An introduction to human brain anatomy

Forstmann, B.U.; Keuken, M.C.; Alkemade, A.

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Chapter 4
An Introduction to Human Brain Anatomy

Birte U. Forstmann, Max C. Keuken and Anneke Alkemade

If you want to understand function, study structure.
(Swaab [75])

Abstract This tutorial chapter provides an overview of the human brain anatomy. Knowledge of brain anatomy is fundamental to our understanding of cognitive processes in health and disease; moreover, anatomical constraints are vital for neurocomputational models and can be important for psychological theorizing as well. The main challenge in understanding brain anatomy is to integrate the different levels of description ranging from molecules to macroscopic brain networks. This chapter contains three main sections. The first section provides a brief introduction to the neuroanatomical nomenclature. The second section provides an introduction to the different levels of brain anatomy and describes commonly used atlases for the visualization of functional imaging data. The third section provides a concrete example of how human brain structure relates to performance.

4.1 Introduction

The human brain is the most complex and fascinating organ of the human body. Over centuries, it has been studied by philosophers, physicians, anatomists, biologists, engineers, psychologists, and in recent times also by neuroscientists. In the Middle ages, anatomical training played a central role in medical education and knowledge of human anatomy was highly valued [60]. However, during early years of the last century and the rapidly developing field of empirical psychology, knowledge of brain anatomy was considered insufficient to understand cognitive functioning. For

B. U. Forstmann (✉) · M. C. Keuken · A. Alkemade
University of Amsterdam, Cognitive Science Center Amsterdam,
Nieuwe Achtergracht 129, 1018 Amsterdam, The Netherlands
e-mail: buforstmann@gmail.com

M. C. Keuken
e-mail: mckeuken@gmail.com

A. Alkemade
e-mail: jmalkemade@gmail.com

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many, brain anatomy became largely irrelevant to the development of psychological models of function and dysfunction [14, 15]. This position was stated succinctly by the American philosopher and cognitive scientist Jerry Fodor: '. . . if the mind happens in space at all, it happens somewhere north of the neck. What exactly turns on knowing how far north?' [16, 32].

In the last decade the advent of ultra-high field 7 Tesla (T) or higher magnetic resonance imaging (MRI) holds the promise to reinstate anatomy to its former important position. In vivo structural and functional brain measurements on the sub-millimeter scale allow researchers to zoom in on fine-grained features such as the layering of cortex [4, 28, 37, 39, 51, 85] and very small nuclei in the subcortex [1, 34, 47] without having to lift the skull. Interest in this new technology is rapidly growing and to date more than 50 ultra-high field MRI scanners are available for human brain research worldwide. However, the importance of studying anatomy with 'expensive' neuroimaging techniques continues to be criticized. Neurosceptics rightly highlight the deficiencies of implausible and theoretically uninspiring research findings (e.g., http://blogs.discovermagazine.com/neuroskeptic/) and one may wonder whether much knowledge has recently been added to the work of the great neuroanatomists of the past centuries.

Recent developments in neuroimaging have provided a powerful tool to the field of the neurosciences, which appears to have regained some of brain anatomy's popularity in neuroscientific research. Traditional postmortem neuroanatomical studies are being replaced, at least partially, by advanced non-invasive techniques that now allow one to study larger numbers, and more importantly, brains of healthy individuals. In its modern form, anatomical studies will continue to contribute to our understanding of brain anatomy and function.

In this chapter, we first provide a brief introduction to the nomenclature of neuroanatomy because it is all too easy to get lost in localization [20]. Next, we introduce descriptive, sectional, and connectional neuroantomy and list grey and white matter atlases that are widely applied to study systematically brain structure. Finally, a concrete example about function-structure relationships zooming in on individual differences will be presented.

4.2 Nomenclature

Nomenclature is a normalized system of exactly defined terms arranged according to specific classification principles and is essential in the field of anatomy [76]. The origins of the anatomical terminology date back to classical Greek and Roman antiquity over 2500 years ago, and explain the current use of Greek and Latin spelling. Due to the early development of terminology and nomenclature, anatomy is considered to be one of the first exact medical fields [42].

The official anatomical nomenclature that is currently used is in Latin and was created by the Federative Committee on Anatomical Terminology (FCAT) and approved by the International Federation of Associations of Anatomists (IFAA). It was

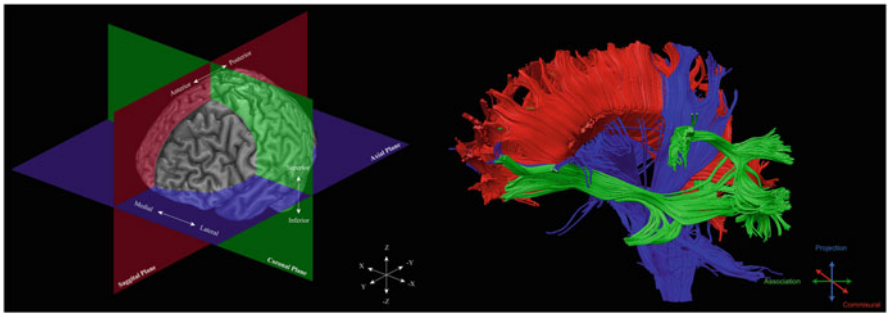


Fig. 4.1 (**a**) Conventions in anatomical terminology; The sagittal plane (*red*) divides the brain in a *left* and *right* part, the axial or transverse plane (*blue*) divides the brain in inferior and superior parts, and the coronal or frontal plane (*green*) is the vertical plane perpendicular to the sagittal plane. (**b**) Connectional neuroanatomy. The corpus callosum and anterior commissure represent the main commissural tracts connecting the *left* and *right* hemisphere (*red*). The associative pathways (*green*) connect specific cortical areas within a hemisphere (*ipsilateral connections*). The ascending and descending projection pathways connect cortical and subcortical structures (*blue*)

published a year later as the Terminologia Anatomica (TA); [30]. Since Latin is taught increasingly less in high schools [17], the TA has been translated in several different languages including English, Spanish, Russian, and Japanese.

Another commonly used way of describing the brain is by differentiating between *descriptive*, *sectional*, and *connectional* aspects of neuroanatomy (see also [16]).

Descriptive neuroanatomy of the nervous system can be defined as the process of identifying and labeling different parts of the brain and spinal cord [16]. The brain can be described from its surface including different views. The surface of the brain can be viewed from above (axial view), from the front (anterior or coronal view), the back (posterior or coronal view), as well as from the side (lateral or sagittal view; Fig. 4.1a). The same terminology is used to indicate different regions of the brain surface (e.g., superior frontal gyrus, Fig. 4.2). The terms distal, proximal, bilateral, unilateral, ipsilateral, and contralateral are used to indicate the location of an area relative to another area. In the following we provide some examples to clarify these terms. Place a finger in your elbow cavity and do the following: Move your finger towards your wrist. This movement is in *distal* direction compared to your elbow cavity. If you move your finger back to the elbow cavity then this movement is in *proximal* direction.

The term *bilateral* indicates that a brain area is represented in both hemispheres. The term *unilateral* refers to only one hemisphere. A well-known example for a unilateral representation is Broca's area, an area essential for language [23, 49]. In the majority of people this area is located in the left hemisphere.

Finally, consider a plane that cuts your body symmetrically into a left and right part. Any connection between two regions that remains on one side is called *ipsilateral*. If the connection crosses from the left to the right side or vice versa, this is called *contralateral*.

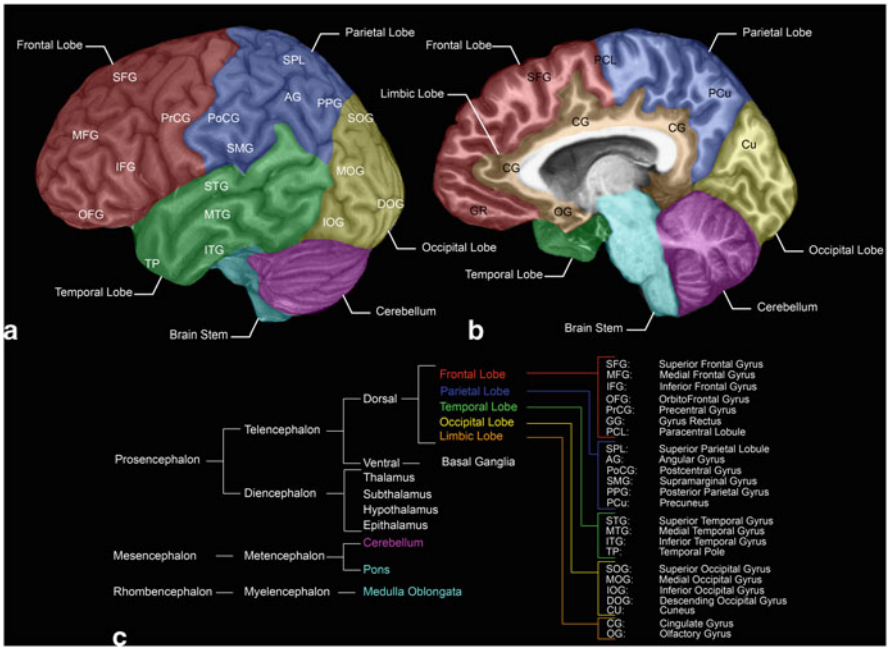


Fig. 4.2 Sectional anatomy. Cortical subdivisions (**a**) *lateral* view (**b**) *medial* view (**c**) brain ontogeny

Sectional neuroanatomy describes the relationship between cortical and subcortical structures, most commonly visualized along orthogonal axial, coronal, and sagittal planes (Fig. 4.1a). Axial planes divide the brain into an upper and lower part. In radiological convention, the axial slices are viewed from the feet upwards to the head. Consequently, on axial slices the left side of the brain is on the right side of the page, whereas in the neurological convention this mapping is inverted. Axial planes are also sometimes indicated as horizontal or transverse planes. To allow generalization and comparison of results, brains in neuroimaging studies are often displayed within a space of reference (e.g., [53, 54, 78] see also the section about grey and white matter atlases). The axial coordinates move in the Z-direction (negative values indicate slices inferior to the anterior commissure, while positive values indicate slices superior to the anterior commissure; Fig. 4.1a).

Coronal planes cut through the brain in the anterior to posterior direction. The coronal planes are conventionally oriented with the left side of the brain on the right side of the page (radiological convention). Slices anterior to the anterior commissure are indicated with positive values on the Y-axis. Finally, the midsagittal plane divides the brain into two hemispheres. Parasagittal slices through the left hemisphere are indicated by negative values on the X-axis.

Connectional neuroanatomy delineates the origin, course, and termination of connecting pathways. Post-mortem dissections of white matter tracts, i.e., the paler tissue of the brain and spinal cord, require special preparation and are particularly difficult

to perform. Recent developments in diffusion MRI tractography have revitalized the field. The tracts are classified according to their course and terminal projections (Fig. 4.1b). So-called commissural pathways run along a horizontal axis and connect the two hemispheres. The majority of projection pathways follow a vertical course along a dorso-ventral (descending) or ventro-dorsal (ascending) axis and connect the cerebral cortex to subcortical nuclei, cerebellum, and the spinal cord. Association tracts run longitudinally along an anterior-posterior axis from front to back and vice versa and connect cortical areas within the same hemisphere.

4.3 Different Levels of Brain Anatomy

For more than five centuries, the nervous system has been divided into grey matter and white matter [82]. Grey matter contains cell bodies, neuronal extensions including axons and dendrites as well as synapses between extensions, glia, and blood vessels (cf. [77]). Grey matter compartments consist of relatively low numbers of cell bodies and are composed of mostly unmyelinated axons, dendrites, and glia cell processes which together form a synaptically dense region which is called the neuropil (cf. [63]). White matter is indicated as such due to its white appearance as a result of mainly myelinated axons, although it also contains unmyelinated axons. White matter is used as a generic term for nervous system volumes where axons predominate connecting grey matter regions. It can also include neurons when it is in close proximity to grey matter [63, 72].

In this section we will describe in more detail sectional neuroanatomy including grey matter regions such as the cerebral cortex and the basal ganglia. Next connectional anatomy will be discussed including white matter compartments and pathways.

4.3.1 Sectional Anatomy

Sectioning of the brain in three orthogonal planes allows us to investigate anatomical structures located deep inside the brain. Deep brain structures include the ventricular system, deep grey nuclei, and a number of white and grey matter structures. The ventricular system is filled with cerebrospinal fluid (CSF) produced by the choroid plexus which provides a highly protective bath with great buffering capacity in which the brain is immersed. The ventricular system consists of a number of brain cavities which are interconnected and allow for a CSF flow towards the submeningeal space. The mediobasal part of the brain and the areas bordered by the lateral ventricles are made up by a number of grey matter nuclei. These nuclei are separated by many fiber tracts which form the cerebral white matter. The outer aspect of the cerebral white matter forms the cerebral cortex. Below we will describe the aforementioned structures in more detail.

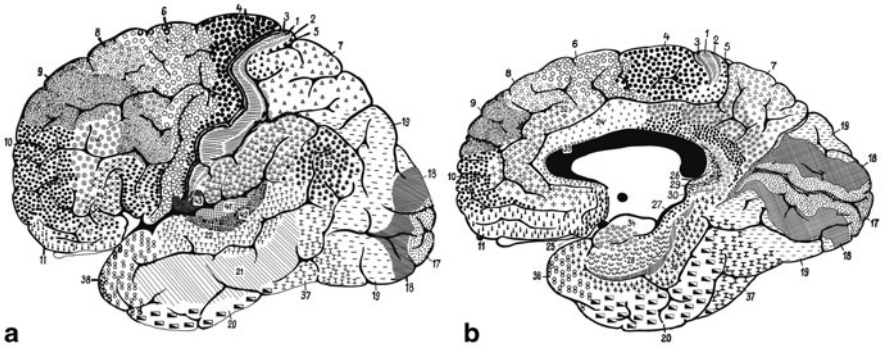


Fig. 4.3 Reproduction of the classical Brodmann map. (**a**) *lateral* view, (**b**) *medial* view. Individual numbers indicate Brodmann area numbers

4.3.1.1 Cerebral Cortex

The outer surface of the cerebral hemispheres is called cerebral cortex which consists of a densely folded strip of grey matter. The cerebral cortex displays a multi-layered organizational pattern. The architecture of the cortical layers varies across the brain. The majority of the cortex is six-layered (neocortex), and can be further parcellated in distinct areas or fields. The cytoarchitecture reveals variations in cell shape, size, and density; characteristics which are used as anatomical landmarks to divide the cortex into distinct areas.

According to the work of individual groups and authors, the number of areas that are distinguished varies from a minimum of 17 [13] to a maximum of 107 [26]. The most widely used maps are provided by Brodmann [9] (Fig. 4.3) and his original atlas contained 52 areas.

According to Brodmann's classification, the frontal lobe consists of eleven fields, which are grouped in five main regions. (1) Area 4 corresponds to the primary motor cortex, containing neuronal bodies, as well as cortico-spinal projection fibers which show a somatotopical organization; (2) Area six contains the premotor region and is subdivided into the lateral premotor cortex (PMC), and the pre-supplementary motor area (pre-SMA); (3) Area 44 and 45 correspond to Broca's area; (4) Area 8–10, and 46 include dorsolateral prefrontal areas, and 47 to the ventrolateral prefrontal corex; (5). Finally, areas 11 and 47 represent the main parts of the orbitofrontal cortex.

The parietal lobe is divided into four regions consisting of a total of nine separate fields by Brodmann. (1) Areas 1–3 correspond to the somatosensory cortex and its cytoarchitecture strongly resembles that of the primary motor cortex; (2) The more laterally located areas 5 and 7 together form the superior polymodal parietal cortex; (3) Areas 39 and 40 are located in the inferior polymodal parietal cortex, corresponding to the Geschwind's territory; (4) The medial parts of areas 31, 5, and 7 form the precuneus, and area 43 is considered a transition region of the fronto-parietal operculum.

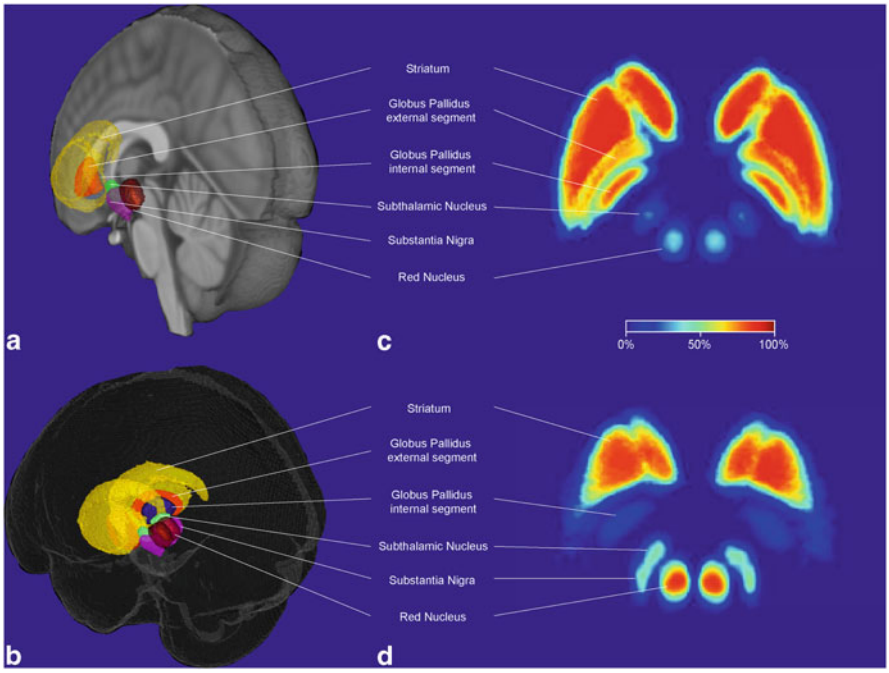


Fig. 4.4 Probabilistic Basal Ganglia atlas. (**a**) Probability maps for the striatum, globus pallidus external segment, globus pallidus internal segment, subthalamic nucleus, substantia nigra, and *red* nucleus of the *left* hemisphere. (**b**) Bilateral representation. (**c**) Axial presentation, level of the globus pallidus. The color intensity reflects the percentage overlap across the 30 participants. (**d**) Axial presentation, level of the *red* nucleus. The color intensity reflects the percentage overlap across the 30 participants. (adapted from [46])

The temporal lobe is also divided into four main regions consisting of seven separate fields. (1) Area 41 is the primary auditory cortex; (2) Adjacent is the auditory association cortex consisting of area 42 and 22, which in part overlays with Wernicke's area; (3) The temporal visual association cortex is formed by areas 20, 21, and 37; (4) Finally, area 38, one of the paralimbic areas, occupies the temporopolar cortex.

The occipital lobe consists of three areas (17–19). The primary visual cortex corresponds to area 17, and area 18 and 19 form the visual association cortex.

The limbic lobe includes as much as 15 fields. Areas 11, 24, 25, 32, 33, 36, and 47 form an olfactocentric group and areas 23, 26–31 form a hippocampocentric group. Additionally, many white matter tracts are present in the cerebral cortex with two main orientations: tangential and radial. Further myeloarchitectonic subdivision within the cerebral cortex reveals over 200 additional areas [84].

Basal Ganglia The basal ganglia are located deep in the white matter of the cerebral hemispheres anterior to the thalamus positioned medial to the lateral ventricles (Fig. 4.4). They consist of two major functional divisions, the striatum and, more medially located, the globus pallidus. The striatum in turn is composed of two highly interconnected masses, the putamen and caudate nucleus.

The caudate nucleus shows a somewhat elongated shape with a large anterior head, which becomes more narrow towards the thalamus and continues to narrow down and forward towards the temporal lobe along the wall of the lateral ventricle. Towards the antero-ventral part of putamen, distinguishing between the caudate nucleus and putamen around the inferior border of the internal capsule is difficult.

The globus pallidus is further divided into an external and internal segment. The putamen and globus pallidus together form the lentiform nucleus and are located lateral to the internal capsule. Finally, two areas that are functionally but not ontologically considered to be part of the basal ganglia are the subthalamic nucleus (STN) and the substantia nigra. The STN forms a small lens-shaped nucleus, which is high in iron content and a main target region for deep-brain stimulation for the treatment of refractory movement disorders, e.g., Parkinson's disease, and is located adjacent in anterior and lateral direction of the substantia nigra. The substantia nigra is a crescent shaped region that is one of the production sites of the neurotransmitter dopamine and the degeneration of this nucleus is a main hallmark of Parkinson's disease. The substantia nigra is named after its pigmented, melanin containing neurons, which allows it to be clearly distinguished in histological sections.

4.3.1.2 Cerebellum

The cerebellum, or "little brain", is located inferior of the occipital lobe and posterior to the brain stem. The functions of the cerebellum range from maintaining balance, coordination of half automatic movements to cognitive functions such as attention, language, and working memory [6, 38, 73]. Similar to the cerebrum, the cerebellum is distributed across the two hemispheres, which are connected through the vermis. Each hemisphere has three lobes: the anterior, posterior, and flocculonodular lobe. The cerebellum is connected to the brain stem via three peduncles namely the superior cerebellar peduncle, the middle cerebellar peduncle, and the inferior cerebellar peduncle connecting respectively to the midbrain, pons, and medulla oblongata. While the cerebellum occupies only 10 % of the total volume of the entire human brain, it contains many more neurons than the rest of the brain combined, such that for each neuron in the cerebral cortex there are on average 3.6 neurons in the cerebellum [40, 43].

4.3.2 Connectional Neuroanatomy

White matter tracts can be classified in different groups: tracts in the brainstem and projections, association, and commissural tracts in the cerebral hemispheres. Projection fibers connect cortical and subcortical gray matter, association tracts connect two cortical areas, and commissural tracts connect the brain's hemispheres.

Brain regions are connected by white matter tracts which vary across subjects in terms of their position, extent, and course [12]. Even though the regional pattern of connectivity is largely preserved across individuals and these afferent, i.e., conducting incoming, and efferent, i.e., conducting outgoing, pathways strongly influence

the information processing properties of individual brain regions [61]. Consequently, it is often desirable to understand regional activation patterns in terms of an underlying system of neural regions and their interactions [35, 36]. To this end, advances in diffusion weighted tractography, a technique that allows the measurement of white matter fibers, offer the potential for explicitly relating functional and connectional anatomy. For instance, regional connectivity patterns can be used to reliably identify both cortical [3, 41] and subcortical regions [5, 22, 50] even when these areas lack clear macroanatomical borders. Consequently, by collecting connectivity information along with functional data, it is possible to directly relate structure to function in individuals. The final section of this chapter provides a concrete example relating white matter connectivity to function by zooming in on interindividual differences.

Finally, the *brainstem* consists of five major white matter tracts: the superior, middle, and inferior cerebellar peduncles, the corticospinal tract, and the medial lemniscus.

Projection fibers connect the cortex with distant regions located in the lower parts of the brain and spinal cord. These fibers can be differentiated into two classes: the corticothalamic/thalamocortical fibers (collectively called thalamic radiations) and the long corticofugal (corticoefferent) fibers. The corticofugal fibers include such fibers as the corticopontine, corticoreticular, corticobulbar, and corticospinal tracts. These fibers all penetrate the internal capsule either between the thalamus and the putamen or between the caudate nucleus and the putamen. When approaching the cortex, they fan out forming the corona radiata. The thalamus is known to have reciprocal connections to many areas in cortex.

Association fibers connect different ipsilateral cortical areas and are classified into short and long association fibers. The former connect areas within the same cerebral hemisphere and include the fibers connecting adjacent gyri, so-called U-fibers. The long association fibers connect different lobes, forming prominent fiber bundles. Some of the main association fibers are (1) the superior longitudinal or arcuate fasciculus connecting the frontal, temporal, and parietal lobe; (2) the inferior longitudinal fasciculus connecting the temporal and occipital lobe; (3) the superior fronto-occipital fasciculus, connecting the frontal and parietal lobe; (4) the inferior fronto-occipital fasciculus connecting the orbital cortex to the ventral occipital lobe, and; (5) the uncinate fasciculus connecting the anterior temporal lobe and lateral orbital frontal regions. Three major fibers connecting the limbic system (hippocampus), namely (1) the cingulum connecting the prefrontal, parietal and occipital cortex to the temporal lobe and hippocampus; (2) the stria terminalis connecting the hypothalamus to the amygdala, and; (3) the fornix, which is a projection fiber, connecting the medial temporal lobe to the mamillary bodies and hypothalamus.

Commissural fibers interconnect the two cerebral hemispheres and contain more than 300 million axons [58]. Most of the commissures interconnect homologous cortical areas in roughly mirror-image sites, but a substantial number have heterotopic connections ending in asymmetrical areas. The largest of the commissural fiber tracts is the corpus callosum, which connects the neocortical hemispheres. Inferior to the corpus callosum are two other commissures, namely the anterior and the posterior commissure (AC and PC respectively). The anterior commissure connects the bilateral anterior and ventral temporal lobes. An imaginary line between connecting these

two points, the AC-PC line, is often used for MRI-analyses. See Catani and de Schotten [15] for an in vivo atlas of the projection, association, and commissural fibers.

4.4 Neuroanatomical Atlases

Neuroanatomical atlases are a useful tool because they provide a common reference framework for structural and functional MRI studies. This is important in light of the substantial variability between individual healthy brains [44, 79], even in identical twins [80]. For example, all humans have a transverse gyrus (known as Heschl's gyrus) in the superior temporal lobe that is associated with the primary auditory cortex, but the number and size of these transverse gyri varies across individuals [62, 64]. Similar variability is observed in other cortical regions [2, 19, 59, 65, 66]. The shape and relative locations of subcortical structures also differ between individuals and change with age [24, 47, 48]. The same can be observed for commissural fibers. This variability in brain structure across individuals is of critical importance because it implicates that no two twin brains are identical at a macroscopic level and therefore no single brain can be considered representative of a population. Consequently, any atlas based on a single 'template' brain will necessarily provide limited accuracy. In theory, it may be possible to determine a topological transformation that could morph one brain into precise correspondence with another, although current spatial normalization procedures tend to correct only for gross anatomical variability.

4.4.1 Grey Matter and White Matter Atlases

Prior to the development of MRI scanners, atlases were solely based on the analysis of post-mortem tissue. Classical examples include for instance the work by Brodmann [9]. As described earlier, Brodmann's atlas is based on cyotarchitectonics, i.e., the density and types of cells present in different cortical layers. Other cytoarchitectonic atlases have been published by von Economo and Koskinas [26], Ngowyang [57], Sarkisov and colleagues [69], and Braak [8]. Strikingly, all these atlases vary substantially in the number of areas, the size of the areas, and the exact location of delineated areas. The most recent cytoarchitectonic atlas is provided by Duvernoy which covers both cortical and subcortical brain areas including the brain stem [25].

A different class of atlases is based on the myeloarchitecture, i.e., the distribution of myelinated axons in the brain. The most prominent myeloarchitecture atlases were published by Reil [67, 68], Burdach [11], Smith [71], Flechsig [31], Vogt [83], and Strasburger [74].

Other classes of atlases that are used in the cognitive neurosciences are based on non-human primate data. An example of such an atlas is provided by Schmahmann and Pandya [70] which includes tracer sections. Postmortem sections were analyzed after the in vivo injection with chemical tracers.

4.4.2 Standard Space Atlases

With the advent of MRI, the need for a common reference space increased because a common reference allows the comparison across individuals' functional and structural brain maps. A first attempt at a standard 3D space was developed by Talairach and Tournoux [78] which was based on a single post-mortem brain from a 60-year old woman. This brain template, together with the anatomical labels, provided the opportunity to compare individuals' functional brain maps in a common reference space. However, while this approach was considered state of the art for many years, further progression of the research field now allows for better alternatives. In the beginning of the 1990s, a template was developed which has now become the standard space in MRI research: the Montreal NeuroImaging (MNI) template. Several versions of this template exist with the most recent one including 452 subjects' anatomical MRI scans [29] specifying 142 brain areas. Other MRI atlases are based on macroscopic delineations of cortical and subcortical areas, such as the Harvard-Oxford atlas which includes 96 brain areas and is created based on 37 subjects [21, 52]. Eickhoff and colleagues [27] created an atlas which is based on cytoarchitectonic properties and includes ten ex vivo brains. More recently, specialized atlases partly relying on ultra-high resolution 7 T MRI have been developed including the STN [34, 47] (http://www.nitrc.org/projects/atag), the locus coeruleus [46], and the thalamus [56].

4.5 Structure-Function Relationships

In the final section of this chapter, we will discuss a concrete example how structure-function relationships can be established in a model-based framework. This example focuses on interindividual differences in the speed-accuracy tradeoff (SAT), both in behavior and in structural features of the human brain. The SAT describes a behavioral regularity that explains why the temporal benefits of responding more quickly come at the cost of making more errors. A possible mechanism for the SAT is that the response threshold can be adjusted depending on the strategy. If the response needs to be very accurate, a high response threshold is adopted so that sufficient information can be accumulated. If a speeded response is required, a low response threshold ensures responses that are quick but error-prone.

Non-human primate and human studies have provided handles on how the mechanism of flexibly adjusting response thresholds could be implemented in the human brain (for a review see [7]). Specifically, the anatomical substrate that could subserve the SAT mechanism is the interplay between cortex and the basal ganglia. There are two main pathways that connect the cortex to the basal ganglia namely the cortical-striatal pathway and the cortical-subthalamic pathway. The striatal hypothesis poses that an emphasis on speed promotes excitatory input from cortex to striatum; the increased baseline activation of the striatum acts to decrease the inhibitory control that the output nuclei of the basal ganglia exert over the brain, thereby facilitating faster but possibly premature responses. Alternatively, the STN hypothesis posits

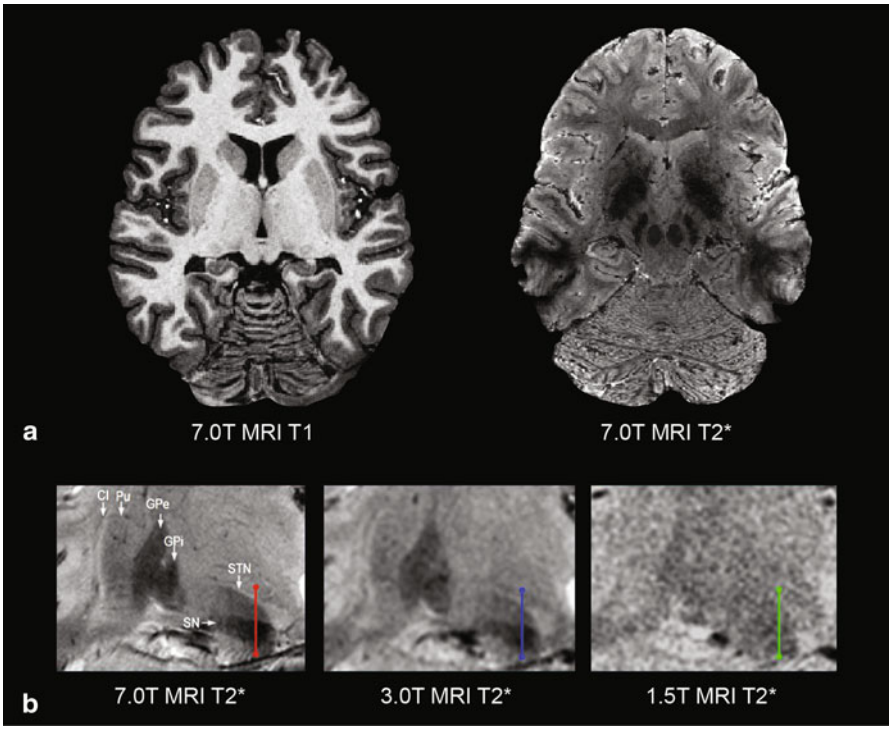


Fig. 4.5 Visualization of the STN with different MRI contrasts at different field strengths. (**a**) The *left* panel shows a 7 T T1 weighted anatomical MRI scan. Note the low contrast in the midbrain. The *right* panel shows a 7 T T2* weighted anatomical scan. Note the improved contrast in the subcortical regions. (**b**) The *lower left* panel shows a 7 T T2* weighted anatomical scan. The use of high field strength yields excellent contrast allowing differentiation between individual subcortical nuclei including the STN and SN. The *middle* panel shows a 3 T T2* weighted anatomical scan and the *lower right* panel shows a 1.5 T T2* weighted anatomical scan for comparison. (adapted from [18])

that an emphasis on accuracy promotes excitatory input from cortex (e.g., anterior cingulate cortex) to the STN; increased STN activity may lead to slower and more accurate choices.

These two hypotheses result in competing anatomical predictions. In particular, the striatal hypothesis predicts that participants who display better control of the SAT have stronger white matter tract connections between cortex and striatum, whereas the STN hypothesis predicts stronger white matter connections between cortex and STN. Testing of these distinct hypotheses has been technically challenging, but a first step has been made by visualization of the STN using 7 T MRI [33, 34, 47]. Since the STN is a very small lens-shaped nucleus in the subcortex, it is barely visible on 3 T anatomical MRI scans (Fig. 4.5). From an anatomical point of view, the technical development of ultra-high resolution MRI has therefore already been proven crucial.

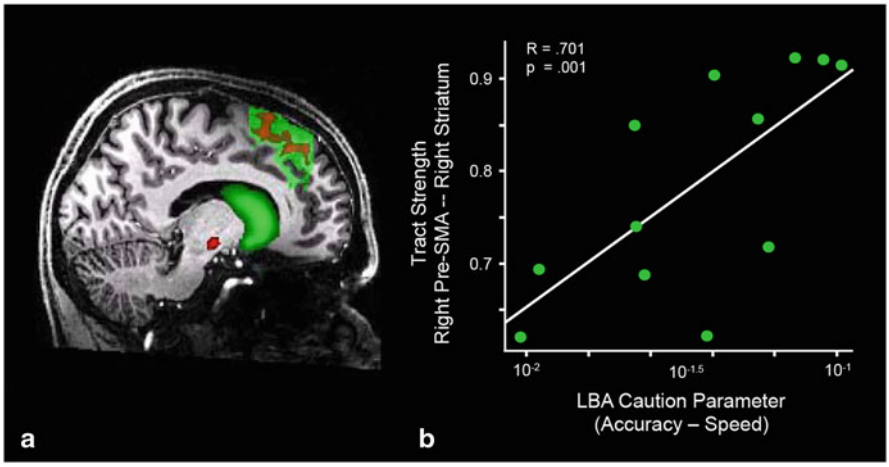


Fig. 4.6 Structural differences in brain connectivity predict individual differences in decision making. (**a**) Connectivity-based seed classification for the pre-SMA projecting into the striatum (*green*) and STN (*red*). (**b**) Individual differences in tract strength between right pre-SMA and right striatum are associated with flexible adjustments of the speed-accuracy tradeoff. (adapted from [33])

The STN contains iron, yielding hypointensities which in turn results in a loss of the MR signal. Moreover, there are large interindividual differences in the STN's location [47]. (Fig. 4.5)

Next, diffusion weighted imaging (DWI) was applied to calculate the tract strength between cortex and striatum and cortex and STN, respectively. Additionally, behavioral data from a moving dots kinematogram with a SAT manipulation was analyzed. The behavioral data were then modeled using the linear ballistic accumulator (LBA) model to account for latent cognitive processes such as individuals' response caution ([10] see also the chapter 1B Cognitive models in action). Statistical model selection techniques confirmed that the LBA explained the data best when only the response caution parameter was free to vary between the speed and the accuracy condition. Interindividual differences in efficacy of changing response caution were quantified by the differences in LBA threshold estimates between both conditions. These differences were then related to participants' tract strength measures between pre-SMA and striatum and pre-SMA and STN, respectively.

Results showed that individual tract strength between pre-SMA and striatum translate to individual differences in the efficacy with which people adjust their response thresholds (Fig. 4.6). This supports the striatal hypothesis of how the brain regulates the competing demands for speed vs. accuracy and show that individual differences in brain connectivity affect decision making even in simple perceptual tasks. The findings also show that, inconsistent with the STN hypothesis of SAT, there is little or no evidence that strong connections from any cortical region to STN lead to more flexibility in threshold settings (see [33] for more details regarding these findings).

Importantly, this research could only be performed using ultra-high resolution 7 T MRI, which allowed accurate localization of the STN.

In sum, this example highlights structure-function relationships as revealed through individual differences in brain connectivity. This approach provides a window to human cognition that exploits individual anatomical variability and complements popular methods such as functional MRI.

4.6 Concluding Comments

In contemporary neuroscience, the anatomy of the central nervous system has essentially become the anatomy of the connections between brain regions. Understanding patterns of connectivity and how neurons communicate is probably one of the next frontiers in the neurosciences [55]. It is important to delineate fine-grained cerebral and subcortical structures using ultra-high resolution MRI [81]. Ultimately, by linking information from large-scale networks with macro- and microanatomical knowledge we can reach a deeper understanding of descriptive, sectional, and connectional neuroanatomy.

Finally, capturing the interindividual variability in the form of probabilistic atlases and maps both from in vivo and postmortem brains holds a great promise. It will facilitate our understanding of functional neuroanatomy including changes associated with development, aging, learning, and disease. Informing mathematical and neurocomputational models of the human brain with the anatomical knowledge gained by using ultra-high resolution MRI promises exciting new avenues of understanding human cognition.

Exercises

Q(1)

Step (1) Imagine a human brain floating in front of you with the eyes pointing towards the cutter.

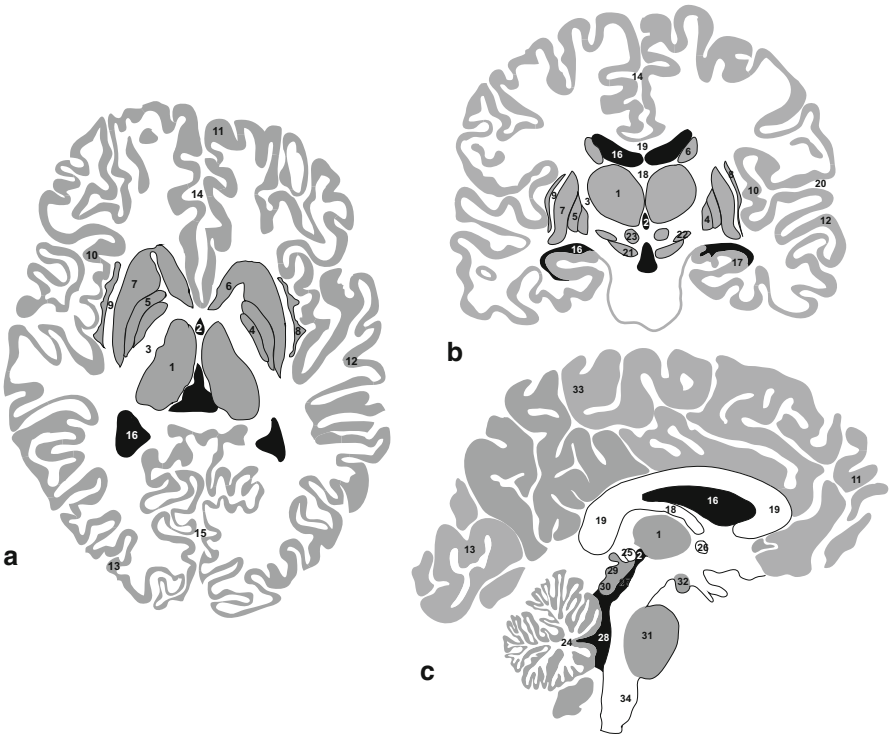
Step (2) Take out your imaginary knife and make the following cuts:

a. Cut the midline.
b. Take the left part and cut it in half again so that you have a superior and inferior part.
c. Take the inferior part and cut it again in half so that you have an anterior and posterior part.

Q1(a) Which two parts did you have after step 2a?
Q1(b) In which part is the cerebellum located after step 2b?
Q1(c) In which of the two parts is the temporal pole located after step 2c?

Q(2)

Q2(a) Which panel shows the brain in an axial view?
Q2(b) Which panel shows the brain in a sagittal view?
Q2(c) Name all the different anatomical structures in the following figure:



Q(3) What is the difference between myeloarchitecture and cytoarchitecture?

Further Reading

1. For a more in depth textbook on anatomy see Catani and de Schotten [16]. *Atlas of human brain connections* (1st ed., pp. 1–515). Oxford University Press.
2. See http://brancusi.usc.edu for an extensive resource for information about neural circuitry.
3. See www.brain-map.org for a large online collection of neuroanatomical atlases, gene expression and cross-species comparisons.
4. See http://www.unifr.ch/ifaa/Public/EntryPage/ViewTAOnLine.html for the anatomical nomenclature.
5. See https://bigbrain.loris.ca/main.php for an ultra-high resolution image of a post-mortem stained brain.
6. See http://www.appliedneuroscience.com/Brodmann.pdf for the English translation of the seminal work by Korbinian Brodmann.

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