my intention had been to expose our ignorance rather than to present some means and ways of approaching these exciting problems.

4

Encephalization, Cortical Maps, and Redundancy

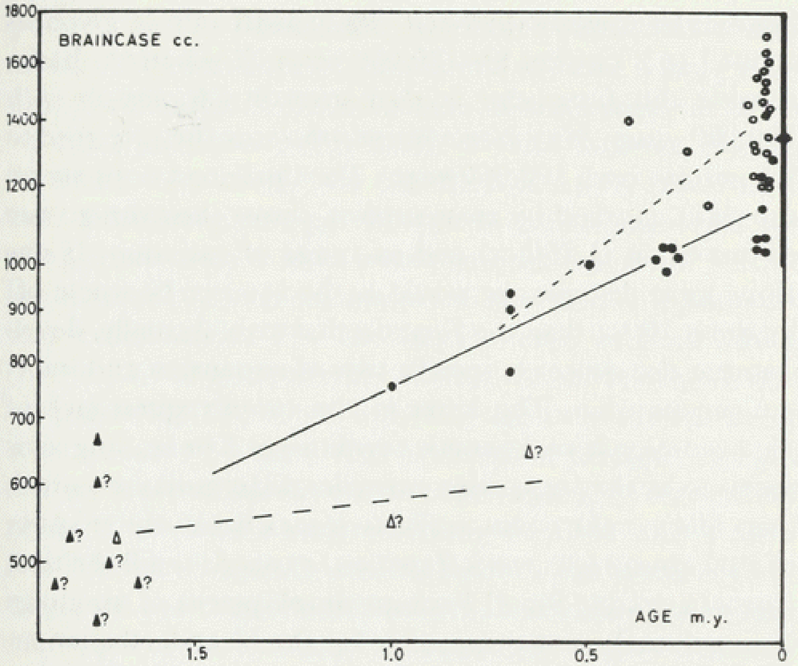
If we refuse to admit that discrimination is in some way based on different anatomical constituents differently located in the brain, we may as well give up altogether. (Author, in his Silliman Lectures, published as *Receptors and Sensory Perception*, by Yale University Press, 1955.)

Encephalization

The highly developed adaptability of man, as studied in Chapter 3, suggests that perfection of this talent could be ascribed to the existence of a roof brain or cortex greater than that of other mammals. While this structure has acquired the role of a supreme governor, it has also had to become cognizant of whatever happens outside the body or inside it (Chapter 8), which, of course, presupposes that it is informed by messages from its sense organs or in some cases by changes of blood chemistry. The role of information is to elicit action, most of it motor. For this reason Sherrington considered that the biological origin of the mind was its usefulness for motor acts.[62]

Developing in size and importance, the roof brain took over checking processes that in phylogenetically primitive vertebrates were wholly governed by lower stations. This is often spoken of as an increasing degree of encephalization (corticalization) or in some old papers as von Monakow's law of movement (that is, of controlling functions) to the higher centers. For example, the pyramidal path descending from the cortical motor area is a puny tract in the rat, but it contains about 186,000 fibers in the cat and is a mighty bundle of 1.2 million fibers in man. A more surprising example is the fact that the retina of the frog differentiates edges and direction of movement with the aid of individual ganglion cells, something that a monkey can do only with cells in its cortex (Chapter 6).

The growth of the skull from the hominids to ourselves, *Homo sapiens*, is illustrated in Figure 4.1 (Kurtén).[63] Modern methods of dating fossils have made it possible to plot size of brain cavity against geological time. The brain of the hominids (*Australopithecus*) scarcely increased at all in size



4.1. Semilogarithmic diagram representing braincase volume and absolute age in millions of years in 50 fossil hominid skulls (open triangles, *Australopithecus robustus*; filled triangles, *A. africanus*; open circles, Neanderthal group; filled circles, *Homo erectus* group). Question marks indicate doubtful age or size. Continuous line: *H. erectus* regression. Upper dashed line: regression for Neanderthal group combined with early *H. erectus* (older than 0.4 million years). Lower dashed line: approximate *Australopithecus* trend. Mean and range for modern *H. sapiens* indicated along right margin of graph. From Björn Kurtén. *Commentationes Biologicae Soc. Sci. Fenn.* (1971), 36.

before this species died out. Its growth rate is given as about 1 to 2 percent for 100,000 years. *Homo erectus* had a considerably faster rate of skull growth, 4.6 percent each 100,000 years. With *Homo Neanderthalensis* the rate rose to 7.5 percent each 100,000 years. The thickened ordinate on the right, marked by cross-strokes, shows the average size of our brain (1,350 cc) and its range of variation. If size alone were decisive, we would in the average be worse off by about 100 cc than the Neanderthal man. Actually, development also concerns specific sites of expansion and internal organization. The kinks in the curve suggest lack of data or unexplained genetic revolutions. The leading view seems to be that expansion precedes differentiation, which then fills out the room available somewhat in the manner of Parkinson's law: work (function) expands to fill the time (space) available for it! Perhaps development of language can explain the rise responsible for the Neanderthalian increase from 4.6 percent to 7.5 percent each 100,000 years.

A gradual increase in the size of the body is likely to be a factor in the pre-Neanderthalian curve. On the average, brain weight B is proportional to body weight W raised to an exponent 0.63 ($B = kW^{0.63}$). Much the same relation prevails between body weight and body surface so that the decisive factor apparently is the surface an animal turns toward the external world. A species-dependent factor k expresses the degree of encephalization. The literature on this subject is interesting.[64] "The encephalization of man is higher than that of all other mammals so far investigated" (Stephan, p. 162). There is a large gap between recent nonhuman primates (higher apes) with an encephalization factor of 10 and man with one of 30.

The increase of brain size in these terms is responsible for the success of our highly adaptable species, though, as

pointed out by Dobzhansky, there are considerable variations from the mean (1,350 cc) that indicate a large margin of tolerance.[24] For example, of the ranges in brain volume, Jonathan Swift, 2,000 cc, and Anatole France, 1,100 cc, were cited. The late Beritoff had a remarkable case, a microcephalic girl brought to the hospital at an age of approximately 8 to 10 years, parents unknown.[65] After she died at 10 to 12, the brain was subjected to a postmortem examination. The two hemispheres weighed 289 g (normal 1,160 g); its cortical surface measured 44,041 mm as against 173,782 mm in a child of age 10 to 11. The brain stem was only 7 g below that of a child of her age. This girl did not learn to speak, nor was she capable of elementary planned behavior such as reaching for food with a cane. She reacted adequately to stimulation of all sense organs, displayed emotional manifestations, and some vocalization. Her capacity for learning corresponded roughly to that of a dog. Beritoff concluded that the number, connectivity, and organization of the cortical elements "were perfectly sufficient for psychoneural activity characteristic of higher vertebrates; they were not sufficient for eliciting the human type of planned psychoneural behaviour" (p. 53). Microcephaly is reviewed by Halloway.[66]

Because there are no fossil brains, we can compare cortical areas in man and orangutan, two land animals of much the same size with many features in common. Both have convoluted or "corrugated" (Le Gros Clark's expression) brains; that is, they possess the gyri and sulci that anatomists and physiologists use as important landmarks in brain research. Lower in the phylum this mode of cortical expansion is absent. The rabbit, for instance, has a smooth cortex; the cat a corrugated one.

If one compares those areas of Table 4.1 in ape and man

Table 4.1 Area of Regions of Cerebral Cortex

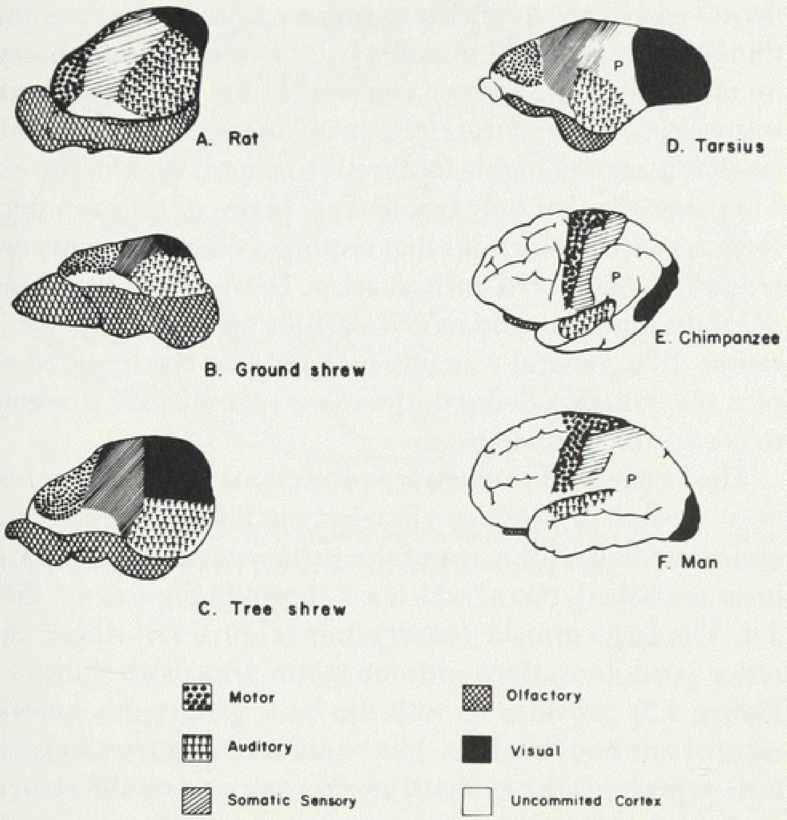
Lobes	Orangutan	Man
Occipital	47	103
Inferior parietal	9	79
Limbic	9	17
Precentral	42	63
Frontal	33	208
Temporal	100	193
Miscellaneous		177
Total	240 cm²	840 cm²

Source: D. Ploog and T. Melnechuk in *Neurosci. Res. Symp.* 6 (1970).

that are largely motor in function (the precentral ones), the difference is not large. The great expansion is reserved for the frontal, temporal, and parietal fields that represent complex functions. This line of development is seen from another angle in Figure 4.2. Although the rat and the ground shrew have cortical areas committed largely to motor action or sensory projections, the rest of the cortex (white in the figure) increases from monkey to man. Speech, for instance, concerns the temporal and inferior parietal lobes, which are much larger in man than in the orangutan. Extensive areas are devoted to "higher functions," as I will show.

Maps and Mapping

The idea of a cortical localization of specific functions had to fight its way to recognition against the notion prevailing at the end of the last century that the cortex was functionally uniform.[67] Most serious disputes in science, like this one,

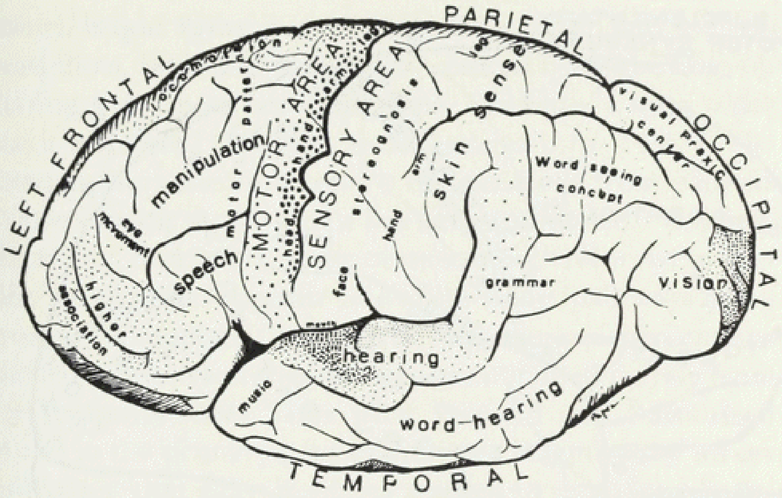


4.2. Mammalian brains from rat to man prepared by Stanley Cobb to illustrate the proportional increase of uncommitted cortex (or undetermined cortex) as compared with sensory and motor cerebral cortex.

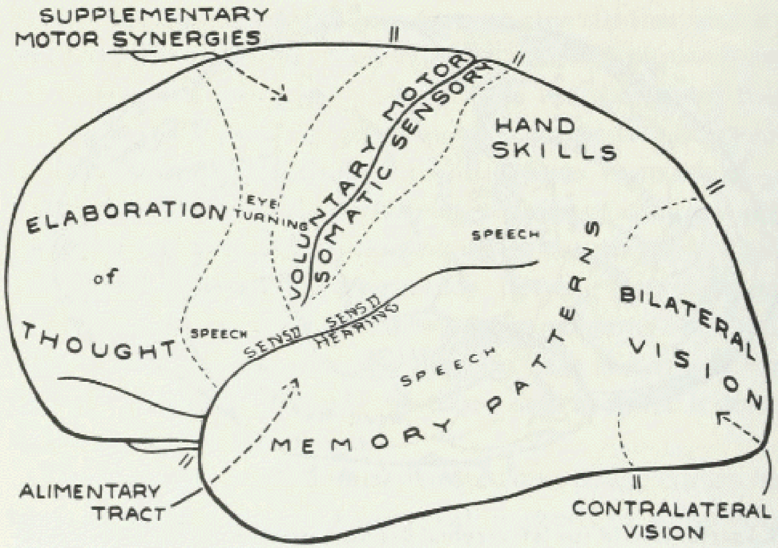
do not end in absolute victory for one side. In this case our thinking has acquired nuances from new techniques based on electronics, the science responsible for the use of both microelectrodes and the electron microscope. We now realize that there are highly localized functions, even tricks—if I may say so—that only certain aggregates of cells can perform, as well as functions that require a coactivation of several widely separated cortical areas. Delving into problems of localization, we tend to end up with problems of organization. In a general way one may say that the more complex the function defined, the more neural space it seems to occupy in all dimensions.

The "wiring" of the sensory projections to the cortex has been studied in detail by electrical methods of stimulation and recording, and maps of the primary end stations have been published, two of which are shown in Figures 4.3 and 4.4. The large somatic sensory area (Figure 4.4) whose anterior portion overlaps with the motor area (both shown in Figure 4.3) provides us with the basic geographic knowledge of our body surface. The visual area (Figure 4.4) similarly represents the external world projected on the retinal surface, the binocular overlapping part as well as the smaller monocular portions; the somatic sensory area reproduces the body surface.

Such primary sensory projections do not represent sites of conscious perception. Rather, they should be called sites of sensation to distinguish these areas from those required for full perceptual elaboration aided by memory. The primary areas are chiefly to be regarded as junctions on the route in which some reorganization of incoming messages takes place. Stimulating them electrically in man does not lead to perception of anything meaningful. From the visual area there are reports of "flickering lights, dancing lights,



4.3. Lateral view of the left cerebral hemisphere showing functional localization. From James W. Papez, *Comparative Neurology* (New York: Crowell, 1929).



4.4. Representation, according to a Congress Report by the late Wilder Penfield, of the localization of certain functions in the dominant hemisphere of man.

colors, bright lights, stars, wheels, blue, green and red colored discs, fawn and blue lights, colored bells whirling, radiating grey spots becoming pink and blue, a long white mark et cetera" (Penfield and Rasmussen, p. 145).[67] The same authors mention reports of sensations from patients whose somatic sensory area has been stimulated: "tingling, electricity, numbness, sense of movement" referred to specific parts on the opposite side of the body (pathways being crossed). Complete meaningful sequences of perceptions elicited by electrical stimulation were obtained merely from the temporal lobe. Thus what Penfield and Rasmussen found in the primary projections were fragments of an organization that since has been studied in considerable detail by microelectrodes (see Chapters 6 and 9).

Localization in the areas of elaboration, often called "association areas" (Figure 4.3) cannot be defined with the same amount of precision. The terms in which they are described in the figures refer to mental operations that acquire full meaning only with human subjects, but then of course we are interested in ourselves, and these areas are also much larger in man than in other animals. They do not respond to electrical stimulation in the manner of primary projection areas. Sensory and motor elaboration is needed, for instance, for skillful hand movements and for speech, but electrical stimulation of those areas merely stops performance. The temporal cortex with its peculiar access to things remembered is an exception (Chapter 5). For this reason much of what is known about elaboration areas has come from patients with head injuries, epilepsy, or ablations in conjunction with testing procedures, for example, and consequently is somewhat anecdotal. Clearly these areas are activated from the inside. Much of our information about them cannot be reviewed without knowledge of anatomy and physiology beyond the level of presentation in this book. Recent attempts at analyzing cellular responses in these areas will be taken up in Chapter 9.

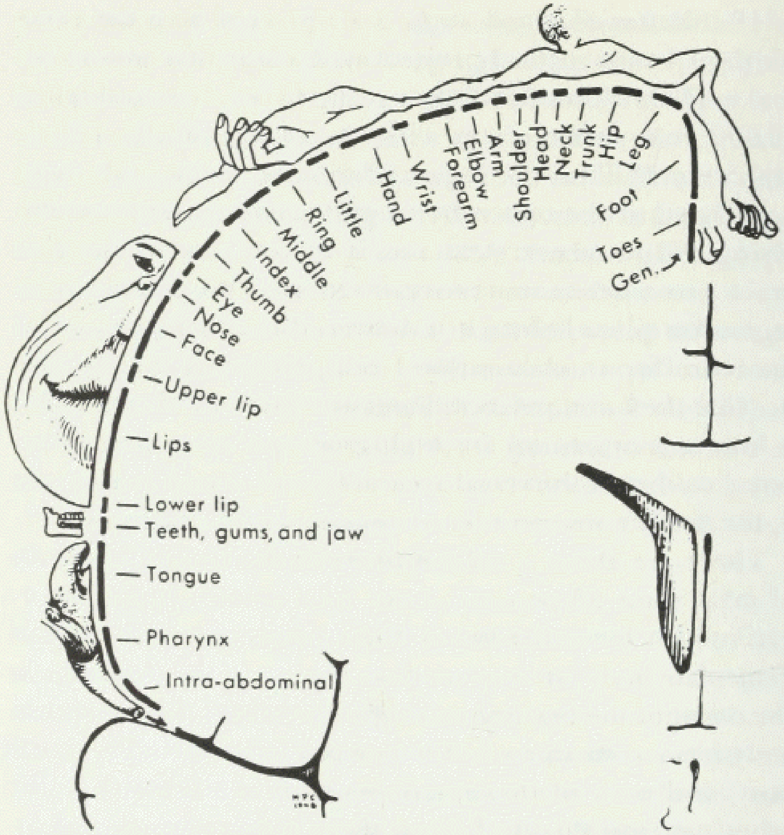
Though the huge expansion of the cortex distinguishes man from other species in the phylum, we share with other mammals the subcortical structures, just as we also share with them states of sleep and wakefulness, emotional attitudes, and basic reflexes of orientation and posture. As we shall see, subcortical components participate in all our responses to the environment and sometimes acquire a dominant role (discussed separately in Chapters 9 and 10). In preparing a background for some general comments on the principles of localization we are, however, best served by presenting the necessary facts in terms of results from the field of cortical physiology.[68]

General Significance of Cell Number

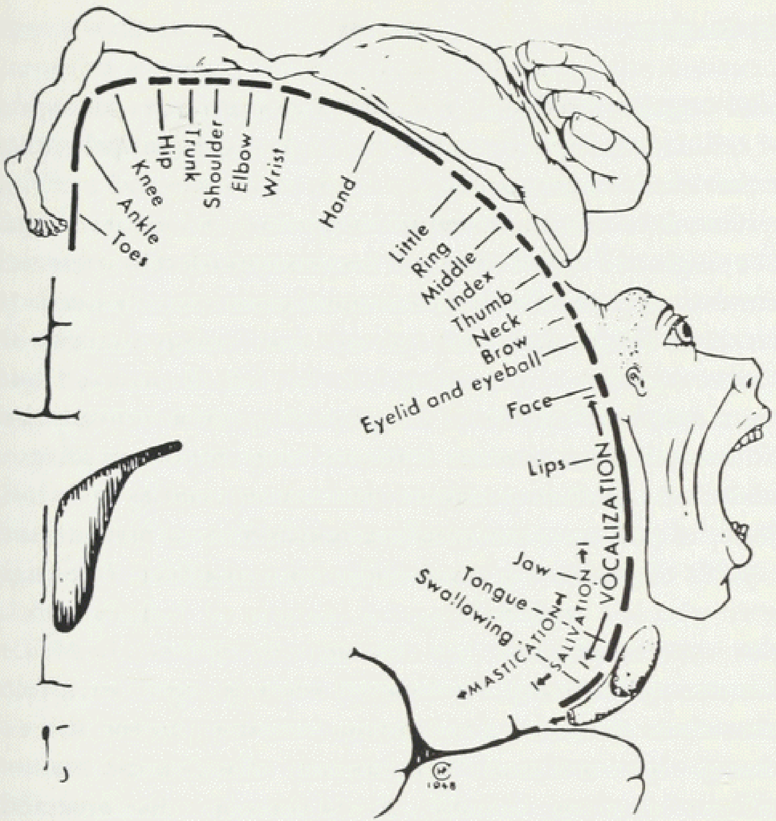
Importance, precision, and detailed specification are aspects of localization that within any particular cortical area are furthered by an augmentation of the number of participating cells. This is shown in brief outline by the homunculi of the motor and sensory fields of Figures 4.5 and 4.6. The large face and hand areas of the sensory and motor fields represent the need for highly discriminative sensitivity and finely controlled motor action respectively. The representation of the fovea of the eye demonstrates the same principle for the visual area, for which some figures are available.

In monkeys, in the foveal part of the retina, which is its most important focusing region, 2 minutes of visual angle at the retina is rerepresented within a millimeter at the cortex, whereas at 5° toward the periphery of vision as much as 18 minutes of visual angle are squeezed into the same width of 1 mm cortical projection. A circle of 1 minute visual angle encloses 0.005 mm at the fovea. It is multiplied 10,000 times at the cortex where it corresponds to a circle of 0.5 mm.[69] Thus the region of optimal vision in daylight is analyzed at the cortex by magnification based on multiplying cell numbers. And this is merely one of the first brain sites where some reorganization of the sensory message takes place before it is delivered to other portions of the brain for an elaboration I call perception. Small wonder that the brain needs millions and millions of cells if this is how it is organized for high-grade performance. Functional studies of the visual area will be dealt with in Chapter 6, but for the moment let us remain within anatomy.

There are about 2 million fibers in the two optic nerves of man, some 38 percent of our total sensory input. Reorganized for binocular vision, these project on to the lateral geniculate body, an intermediate station in the thalamus in the midst of the brain. Any single fiber from the geniculate body has terminals on 5,000 neurons in the primary visual area, and each of these neurons is in contact with 4,000 other neurons (Sholl).[49] Thus there is interaction, and interaction is the raison d'être of cellular multiplication. For the individual cells interaction may be in the nature of an enhancement (excitation) or a suppression (inhibition) of their activity. The nature of such interactions can in specific cases be analyzed by electrical techniques, as has been done for primary visual projection (Chapter 6) and the motor area (Chapter 8). At this point the problem of localization turns into an analysis of organization that should indicate what precisely is the function that is being localized.



4.5. Sensory homunculus. The right side of the figure is on a cross-section of the hemisphere, drawn somewhat in proportion to the extent of sensory cortex devoted to it. The length of the underlying block lines indicates more accurately the comparative extent of each representation. Compare with 4.6. From Wilder Penfield and Theodore Rasmussen, *The Cerebral Cortex of Man* (New York: Macmillan, 1950).



4.6. Motor homunculus. The right side of the figure is on a cross-section of the hemisphere. Compare with 4.5. From Wilder Penfield and Theodore Rasmussen, *The Cerebral Cortex of Man* (New York: Macmillan, 1950).

Redundancy

Like negative feedback, redundancy emphasizes an aspect of cellular multiplication that belongs to general principles rather than to any particular locus in the central nervous system. It means that a central response, indeed, even that of a single cell in the visual cortex, is supported by a greater number of pathways and neurons than it actually needs to function. Redundancy is a concept that biology shares with communication engineering.* In his less formalized and more empirical approach the physiologist also realizes that Nature takes no chances with anything important. Everywhere one finds important functions secured by a redundancy of pathways and also by a multiplicity of mechanisms capable of producing much the same end effect. The engineer who is a reasonably good imitator of Nature's tricks also uses redundancy, but on a considerably smaller scale. For example, though "individual wires going to each telephone are necessary for function . . . deep inside the exchange there are many 'senders' any of which can assume various functions. If only a few of them are disconnected, there would be little or no noticeable functional difference in the exchange. It would be a little bit slow in answering or setting up some of the calls, but these behavioral deficits would be detectable only through very subtle tests" (Shannon).[70] Similarly, as sometimes happens when the neurosurgeon has been forced to remove the cerebellum, a large

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*In information theory the amount of information or "entropy" is defined by the letter *H* in Shannon's formula (see any textbook in the field, e.g., F. H. George, *Cybernetics and Biology*. Edinburgh and London: Oliver & Boyd, 1965). Redundancy is the complement of information that could have been passed relative to the amount that actually was communicated. With the aid of the formula it can be measured quantitatively.

organ with some 10 billion cells, very special tests may be required to detect an abnormality of gait if the patient is allowed to keep his eyes open and thus has access to visual compensatory control.

The electronic engineer is much concerned about the irregular low-level activity in his circuits called "noise" because his signal must exceed the noise level. There is much spontaneous activity going on in the afferent input to the central nervous system; this has also been regarded as biological noise. In the nervous system, as in other circuits, a message has to exceed the noise level. Redundancy is one organizational feature by which noise is counteracted but there are others, particularly mechanisms based on inhibition, which is of fundamental importance at several levels as a filter enhancing the relevance of a message by restructuring it.

The central nervous system by no means behaves as a passive receiver of input (Chapter 9). It selects its information actively by processing it in the periphery, at the subcortical level, and within the cortex, where the ultimate selection takes place with the aid of consciousness. The mechanisms for rejection of noise are so highly developed that the physiological problem bears a merely superficial likeness to that of the communication engineer. Spontaneous impulse activity plays a most important role by maintaining a certain level of facilitation in the cells. Against this background of increased excitability nervous inhibition has a chance of modulating a response for greater pregnancy with regard to the permanently or momentarily needful. As yet no mathematics are available to formalize the role of cell multiplication in localizing highly discriminative responses because the fundamental variables of a quantitative treatment would have to be known. We are still too ignorant about them to use the mathematical instrument. To make some preliminary sense out of these intricate organizations, the investigator has to rely on an empirical approach with the aid of electrical recording and on behavioral abnormalities in man or animals with verifiable local destructions.

Expansion, Encephalization, and Localization

The three general aspects of cortical physiology surveyed clearly have a purpose in common that is best illustrated by referring to the localization of the structures handling speaking and the understanding of language (marked *speech* in Figure 4.4). The language areas have long been known to be located in the left hemisphere, but the two hemispheres are also connected by a system of communicating fibers, the corpus callosum, which permits them to cooperate harmoniously (see Chapter 5). Whether this communication with the right hemisphere meant anything for the understanding of language was until fairly recently unknown. There are pathological cases in which surgical section of the corpus callosum has been a justifiable cure; in them it has been possible to demonstrate that the right hemisphere actually is incapable of communicating by language while its left partner remains in full possession of this talent (next chapter and note 81). It is thus possible to compare the anatomy of corresponding regions, one with and the other without a role in communication. The two sites in the left and the right hemisphere are actually highly asymmetrical, the left side containing the speech areas, being both larger and more richly differentiated (Geschwind).[53] In a small number of people speech is represented in both hemispheres. What this implies in the way of

anatomical development is at the moment unknown.

The question of what is being localized—which will concern us in specific cases in the next chapters—has been pursued along two main lines: (1) the neurophysiological, tightly stimulus-bound, experimental approach, and (2) the other proceeding to some kind of understanding by psychological definitions (in man) or using behavioral observations (in animals) in the belief that the recorded motor reactions would not as such contribute essentially to the behavioral act. While we are aiming at combining—as far as it goes—neurophysiological and anatomical knowledge with clinical experience and psychological or behavioral responses, there is a limit beyond which only psychology can take over, aided in some cases by anatomy, and possibly caught up in a distant future by neurophysiology. An example of this is speech, as spoken and understood. At their best the neurophysiological analyses of today carry us to the level of the primary projections in the visual, acoustic, somatic, and other sensory areas and sometimes a bit beyond them.

Our present knowledge of localized functions in the brain is steadily expanding. Modern anatomy is at a high technical level. It makes use of refined staining methods aided by improved light microscopy and the electron microscope. In the last instance, however, a functional criterion is needed to define what is being localized. At the moment we are trying to understand encoding and decoding of information, mechanisms of cellular interaction, what fraction of experience is handled by a single cell, how conscious percepts result from available bits of information, and a host of other questions.

In relation to the enormous task of understanding nervous action and perception, the insight laid down in the principle of differentiation by localization may seem insignificant as an attempt at classifying brain activity. Nevertheless it serves as the backbone on which the rest of our body of knowledge hinges. Another matter is then how to proceed to the next step in classification and decide to what class of phenomena a living nervous system belongs. It is a unique phenomenon in this world—unique also in ultimately trying to understand itself.

5

Some Approaches to Conscious Awareness

Any science that deals with living organisms must needs cover the phenomenon of consciousness, because consciousness, too, is part of reality. (Niels Bohr in a discussion recorded by Heisenberg in *Physics and Beyond,* London: Allen and Unwin, 1971, p. 114.)