reflected this view when he explained the frequent co-occurrence of right-hemiplegia with speech loss:

> because . . . the seat of the faculty of language, or of articulate language, is near the upper part of the motor tract—the corpus striatum; so that, from mere relation of contiguity, they [speech and motor functions] often suffer together. [1864/1915, p. 39]

In 1861, Broca did the same when he explained Leborgne's aphasia. Leborgne's lips and tongue were not paralyzed because he could use them for other tasks. The problem was that he could not remember how to use them to articulate words. In calling F3 on the left side "the seat of articulate language," Broca meant that it was where memories were stored for performing linguistic-articulatory acts. Leborgne's aphasia therefore was a memory disorder, not a motor disorder. What *was* a motor disorder was his right hemiplegia, which, as Broca (1861*a*) said, signified that his frontal lesion extended down into the corpus striatum, "the motor organ nearest the anterior lobes" (p. 347). Broca returned to this point in 1865:

> [I]t is neither in the muscles, nor the motor nerves, nor the cerebral motor organs such as the optic beds [*les couches optiques*, that is, the optic thalamus] or the striate body, that the essential phenomenon of articulate speech lies. If one had only these organs, one would not speak. These organs exist sometimes, perfectly healthy and perfectly developed, in individuals who have become completely aphemic, or in idiots who have never been able to learn or to understand any language. Therefore, articulate speech depends on the part of the encephalon that is given over to intellectual phenomena, and whose cerebral motor organs are, in a way, only its ministers. [p. 384]

The Left Hemisphere Is Not the Exclusive Seat of the General Faculty of Language. In declaring that we speak with the left hemisphere, Broca (1865) was not making the left hemisphere the seat of all language functions. Indeed, he disavowed this view: when speech [*la faculté du langage articulé*] is lost following left-hemisphere injury, "this does not allow us to say that the left hemisphere is the exclusive seat of the general faculty of language" [*la faculté générale du langage*] (p. 385). The reason is that the individual has "generally lost only the ability to reproduce the articulate sounds of the language [*les sons articulés du langage*]; he continues to comprehend what is said to him, and consequently, he knows perfectly the relation between ideas and words" (pp. 385–386). It followed that

> the faculty of creating those relations belongs simultaneously to the two hemispheres . . . but the faculty of expressing them by coordinated movements . . . would appear to belong only to one hemisphere, which nearly always is the left hemisphere. [p. 386]

In these passages, Broca made two propositions beyond his main point that the left hemisphere was not the seat of all language functions: first, that in aphasia, comprehension is unaffected; and second, that the seat of comprehension lies equally in both hemispheres. Both propositions later would be overturned. Broca (1861*a*) himself provided evidence against the first when he described what seem to have been comprehension deficits in Leborgne. Although "certain" that Leborgne could understand "nearly all that one said to him" (p. 345), as shown by his answers to questions, which he gave using left-hand gestures, Broca acknowledged that there were other questions that Leborgne should have understood but to which he answered wrongly or not at all.

Challenges to Broca's Principle. I said that Bouillaud's anterior localization hypothesis was challenged by reports of patients *not* made aphasic by anterior lesions, even when the regions had been destroyed bilaterally. Broca (1861*a*), having concluded that F3 was the critical anterior region, replied that the critics had erred through "an unfortunate confusion [*une confusion fâcheuse*]," namely that where the "entire anterior part" had reportedly been destroyed without loss of speech, the term "anterior" had been defined as the part rostral to the optic chiasm and as the most rostral part of the temporal lobe, but in either case excluding F3 (p. 342).

After 1865, by which time Broca had declared that the critical structure was F3 on the left side, a different kind of challenge was posed, namely, by reports of patients who were made aphasic following lesions in F3, but in the right hemisphere instead of the left. To understand how Broca dealt with these cases, we must examine his views about the nature of cerebral control, not just for speech but for handedness as well. (The following account is based on Harris 1991, 1993.)

Cerebral Control for Handedness and Speech. Xavier Bichat (1805/1809) had called handedness a product of social habits. Broca (1865) acknowledged that social habits (education and imitation) "undoubtedly contribute much" (p. 381) but argued that handedness was rooted in an "organic predisposition" that gives one hand "a natural and unchangeable pre-eminence" (p. 386). Drawing on the principle of contralateral innervation, he declared the seat of this predisposition to lie in the hemisphere opposite the dominant hand, meaning the left hemisphere for right-handers, the right hemisphere for left-handers. Just as left-handers have right-hemisphere control for handedness, Broca suggested that certain "exceptional individuals" have right-hemisphere control for speech. For speech, they would be "comparable to what left-handers are with respect to the functions of the hand" (pp. 385–386). The existence of a "small number" of such individuals "would explain very well the exceptional case where aphemia is the consequence of a lesion of this hemisphere" (p. 386).

Who Speaks With the Right Hemisphere? Who were these exceptional individuals? Broca compared them to left-handers but said that they were not necessarily left-handers themselves. The reason was that

> it does not seem to me at all necessary that the motor and the intellectual part of each hemisphere are bound up together [*solidaires l'une de l'autre*], taking into account the rate of their respective development in the two hemispheres. [p. 386]

By the "motor and the intellectual part," one might suppose that Broca was distinguishing primary motor cortex (precentral gyrus), especially the hand-arm region, from premotor areas, especially F3 (what David Ferrier later would call "Broca's area"). This sounds reasonable given the view that primary cortical regions develop earlier (as indexed by myelination) than premotor and prefrontal regions (secondary and tertiary cortex) (e.g., Conel 1939–1967). But this cannot be what Broca meant. It is not that cortical regional maturation was unknown in 1865. It is, as I said before, that the motor excitability of the cerebral cortex was not yet established, so the corpus striatum and other basal ganglia (along with the cerebellum) were still seen as the only motor centers. When Broca spoke of the motor and intellectual parts, he therefore would have meant the corpus striatum and cerebral cortex, respectively. This suggests that the developmental dysynchrony that he proposed as underlying a possible disjunction of hemispheric control of speech and handedness was between subcortex and cortex rather than between different regions of the cortex itself. Broca presumably meant that subcortical structures develop before cortical structures. This principle was well-established in his time; Gall himself had advanced it a half-century before (Gall and Spurzheim 1810; see also Gall 1835, vol. 6).

In supposing that the motor (corpus striatum) and intellectual (neocortex) parts of each hemisphere are not necessarily "bound up together" developmentally, Broca presumably was referring to a dysynchrony of interhemispheric as well as intrahemispheric development. That would allow for right-hemisphere speech control without right-hemisphere handedness control (i.e., without left-handedness) or left-hemisphere speech control without left-hemisphere handedness control (i.e., without right-handedness). In that way, the seats of neocortical control for speech and subcortical control for handedness could be laterally dissociated.

The Problem of "Crossed Aphasia." Broca's own view to the contrary notwithstanding, many investigators supposed that the seats of control for speech and handedness were necessarily conjoined—in effect, tightly linked anatomically and functionally in the same hemisphere. That meant that if right-handers spoke from the left hemisphere, then left-handers spoke from the right hemisphere. It also implied that individuals made aphasic by a right-hemisphere lesion were left-handers. This "tight-link" rule, however, also found exceptions—reports of aphasia associated with injury to the hemisphere ipsilateral rather than contralateral to the dominant hand, a phenomenon that Byrom Bramwell (1899) called "crossed aphasia." A few crossed aphasics were right-handers, but most were left-handers.

Different attempts were made to account for crossed aphasia and, thereby, to save the "tight-link" rule. For example, William Ogle (1871) suggested that right-handers with crossed aphasia had a "natural left-handed tendency" but one "so feeble that its external manifestations become completely masked by education" (p. 292). The suggestion was not unreasonable given the social and educational practices of the day, especially the practice of making all children write with the right hand (Harris 1985*a*, 1990). Where this explanation of crossed aphasia in right-handers could not be invoked, Bramwell (1899) offered another: "[S]ome of the [individual's] near relations or ancestors . . . would probably have been left-handed" (p. 1477).

To explain crossed aphasia in left-handers, the practice of requiring the use of the right hand for writing was seen as having a different and more radical effect: it caused speech (and language generally) to shift from its original site in the right hemisphere to a new site in the left hemisphere.

The Principle of Suppléance. Broca (1865) himself offered still another explanation for anomalous (right-hemisphere) speech lateralization. Just as a child born without a right hand "becomes as skillful with his left hand" as he ordinarily would have been with his right, so "someone with congenital atrophy [*atrophiée depuis la naissance*]" of F3 of the left hemisphere would learn to speak with F3 of the right hemisphere (p. 387). Broca called this principle *suppléance*, or substitution. His test case was a 47-year-old woman, epileptic since early childhood (*"depuis sa plus tendre enfance"*) and with right hemiplegia, whose autopsy revealed atrophy of "the whole part of the left hemisphere" bordering the Sylvian fissure (p. 387). The woman was not aphasic but "should have been if the third *left* convolution had been the exclusive and constant seat" of the faculty of speech (p. 387). The absence of aphasia suggested that speech developed in her right hemisphere. Broca added, "[P]arenthetically, she sewed with her left hand" (p. 388).

Broca invoked the principle of *suppléance* for congenital or early injuries. Some clinicians also invoked it for injuries of adult onset, supposing that when right-handed adults with left-hemisphere lesions failed to become aphasic or showed only transitory symptoms, the healthy right hemisphere had substituted, or compensated, for the injured side. They assumed, reasonably, that substitution was most likely when F3 was slowly and gradually destroyed, as in cases of neoplasm; but some clinicians saw substitution as a possibility in acute cases as well (Bramwell 1899; Redlich 1908; Gordon 1920–1921).

The Discovery of Left-Hemispheric Specialization for Comprehension

So far, our focus has been on speech (*langage articulé*) and on evidence linking deficits in speech production (now called motor aphasia, nonfluent aphasia, or Broca's aphasia) to left-hemisphere dysfunction. There is, of course, another kind of language deficit associated with left-hemisphere dysfunction, namely in reception, or comprehension.

Early Descriptions of Sensory Aphasia. Like accounts of motor aphasia, reports of what came to be known as sensory or fluent aphasia long antedate the discovery of hemispheric specialization (Benton and Johann 1965; Goldstein 1974; Boller 1978). The earliest report may be that of the German physician Johann Gesner (1769–1776), who described a patient with fluent but unintelligible speech (in Benton and Johann 1965). Most famously, there is the self-report by the Montpellier physician Jacques Lordat (1843). Lordat recalled that, in 1825 at age 52, he suddenly noticed that he had become "incapable of understanding the sounds I heard quickly enough to grasp their meaning" (translation by J. Hubert, quoted in Riese 1954, p. 237). The Lordat case is not a perfect example of fluent aphasia, however, because Lordat's speech was also affected. His condition therefore is conventionally diagnosed as transient mixed aphasia, comprising elements of motor and sensory aphasia (Riese 1954; see also Goldstein 1974; Boller 1978).

Sensory Aphasia and the Temporal Lobes: The Work of Theodor Meynert, Carl Wernicke, and Their Students and Associates. Following the discovery of hemispheric specialization came further reports of sensory aphasia (e.g., Bastian 1869*b*; Schmidt 1871; Broadbent 1872 [see Boller and Schmidt 1977]). Some linked the symptoms to posterior rather than anterior lesions, but these reports usually lacked postmortem data as well as a clear theoretical rationale. Both elements were provided by Carl Wernicke, a 26-year-old medical student who had studied with Theodor Meynert in Vienna. In 1874, in his doctoral dissertation, *Der Aphasiche Symtomencomplex [On the Aphasia Symptom Complex*], Wernicke gave dramatic accounts of sensory aphasia. His first case was a 59-year-old widow, Suzanne Adam, who, after falling ill from an unknown cause, could "comprehend absolutely nothing which was said to her." Her speech was confused as well:

> [T]he sentences were incorrectly produced, containing meaningless and garbled words. And yet the overall meaning of a sentence, which could be grasped in a general way, was always reasonable. There was no trace of flight-of-ideas. Her behavior was calm and appropriate. [quoted in translation in Eggert 1977, p. 120]

To show how Wernicke explained these deficits and to appreciate his theoretical contribution to aphasiology, we must start with his teacher, Meynert, because what Wernicke had done, as he himself acknowledged, was to apply Meynert's neuroanatomical approach to the study of aphasia, or, as Geschwind (1974) put it, "to complete the cycle started by Meynert" (p. 288). In this approach were three components critical for Wernicke's aphasiological theory. The first has already been mentioned: it was Meynert's proposal that the anterior parts of the brain were motor, the posterior parts sensory. The second was the order Meynert brought to the tangle of white-matter tracts by clearly distinguishing among the ascending and descending pathways (cortical–subcortical connections), association pathways (intrahemispheric connections), and commissural pathways (interhemispheric connections) (Meynert 1872). The third, and according to Eggert (1977, p. 21), probably most important for Wernicke, was Meynert's article "Ein Fall von Sprachstörung," published in 1866 in *Medizinische Jahrbüch der Zeitschrift ges Artze*. Here, Meynert described what Boller (1978) called "probably the first autopsy report in a case of sensory aphasia"—that of a 23-year-old man who suffered (presumably) from rheumatic heart disease and who suddenly developed paraphasic speech and an inability to understand, but without hemiplegia. The autopsy showed an infarct in the parietal operculum and the posterior part of the insula (Island of Reil). From this case, Meynert (1866) postulated that "the Sylvian fissure was related to language, that its posterior part contains the auditory cortex [*Klanhsfeld*]" and that this is where " 'sound-images' [*Klangbilder*] are formed" (p. 155).[6]

As Heilbronner (1901) observed (see Eggert 1977, p. 21), the significance of Wernicke's (1874) dissertation is revealed in its subtitle: *Eine Psychologische Studie auf Anatomischer Basis* [A Psychological Study on an Anatomical Basis]. According to Wernicke, localizationists like Gall and antilocalizationists like Flourens were both mistaken. What was localizable were simpler perceptual and motor functions, and what the cortex did to achieve higher integration was to store sensory traces in cells for long periods and then to use the association pathways to link different parts of the system together. Building on Meynert's proposition that cortical motor regions were anterior and sensory regions posterior to the central sulcus, Wernicke proposed that traces of motor patterns and sensory impressions are stored in cortical regions adjacent to the appropriate elementary (primary) functional cortical zones. As applied to speech and language, the model took account of two other features: the location at the lower end of the primary motor area (precentral gyrus) of a zone that, when stimulated, led to mouth and tongue movements; and the location of the central projection end of the acoustic pathway in the region of the posterior Sylvian fissure. Wernicke hypothesized that patterns of articulating movements were stored in the region just rostral to the anterior zone (Broca's area) and that traces of the sounds of words were stored in the posterior zone. From these hypotheses, it followed that posterior lesions should cause loss of comprehension but not loss of articulation. It also followed that a lesion that spares the motor and sensory speech areas but destroys the pathway, or connection, between them should lead to a new syndrome, *conduction aphasia,* with two characteristics: paraphasic speech because of the loss of the internal correction of the motor speech area by the receptive (sensory) speech area, but normal comprehension of the speech of others. Wernicke (1874) supposed, presumably following the autopsy data in Meynert's (1866) case, that the pathway lay within the fiber tracts of the insula, but Wernicke's own autopsy data were inconclusive on this point. Wernicke (1908) later named the arcuate fasciculus as the pathway, based on new anatomical evidence from Constantin Von Monakow.

The model had still other novel implications. For example, finding that aphasic patients often were impaired in their comprehension of written language as well as in their ability to write, Wernicke suggested that the reason

[6]For a translation of Meynert's (1866) article and an analysis of why it should be seen as the precursor of Wernicke's (1874) theory, see Whitaker and Etlinger (1993). See also Geschwind (1967), on which the following summary is based.

for both disorders was that script is taught as an association to sound. He also named the angular gyrus of the left hemisphere as the region where visual patterns of words are converted into auditory patterns, thereby allowing seen words to be comprehended.

In summary, by the 1870s, two left-hemisphere regions—one inferior frontal, the other superior-posterior temporal—had come to be regarded as primary centers for the production and comprehension of oral language, respectively; other regions later were identified as centers for aspects of written language. With the identification of different kinds of language centers, interest turned to the white-matter connections or associations between centers. The view was that one kind of language disorder was produced by lesions in the centers, another kind by lesions in the connections between centers. The key representatives of this new connectionist-associationist school included H. Charlton Bastian (1869*a*), Siegmund Exner (1881), Jean-Martin Charcot (1887–1888), and, above all, Ludwig Lichtheim (1885), who was responsible for the major elaboration of Wernicke's model (see Goodglass 1993, chapter 2).

Wernicke's (1874) initial contribution to the study of sensory aphasia ironically inspired a savage attack, some three decades later, on the work of his predecessor, Paul Broca, by Pierre Marie (1906*a*, 1906*b*, 1906*c*), formerly one of Charcot's interns at the Salpêtrière. Marie accepted the core principle that linked aphasia to left-hemisphere injuries but, based on "clear-cut cases of Broca's aphasia in which there is complete integrity" of F3 on the left side, concluded that "the third left frontal convolution plays no special role in the function of language" (Marie 1906*a*, p. 241). Instead, Marie argued that there was but one kind of aphasia—Wernicke's—and that *"the aphasia of Broca is the aphasia of Wernicke with speech missing"* (p. 239), that is, aphasia with anarthria, a disorder of the movements of respiration, phonation, and articulation in speech. It followed that "since aphasia is *one*, its localization ought equally to be *one*," and "so it is in reality" because, in Marie's view, only lesions to Wernicke's area produce aphasia (p. 236). Therefore, when a lesion to F3 is found to be associated with aphasia, it is "purely and simply a coincidental factor due to the extension of the obliterated vascular territory and nothing more" (p. 241). Noting also that Broca had failed to section the brain of his first patient, M. Leborgne, Marie (1906*c*) asserted that Leborgne's lesion actually extended well into the temporal lobe, an assertion supported by his student François Moutier's (1908) drawing of Leborgne's brain. Marie even suggested that Leborgne, rather than being aphasic, was a senile man who may not have had a focal lesion in the first place. Marie's views were highly controversial and led to a bitter dispute with Jules Dejerine (see Brais 1992).

The Role of the Corpus Callosum in the Pre- and Post-Broca Eras

In his analysis of conduction aphasia, Wernicke (1874) predicted the effects of lesions to intracerebral pathways. He also showed a way to think about the effects of lesions to intercerebral pathways, the corpus callosum in particular. Except when I noted the clarity that Wernicke's teacher, Meynert, brought to the classification of the white-matter tracts, including the corpus callosum, this structure so far has gone unmentioned in our story.

In the pre-Broca era, localizationists as well as anti-localizationists could see the corpus callosum only as a bridge between functionally symmetrical hemispheres. Recall that Gall (1835) described the 27 organs of his craniological system as duplicate sets, one in each hemisphere (vol. II, pp. 163–168). Recognizing that each pair of organs must be "united for mutual influence and the attainment of a common end," Gall saw that there had to be a physical connection between them. The corpus callosum was the chief candidate:

> [T]he congenerous systems of the two sides [of the brain] are joined together and placed in reciprocal action by transverse layers of fibers [commissures]. . . . All parts of the cerebrum are connected with analogous parts of the other hemisphere by a similar mechanism. [Gall and Spurzheim 1810; quoted in Clarke and O'Malley 1968, p. 600][7]

In the post-Broca era, by contrast, the corpus callosum could be seen as linking functionally asymmetric hemispheres—the linguistic left and the presumbly silent right. On this view, altogether new questions could be posed: What if a lesion destroyed the left visual cortex and the splenium of the corpus callosum, preventing information sent to the healthy right visual cortex from reaching the angular gyrus of the left hemisphere? Or what if a verbal command to use the left hand could not reach the motor cortex of the right hemisphere because of a lesion to the anterior corpus callosum? Both questions figured in new and important clinicopathologic studies: in France, studies of acquired reading disorders ("pure alexia" and alexia with agraphia) by Jules Dejerine (1892; see Geschwind 1965; Henderson 1984) and, in Germany, studies of apraxia by Wernicke's own student,

[7]Similar views are reflected in the work of other anatomists of the day. For example, John and Charles Bell (1827) wrote: "Betwixt the lateral parts there is a strict resemblance in form and substance: each principal part is united by transverse tracts of medullary matter; and there is every provision for their acting with perfect sympathy" (p. 26). See Harris (1995, 1996) for accounts of early theory and research on the role of the corpus callosum and hemispheric communication.

Hugo Liepmann (1900, 1905, 1907; Liepmann and Maas 1907).

The Left Hemisphere and Control of Voluntary Movement

Liepmann did more than elucidate the functions of the corpus callosum. He provided evidence that the left hemisphere, along with its leading role in speech and comprehension, also led in praxis and in the planning and purposeful execution of movements. In the case, say, of movements involving the hands, such as waving good-bye or saluting, he proposed that there was a level of motor control superordinate to the final cortical outflow, or executive pathway, to the spinal motor neurons for the hands, and that this superordinate level supplies the motor programs, or "formulas," necessary for purposeful, skilled movements. This analysis served as the framework for a new view of apraxia, or the inability to perform such movements as waving good-bye or saluting on command. As Kimura (1993, p. 79) has noted, because these problems were usually found in association with speech disorders, they were originally interpreted as a difficulty in making representational, or expressive, movements. However, Liepmann argued that aphasia and apraxia were essentially similar and that both were manifestations of the loss of an ability to make certain kinds of movements (see also Harrington 1987, chapter 5; Brown 1988; Harris 1990).

The Discovery of Right-Hemisphere Specialization for Spatial Perception

John Hughlings-Jackson and Studies of "Imperception." So far, we have focused on language and the left hemisphere. What of the nonverbal faculties associated with the right hemisphere? We saw that Gall incorporated several such faculties, including the sense of "places and space" and "people" in his so-called symmetrical organological theory of mind. We also saw that in 1874, in the era of hemispheric specialization, Hughlings-Jackson, citing clinical evidence, posited a special role for the posterior right hemisphere in recognition of "objects, places, persons, &c."—essentially the same faculties named by Gall. In 1876, Hughlings-Jackson offered further evidence provided by a patient, a 59-year-old woman, Eliza T. Two months after Eliza T. first complained of headache and "neuralgia," she began to show remarkable new symptoms:

> She was going from her own house to Victoria Park, a short distance and over roads that she knows quite well, as she has lived in the same house for 30 years, and has had frequent occasions to go to the park; on this occasion, however, she could not find her way there, and after making several mistakes she had to ask her way, although the park gates were just in front of her. When she wished to return she was utterly unable to find her way, and had to be taken home by a country relation to whom she was showing the park for the first time. When she got home she seemed as usual, but from the time she began to alter, and during the next three or four weeks she seemed to age rapidly, got weaker and more feeble. Now and then too she would do odd things, she would put sugar in the tea two or three times over, she made mistakes in dressing herself; put her things on wrong side before, and did little things of that kind. [Hughlings-Jackson 1876/1958, p. 148]

After Eliza T. was admitted to hospital, more symptoms appeared. She was unable to name certain common objects, "could not remember events from one hour to another," and mistook the people around her:

> [S]he called all the nurses "Annie" (her daughter's name). She would say to one nurse, "Are you the one that came just now?" when she had previously been visited by another nurse. She asked the under-nurse how she was to know her from that one who had long tails, *i.e.*, strings to her cap. [p. 149]

Eliza T. died soon after, and the autopsy revealed a "large gliomatous tumor" in the temporo-occipital region of the right hemisphere (p. 151). Hughlings-Jackson called her constellation of symptoms—visual disorientation, facial agnosia, and dyspraxia for dressing—"imperception" and proposed that it was as characteristic of posterior right-hemisphere disease as aphasia was of anterior left hemisphere disease.

The years that followed brought further reports linking spatial faculties to the right hemisphere. Two examples will serve. In 1895, the American ophthalmologist Thomas Dunn reported the case of a 68-year-old man with defects in topographical orientation following a right-hemisphere stroke. Dunn postulated "a centre (which may, for convenience, be named the geographical centre) on the right side of the brain for the record of the optical images of locality, analogous to the region of Broca for that of speech on the left side" (p. 54). In 1905, the German ophthalmologist Georg Lenz (1905) described eight patients with homonymous hemianopia with visual disorientation. Finding that seven had a left-field defect, Lenz suggested that "the right occipital lobe is perhaps more stongly related to orientation than the left" (quoted in translation in Benton 1972, p. 11).

The Discovery of Right-Hemisphere Specialization for Emotion

Along with reports suggesting right-hemisphere specialization for spatial functions came reports suggesting that the right hemisphere also played a role in emotion. There had already been a hint of this role in Broca's (1861*a*) first report on Leborgne when Broca said that Leborgne, though able to say voluntarily only the monosyllabic "tan," could utter a curse [*un gros juron*] when angry (p. 344), but it was Hughlings-Jackson and especially Jules Luys who made the point explicit. Hughlings-Jackson (1874/1915) noted that, under strong emotion, speechless patients could utter oaths and other involuntary, or "automatic," phrases (p. 85), and, at the Salpêtrière, Luys (1881) described certain differences between patients with left-hemisphere lesions and patients with right-hemisphere lesions, in most cases as indicated by right-hemiplegia and left-hemiplegia, respectively, and then confirmed by autopsy:

> Whereas ordinary hemiplegics, *right hemiplegics,* are more or less apathetic, more or less silent, passive and stricken with hebetude;—left emotional hemiplegics are more or less afflicted with an abnormal impressionability. They respond, when one questions them, in a limping voice, broken up by a kind of sobbing [*des espèces de sanglots*]. . . . In other circumstances . . . they are boisterous and loquacious, their face is congested, their eyes sparkle, they are in incessant motion. During the night, they cannot remain in bed. They are always getting up and going out without reason, and it is not unusual to see them in the grips of a veritable fit of excitation, maniacal, having false conceptions, delusions of persecution, and even making attempts at suicide. [pp. 379–380]

In light of this evidence, and given the left hemisphere's role in language and the conventional view that language was uniquely the basis for reason and logic, the left hemisphere began to be seen as representing the individual's rational, logical side and the right hemisphere as the irrational, emotional side. Luys (1879, 1881) was among those promoting this view.

Explanations of Hemispheric Specialization

What accounted for hemispheric specialization? The question was no less challenging for right-hemisphere than for left-hemisphere functions, but given the preeminent role assigned to the left hemisphere for the so-called higher functions of the intellect and given the far greater body of evidence for left- than for right-hemisphere specialization, the search for explanations focused mostly on the left side.

Explanations of Left-Hemisphere Specialization. For Broca (1865), the search posed a special challenge because, even while naming the left hemisphere as the seat of control for speech and right-handedness, Broca embraced what he called the "physiological law of symmetry" (p. 380), meaning Bichat's law. It fit the evidence as Bichat, Gall, and Broca himself saw it, namely that, except for variations in certain secondary convolutions, the cerebral hemispheres were "perfectly alike" (p. 380), or as Charcot (1878) would later say, "nearly symmetrical, and so nearly identical in their structure that whatever may be said of the one may, anatomically speaking, rigidly apply to the other" (p. 3). How, then, Broca (1865) asked, could cerebral control for speech and for handedness be asymmetrical, and how could that asymmetry be reconciled with the "general truths [referring again to Bichat's law] that it seems to contradict" (p. 382)?

Growth gradient. For Broca, the answer lay in the possibility of a maturational, or growth, gradient. He had already suggested that dysynchronous growth of the "motor" and "intellectual" parts of the brain could lead to a dissociation, both within and between the hemispheres, for the control of speech and handedness. Perhaps growth differences also underlay the differences in hemispheric function. A few years earlier, the anatomist Pierre Gratiolet had reported that in human fetal brains, anterior (frontal) convolutions appear earlier in the left hemisphere than in the right (Leurat and Gratiolet 1857). Such a growth difference, Broca (1865) suggested, could account for right-handedness:

> One therefore understands why, from the first moments of life, the child shows a preference for the limbs having, at that time, the more complete innervation, why, in other words, he becomes right-handed. The superior right limb, being stronger and more skillful than the left from the beginning, for that very reason is called on to work more often; and from that moment it acquires a superiority of strength and skill that only grows with age. [p. 383]

And, in the same way, it could dispose the left hemisphere to lead in more complex intellectual acts, including speech and language (p. 393).

In this linking of speech and handedness, Broca seems to be implying that the neocortex has motor as well as intellectual functions. As already noted, Broca credited only subcortical structures with motor functions. In this statement, then, Broca presumably was assuming that the neocortex and sub-cortex were developing together, so that if the left frontal regions developed earlier than the right, so did those subcortical structures with intimate connections to the frontal lobe. (This is one instance where Broca's (1865) wording could be construed as endorsing a "tight-link" rule for cerebral control of speech and handedness. Another is Broca's (1877) comments on vascular theories of hemispheric specialization and handedness (see Harris 1991, 1993).)

As applied to speech and language, Broca's hypothesis was hardly noticed. For handedness, it won more attention but only mixed reviews. On the positive side, Jules Luys (1865), William Ireland (1880), and Louis Jobert (1885) reported finding earlier left-hemisphere growth. Luys and Ireland also agreed with Broca that this would mean earlier use of the right hand. On the negative side, Alexander Ecker (1868) found no lateral differences, and Jules Parrot (1879) found differences in the reverse direction. The discrepancies were never resolved. As Ireland (1886) later remarked, "the question which side is first developed seems still doubtful" (p. 293).

Blood supply. In seeking explanations of left-hemisphere specialization, many investigators also emphasized the role of blood. Their reasoning was straightforward: Whereas before Broca's time, more blood was believed to flow to the right arm through the right subclavian artery because it was reportedly larger in diameter, now more blood was assumed to flow, under greater pressure, to the left hemisphere through the left internal carotid artery because its source, the left common carotid, arose directly off the aorta, whereas the right common carotid, like the right subclavian, was a branch off the brachiocephalic artery. William Ogle (1871) and Armand de Fleury (1873) were probably the first to make this argument. They also reported finding that the left common carotid was larger in diameter. According to Bennecke (1878), however, it was the right carotid that was larger. Broca (1877), for his part, was dubious about all such reasoning because, as he noted, if "the mode of origin" of the two carotids exerted a decisive influence on the distribution of work between the hemispheres, then all left-handers would show an inversion of the normal vascular structure. In the "overwhelming majority of cases," however, "left-handers are free from this rare anomaly" (p. 526).

Generally, blood-supply explanations began to wane in the face of new anatomical evidence. Daniel J. Cunningham (1902) compared the total areas of the left and right internal carotid arteries from wax casts. In 24 specimens, there were considerable differences in size, some favoring the left and some the right, but the overall difference was negligible. James Crichton-Browne (1907) found much the same thing. Crichton-Browne, however, dismissed the entire argument as moot because the cerebral blood supply is pooled by the Circle of Willis, equalizing the blood supply (and pressure) to both hemispheres (see also Kellogg 1898, p. 358; Huber 1910, p. 261; Beeley 1919, p. 391).

Brain weight and density. Comparisons also were made of hemispheric weight and density (measured by specific gravity). Some comparisons favored the left (e.g., Boyd 1861; Bastian 1866), and these reports were seized on by investigators, such as Luys (1879, 1881), who saw them as consonant with their views that the left hemisphere was rational and logical, the right hemisphere irrational and emotional. That is, for rationality to predominate, it followed that the "rational" left hemisphere should be heavier and denser than the "irrational" right. Other comparisons, however, went in the other direction (e.g., R. Wagner 1860–1862; H. Wagner 1864 [see review in Bonin 1962]; Thurnam 1866; Braune c. 1891 [cited without date in Cunningham 1902, p. 289]).

Finally, a report by Broca suggested that any comparisons had to take the specific region into account. In a report to the *Société d'Anthropologie* in 1875, Broca presented data on 37 brains from patients from the Bicêtre and Saint-Antoine hospitals. The right hemisphere was heavier overall, but by less than 1.5 grams. In contrast, the left frontal lobes, on average, were 3.5 and 4.5 grams heavier than the right in the Bicêtre and Saint-Antoine groups, respectively. When asked whether the difference reflected a difference in the weight of the third frontal convolution, Broca said he was inclined to this view but was reluctant to make a strong statement in light of the difficulty in surgically isolating the third convolution (Assézat 1875).

A disagreement followed about the reliability of Broca's data. Louis J.F. Delasiauve (1875), an alienist (the term used before *psychiatrist* came into common use—from the Latin, *alienatus,* alienated from oneself) at the Salpêtrière, reported finding no differences in his own studies, and Jules Lunier (1875), another alienist and the coeditor of *Annales Médico-Psychologique,* said that there were not enough observations (referring perhaps not only to Broca's but to all studies) to permit any general conclusions. Curiously, Broca neither identified nor was asked about his subjects' handedness.

Brain convolutions. Along with weight and density, the brain convolutions also were scrutinized as they had been by Gratiolet (Leurat and Gratiolet 1857), except that the focus now was on the adult rather than fetal brain. Broca was among those reporting differences on this measure. In 1865, he had called the hemispheres "perfectly alike" (p. 380) except for certain secondary convolutions. Later, according to Bateman (1869), he examined

40 brains and concluded, in Bateman's words, that the convolutions "are notably more numerous in the left frontal lobe than in the right" (p. 380; Broca reference not identified). It was but another small step for others to suppose that the difference was reversed in left-handers (e.g., Ogle 1871).

Length and angle of the Sylvian fissure. Finally, asymmetries were found in the Sylvian fissure. Oskar Eberstaller (1884) reported that in the adult brain, the fissure was longer on the left than on the right—58.2 mm versus 51.8 mm (cited in Bonin 1962, p. 5). Later, Cunningham (1892, 1902) measured the upward angle of the posterior ramus of the Sylvian fissure (an indirect measure of length) in the brains of human fetuses as well as adult gorillas, chimpanzees, and orangutans. Finding a smaller angle on the left in all cases, he concluded that the cortical region bounded ventrally by the Sylvian fissure (the region of the planum temporale, part of Wernicke's area) was larger on the left.

Judging from the citation record, these reports had little or no effect. In Cunningham's (1902) case, the reason seems clear: He questioned the significance of his own discovery:

> That this [smaller angulation, or greater depression of the left Sylvian fissure] is in any way associated with right-handedness, or even with the localization of the active speech centre in the left cerebral hemisphere, I am not prepared to urge, because the same condition is also a characteristic of the ape. This it is true would offer no impediment to the acceptance of this explanation by those who believe that the ape is right-handed, but, as I have already stated, I cannot persuade myself that the ape possesses any superior power in either arm. [p. 293]

Nevertheless, Cunningham (1902) was confident that a structural explanation of hemispheric specialization would be found: "[My inquiry] has been conducted up to the present along wrong lines, and I do not doubt that the problem will ultimately be satisfactorily explained" (p. 293).

Explanations of Right-Hemisphere Specialization. As I said, most attempts to explain hemispheric specialization focused on the left hemisphere rather than the right. A few clues about the source of right-hemisphere specialization, however, emerged from two of the aforementioned studies of the cortical convolutions. The first was Gratiolet's developmental study (Leurat and Gratiolet 1857). As already noted, it showed that the left frontal convolutions develop earlier than the right, but it also showed that the temporal and occipital convolutions of the right hemisphere develop earlier than those of the left. Hughlings-Jackson (1874/1915) cited this latter difference as support for his hypothesis that the posterior right hemisphere takes the lead in perception. The second was Broca's examinations of the adult brain, which found that just as the left frontal lobe is more convoluted than the right, so "the right [occipital lobe] is richer in convolutions than the left" (in Bateman's words, 1869, p. 380; Broca reference not identified).

Speaking of these studies, Hughlings-Jackson (1874/1915) said, "These anatomical facts, I submit, support the view . . . that the posterior lobe—or let us speak more generally—the hinder part of the brain on the right side, is the chief seat of the revival of images in the *recognition* of objects, places, persons, &c." (p. 101).

A Neo-Bichatian Response

We saw that Gall's organology theory won praise and disdain in equal measure. The evidence for hemispheric specialization enjoyed a far better reception, but it, too, did not convince everyone. Certain critics—call them *neo-Bichatians*—attacked the core principle of hemispheric specialization on the grounds that it violated the law of symmetry. For example, in 1863, when Broca was still tentative about the possibility of hemispheric specialization, someone identified only as Laborde (presumably the physician J.-V. Laborde) expressed his "repugnance to admit that two parts of one and the same organ, whose position, dispositions, and structural details are absolutely alike would not be given the same uses by nature" (1863, p. 386). That would constitute a grave exception to "the law of organic duality" and, by implication, of functional unity (p. 386). In 1869, well after Broca's (1865) declaration, the British neurologist H. Charlton Bastian (1869*a*) expressed the same misgivings. He noted that the "various avenues of knowledge" (i.e., the sense organs) are bilaterally symmetrical and, for this reason, thought it

> only fair to infer that the cerebral hemispheres on each side of the body, which are the ultimate recipients of these various impressions, should be endowed with like functions, since they too may be said to have a bilateral symmetry. I am therefore strongly inclined still to believe in the similarity of function, and practical equality of education of the two cerebral hemispheres, notwithstanding all that has been said of late in opposition to this doctrine. [p. 455]

Bastian (1869*a*) did acknowledge the opinion "of the best judges" that in man, in contrast to the higher apes, "there has risen a very slight though still perceptible want of symmetry between the convolutions of the two hemispheres" (p. 455, footnote). Evidently, he gave little if any weight to his own earlier discovery that the specific gravity of the left hemisphere exceeded that of the right (Bastian 1866).

The clinical evidence also did not consistently support Broca's principle. As the neurologist Charles E. Brown-Séquard (1877) and, later, the educator John Jackson (1905; see Harris 1985*a*, 1985*b*) argued, it suffered too many exceptions, namely, people who either did not become aphasic after injury to either of the putative left-hemisphere language zones or who became aphasic after right-hemisphere injury. Brown-Séquard (1877) regarded such exceptions as too common to be explained away as left-handers. In any case, to the extent that aphasia was associated with left-hemisphere disease, these critics did not see the association as reflecting intrinsic specialization of the left hemisphere. In their view, the specialization had been induced *de nouveau* by right-hand writing. They reasoned that because writing is an implicit act of speech and comprehension, right-hand writing provides the left hemisphere with sufficient exercise to develop cortical centers for writing, speech, and comprehension. We can recognize this explanation as a radical version of the view, mentioned earlier, that the left hemisphere is intrinsically specialized for language but that this specialization can be overridden, or switched, by hand training.

Further Contributions by Hughlings-Jackson

Hughlings-Jackson (1874/1915), although not opposed to the principle of hemispheric specialization, made two crucial contributions to a better understanding of the phenomenon. First, he identified what he saw as a common problem in the interpretation of the clinical data. The reports linking speech disturbances to damage of F3 of the left hemisphere were widely taken to mean that speech therefore was located in that part of the left hemisphere. The error lay in equating localization of symptoms with localization of function:

> Whilst I believe that the hinder part of the left third frontal convolution is the part most often damaged [when speech is lost], I do not localize speech in any such small part of the brain. To locate the damage which destroys speech and to locate speech are two different things. [p. 81]

Hughlings-Jackson instead saw speech, and language more generally, as a dynamic process deriving from the integrated functioning of the entire brain, such that the more complex the task, the more brain regions involved, with each making its own contribution. The question was not, where is language located? It was, rather, what is each region's contribution to language? Hughlings-Jackson's answer was that language is represented in both hemispheres but at different functional levels: Emotional utterances (the lowest level or most primitive utterances) were the least lateralized, or most bilateral—this explained the preservation of "emotional" speech in speechless individuals with left-hemisphere damage; comprehension was more lateralized; and "propositional speech," together with the background of conceptual thought that it requires, was wholly dependent on the integrity of the left hemisphere.[8]

Hughlings-Jackson's second contribution was to apply the concept of functional levels for clinical diagnosis. Using a distinction introduced by the physician John Russell Reynolds (1858, 1861; see Berrios 1985), he identified two kinds of symptoms following brain damage. Negative symptoms referred to loss of function, that is, to behaviors that are absent after brain damage and that, by implication, depend on the integrity of the damaged region. Positive symptoms referred to behaviors that emerge, or become more common, after brain damage and that, by implication, reflect the action of the remaining neural structures. To use Luys' (1881) example, if, following right-brain injury, someone becomes manic and hyperemotional, the negative symptoms are the absence of normal activity and affect, the positive symptoms are the mania and hyperemotionality.

The distinction between positive and negative symptoms promised a new view of how hemispheric damage affects mental function. During normal function, the cerebral hemispheres work together in dynamic balance, each modulating the other. Unilateral injury upsets the balance so that the behavioral changes described above—the mania and hyperemotionality following right-hemisphere injury—could be seen as having been generated by the healthy, uninjured left hemisphere, now no longer modulated by (i.e., in dynamic balance with) the injured right hemisphere. This analysis squared with Luys' (1881) own views. Luys proposed that the mania and hyperemotionality of the left-hemiplegics could be explained on the hypothesis that certain moderating centers (*centres modérateurs*) for emotion had been destroyed by a lesion other than the lesions causing the hemiplegia. He localized the lesions causing the hemiplegia in the corpus striatum and the insula of the external capsule and localized the lesion causing emotional mani-

[8] *The difference that Hughlings-Jackson proposed in the degree of lateral specialization between speech and comprehension was nearly anticipated by Broca. Recall that Broca (1865) had supposed that comprehension ("the faculty of creating relationships [between ideas and words] belongs simultaneously to the two hemispheres"), whereas articulate speech belongs to only one. For more on Hughlings-Jackson, see Head (1926), Greenblatt (1965, 1977), and Schulte (1994).*

festations in the superior temporal lobe of the right hemisphere (p. 397).

Hemispheric Specialization and Madness

So far, our focus has been on normal people made abnormal by "accidental mutilations" to their brains. Whether disabled by aphasia, by imperception, or by mania and hyperemotionality, however, they were not generally regarded as demented, insane, or mad. Others were so regarded, and early theory and research on the brain, and on hemispheric specialization in particular, were directed toward understanding their condition as well.

Madness and Symmetry. Before the discovery of hemispheric specialization, clinicians—"mad doctors" (alienists) and general practitioners—who saw mad, or demented, patients based their diagnoses and treatments on the following assumptions: Unity of mind and consciousness is the *sine qua non* of mental stability, and to achieve this unity, the cerebral hemispheres must work symmetrically and synchronously. Disruption of this synchrony, or balance, can bring instability or madness. Madness thus was seen as stemming from the disruption of hemispheric balance in the same way that Gall supposed that damage to the speech organ on one side caused the loss of speech in his patient Édouard de Rampan. In cases of madness, however, the source of the disruption was not always stated. Some reports refer vaguely to chronic or acute injury or disease of one hemisphere, others to a difference in "excitation." Like the Rampan case, however, it did not matter whether the disruption originated in the left or right hemisphere because, for localizationists and antilocalizationists alike, the hemispheres were symmetrical.[9]

Gall (1835) himself described several patients of this sort. A minister with disease in one hemisphere

> continually heard insults uttered against him [on the left side], so that he always turned his eyes that way, although, with the right side, he distinctly perceived, that these sounds came from no other source than a derangement in the left side of his head. [vol. II, p. 164]

Another patient, a young woman, told Gall of her "apprehension of falling into dementia on one side of her head, because she observed that the process of thought was not the same on this side as on the other" (vol. II, p. 164). A third patient, "a woman of infinite sense," said that

> she distinctly felt . . . that she perceived every thing differently with her left side from what she did with the right; that every thing affected her differently on different sides . . . that sometimes her faculty of thinking was completely shackled on that side, and that this inability was accompanied by an icy torpor: it seems to me (these are her own words, and she applied her hand perpendicularly upon the middle of her forehead) that from the front to the back of my head, the brain is divided into two distinct halves. [vol. II, p. 165; see also Elliotson 1847, pp. 212–213]

If all these patients had neurological diseases, we can only guess at their type or location because Gall identified neither. For example, Gall's account of the minister's symptoms perhaps suggests a right-hemineglect following a left-hemisphere lesion.

After Gall, several more cases appeared. They included reports by Jean-Etienne Dominique Esquirol, a former student of Phillipe Pinel at the Salpêtrière and later the reform-minded physician-in-chief of the Maison Royale des Aliénés de Charenton. In his treatise *Des Maladies Mentales* (1845), in the chapter on homicidal monomania, Esquirol described persons who, in an extreme state of passion, or "delirium," are "drawn away *irresistably*" to commit heinous, irrational acts.[10] Aware of their condition and able to judge their acts correctly and to deplore them, they nonetheless are "drawn away" again. Esquirol (1845) concluded that someone in this condition

> no longer has the faculty of directing his actions, because he has lost the unity of his mind. He is the *homo duplex* of St. Paul and of Buffon;[11] impelled to evil by one motive, and restrained by another. This lesion of the will, may be, with much propriety, compared with an oversight, and can be conceived of, as resulting from the duplicity of the brain, whose two halves, not being equally excited, do not act simultaneously. [p. 363]

[9]In these assumptions about mental balance and the consequences of unilateral damage, one can see an anticipation of Hughlings-Jackson's idea about the circumstances giving rise to positive and negative symptoms. The difference is that Hughlings-Jackson accepted the principle of hemispheric specialization, so the nature of the symptoms depended on which side was damaged.

[10]Such individuals were in ample supply at Charenton, the hospital-prison where the Marquis de Sade was incarcerated in the 1790s and where Jean Paul Marat, the French revolutionist, was stabbed to his death in his bath by Charlotte Corday.

[11]The *homo duplex* of St. Paul refers to Romans 7:14–15: "For we know that the law is spiritual: but I am carnal, sold under sin. For that which I do I allow not: for what I would, that do I not; but what I hate, that do I." Buffon (George Louis LeClerc Comte de Buffon, 1707–1788), in his essay "De la nature de l'homme" (1750/1971), likewise describes man as a being compounded of two distinct and conflicting natures, body (flesh) and soul.

In America, the pioneer psychiatrist Benjamin Rush gave similar accounts in his lectures at the College of Philadelphia from 1795 to 1811. For example, a young epileptic man, during a seizure, remembered what happened in the preceding seizure but nothing that happened during the interval. He "seemed to have *two distinct minds* which acted by turns independently of each other" (Rush 1981, p. 669). That led Rush to wonder whether such cases could be ascribed "to all the mind being, according to Dr. Gall, like vision a double organ occupying the two opposite hemispheres of the brain" (p. 670; see also Harrington 1987, pp. 18–19).

In England, the physicians Arthur Ladbroke Wigan and Sir Henry Holland weighed in with still more evidence. In his book, *A New View of Insanity: The Duality of the Mind,* Wigan (1844) drew partly on Gall's own reports in proposing

> [t]hat when the disease or disorder of one cerebrum [i.e., one hemisphere] becomes sufficiently aggravated to defy the control of the other, the case is then one of the commonest forms of mental derangement or insanity; and that, a lesser degree of discrepancy between the functions of the two cerebra constitutes the state of conscious delusion. That in the insane, it is almost always possible to trace the intermixture of two synchronous trains of thought, and that it is the irregularly alternate utterance of portions of these two trains of thought which constitutes incoherence. [pp. 26–27]

Wigan (1844) also proposed a way to prevent madness, or insanity, or to overcome it when it strikes. Each hemisphere would serve as a "sentinel and security for the other while both are healthy," and, when one hemisphere is "disordered," the healthy hemisphere would "correct and control" its "erroneous judgments" (p. 29).

Holland outlined his views in 1839 in his essay "On the brain as a double organ," reprinted in *Chapters on Mental Physiology* (Holland 1852). Like Bichat, Gall, and others before him, Holland (1852) believed that unity of mind depends on the two halves of the brain functioning symmetrically and synchronously and that "some of the aberrations of mind, which come under the name of insanity [could be] due to incongruous action of this double structure" (p. 172). For examples, he described deranged persons who appeared to have "two minds, one tending to correct . . . the aberrations of the other," and persons torn between two contradictory impulses leading to "a painfully exaggerated picture of the struggle between good and ill" (p. 185). As Harrington (1987) has noted, Holland rejected the materialistic implications of the phrenological view of the brain's functional duality. Instead, he favored a dualistic analysis according to which the human brain was double, but "standing *over and above* that brain" there was a single immaterial mind (quoted in Harrington 1987, p. 21; see also Harris 1983, 1985*a*, 1985*b*).

Madness, Neural Integration, and the Corpus Callosum. Because Gall named the corpus callosum as the integrative structure in his organological theory of mind, it is puzzling that it is not mentioned in his accounts of insane patients. Wigan (1844), however, went much further: He called the corpus callosum "an organ of no importance . . . not necessary to the functions of the brain" (p. 49). It was Holland (1852), evidently, who first named the corpus callosum as the critical organ in insanity. When healthy, it afforded sanity (wholeness of mind); when damaged or diseased, it caused mental disintegration:

> On the connexions afforded by the Corpus Callosum and the other commissures depend, it may be presumed, the unity and completeness of the functions of this double organisation, . . . And any breach in the integrity of the union, and of the relations thus established, may tend no less than disease in the respective parts themselves, to disturb the various actions of the brain and nervous system. [p. 175]

Holland (1852) also supposed that the corpus callosum made it possible for "translation of morbid actions from one side to the other" (p. 175). Did he mean that a disorder that begins unilaterally can become bilateral? If so, he would have anticipated the much later discovery of the role of the corpus callosum in the spreading of epileptic discharges (Erickson 1940).

Despite their different views about the corpus callosum, Wigan and Holland found support in the same kind of clinical evidence, namely, accounts of the mental faculties of persons with callosal agenesis or callosal lesions. Wigan (1844) cited a report by the physician Richard Bright (1831) of a man, James Cardinal, with callosal agenesis brought on by chronic hydrocephalus. According to Bright's account, as quoted by Wigan (p. 50), the man's mind was *unimpaired:* "His mental faculties were very fair: he read and wrote pretty well; his memory was tolerable."[12] Speaking of this case, Wigan said, "[I]t is quite evident that the corpus callosum is not an essential commissure" (p. 52).

[12]Wigan omitted a further detail by Bright (1831, p. 432) that paints a darker picture, however: Cardinal's memory, though "tolerable," "did not retain dates and periods of time." Later, there were other reports that Wigan would have been able to cite in support of his view, that is, reports giving few if any indications of mental "unbalance" in persons with callosal agenesis, for example Paget (1846), Jolly (1869), Malinverni (1875, French abstract; original report in Italian, 1874), Bruce (1889–1890). For a review, see Harris (1995).

Holland (1852) was more cautious. He cited "observations of [Johann Christian] Reil, [Luigi] Rolando, and other physiologists," which "though valuable, cannot be considered as leading to any assured conclusions" (p. 175). The reason is that these observations, "made through experiments or accidental lesions of these commissures, give results quite as equivocal as those on other portions of the brain" (p. 175).[13] Nonetheless, he remained convinced of the importance of the commissures, saying "it is probable, or even certain, that many phenomena of sensorial disorder have their origin in these connecting parts more especially, as the seat of disease" (p. 175).

Madness or Aphasia? The discovery of hemispheric specialization, Wernicke's work in particular, also had a profound effect on diagnosis and nosology. Before this time, patients with sudden loss of speech or, especially, of fluent speech with paraphasic symptoms often were diagnosed as hysteric, confused, or psychotic, especially if they did not show any classical physical symptoms of brain injury such as paresis or paralysis. In hospitals like the Salpêtrière, they would have been placed with the insane—the *aliènées*—in the psychiatric wing, rather than with the patients in Charcot's neurological service (see Goetz et al. 1995, chapter 3). Wernicke's work raised the possibility that, in at least some cases, the symptoms, in the absence of general dementia, could be traced to a discrete brain lesion of the left temporal lobe. Wernicke himself corrected a misdiagnosis of his patient Suzanne Adam, whose symptoms were described earlier. No physical illness being apparent, namely paresis or paralysis, her condition initially "was diagnosed as dementia" and "she was placed on a psychiatric ward" (Wernicke 1874, quoted in translation in Eggert 1977, p. 119). Wernicke (1874) showed that for Suzanne Adam and other patients, the symptoms actually result from a discrete neurological condition—a posterior lesion:

> That cases with such manifestations have not been observed, or at least not published, until now, rests not only on the rarity of such cases but also on the fact that thoroughly experienced and intelligent physicians regard this condition as a confusional state—as I myself have had the opportunity to experience. For the psychiatrically trained man who knows the clinical forms of confusional states, the diagnosis has not the least difficulty. [quoted in translation in Geschwind 1974, p. 290]

Even as Wernicke's theory made correct neurological diagnoses possible, it allowed for misdiagnoses in the other direction, for example, for hysteric loss of speech to be misdiagnosed as organic aphasia. This possibility was raised in the Lordat (1843) case. Against the conventional view (Riese 1954) that Lordat's self-reported speech and comprehension problems were symptoms of a transient mixed aphasia, comprising elements of motor and sensory aphasia, Bay (1969) suggested that they were "largely hysteric," that the "only clearly identifiable syndrome" was a transient bulbar paresis, and that the selection of symptoms had been guided by Lordat's preconceived theory of "alalia" (or "aphasia") triggered by the paresis. Bay (1969) added that Lordat's "unquestionable experience with aphasic patients could furnish a good model for such a psychogenic 'alalia'" (p. 307).

Madness and Hemispheric Specialization: The Rational Left and the Emotional Right. Wernicke showed that the fluent but paraphasic speech that sounded like madness was actually aphasia brought on by posterior left-hemisphere disease. His contribution to diagnosis thus relied on the discoveries of the new era of theory and research on hemispheric specialization, in which he himself had played a key role. One might have expected the same discoveries to have figured as well in cases where madness was accurately diagnosed and laid to a breakdown of one cerebral hemisphere, but where, as Charcot (1885) might have said, the lesion was obscure, neither circumscribed nor grossly destructive, one that "for want of a better term, we designate *dynamic* or *functional*" (quoted in translation in Goetz et al. 1995, p. 206). Most such cases, however, were discussed much as they had been in the pre-Broca era, that is, as though it made no difference which hemisphere broke down. Ireland (1886) provides many examples, including reports of dual personality, sleepwalking, hypnotism, alternate consciousness, double memory, and hystero-epilepsy, a kind of hysterical attack that included convulsions, paralyses, contractures of limbs, and other signs that mimicked grand mal epilepsy (see especially pp. 336ff.).

There were at least two exceptions to this pre-Broca-era style of analysis. One was the work, mentioned ear-

[13] I have not located the reference to Rolando. The reference to Reil was, presumably, to his 1812 report on callosal agenesis, which appeared just 3 years after the publication of his first anatomical study of the corpus callosum. Reil (1812) described a "woman about 30 years old, who was otherwise healthy, but dull in intellect." The woman "was able to do errands in town for others from her village" (p. 341). After a fall, she suffered an apoplectic seizure and died. The autopsy disclosed "ventricles moderately full of water" and a corpus callosum "divided longitudinally in the middle," the hemispheres being held together only by the anterior commissure, optic chiasm, isthmus of crura cerebri in front of the pons, and corpora quadrigemina (pp. 341–342; for brief accounts of the case, see Paget 1846, p. 62; Bruce 1889–1890, p. 176). Reil's case thus seemed to indicate that the corpus callosum was important for normal intelligence, although Holland (1852) clearly was justified in calling the results "equivocal."

lier, of Jules Luys (1879, 1881). Recall that Luys had linked mania and hyperemotionality with right-hemisphere lesions in normal persons. From these findings, it sometimes was supposed that the same symptoms, in the absence of explicit neuropathology, reflected dynamic or functional abnormalities in the right hemisphere. The view that ascribed rationality to the left hemisphere and emotionality to the right also was invoked to explain reports that hysterics more often had symptoms on the left than on the right side of the body (see Harrington 1985, 1987). The symptoms could be in the form of paralyses or contractures, mimicking epilepsy, as though when the "emotional" right hemisphere broke down, it affected not only the mind but also the parts of the body on the opposite side. Pierre Paul Briquet (1859), an alienist at the Charité in Paris, estimated the ratio of left to right paralyses of hysteric origin to be 3 to 1. The state of madness also was said to be manifested in the weight of the hemispheres. Thus, Luys (1879, 1881) reported finding that just as in normal people the left hemisphere was heavier, so in the madman the right hemisphere was heavier. Finally, Charcot (1888–1889) interpreted certain signs, such as mutism, in hysteric patients with no identifiable anatomical damage as involving physiological dysfunction of the same brain region known to be affected in patients with static anatomical lesions (see Goetz et al. 1995, p. 131).

Madness and Handedness. The supposed connection between madness and either the strength of the emotional, "irrational," right hemisphere or the weakness of the rational left hemisphere was invoked to explain still another connection—among madness, criminality, and left-handedness. According to the Italian criminologist Cesare Lombroso (1903):

> This is a new characteristic, which connects criminals with savages, and differentiates them from sane people as well as lunatics [so that in criminals the right lobe] predominates very much more often than in normal persons. While the healthy man thinks and feels with the left lobe, the abnormal wills, and feels more with the right—thinks 'crooked,' as the popular proverb has it. [p. 443]

Lombroso (1903) noted that long before he had reached his own conclusion "after much clinical observation," "the people in the provinces of Emilia, Lombardy, and Tuscany had already declared the same when they framed and used the saying, 'He is left-handed,' to express the idea that a person is untrustworthy" (p. 444). Lombroso's report was widely cited, and apparent corroborations soon appeared. For example, Audenino (1907) and Lattes (1907) summarized research indicating more frequent left-handedness among criminals as well as prostitutes, epileptics, and other "degenerates." Lombroso (1903) also acknowledged, however, that someone with a "single hereditary trait" such as left-handedness is not necessarily "in a state of arrested development or of inferiority" because left-handedness "signifies nothing" until associated with other symptoms, such as "exaggerated cranium asymmetry" (p. 444). In this connection, he reported finding that in 44 heads of criminals in his museum at Turin, asymmetry was "very prevalent in the right lobe" in 41 percent (i.e., the right lobe was larger), and in the left in 20 percent (p. 444).

Lombroso's qualification seems to anticipate the distinction made by Lattes (1907) between two kinds of left-handedness: the atavistic or constitutional type, resulting from an inversion of normal cerebral asymmetry, and the pathologic type, manifested after a left cerebral lesion—the type that Lattes supposed was predominant in epileptics and delinquents (see Harris 1980, pp. 51ff.). The same distinction was made by the geneticist Henry E. Jordan (1922), who said that left-handedness "is not necessarily a stigma of inferiority" and who distinguished the anomalous left-handers described by Lombroso (1903) from the "pure, uncomplicated type." Jordan (1922) supposed that the latter "constitutes the bulk of the left-handed population" and which, "instead of being regarded as something inherently derogatory . . . deserves appreciation and understanding" (p. 379; see also Jordan 1911).

Handedness was related to madness in still another, more dramatic way in some of the reports of dual personality. One such case, reported in 1895 by a Scottish physician Lewis C. Bruce, was that of a 47-year-old Welsh sailor. In one state, the sailor spoke English, used only his right hand, and was "the subject of chronic mania," playing practical jokes, stealing, and acting destructively; in the other state, he spoke Welsh (almost unintelligibly), used only his left hand, and was "the subject of dementia," acting "shy and suspicious," sitting "doubled up in a chair for hours," and "constantly on the lookout for unseen danger" (pp. 60–62). Because the man's handedness seemingly changed with his state, Bruce assumed that the right-handed and left-handed states represented the actions of the left and right hemispheres, respectively. (For an account of this and similar cases, see Harrington 1987, chapter 5; see also Ireland 1886.)

Some Threads Linking Past and Present

Here, then, are main themes and representative studies from early theory and research on hemispheric specialization. What of current work and the threads that link the present and past? At an accelerating pace since the early 1960s, neuropsychologists have been providing ever more detailed accounts of what each cerebral hemisphere contributes to higher-order functions (e.g., Benson and Zaidel 1985; Trevarthen 1990; Kitterle 1991), and of this work, there is space to mention just a few examples.

Cerebral Control for Speech and Handedness. Much of the new research has confirmed and extended what was once only mere surmise. For example, research on cerebral control for speech and handedness shows that Broca (1865) was right to suggest that control for these functions was not necessarily tightly linked, even though he did not foresee that this would be so largely in left-handers. That is, it shows that whereas nearly all right-handers (95% to 99%) are left-hemisphere dominant for speech, in left-handers the majority are left-dominant, with only about 15 percent right-dominant, and another equally small percent bilateral (see review in Harris 1992).

The Principle of Suppléance. A vast amount of new research also has been devoted to testing Broca's (1865) principle of *suppléance,* or substitution, that when the left hemisphere is injured early in life, the right hemisphere can take over its speech and language roles. The results from studies of early brain injury as well as studies of individuals who undergo early hemispherectomy strongly support the principle. As Oliver Zangwill (1964) said, "[Broca's] inspired guess has been brilliantly vindicated" (p. 107). The research also shows, however, that the compensation is incomplete, particularly for syntactic comprehension and rapid-rate auditory processing (e.g., Aram and Whitaker 1988; Stark et al. 1995).

One or Many Kinds of Aphasia? New research also has corrected past mistakes. One example is Pierre Marie's (1906*a*, 1906*b*, 1906*c*) contention that there is only one kind of aphasia—Wernicke's—and that only lesions to Wernicke's area cause aphasia. We now know that Marie was mistaken and that Broca's aphasia and Wernicke's aphasia are, indeed, different both clinically and neuropathologically (e.g., Kertesz 1983; Levine and Sweet 1983). Marie also wrongly supposed that Leborgne ("Tan") may not have had an anterior focal lesion in the first place. A computed tomography study of Leborgne's brain (Signoret et al. 1984) shows that Wernicke's area was preserved, confirming Broca's original diagnosis that Leborgne's frontal lesion was the source of his aphasia. What remains uncertain is the centrality of F3 in Broca's aphasia. Evidence shows that persisting, severe Broca's aphasia usually involves extensive lesions that extend beyond F3 to the precentral gyrus, especially ventrally, and to the inferior parietal area (Mohr 1976; Levine and Sweet 1983). Finally, the differences once thought to perfectly distinguish the two kinds of aphasia no longer hold. Although difficulty in speech production is the principal feature of aphasias associated with damage to Broca's area, agrammaticism and comprehension problems are also common (e.g., Swinney and Zurif 1995; Hickok and Avrutin 1996). Marie, therefore, was correct in asserting that both kinds of aphasia involve comprehension difficulties.

Explanations of Hemispheric Specialization. The search for the explanation of hemispheric specialization goes on more intensely than ever, with most of the focus on possible anatomical substrates. The results have been encouraging. Thus, new data amply support early reports that the language region of the temporal cortex is larger on the left side than on the right. The new data point to the planum temporale in particular. Studies also reveal left–right differences in the anterior speech region, including Broca's area (see reviews in Witelson and Kigar 1988; Kertesz and Naeser 1994).

Although the brains in most of the new studies are of individuals of unspecified handedness, it is noteworthy that the percentages of brains showing larger or cytoarchitecturally more complex left than right regions correspond at least roughly with the handedness distribution in the general population. When handedness is specified, the possibility of a connection becomes stronger because certain asymmetries are clearer in right-handers than in left-handers (for reviews, see Witelson 1980; Witelson and Kigar 1988).

Growth-gradient hypotheses, likewise, still figure in theories of hemispheric specialization but seem to remain as inconclusive as they were in Broca's time (Harris 1984). Some researchers follow Broca in proposing that maturation normally favors the left hemisphere, with right-handedness and left-hemisphere language specialization as modal results (Corballis and Morgan 1978; Geschwind and Galaburda 1984). Others question this scenario and point, instead, to evidence that they see as indicating earlier right-hemisphere functioning (Whitaker and Ojemann 1977). Still others posit the simultaneous occurrence of more than one growth gradient, involving different cortical regions along the longitudinal as well as the lateral axis (Koop et al. 1986; Best 1988).

Putting It All Together: Studies of the Role of the Corpus Callosum. Having made so much progress in describing hemispheric differences, neuropsychologists have increasingly come to appreciate that we are only part of the way to understanding the neural bases of higher cognitive functions, and the focus on interhemispheric communication is no less important. More and more, then, neuropsychologists are asking how the hemispheres actually communicate, how they impart, share, and make common the information they take in about the external world and then process in their respective ways, and how they coordinate their work to achieve normal cognition and action (e.g., Trevarthen 1990; Kitterle 1995).

Hemispheric Specialization and Mental Illness. Today, a major emphasis in clinical neuropsychological research is the relationship between hemispheric specialization and mental illness. Here, too, certain older ideas have reappeared in one form or another. Consider two popular hypotheses about schizophrenia and depression. In a way reminiscent of the old idea linking the left hemisphere to rationality and reason, it has been suggested that the main disturbance in schizophrenia is hyperarousal of a dysfunctional left hemisphere (e.g., Flor-Henry 1976; Gur 1978; Gur et al. 1989). Similarly, it has been suggested that clinical depression is associated with hyperarousal of a dysfunctional right hemisphere, or perhaps hypoarousal of the left (e.g., Gainotti 1989; Henriques and Davidson 1991). Researchers looking for possible structural foundations are also comparing anatomical asymmetries in the brains of normal persons and persons with schizophrenia.

Another old idea being revisited is that left-handedness is more common in people with schizophrenia or other psychiatric disorders than it is in the general population. Following Lattes' (1907) and Jordan's (1922) distinction between pathological and normal left-handedness, one hypothesis is that the excess represents pathological left-handedness stemming from early (probably intrauterine) left-hemisphere dysfunction. As Satz and Green (1999) report elsewhere in this issue of the *Bulletin*, recent studies do indicate a leftward shift in the handedness distribution of people with schizophrenia. They note, however, that the surplus left-handers often show a more variable and less completely lateralized pattern of manual preference that is better described as mixed or ambiguous handedness that as (pathological) left-handedness. In their view, the handedness data therefore are more consonant with a diagnosis of bilateral or multifocal insult.

There also is renewed interest in the possibility, raised earlier by Bruce (1895), that psychosis, to the extent that it is associated with alterations in hemispheric functioning, is accompanied by changes of lateral motor preference, even handedness. Flor-Henry (1990) has made this proposal in a series of papers (Flor-Henry 1979, 1983; Flor-Henry and Koles 1980) and has described two cases reminiscent of Bruce's (1895) sailor, cases that Flor-Henry (1990) calls "admittedly exceptional" but "illuminating" (p. 428). One was a young man with unipolar depressive psychosis. When well, he was ambidextrous; when depressed, "he lost the manual skill of his left hand, becoming completely dextral except for writing" (p. 428). The second case was a woman in her early fifties who was completely sinistral during a manic episode but completely dextral when asymptomatic. Flor-Henry sees these examples as suggesting that depression and mania, by altering the organization of the right and left hemispheres, respectively, interfere with the dexterity of the corresponding hands.

Madness or Aphasia? As we have seen, many of the threads between past and present reflect the vigor of old hypotheses—old ideas that new research has shown to be fundamentally correct. Some threads, however, may reflect the persistence of the same old mistakes. One example is the lingering confusion of dementia with aphasia. We saw that in 1874 Wernicke demonstrated that fluent paraphasias, rather than signifying dementia, could signify instead a discrete neurological condition stemming from a posterior lesion. Writing in 1967, nearly a century later, Geschwind suggested that many patients with fluent paraphasias were still being misdiagnosed as confused or psychotic, and, in 1994, after 20 more years, the error evidently was still common enough to warrant mention in a standard psychiatric handbook (Kaplan et al. 1994):

> Because Wernicke's aphasia can present without other major neurological symptoms, a clinician may misclassify a patient with Wernicke's aphasia as having a thought disorder associated with a psychiatric disorder. [p. 102]

Localization of Symptoms Is Not the Same as Localization of Function. There is at least one other error from the past to which we may still fall victim today, and for the study of hemispheric specialization, it probably surpasses all others in importance. When Hughlings-Jackson (1874/1915) said, "[T]o locate the damage which destroys speech and to locate speech are two different things" (p. 81), he was pointing out the error of treating localization of symptoms and localization of function as one and the same, an error that he believed obscured the true nature of speech and language and other complex cognitive functions. Today, given the power of CT and other structural neuroimaging techniques to pinpoint areas of damage in brain-injured patients, and of positron emission tomography, functional magnetic resonance imaging, and other functional neuroimaging techniques to allow the visualization of activated cerebral regions under different cognitive and emotional conditions in normal subjects, the risk of "over-localizing" can be no less great than in earlier times. The neuropsychologist Justine Sergent (1994) has alerted us to this possibility. The benefits of the new functional neuroimaging techniques, she said, "should not mask [their] inherent limitations" or the "risk of promoting a modern type of phrenology that would disregard evidence of interactive and distributed processing carried out in cerebral structures" (p. 491). Hughlings-Jackson surely would have been heartened by Sergent's cautionary words. They would have told him that his wise counsel had been taken to heart. They also provide a fitting coda to our historical review.

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Dedication

This article is dedicated to the memory of Justine Sergent.