# Brain

Curator: William E. Skaggs

Valentino Braitenberg

Eugene M. Izhikevich

Javier Elkin

Benjamin Bronner

Marc-Oliver Gewaltig

Robert P. O'Shea

Dr. Valentino Braitenberg, Max Planck Institute for Biological Cybernetics, Tubingen, Germany

The brain is encased in the head, the part of the body which in most walking, flying or swimming animals is the leading end of the moving body (with few exceptions: starfish, cuttlefish, humans, penguins when they are not swimming). The obvious risks which this localization entails are apparently compensated by the advantage of direct short connections with the sense organs localized in or on top of the head (olfaction, taste, vision, audition, vestibular sense), which together with the brain could be seen as something like the cockpit of the animal, or the pilot if one prefers.

The intimate relation of the brain to the sense organs points to the brain’s essential role as an information handling device. Meaningful events to which the animal reacts are but rarely signaled by a single sense organ. More commonly it is a combination of information from different sensory modalities that gives away the aggressor, or the prey, or the sexual partner, or the dangerous cliff etc. Thus the brain is there to make concepts out of sensations, at a higher level of abstraction. It is not only the different senses that contribute to the formation of concepts. Equally important, the monitoring of motor behavior, both in its planning and in its execution, provides crucial information necessary for the correct interpretation of any situation signaled by the senses. All of this requires a brain.

Although the brain is not insensitive to some chemical signals that reach it through its blood supply (e.g. concentration of CO2, concentration of sugar, various hormones in the blood), and is in turn capable of emitting chemical messages addressed to other parts of the body, by far the greatest part of the information traffic in which the brain is involved uses nerve fibers as carriers of signals. In humans, a few million fibers enter the brain on the sensory side, and about as many connect it to the motor output.

The bulk of the brain itself is also made up of masses of fibers: axons, dendrites, glia. From the volume of the brain and the average thickness of the fibers (not including the glia), we get an estimate of the sum total of the length of all fibers contained in a single (human) brain as reaching from the earth to the moon and back. This astronomical length is impressive, but hardly conducive to a functional interpretation of the anatomical structure of the brain. Rather, it is the network woven out of the fibers which provides clues to the workings of the brain.

Nerve fibers of two sorts, dendrites and axons, emanate from neural cell bodies. Thus the neuron, the anatomical unit of brain tissue, is star shaped, a fact which has important consequences for connectivity. Since what happens within the brain is essentially based on the exchange of signals among neurons, and since such exchange can only happen where neurons come in close contact with each other, it is advantageous to provide for each neuron contacts with as many other neurons as possible. Were neurons spherical and closely packed, each of them could touch at most as many other neurons as are the nearest neighbours of peas in a jar, namely twelve for each pea. In reality, the synaptic neighbours of a single neuron, both on the giving and on the receiving side, thanks to the long neural cell processes number several thousands on an average, ranging from a minimum of very few (exceptionally perhaps only one) to several hundreds of thousands (synapses between parallel fibers and a single Purkinje cell in the cerebellum). Convergence and divergence of signals, from many neurons onto one and from one to many, are thus guaranteed and certainly play a crucial role in brain function.

The length of the individual fibers in the brain varies a great deal, from less than one tenth of a millimeter to over hundred millimeters, corresponding to the diameter of the whole (human) brain. Evidently, the synaptic neighbours of a single neuron, i.e. the neurons with which it enters into direct synaptic contact, can be distributed widely in disparate parts of the brain, including the immediate neighbourhood as well as far away regions.

There is a distinction of two kinds of brain “substance”, or better, of two distinct compartments of the brain (Figure 3), which coincides roughly with a distinction of regions containing long, mostly insulated (“myelinated") fibers on the one hand, and regions containing a multitude of short fibers and neural cell bodies on the other. There is another, more fundamental distinguishing feature between the two. In the so-called white substance (or white matter), the one predominantly made up of long fibers, there are no synapses, whereas synapses abound in the grey substance (or grey matter). Apparently, elaboration of information in a synaptic network, and projection of information from one place to another are two functions which are kept locally separate in the brain, in line with the multi-level hierarchy both of information processing in the brain and of behaviour.

Although the equipment of elementary components in the grey substance (dendrites, axons, excitatory and inhibitory synapses, glia) is remarkably similar in different places (and in different animal species), there are striking local differences in the architecture in which these components are arranged. For one thing, the outlines of the territory in which an individual neuron spreads its dendritic ramifications vary a great deal both in shape and in size, and even more striking are the differences in the axonal trees. Obviously, the geometry of dendritic and axonal cell processes of neurons located in the same piece of grey substance determines for each neuron the choice of partners with which it may establish synapses.

In some places, neighbouring dendritic trees are intimately interwoven so that they largely share the same territory and hence also the same set of axons to establish synapses with. This is the situation with the pyramidal cells in the cerebral cortex. In other parts of the brain, dendritic trees (e.g. of Purkinje cells in the cerebellum) stand neatly separated with no overlap, each defining its individual choice of synaptic contacts.

The varying statistics and geometry of neural elements in different regions of the grey substance are undoubtedly related to different schemes of neural computation, or perhaps more cautiously, of elaboration of information. Besides the differences already mentioned, in different parts of the brain there are striking differences in the numerical relations between the neurons of various kinds that compose the tissue. There are places in the brain where the fibers which carry the input are connected directly to the neurons which relay the output to distant places, whereas in other regions complicated networks of so-called interneurons are interposed between input and output, sometimes vastly outnumbering the output and input elements (as in the case of the cerebral cortex). There are also differences in the number of inhibitory neurons with respect to that of the excitatory ones, differences in the “plasticity”, i.e. the possibility of changing the connections by learning. Most importantly, the distribution and orientation of fibers in the fiber felt is quite different in different parts of the grey substance. There are lumps of grey substance where there is no apparent preferential direction of fibers in the three directions of space (e.g. many “nuclei” of the brain stem). Other, quantitatively imposing parts of the grey substance (cerebral cortex, cerebellar cortex, visual ganglia of many invertebrates) are arranged in layered structures where the fibers within one layer, confined to a two-dimensional space, are neatly distinct from those connecting different layers to each other. Moreover, even between different instances of such layered structures there are striking differences in the layout of the fibers. In the cerebral cortex, within each layer the connections are spread in all directions, whereas in the cerebellar cortex all the excitatory fibers run in one and the same (roughly latero-lateral) direction of the cortical plane, while the inhibitory ones are oriented at right angles to them.

The fact that different parts of the brain are involved in different aspects of behaviour has been known for many years to clinical neurologists. The evidence is derived from a variety of symptoms which follow localized lesions of the brain, either due to some pathological process or to surgical experimentation in animals. In the simplest case, the localization of function is simply a consequence of the point of entry of the sensory fibers involved in a particular sensory modality. Thus there is a “visual cortex”, an “auditory cortex”, a “somatosensory cortex”, and similar subdivisions of the brain stem defined by the kind of sensory inputs they receive. The origin of the motor output also provides the name for various regions: there is a “motor cortex”, there are “oculomotor nuclei”, “motor speech centers”, etc.

However, local specialization of the brain goes beyond the distinctions imposed by different sensory modalities. One and the same sensory input may be perceived in different contexts and these can be represented in different places in the brain. The same acoustic input from the cochlea at one time (and in one place) may be used to determine the localization of the source, at another time (and in another place in the brain) it may elicit a startle reaction, or (in humans) it may be understood as a linguistic utterance. The visual input, possibly, has even more multifarious destinations in the brain. It would be surprising, if it was the same piece of cerebral cortex that could establish the velocity with which a certain smudge moves through the visual field, or what kind of animal it is if it is an animal, or which letter of the alphabet it may represent. And indeed, these questions and some more are answered in different areas within the visual cortex, by now rather well known in their different specialization.

To a certain extent, the different roles of cortical areas, as well as of various subcortical organs, can be inferred from the position they occupy in the global organization of the brain between sensory input, associational regions and motor output. In some cases, both in sensory and motor regions of the brain, different areas, or different levels of analysis, are arranged in series, with the output of one serving as the input to the next one. In other cases, the information arriving at one point is duplicated and elaborated in parallel in different “streams” of analysis. In others again, we observe a restricted region of the brain having contacts with a multitude of other regions, as if broadcasting messages “to whom it may concern”. The macroscopical layout of compartments in the brain is also reflected in the structure of the white substance which contains the long fibers, mostly bundled to form several distinct “fascicles”, responsible for the functional relations of the various compartments with each other.

Both in vertebrates and invertebrates the shape of the brain clearly suggests anatomical subdivisions which in part coincide with the distinctions made above on the basis of functional specialization and variation of fine structure. In the insect (and generally, arthropod) brain the optic lobes with their associated ganglia are most impressive. In the vertebrate brain the two cortices, cerebral and cerebellar, leap to the eye, as well as the optic tectum (in “lower” vertebrates) and the brain stem. The cerebral cortex in the human brain is the largest piece of grey substance and is in itself composed of separate lobes (frontal, temporal, parietal, occipital) well demarcated by particular deep furrows, although parts of a continuous sheet of grey substance. The cerebral cortex, like most of the subdivisions of the vertebrate (and invertebrate) brain is paired, with separate, symmetrical pieces of grey substance arranged at both sides of the midline. Only some small nuclei of the brain stem situated near the midline are unpaired (e.g. the interpeduncular nucleus), and so is the conspicuous cerebellar cortex, which straddles the midline without any interruption of its structural continuity.

The weight of the brain varies a great deal in different animals, ranging from a few milligrams in insects to 1.3 kilograms in humans, and further to the brains of elephants and whales with brain weights about 5 times that of a human brain. The weight of the brain increases with the size of the body, not proportionally to its mass, but rather to its surface. This rule is valid within each order of related animal species. Between different orders, differences in brain weight (relative to the weight of the body) are said to indicate different degrees of “encephalisation”, by which term is meant a hypothetical tendency of evolution to produce, in the long run, ever bigger and better brains in successive generations of animals.

The number of neurons in animals of different sizes grows with the size of the brain but stays behind the volume of the brains. In fact, in small brains the neurons are packed more densely than in larger brains. In the mouse cortex there are about three to ten times more neurons per cubic millimeter than in the human brain. This is due to the proportion of volume occupied by the neuronal cell processes, which in larger brains tend to be longer for obvious geometrical reasons.

It is tempting to take the volume of the brain, or the number of neurons in it, as a measure of its efficiency. Also, the relative sizes of various subdivisions of the brain in different animal species (and even in individual human beings) are sometimes taken as indicating different attitudes or different proficiencies in various performances. These claims usually do not go much beyond the journalistic level.

Brodal, A. (1981). Neurological Anatomy (In Relation to Clinical Medicine), Oxford  
University Press.

Ramon y Cajal, S. (1995). Histology of the Nervous System, two volumes [1909-1911], Oxford  
University Press.

Nicholls, J. G., Martin, A. R., Wallace, B. G., &amp; Fuchs, P. A. (2001). From Neuron to Brain 4th ed.: Sinauer.

Thompson, R. F. (2000). The Brain. A Neuroscience primer, Freeman &amp; Co.

Internal references

Cerebellum, Cortex, Glia, Neuroanatomy, Neuron, Synapse, Synaptic Plasticity, Thalamus