Gennari never published again, and died a young, penniless compulsive gambler.88

THE BEGINNING OF THE MODERN ERA OF CORTICAL LOCALIZATION

Gall and Phrenology

The localization of different psychological functions in different regions of the cerebral cortex begins with Franz Joseph Gall (1758–1828) and his collaborator J. C. Spurzheim (1776–1832), the founders of phrenology.89 Before they developed their phrenological system, the two men made a number of major neuroanatomical discoveries that would have fixed them in the history of neuroscience even if they had never begun their project of correlating the morphology of the cranium with psychological faculties (figure 1.17). Among Gall’s significant anatomical contributions were the recognition that the grey matter is functioning neural tissue connected to the underlying white matter (to which he attributed a conductive function), the first description of postembryonic myelinization, proof of the decussation of the pyramids, the first clear description of the commissures, demonstration that the cranial nerves originate below the cerebrum, and the realization that the brain is folded to conserve space.90

The central ideas of their phrenological system were that the brain was an elaborately wired machine for producing behavior, thought, and emotion, and that the cerebral cortex was a set of organs with different functions.91 They postulated about “thirty-five affective and intellectual faculties” and assumed that (a) these were localized in specific organs of the cerebral cortex; (b) the development or prominence of these faculties was a function of their activity, and the amount of activity would be reflected in the size of the cortical organ; and (c) the size of each cortical organ was indicated by the prominence of the overlying skull, that is, in cranial bumps.

The primary method of data collection used by Gall and Spurzheim was examining the skulls of a great variety of people from lunatics and criminals to
the eminent and accomplished (figure 1.18). Neuropsychological and animal experimental data, even those gathered by themselves, they considered only minor and ancillary evidence.92

Phrenology had wide popular appeal, particularly in England and the United States, and among many leading intellectuals, such as Honoré de Balzac, A. R. Wallace, Horace Mann, and George Eliot.93 However, it met considerable opposition from the religious, political, and scientific establishments of the day. For example, Gall's public lectures were banned in Austria because they led to materialism and opposed religion and morality. His works were
placed on the Index of the Catholic Church for similar reasons. In 1908 the French Institute, later the Academy of Science, under the leadership of the great Cuvier, totally rejected even the anatomical parts of a paper that Gall submitted.

*Florense Attacks Gall, but the Cortex (Re)emerges as a Higher Structure*

In the scientific world the most important and influential critique of Gall came from Pierre Flourens (1794–1867), later professor of natural history at the Sorbonne. A technically brilliant experimenter, Flourens quickly rose in the French scientific establishment and at the age of thirty-five was elected to the Academy that had rejected Gall. Starting in the 1820s and continuing for over twenty years, he carried out a series of experiments on the behavioral effects of brain lesions, particularly with pigeons. Flourens reported that lesions of the cerebral hemispheres had devastating effects on willing, judging, remembering, and perceiving. However, the site of a lesion was irrelevant: all regions of the hemispheres contributed to these functions. The only exception was vision, in that a unilateral lesion produced only contralateral blindness, but again there was no localization within the hemisphere. These holistic results tended to eclipse Gall’s ideas of punctate localization, but only in scientific circles and only temporarily.

Flourens’s finding of cognitive losses after hemispheric lesions was actually a confirmation of Gall’s emphasis on the cognitive role of the cortex, a concept that had been virtually absent before Gall. This change in attitude toward the cortex was reflected in mid-nineteenth-century textbooks that now routinely attributed intellectual function to the cortex. William Carpenter, in his authoritative *Principles of Human Physiology*, wrote that the convolutions of the cerebrum were:

Figure 1.18 Frontispiece and its legend from J. G. Spurzheim’s *Phrenology or the Doctrine of the Mental Phenomena* (1834). Note that none of the faculties were sensory or motor, but were all “higher” ones.
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... the centre of intellectual action ... the site of ideas ...
restricted to intellectual operations ... the sole instrument of
intelligence ... It is probably by them alone that ideas ... of
surrounding objects are acquired ... and that these ideas are made
the groundwork of mental operations ... that would also seem to
be the exclusive seat of Memory ... and Will.

The cortex was termed a "superadded" structure lying hierarchically and
physically above the highest sensory structure, the thalamus, and the highest
motor structure, the corpus striatum (figure 1.19). The general idea that the
thalamus had major sensory functions and the corpus striatum major motor
functions was generally accepted by the middle of the nineteenth century on
the basis of a number of studies that traced sensory and motor tracts from the
periphery and made experimental lesions in animals. 96

This view of the higher functions of the cortex, common for the period,
combined Haller's notion of insensitivity and both Gall's and Flourens's attri-
bution of higher faculties, but neither sensory nor motor functions, to the
cortex.

Bouca Confirms Gall

Despite the bitter attacks by Flourens, Gall's theory of punctate localization,
and even many of his specific localizations such as language in the frontal lobes
and sexuality in the cerebellum, continued to be actively debated in the middle
of the nineteenth century. 97 At least in the scientific community, the supposed
correlations between skull and brain morphology were quickly recognized as
erroneous. Yet, Gall's ideas stimulated the search for correlations between the
site of brain injury and specific psychological deficits in patients as well as in
experimental animals. Reports of such correlations were published in both the
phrenological and mainstream neurological literature, and the question of the
localization of psychological function in the brain was hotly debated at scientific
meetings.
Thus, in 1848, J. B. Bouillard (1796–1881), professor at la Charité in Paris and a powerful figure in the medical establishment, offered a cash prize for a patient with major frontal lobe damage who did not have a language deficit. The debate about localization reached a climax at a series of meetings of the Paris Société d’Anthropologie in 1861. At the April meeting, Paul Broca (1824–1880), professor of pathology at the Sorbonne and founder of the society, announced that he had a critical case on this issue. A patient with long-standing language difficulties—nicknamed “Tan” because that was all that he could say—had just died. The next day Broca displayed his brain at the meeting, and indeed it had widespread damage in the left frontal lobe. Over the next few months he presented several similar cases. Not only did these cases finally establish the principle of discrete localization of psychological function in the brain, but the discovery was hailed as a vindication of Gall. Broca himself regarded Gall’s work as “the starting point for every discovery in cerebral physiology in our century.”

**Evolution and Brain Function**

Contributing to the growing interest in the cerebral cortex were ideas about organic evolution that were in the air in the decades before the publication of Darwin’s *Origin of Species* (1861). In J.B. Lamarck’s (1809) theory of evolution, the first coherent one, evolution involved continuous upward progress, the inevitable transformation of lower into upper forms. The anonymous and widely influential best-seller *Vestiges of the Natural History of Creation* (1844) took a similar progressive view of evolution. (See chapter 4.)

Herbert Spencer (1820–1903) was the first and most important figure to apply evolutionary ideas to the nervous system and psychology. Spencer had virtually no formal education, but read widely in the sciences as a boy. A seminal experience at age 11 was hearing a lecture on phrenology by Spurzheim, and it was decades before he decisively parted from a phrenological position. Before he did so he published in phrenological journals and invented a more accurate device for measuring skull bumps. After a few years as a railway
A. The cortical substance or mental portion.
B. B. The sensitive column.
C. C. The motor column.
D. The passage of motor fibres to the cerebellum.
E. E. E. Fibres of volition and consciousness.
F. F. Sensitive and motor fibres.
engineer he drifted into political journalism, where he came into contact with T. H. Huxley, Thomas Carlyle, and George Henry Lewis (and, to use a modern but particularly apt expression, Lewis's partner, George Eliot), and was exposed to the scientific and political issues of the day.

In his first book, *Social Statics* (1851), Spencer set out a quasi-Lamarckian progressive theory of evolution. He argued that it justified survival of the fittest (a phrase Darwin later adopted) in human society. This led him to oppose such things as government help for the poor, public health, and public education. These views were the theoretical bases of the ultraintividualist and conservative ideology that later became known as social Darwinism, although Spencerism would have been a more appropriate designation. Spencer's social theories were particularly welcome among the elites in postbellum America. As John D. Rockefeller put it in a Sunday school address:

> The growth of a large business is merely survival of the fittest. . . .
> The American beauty rose can be produced in the splendor and fragrance which bring cheer to its beholder only by sacrificing the early buds which grow up around it. This is not an evil tendency in business. It is merely the working-out of a law of nature and a law of God.

In his next work, *Principles of Psychology* (1855), Spencer combined association psychology with evolutionary theory to produce "evolutionary associationism." From evolution he took the idea of a progressive increase in the complexity of the nervous system both phylogenetically and ontogenetically. This led to the conception of the cortex as the newest, highest, and most important level of the nervous system. Furthermore Spencer posited that

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Figure 1.19 This figure from a 1837 dissertation illustrates the prevailing view at this time that the highest sensory and motor structures were subcortical (the thalamus and the striatum, respectively, although not so labeled here), and only the cortex had mental functions (Bennett, 1837).
function must be localized in the cortex just as it clearly is in lower nervous structures:

But no physiologist who calmly considers the question . . . can long resist the conviction that different parts of the cerebrum subserve different kinds of mental action. Localization of function is the law of all organization whatever: separateness of duty is universally accompanied with separateness of structure; and it would be marvellous were an exception to exist in the cerebral hemispheres. Let it be granted that the cerebral hemispheres are the seat of higher psychical activities; let it be granted that among these higher psychical activities there are distinctions of kind . . . more or less distinct kinds of psychical activity must be carried out in more or less distinct parts of the cerebral hemispheres . . . It is proved experimentally, that every bundle of nerve fibers and every ganglion, has a special duty; and that each part of every bundle of nerve fibers and every such ganglion, has a duty still more special. Can it be, then, that in the great hemispherical ganglia alone, this specialization of duty does not hold?

When the *Origin of Species* was published in 1859, Spencer became a enthusiastic follower of Darwin. He set out to unify all knowledge along the principles of Darwinian evolution and attempted to do so in his massive, multivolume *Principles of Synthetic Philosophy*. Today, his synthetic philosophy is all but forgotten, whereas the disastrous consequences of his social views are still reverberating. However, Spencer did make one permanent and major contribution to modern neuroscience. That was the profound influence of his views of the evolution of the nervous system on John Hughlings Jackson.

John Hughlings Jackson (1835–1911) is the perennial holder of the title, “father of English neurology.” As a medical student in Yorkshire, he was so enthralled with Spencer’s writings that he almost abandoned medicine to pursue their study full time. Instead, he spent forty-five years as a clinical neurologist
at the National Hospital, Queen Square, London, applying Spencer’s ideas on
the evolution and dissolution of the nervous system. Many of his over 300
papers began with such sentiments as “I should say that a very great part of this
paper is nothing more than the application of certain of Herbert Spencer’s
principles.”

Spencer taught that evolution implied a continuity of nervous organiza-
tion from spinal cord to cerebral cortex. Therefore, as Jackson put it, “If the
doctrine of evolution be true, all nervous centers [including the cortex] must
be of sensory-motor constitution,” that is, they must have both sensory and
motor functions.104 It was the combination of Spencer’s theory of cortex as a
sensorimotor structure and his insistence on cerebral localization of function,
and Jackson’s many observations of seizures (including his wife’s) that led him
to the brilliant clinical inference that the seizures we now call Jacksonian reflect
a somatotopically organized cortical motor mechanism.

Jackson’s ideas on the motor mechanisms of the cerebral cortex were
dramatically confirmed in 1870 by Fritsch and Hitzig’s demonstration of specific
movements from electrical stimulation of the cortex of the dog.105 These
authors were not reticent about the more general implications of their results,
as shown by the final lines of their paper:

It further appears, from the sum of all our experiments . . . certainly
some psychological functions and perhaps all of them . . . need
certain circumscribed centers of the cortex.

In summary, despite their temporary eclipse under the shadow of
Flourens’ experiments, Gall’s general ideas of punctate localization in the cortex
were essentially vindicated by the third quarter of the nineteenth century. By
that time, they were considered confirmed by Broca’s demonstration of an
association between damage to the frontal lobe and aphasia, and again by Fritsch
and Hitzig’s experiments on stimulation of motor cortex. Gall’s ideas on the
localization of mental function had a deep and lasting influence through stress-
ing (a) that the human mind could be subdivided into specific functions,
(b) that these specific functions were mediated by discrete brain structures, and
(c) that the cerebral cortex was crucially important in mental activity. It is
interesting to note that one of the first accurate drawings of the cerebral cortex
was by Gall and Spurzheim (figure 1.17). Before them the cortex was often
portrayed as a pile of intestines (figures 1.13 and 1.14) or in a crude schematic
way with no attention to detail (figure 1.15). Perhaps it is necessary to believe
a structure has important functions before one goes to the trouble to portray it
accurately.

The Search for Sensory Areas in the Cerebral Cortex

The last quarter of the nineteenth century saw an intense search for the
localization of sensory centers in the cortex. In addition to increasing interest
in the cortex from the work of Gall, Flourens, Spurzheim, Jackson, and Fritsch
and Hitzig, a major spur to the search for sensory centers was Johannes Müller's
doctrine of specific nerve energies. Müller (1801–1858), professor of anatomy
and physiology at Berlin, dominated midnineteenth-century physiology
through his personality, his many influential students, and his massive Handbuch
der Physiologie (1833–1840).

Müller's doctrine had three essential elements. The first and most funda-
mental asserted that sensation was the awareness of the states of sensory nerves,
not of the outer world itself. This was a radical departure from the widespread
view, derived from the presocratic philosophers Leucippus and Democritus,
that images (eidola) from objects in the world enter the eye and travel to the
brain. The second element was that when a given nerve type or nerve energy
was excited, the same type of experience is produced no matter what the
stimulus. Thus, photic, mechanical, and electrical stimulation of the eye all
produce visual sensations. Müller, following Aristotle, assumed that there were
five nerve types or nerve energies; today, we would call them qualities or
modalities. The third element of the doctrine was that the same physical
stimulus applied to different sense organs gives rise to different sensations. Thus,
a blow to the eye and one to the ear produce visual and auditory sensations,
respectively.
Müller was unsure of the locus of nerve specificity. As he put it:

It is not known whether the essential cause of the peculiar “energy” of each nerve of sense is seated in the nerve itself or in the parts of the brain and spinal cord with which it is connected.

A student of Müller, however, the great Hermann von Helmholtz, philosopher, physicist, and psychologist, located the specificity squarely in the nerve terminations. Helmholtz, who was the first to measure the speed of nerve conduction, in the original comparison of the nervous system with a telegraph system, noted that with wires:

according to the different kinds of apparatus with which we provide terminations, we can send telegraph despatches, ring bells, explode mines, decompose water, move magnets, magnetize iron, develop light and so on. So with the nerves the condition of excitement which can be produced in them and is conducted in them, is, so far as can be recognized in isolated fibres of a nerve, everywhere the same, but when it is brought to various parts of the brain, or the body, it produces motion, secretions of glands, increase and decrease of the quantity of blood, of redness and of warmth of individual organs, and also sensations of light, of hearing, and so forth.

Emil Du Bois-Reymond, another one of Müller’s students, his successor in the Berlin Chair, and discoverer of the action potential, went further and claimed that if it were possible to cross-connect the auditory and optic nerves, we would see with our ears and hear with our eyes.

The idea that the specificity of nerves derived from their central connections was not new. On the basis of his clinical practice among gladiators in Pergamon, Galen distinguished between sensory and motor nerves, and proposed that sensory nerves were connected to the anterior part of the brain and motor nerves to the posterior. Charles Bell (1774–1842), codiscoverer of the
law of spinal roots, or rather, the sensory half of it, extended the idea of specificity inherent in that law to the five senses to yield in 1811 an account of nerve specificity essentially identical to Müller’s later published one. As Bell put it:112:

the nerves of sense depend for their attributes on the organs of the brain to which they are severally attached . . . the properties of the nerves are derived from their connections with the parts of the brain.

It is important to note that for both Bell and Müller it was not the terminations in the cerebral cortex that conveyed specificity on the sensory nerves. Rather, for both of them, and, as noted above, more generally for almost all the physiologists and anatomists of the first half of the nineteenth century, the cortex still had no sensory (or motor) functions. The main support for this view was still Haller’s that since the cortex was insensitive to touch, it could hardly be sensory. Instead, it was believed to be the site of the highest intellectual functions. This notion was often supported both by the phylogenetic correlation of cortical complexity with intelligence and reports of intellectual deficits after cortical lesions. It was clearly also heavily influenced by Gall’s ideas. Note that of all the thirty-five faculties that Gall put into the cerebral cortex, none was sensory or motor. Some of Gall’s faculties do have sensory sounding names, but on examination they are actually cognitive. For example as to the faculty of color, Gall notes, “I do not mean the simple faculty of seeing or perceiving colors . . . [but rather] distinguishing the relations of colors: the talent for painting.”113

What turned Müller’s doctrine and everybody else’s attention toward the possible sensory functions of the cerebral cortex was Fritsch and Hitzig’s discovery of motor cortex by electrical stimulation in 1870. This unambiguously demonstrated that the cerebral cortex had more than just higher functions.

Müller’s doctrine of specific nerve energies now became directed toward cortex as the locus of specific energies. Thus, under its influence, in the later
part of the nineteenth century. (a) neural pathways were traced from the sense organs into the brain to find the specific regions in which they ended; (b) the cortex was divided up into separate centers or organs on the basis of the pattern of its structure, thereby yielding the techniques of cytoarchitectonics and myeloarchitectonics; (c) cortical lesions were made in animals to find the sensory centers, and (d) in close parallel, attempts were made to correlate sensory losses in humans with the site of cortical damage.

The Discovery of a Visual Center in the Cerebral Cortex

Bartolomeo Panizza: The First Claim

The first person to suggest a discrete localization of visual function in the cortex on the basis of systematic investigations was Bartolomeo Panizza (1785–1867), professor of anatomy at Pavia and a follower of Gall. After examining the brains of several patients who became blind after strokes, he attributed vision to the posterior cortex. He then tested this idea by making lesions and enucleations in a number of species and concluded that the occipital region was the crucial one for vision. He also studied the anatomical and behavioral effects of monocular enucleation as a function of age, and concluded that the effects on the brain were more profound in adults than in infants. Panizza’s work seems to have been totally ignored at the time. One reason for this may have been because he only published in local journals, those of the Royal Institute of Lombardy of Science, Arts, and Letters; however, these journals were exchanged with those of the Royal Society and presumably other scientific societies.

A more likely reason for the lack of impact of Panizza’s work was the prevailing theoretical view of the relative role of cortex and subcortex. As we have indicated, at that time it was thought that the thalamus was the highest sensory center and the basal ganglia the highest motor center. In contrast, the cortex was believed to be concerned not with sensation or movement but with intellectual operations. This view went back at least to Gall, who among his