2. BIOLOGICAL BACKGROUND

The site of the intelligent capabilities of the brain is the *neocortex*; from an evolutionary point of view the most recent and in people the most highly developed part of the brain. Viewed superficially, the human neocortex consists of a layer of nerve cell tissue of about $0.2m^2$ in area and on the average 2–3 mm in thickness, strongly convoluted to save space, and forming the exterior of both brain hemispheres. Within this layer, various areas can be distinguished which are specialized for specific tasks such as visual perception *(visual cortex)*, motor control *(motor cortex)*, or touch *(somatosensory cortex)* (Fig. 2.1). Additional areas *(association areas)* link information affecting multiple sensations.

In the human neocortex, about 100,000 closely interconnected nerve cells, called *neurons*, lie under every square millimeter and constitute the "computational units" of the cortex. Fig. 2.2 shows a vertical cut through the neocortex of a cat and gives some impression of the complexity of the cortical circuitry. Of the neurons actually present in the slice, only a fraction is shown in Fig. 2.2, in order that single neurons be recognizable for the observer. The actual neuron density is a factor of about 100 larger and would correspond to a completely black picture of the slice.

Three main structures can be distinguished in a typical neuron: *dendritic tree*, *cell body*, and *axon*, roughly corresponding to the input, processing, and output functions, respectively. The dendritic tree, a branched structure of thin cell extensions, forms the main input pathway of a neuron. It is spread out within a region of up to 400 μm in radius around the neuron and sums the output signals of the surrounding neurons in the form of an electric potential, which it then sends to the cell body *(soma)* of the neuron. If this potential exceeds a certain threshold value, the cell body produces a short *electrical spike*, which is then conducted along the axon, a nerve fibre ranging from a fraction of a millimeter to several meters in length. The axon also branches out and, in this manner, conducts the pulse to several
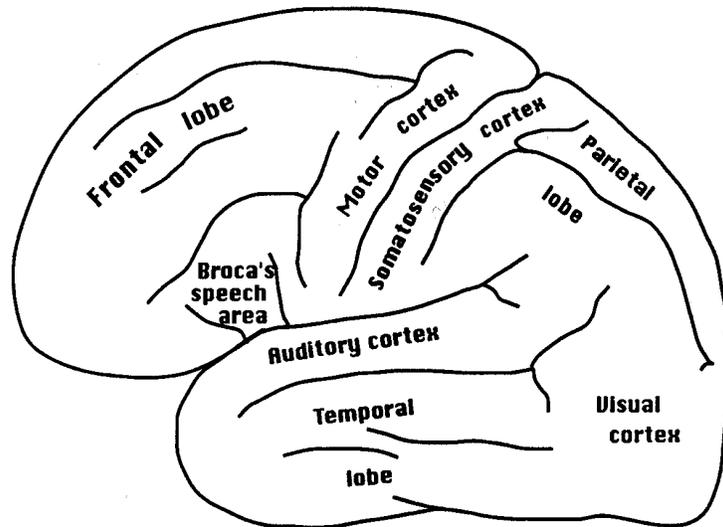
Abb. 2.1: Lateral (schematic) view of the human left-brain hemisphere. Its convoluted surface is composed of a 2–3mm thick cortical area (neocortex). Various cortical areas specialized to specific tasks can be distinguished on this layer.

thousand target neurons. The contacts of an axon are either located on the dendritic tree or direcly on the cell body of the target neuron and are known as *synapses*. Most synapses are "chemical contacts," *i.e.*, at the synapse, the electrical pulse of the axon causes secretion of a transmitter substance (*neurotransmitter*), which in turn leads to a change in the potential at the dendritic tree or cell body of the target neuron. Depending on the type of synapse and its state, an incoming pulse causes a more or less strong potential rise (*excitatory* synapse) or potential drop (*inhibitory* synapse) at the target neuron. Hence, the synapses act like analog switches regulating the communication between neurons and, thus, represent sites where important information is stored.

Two main classes of cortical neurons are distinguished on the basis of their shape: *pyramidal cells* (*Golgi Type I neurons*, comprising about 60% of the total) and star-shaped *"stellate cells"* or *astrocytes* (*Golgi Type II neurons*, about 40%). The pyramidal cells usually have long-range axons with synapses

Abb. 2.2: Vertical section through the neocortex of a cat (the thickness dimension of the cortex lies in the vertical direction of the figure). The pyramidal cells (A–G) are recognizable from their conical cell body, their root-like dendrites, and their long axon which extends to the surface of the cortex (in the upper part of the figure). In contrast, the extensions of the stellate cells (H–M) are spread out only in the immediate neighborhood. Only a fraction of the neurons in the figure section is reproduced. The true packing density is a factor of about 100 higher (Ramón y Cajal 1909).

acting excitatory, whereas in the stellate cells the axon, with its stellate branching, affects only its immediate environment, acting usually in an inhibitory fashion (see Fig. 2.3). It is commonly believed that the important information is coded in the activity state of the pyramidal cells, and the astrocytes serve as stabilizers of the system by inhibiting activity around excited regions (*lateral inhibition*). In many regions of the cortex, groups of adjacent neurons give evidence for aggregation in higher functional units (Mountcastle 1978; Blasdel and Salama 1986). These units, known as *microcolumns*, usually include the neurons of a small vertical cylindrical volume in the cortex of typically tenths of a millimeter in diameter or smaller. Such a cylinder can serve to analyze some particular stimulus feature, such as the
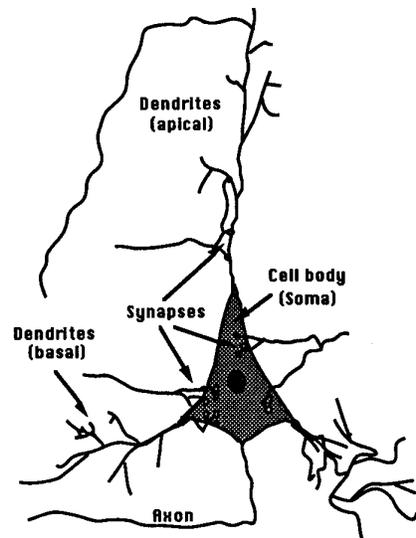
Abb. 2.3: Structure of a neuron (schematic). Besides the "pyramidal cell" shown, numerous other kinds of neurons occur in the brain.

orientation of an edge of an image (as in the primary visual cortex), or the innervation of a common muscle (as in the *primary motor cortex*). Adjacent microcolumns cannot be precisely separated, but rather there is a gradual transition in the membership of individual neurons.

At the next higher level of organization, microcolumns of one type are arranged in specialized areas. Today, about 80 such "cortical areas" are known in the human cortex, each of which represents a highly parallel "special purpose" module for a specific task. For example, one can identify in the visual cortex areas for the analysis of edge orientation, of color shades, and of velocity fields, while other cortical areas host modules for various aspects of speech comprehension, recognition of faces, spatial orientation, and planning and execution of movements. To the extent that simple features can be identified relating to the properties of cortical neurons, one often finds a regular variation of these features along the two directions parallel to the surface of the layer, *i.e.*, there is a *continuous, two-dimensional feature map*. The formation — and the benefits — of such a representation of, *e.g.*, sensory data, constitutes one of the subjects of this book.

Most cortical areas can be assigned to one of three groups: (*i*) *primary* and *secondary* sensory areas, whose input stems directly (via noncortical "relay stations") from sensory receptors or primary cortices, (*ii*) *association fields*, in which the various sensory signals which have been preprocessed by primary and secondary cortical areas converge, and (*iii*) *primary* and *secondary motor areas*, which (again via noncortical intermediaries) are connected with the musculature or the primary motor areas. Each of these cortical areas is also connected to and interacts with numerous additional cortical areas as well as brain and nerve structures outside of the cortex. This leads to a highly coupled and parallel global system. In spite of the differences between the tasks addressed by different cortical areas, the cortex possesses a surprisingly homogeneous structure. For example all cortical areas consist of six layers (I–VI), one above the other, which differ from one another in their relative thickness. At the risk of oversimplifying, one can say that layer IV generally serves as the input layer of a cortical area. Next to this, association fibers project out to other, distant cortical regions. The main source of output is layer V. Layer VI sends out "feedback" nerve fibers to the neurons, which are directed to the input layer IV. Layers II and III are the main output location for short-range association fibers to surrounding cortex points. These fibers themselves form the upper layer I.

The circuitry connecting individual modules with one another is generally subject to a common "topographic" organizational principle: adjacent neurons of an output field are almost always connected to adjacent neurons in the target field. This organizational structure is especially evident in the primary cortical areas, *i.e.*, those that, from the point of view of circuitry, are located "close to the outside world."

Most signals from the environment are received by the brain from "sensory surfaces" which are covered with receptors. Our largest sensory surface is the skin with its touch and thermal receptors; perhaps our most important sensory surface is the retina. The ear gives an example of a one-dimensional sensory "surface:" there, the receptors are arranged along the spiral-shaped *cochlea*.

Although the wiring connecting these sensory surfaces to their primary sensory areas in the cortex passes through several "relay stations," it also exhibits a "topographic ordering" and conducts signals from adjacent receptors to neurons which are adjacent in the cortex. In this way a mapping of the
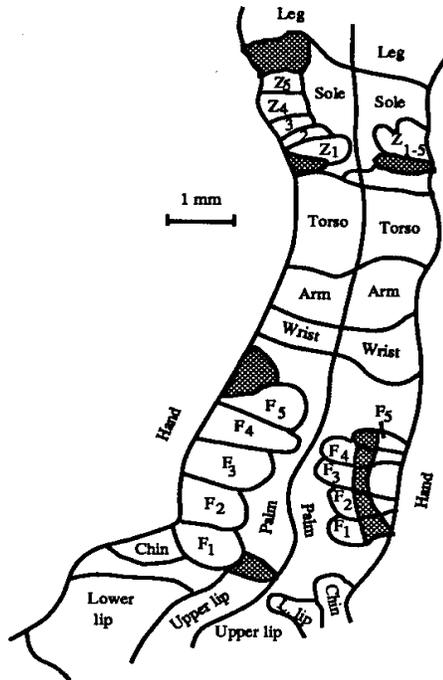
Abb. 2.4: Map of a part of the body surface in the somatosensory cortex of a monkey. Most of the neighborhood relations of the body regions shown are preserved in the map. Richly innervated skin regions (e.g. finger $F_1 - -F_5$) are strongly enlarged in the map (after Kaas et al. 1979).
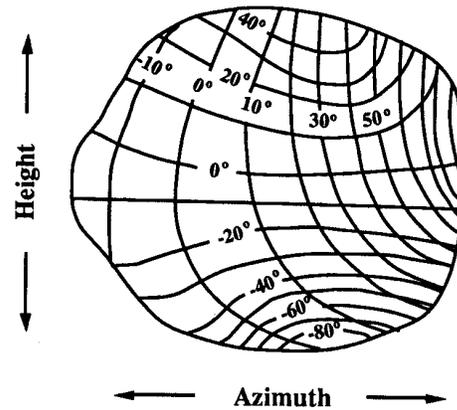
Abb. 2.5: Direction map for sound signals in the so-called "optical tectum" of an owl. The horizontally directed lines connect neurons responding to sound signals from directions with the same longitude. The vertically directed lines connect neurons corresponding to sound directions with the same incident latitude (after Knudsen et al. 1987).

respective sensory surfaces to the relevant cortical area is established. Due to its preservation of adjacency and neighborhood relationships, this mapping can be regarded as a (frequently more or less distorted) *image* or *topographic map* of the sensory surface. For example, in the case of the sense of touch, one finds various such maps of the body surface in the *somatosensory cortex*

(Kaas et al. 1979). An example is shown in Fig. 2.4. A similar situation holds for the primary visual cortex. However, there it is already evident that the brain also constructs *maps of abstract features* of the environment in which, *e.g.*, the association of neurons with local properties of visual images, such as edge orientation or velocity of movement, varies in a regular way with the location of the neurons. An especially illustrative example is the image in the *optical tectum* of owls. There, the direction of sound signals is mapped in a regular way within a layer (Fig. 2.5). A map coding pitch in one direction is found in the *auditory cortex* of many higher brains. In bats, the amplitude of the signal is coded in the direction orthogonal to the direction of pitch. In this way, a "sound spectrogram" is created on the cortex. In addition, bats also possess a map representing the time difference between two acoustic events. This map is important for the sonar orientation of the animal (Suga and O'Neill 1979).

However, maps are not limited to sensory regions. There are also "motor" maps, on which the location of an activity peak specifies the execution of a movement. While sensory maps generate a spatially localized "activity peak" from the activity pattern of preceding receptor neurons whose location represents the signal features being analyzed, motor maps create — from a spatially localized activity peak — an activity pattern (in space and time) among subsequent motor neurons that triggers a particular movement (Lemon 1988). The best investigated example of such a map can be found in the *"superior colliculus"* in the midbrain (Sparks and Nelson 1987). In this map, the spatial location of an excitation peak encodes the direction and amplitude of an eye movement. A map organized in the form of a ring can be observed in the primary motor cortex (Murphy et al. 1977). Localized electrical stimulation within this map triggers flexion and extension movements of the arm joints, varying systematically with the location of the stimulus.

It is highly probable that a large portion of the organization of such maps is genetically determined. However, considering the estimated 1013 synapses of a brain, it would be impossible to specify this organization on the basis of a detailed connectivity scheme. A way out of this dilemma is the genetic coding of mechanisms of structure formation, as a result of whose operation the desired connectivity would then be created. The formation of structure could either take place before birth or as part of a later maturation phase, and in the latter case it could be driven by suitable sensory stimuli. For example, it has been established that the normal formation of an edge orientation

map in the primary visual cortex of a newborn is suppressed in the absence of sufficient visual experience (Rauschecker and Singer 1981). Moreover, experimental investigations, *e.g.*, in the somatosensory cortex, show that even in a mature animal many maps are not at all rigidly determined, but can change slowly depending on sensory stimuli (Jenkins et al. 1984; Harris 1986).

This condensed description provides only an extremely limited impression of the "brain as a neural computer" and its structural variety. Nevertheless, in the last few years we have gained numerous theoretical insights in the functioning of the brain that can be tested by means of mathematically formulated models. In Chapter 3, we discuss some of their most important representatives.