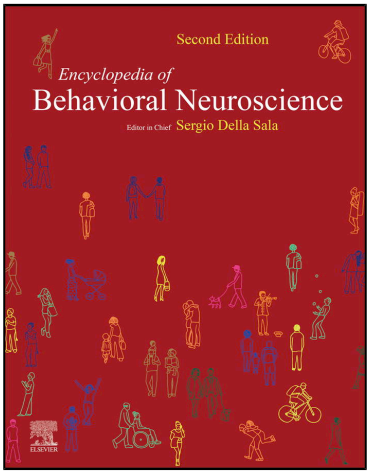

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Principles of Neuroanatomy: A Short Introduction

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Brain Components

The human mind is equally the product and pilot of our nervous system's headquarters – our brain, "The most complex piece of matter in the universe" (Bear et al., 2007). Despite centuries of hard work and unquestionable progress, the mysteries of our most cryptic organ remain unsolved.

Our brain is involved in every aspect of our lives. We use it for a wide range of tasks, including, for instance, processing sensations, storing memories, feeling emotions, decision-making, action-planning, etc. All of these intellectual processes are gathered under one broad term: cognition. Although an adult brain only weighs around 1,5 kg – which accounts for 2% of the total body weight – it consumes, on average, 20% of our daily used energy (Raichle and Gusnard, 2002), which can give us an idea of this organ's importance.

The brain is made of nervous tissue (**Fig. 1**), a sophisticated arrangement of neurons, and the cellular units of a nervous system, all surrounded by an army of glial cells – a support team that feeds and protects neurons.

Unlike other animal cells, neurons present with an original geometry: their cellular body, the soma, has two types of prominent extensions or protoplasmic elongations, one axon and several dendrites (Ramón y Cajal, 1894) (**Fig. 1**). This particular form manifests their unique function. A neuron can process information, receiving it through its dendrites then forwarding it via its axon. Because of this original feature, an isolated neuron would be purposeless.

Neurons are team players like any other cell type of our organism. For example, skin cells are like bricks. An isolated brick is not very useful. However, hundreds of them can make a wall, the skin. In other words, numerous cells assemble to build tissue, and as the structural complexity increases, an additional function can emerge. For skin cells, that would be to protect the organism against external aggressions. For neurons, it is even more elaborate as complex communication between neurons comes into place.

Brain Communication

Naturally, as they carry information, neurons are more complex than bricks. Not only do they have to be in numbers, but they also have to be linked to each other to communicate.

The synapse is the point of connection between two neurons: a sophisticated space between the terminations of an axon and a dendrite where information can unidirectionally pass from a first cell to the next one (**Fig. 1**). Connections with peers are essential to a neuron, and if deprived of them, the neuron will degenerate (Bredesen, 1995; Capurso et al., 1997). A single neuron can be connected to up to 10,000 fellow neurons, and we estimate the total number of synapses in our brain to be somewhere between 100 and 1000 trillion (Seung, 2012) for approximately 100 billion neurons (Herculano-Houzel, 2009). This network forms a very dense circuit of interconnected neurons in which information travels step by step, from cell to cell, and can reach even the most distant cells.

Brain Information

The information that flows within the neuronal network is electrochemical (Ramón y Cajal, 1899). Neurons can generate and convey signals: as ions enter or leave a neuron through channels in its membrane, the electrical potential between the interior and the exterior of the cell changes. When this difference reaches a threshold of 15 mV, a succession of electrochemical events take place, and an electrical impulse called action potential is sent along the axon to convey a message.

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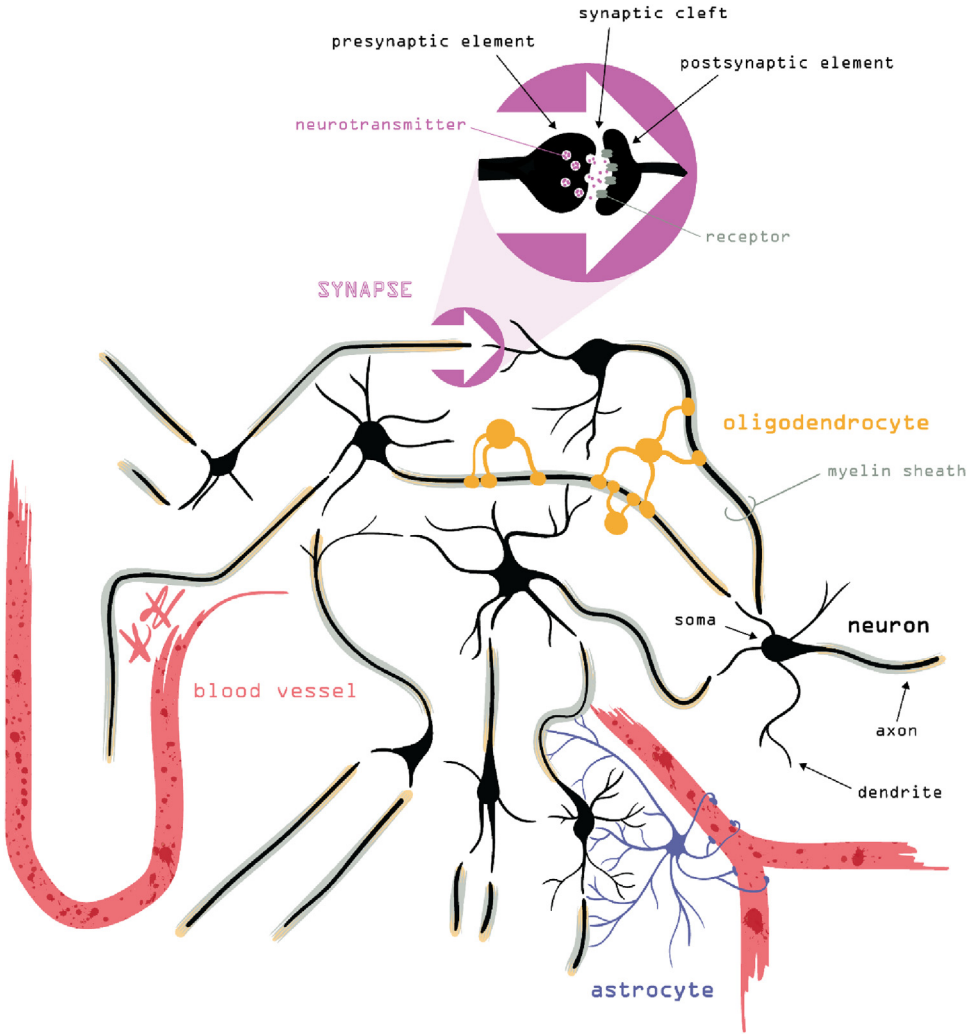

Figure 1 Prototypical representation of the cerebral nervous tissue. This sketch displays the typical interaction between three prominent cerebral nervous tissue cell types: the neurons, the oligodendrocytes and the astrocytes. Note that for clarity purposes, the different elements displayed in this figure are not to scale. A population of neurons conveys and processes electrochemical information inside a neuronal network. To achieve such a task, the geometry of a neuron is very unusual when compared to other animal cells. The neuron's body, the soma, has two types of elongations, one axon and several dendrites that link it to other neurons through equally unusual sophisticated structures called synapses. A close-up view of a synapse can be seen inside a purple circle on the top of the present schema. Electric information diffuses unidirectionally inside the neuronal net. When an electric potential approaches the end of the axon of a neuron, it takes a chemical form to travel the synapse and reach the dendrite of the next neuron. Neurotransmitters contained in vesicles of the presynaptic element are released from the presynaptic element and sent to the synaptic cleft. From there, they can bind with receptors dispatched on the membrane of the postsynaptic element. A second population of cells, the glial cells, including the oligodendrocytes and the astrocytes, supports the neurons in their mission. The oligodendrocytes, with their wrapping processes, cover axons with an insulating myelin sheath that ensures a fast and efficient propagation of electric signals. The remaining space is filled with the most abundant type of glial cells present in the nervous tissue: the astrocytes. For many reasons, they can be considered the caretakers of the cerebral nervous tissue. The most important reason is that astrocytes keep neurons alive by feeding them the nutrients uptaken from capillaries through their vascular end-feet.

The speed of the conduction is not instantaneous; it varies around the range of 300 km/h, subject to the influence of the diameter of the axon (Hursh, 1939) and its myelination (Waxman and Bennett, 1972).

At the axonal termination of a neuron, action potentials are translated into a chemical formula of neurotransmitters – mostly dopamine, acetylcholine, noradrenaline, gamma-aminobutyric acid (GABA), histamine, serotonin and glutamate – that diffuse across the synapse to bind specifically with membrane receptors of the next neuron's dendrite. This transmission is monitored by astrocytes – those glial cells whose function remains arguably the most enigmatic to us. In addition to providing nutrients to neurons and modulating the flow of blood in the nervous tissue, astrocytes can also influence the synaptic exchange by taking up and releasing neurotransmitters (Bear et al., 2007).

As stated before, each neuron has only one axon but many dendrites, meaning that a single neuron can receive several action potentials from various fellow cells. Their most remarkable ability is being able to integrate information – after summing or subtracting the inputs they receive, they purvey the network with an original output that integrates all incoming signals.

This aptitude is at the origin of all cognitive abilities.

This mechanism is similar across all brain neurons. Each neuron can only create one unique type of action potential; thus, the diversity of information does not come from the electrical signal itself but the frequency of its occurrence. As far as we know, neurons cannot produce complex data on their own. Being part of a network, though, they can work together with frequency-coded information. Ultimately, the extreme computational power of the brain arises from the collaborative effort of a tremendous number of single cells.

Brain Organization

Without a crucial extra component, the dense network where information freely travels would end up in a cacophony, which would fail to send information where expected, integrate information when not needed and lead to the opposite of what is required to execute cognitive functions.

A key to managing complex information flow is flawless organization. In an organized neuronal net, the role of each cell is spatially restricted. Thus, every single neuron has a role determined according to its position relative to other neurons in the network.

As expressed by Marcel Mesulam in the foreword he wrote for Schmahmann and Pandya (2006), "Nothing defines the function of a neuron better than its connections," and "the distribution of connections is complex but not chaotic".

Newborns already possess the vast majority of their neurons. As the brain matures and experiences life, the network develops but not randomly. Functionally useful connections will be consolidated: This is called synaptic pruning (Bourgeois et al., 1994; Changeux and Danchin, 1976; Huttenlocher, 1979; Huttenlocher and Dabholkar, 1997; Rakic, 1986). Such a mechanism will lead to a unique, fine-tuned microscopic connectome in every adult. A connectome is an elaborate arrangement of connections that could be charted as a wiring diagram that is ultimately representative of the individual abilities of each particular brain.

Consequently, if the role of any given neuron within the central nervous system depends on its pattern of connectivity with other neurons, distinctive connectivity patterns can be interpreted as an indication that two different regions serve different functions (Fettes et al., 2017).

Brain Structure

On a cellular scale, the search for specific connectivity signatures to infer any functional role might be tedious, but not impossible; a brain network comprises around 100 billion neurons. Fortunately, at a macroscopic scale, a connectome is also apparent, greatly simplifying the functional interpretation of particular structural arrangements.

The nervous system consists of two subcomponents — the central and the peripheral nervous systems. On the one hand, along with the spinal cord, the brain is part of the central nervous system (CNS) that respectively encloses the spine and the skull. On the other hand, bundles of axons called nerves dispatched all over the body, emerging from or arriving at the spinal cord, form the peripheral nervous system (PNS). Note that the nervous system is hollowed with cavities called ventricles where a liquid, cerebrospinal fluid (CSF), is produced and distributed.

The brain itself is made of three distinct portions: the cerebrum, the largest portion, also called the telencephalon; the cerebellum; and finally the brain stem that connects the ensemble to the spinal cord, thus ensuring continuity between the CNS and the PNS.

Arguably the most sophisticated part of the human nervous system is the cerebrum, a spherical structure formed from two roughly symmetrical halves: the left and right hemispheres, separated by a deep sagittal cleavage, the longitudinal fissure. Both hemispheres present on their surface a landscape of hills and valleys (**Fig. 2**). The bumps and grooves, respectively called gyri and sulci, are quite constant from one individual to another. Therefore, they can serve as landmarks to those who study the brain like standard universal pictograms can help tourists find their way when visiting a new city.

Based on these superficial landmarks, four areas of unequal size conventionally divide each hemisphere: the frontal, the parietal, the occipital and the temporal lobes, named according to the overlying skull bones. Prominent sulci often define lobar boundaries (**Fig. 2**); for example, the lateral sulcus separates the frontal lobe from the temporal lobes, whereas the central sulcus is the demarcation between the frontal and the parietal lobes. Moreover, fifth and sixth lobes are sometimes considered and correspond to the insular lobe, hidden within the depths of the lateral sulcus, and the limbic lobe, which is on the medial side of each hemisphere.

The brain is a stratified construction. Its outer layer, called the cerebral cortex, is made of gray matter, whose gray color reflects the collection of cell bodies gathered in it. This thin folded mantle of gray matter gives the human brain its typical convoluted aspect; the folds materialize on the cerebral surface in the landscape of gyri and sulci. This gray coat is uneven: it is 4–6 mm thick in a vast portion called the neocortex, but it can get down to 2–3 mm in the post-central cortex and areas that form the allocortex (Amunts and Zilles, 2015). Under microscopic inspection, the neocortex is not homogenous; it discloses cytoarchitectural variations. To put this differently, neurons are arranged in various ways in different locations. At least 52 regions with distinctive cytoarchitectures have

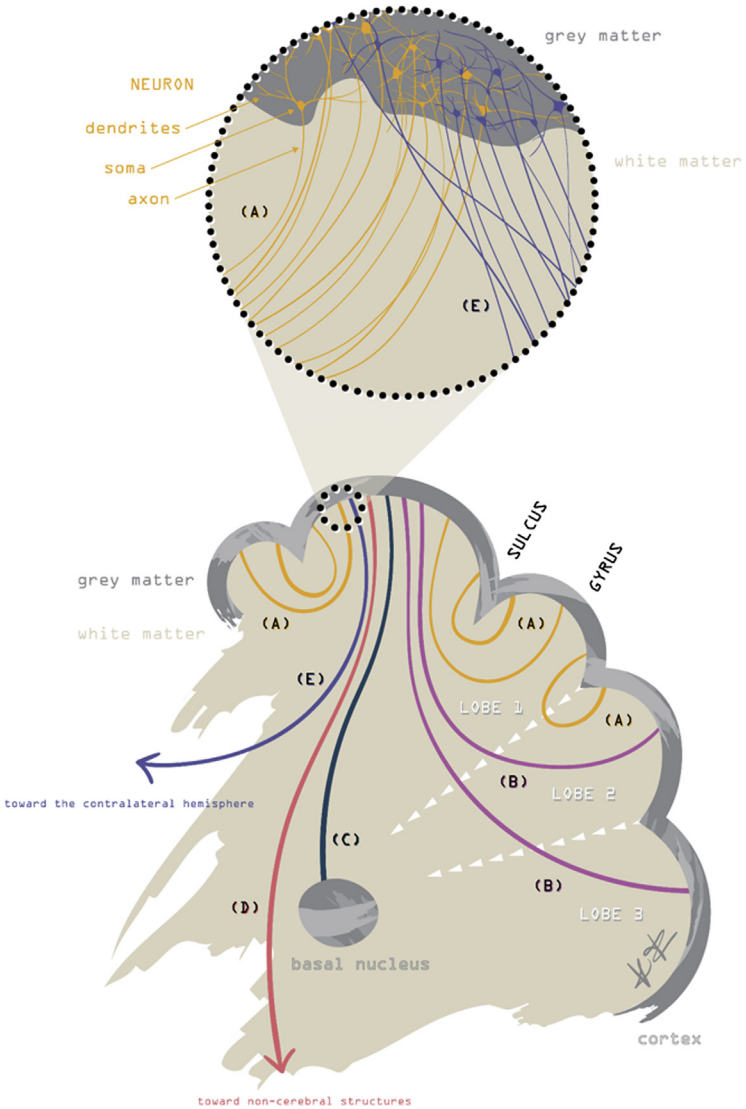

Figure 2 The schematic view of the typical brain white matter layout. The lower part of the figure showcases the typical macroscopic layout of white matter fibres in the human brain. They are presented on a symbolic slice that could be perceived as coronal, sagittal or axial; this is because the typical layout presented in the figure can be found anywhere in the brain independently from any chosen view or orientation. The five most common types of fibres are displayed with at least one termination in the superficial layer of cerebral grey matter (i.e., the cortex) so as to illustrate the basic principles of white matter organisation. White matter connections are layered according to the distance between their termination areas (Forkel et al., 2014). The more superficially a white matter fibre runs, the closer the grey matter areas it connects. The vast majority of white matter fibres in the human brain are superficial and connect adjacent cortical areas in the same hemisphere. These are called short U-shaped fibres (A). Indeed, the most superficial layer of white matter is made of the shortest fibres and has either an intra- or inter-lobar course in a shape similar to the letter "U". Right below, some longer inter-lobar fibres run: the association fibres (B). The most superficial of these fibres connect adjacent lobes of the same hemisphere. The deeper they go, the more distant are the lobes they link, but they are still in the same hemisphere. Deeper than the association fibres run the projection fibres, connecting cortical areas to either basal nuclei (C) or structures outside the cerebrum, for example, the spinal cord (D). The deepest fibres are the commissural ones (E). Unlike the previously described populations of fibres, they link analogous regions of two brain hemispheres. The upper part of the image is an up-close view of the superficial area circled by a dotted line on the slice below. It highlights the fact that macroscopic white matter bundles are made of multiple densely packed axons following a common path. Axonal fibres undergo a fasciculation process during the brain development to form, in an adult brain, the particular layout of white matter bundles presented in this figure. With this close-up view, we highlight in particular how, on a microscopic scale, two populations of axons emerging from the same grey matter area can diverge in two different directions to form two distinct white matter fibres or even tracts ([A] and [E]).

been numbered and mapped on the cortical surface. They are known as Brodmann areas (BA) (Brodmann, 1909), and despite being highly variable across participants (Amunts et al., 1999, 2000), they have proven very helpful in studying brain functions.

Beneath the slender gray-matter mantle, tightly packed axons form a generous inner layer of white matter. The white color occurs due to a distinctive fatty substance, myelin, wrapped around the axons. Myelin acts as an electrical insulator to prevent the loss of

electric charges, similar to a plastic coating on a metallic wire. A very peculiar type of glial cell, known as the oligodendrocyte, produces myelin. With hugging-arm-like elongations, numerous oligodendrocytes encase the entire length of each axon in a myelin sheath (Fig. 1). The myelination not only enables the APs to travel long distances with minimal message fading but also fastens their propagation.

The inside of a brain is mostly made of brain nuclei and white matter.

Brain nuclei, excluding the brainstem and the cerebellum, are classically divided into two classes: basal nuclei and the diencephalon. The basal nuclei are further divided into neo-, paleo- and archistriatum. The neostriatum corresponds to the caudate nucleus that, together with the putamen, receives excitatory inputs from the cortex. The paleostriatum includes the whole of the globus pallidus (medial and lateral), and the archistriatum is the amygdala. The diencephalon consists of the system of nuclei that compose the thalamus and the hypothalamus.

On a macroscopic scale, the white matter of an adult human brain is made of an aggregate of fasciculi (an alternative name for white matter bundles) arranged around the ventricles and a system of subcortical nuclei that are gray matter islands in the depths of each hemisphere.

However, it is not a dull white filling nor tangled myelinated fibers (Steno, 1669). During brain development, neurons grow their axons toward more or less distant candidates for synapse creation. On their way, axons with similar trajectories gather up and, when they are many, they form bundles of white matter. Getting closer to their destination, they unbundle, diverge and spread over the targeted territory. This process called fasciculation (Hau, 2015) creates, by grouping parallel axonal fibers, a connectome accessible to naked-eye inspection.

Tracts are divided into three categories: commissural, projection and associative fibers (Meynert, 1885). These three systems can be further divided in fasciculi that baer a name reminiscent of their shape (e.g., arcuate fasciculus), their location and trajectory (e.g., superior longitudinal fasciculus) or their projection (e.g., corticostriatal tract). Note that the short fibers that connect neighboring gyri are sometimes called U-shaped fibers.

Commissural tracts connect both hemispheres. They include the corpus callosum that was the first discovered due to its evident disposition (Vesalius, 1555). The corpus callosum is the most prominent white-matter connection of the brain. It links the two hemispheres and is visible after trepanation when looking between the two hemispheres. The anatomy of its projections is heterogeneous; however, they preferentially link areas that share a symmetrical, functional organization (Karolis et al., 2019). Commissural tracts are essential for integrating the information processed across the two hemispheres. A typical example is the panoramic vision we have that requires the integration of the left and right visual fields.

Projection tracts connect central structures to the surface of the brain. They habitually link the external environment to the brain. For instance, the corticospinal tract mostly links the motor cortex to the spinal cord, ensuring the transmission of motor commands. Other examples of projection tracts typically include, but are not limited to, the thalamocortical connections, the corticostriatal pathway, the fornix and the optic radiations (that are a particular subgroup of the thalamocortical radiations).

Association tracts connect relatively distant areas within the same hemisphere and are evolutionarily expensive, as they can reach lengths of up to 15 cm in the brain. These tracts allow for the fast transmission of information between areas to ensure the hierarchical or integrative processing of information (Pandya and Yeterian, 1991). Typically, the inferior longitudinal fasciculus is composed of long and short fibers (Catani et al., 2003) that ensure the progressive and hierarchical processing of visual information along the ventral visual stream, or the "what" stream (Mishkin et al., 1983). Similarly, the superior longitudinal fasciculus connects the frontal and parietal areas, whose interactions are necessary to produce awareness of the external world (Thiebaut de Schotten et al., 2005, 2011; Bartolomeo, 2007, 2014) and our own bodies (Pacella et al., 2019). Other examples of association tracts include – but are not limited to – the arcuate fasciculus, the uncinate fasciculus and the inferior fronto-occipital tract. Analogous to Brodmann's parcellation of cortical gray matter, mapping the fascicles that form its underlying white matter can prove greatly advantageous to those who study the brain. Indeed, when starting a scientific study on any tangible object of interest, it is best to know its three-dimensional structure beforehand.

Conclusion

In solving our brain's mysteries, "getting to know your way around the brain is like getting to know your way around a city" (Bear et al., 2007). If the microscopic neuronal network resembles a city subway plan with railways, stations and interchanges, at the scale of the entire brain, the macroscopic connectome reminds us more of a world ship map with sea lanes, seaports and transit hubs. Gray matter areas are like continents, and information can navigate through the white matter sea along channels of packed axons. Therefore, we would like to suggest that future investigators avoid exploring the brain without a good map or excellent knowledge of brain anatomy in order not to get lost on the road.

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