## Morphology of Parietal Sulci: Intraparietal Sulcus, Anterior Intermediate Parietal Sulcus of Jensen, and Postcentral Sulcus with its Relation to Somatic Sensory Representations

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#### Abstract

A comprehensive study of the functional organization of the parietal cortex in the human brain requires a clear understanding of the sulcal-gyral morphology and its variability in individual cerebral hemispheres. In the studies presented in this thesis, the Magnetic Resonance Imaging (MRI) technique is used to advance our knowledge of the morphology of several main parietal sulci, namely the postcentral sulcus, the transverse postcentral sulcus, the intraparietal sulcus, and the anterior intermediate parietal sulcus of Jensen (the sulcus of Jensen) by studying the sulci along their entire course in three planes of section: coronal, horizontal and sagittal. This approach provides critical information concerning the association between the end-points of the neighbouring sulci from the surface of the brain to the fundus and subdivision of the major sulci into basic anatomical units for the study of cortical folding patterns. Comparison of the deeply buried features of the postcentral sulcus, the transverse postcentral sulcus, the intraparietal sulcus and the sulcus of Jensen across multiple brains permits determining the features, which are commonly present and those that vary across subjects. The knowledge of such inter-individual variability in sulcal morphology is required for accurate identification of the parietal sulci and establishing the spatial relationships between the sulcal patterns and functional regions of the parietal lobe in individual brains. In this thesis, the details of morphology, variability in morphology and patterns of the postcentral sulcus, the transverse postcentral sulcus, the intraparietal sulcus and the sulcus of Jensen are well-defined in individual subjects with the structural MRI approach. Furthermore, the morphological features of the postcentral sulcus are related to functional regions in the anterior parietal lobe of individual subjects with functional MRI.

The first study of this thesis is a morphological examination of the region of the anterior parietal lobe in a large sample of MRI brain scans. The anterior parietal lobe is composed of the somatosensory cortex on the postcentral gyrus and it is bounded posteriorly by the postcentral sulcus. In this study, the anatomical variability and patterns of the postcentral sulcus are described with respect to its submerged structure (the banks and the fundus) in multiple cerebral hemispheres registered in the Montreal Neurological Institute (MNI) standard stereotaxic space, which is commonly used for reporting functional neuroimaging data. Description of sulcal landmarks in the MNI space is a prerequisite for detailed structure-function studies. The results demonstrate that the postcentral sulcus is a complex of distinct segments, which extend from the medial edge of the hemisphere to the lateral fissure. In certain hemispheres, the postcentral

sulcus merges with a prominent sulcus of the posterior parietal lobe, the intraparietal sulcus, on the surface of the brain, but the sulci are always separated by a small gyral passage in the depth. Another sulcus, the transverse postcentral sulcus, extends in parallel with the postcentral sulcus on the ventral part of the postcentral gyrus. The transverse postcentral sulcus may be considered an inferior part of the postcentral sulcal complex because its presence in the brain coincides with an overall shorter length of the postcentral sulcus and, in some cases, it overlaps with the ventral end of the postcentral sulcus.

The second study examines the intraparietal sulcus and a sulcus closely associated with it, namely the sulcus of Jensen in many MRI brain volumes. The cortex of the intraparietal sulcus is implicated consistently in studies of visual-motor coordinate transformations, visual-spatial attention, and visual guidance of movement in space. However, the current knowledge of interindividual variability in the morphology of the intraparietal sulcus is insufficient to identify the intraparietal sulcus accurately in cerebral hemispheres of individual subjects, which complicates the establishing of consistent structure-function relations in the posterior parietal lobe. The findings demonstrate that, most frequently, the intraparietal sulcus may be divided into two branches, the anterior and posterior rami, by a gyral bridge, submerged or visible from the surface of the brain. The sulcus of Jensen is located close to this gyral bridge between the two rami of the intraparietal sulcus and it forms a number of patterns with the intraparietal sulcus, most frequently occurring as a side-branch of the intraparietal sulcus or a shallow sulcus associated with it. Commonly, the ventral termination of the sulcus of Jensen is located between the first and second caudal branches of the superior temporal sulcus, which terminate in the inferior parietal lobe, but in a small number of hemispheres it may merge superficially with the first caudal branch of the superior temporal sulcus.

The third study applies the morphological findings from the first study to demonstrate a relationship between the structure of the postcentral sulcus and the sensorimotor representations of different body parts in the anterior parietal lobe. In this study, movements of the lower limb (foot and leg), upper limb (arm and hand) and face (eye-blinking, mouth and tongue) produced by subjects in the MR scanner elicited functional changes in activity in the pericentral region and the posterior boundary of functional activity clusters in the postcentral gyrus was related to the position of the distinct segments of the postcentral sulcus on a participant-per-participant basis. The findings demonstrated that the posterior border of the sensorimotor representation of a specific body part was formed by a specific segment of the postcentral sulcus. In addition, the

transverse postcentral sulcus functionally related to the sensorimotor representations of the mouth and tongue on the postcentral gyrus in the hemispheres in which it was present. Thus, the morphology of the anterior parietal lobe relates strongly to the functional sensorimotor activation patterns.

The results of the morphological examination of the parietal cortex in the MNI proportional stereotaxic space, presented in this thesis, may be used to relate specific functional changes in activity obtained in neuroimaging studies to details of sulcal and gyral anatomy in individual subjects. Our experimental findings have already clarified the functional organization of the anterior parietal lobe by establishing a strong relationship between the sensorimotor representations of different parts of the body and the distinct segments of the postcentral sulcus. Furthermore, based on the review of the available literature, possible functional relevance of the anatomical structure of the intraparietal sulcus and the sulcus of Jensen has been discussed and needs to be studied explicitly in individual subjects in future research, as the details of morphology of these parietal sulci have now been provided.

#### Résumé

Une étude approfondie de l'organisation fonctionnelle du cortex pariétal dans le cerveau humain nécessite une claire compréhension de la morphologie des sillons et gyrus et de leur variabilité au niveau des hémisphères cérébraux individuels. Les études présentées dans cette thèse utilisent la technique d'imagerie magnétique par résonance (IRM) à fin de faire avancer notre connaissance de la morphologie des trois principaux sillons pariétaux, le sillon central postérieur, le sillon intrapariétal et le sillon pariétal intermédiaire antérieur de Jensen (le sillon de Jensen) en étudiant le sillon sur la totalité de son parcours dans les trois plans de coupes, frontal, horizontal et sagittal. Cette approche donne d'importantes informations concernant les associations entre les extrémités de sillons voisins, de la surface du cerveau au fond et sur les subdivisions des sillons principaux en unités anatomiques de base pour l'étude des motifs de replis corticaux. La comparaison des caractéristiques profondément enfouis du sillon central postérieur, du sillon interpariétal et du sillon de Jensen sur plusieurs cerveaux permet de déterminer les caractéristiques communément présentes dans ceux-ci ou variant entre sujets. La connaissance d'une telle variabilité interindividuelle dans la morphologie des sillons exige une identification précise du sillon pariétal et l'établissement de relations spatiales entre les motifs du sillon et les régions fonctionnels du lobe pariétal dans les cerveaux individuels. Dans cette thèse, les détails morphologiques, la variabilité de morphologie et les modèles des sillons, central postérieur, interpariétal et de Jensen, sont bien définis dans les sujets individuellement par une approche d'IRM structurelle et liés aux régions fonctionnelles du lobe pariétal antérieur de chaque sujet avec une IRM fonctionnelles.

La première étude de cette thèse est l'examen morphologique de la région du lobe pariétal antérieur sur 40 scanners (IRM) cérébraux. Le lobe pariétal antérieur est composé de cortex somatosensoriel au niveau du gyrus central postérieur et il se termine postérieurement par le sulcus central postérieur. Dans cette étude, la variabilité anatomique et les motifs du sillon central postérieur sont décrits en ce qui concerne sa structure immergée (les berges et le fond), dans de multiples hémisphères cérébraux enregistrés dans l'espace stéréotaxique standard de l'Institut Neurologique de Montréal (MNI) qui est communément utilisé pour analyser des données de neuro-imageries fonctionnelles. La description des points de repères des sillons dans l'espace du MNI est un prérequis pour les études structures-fonctions détaillées. Le résultat montre que le sillon central postérieur est un ensemble de segments différents, qui s'étend du coin médial de l'hémisphère à la fissure latérale. Dans certains hémisphères, le sillon central postérieur se fusionne avec le sillon principal du lobe pariétal postérieur, le sillon intrapariétal, à la surface du cerveau mais les sillons sont toujours séparés dans la profondeur par un petit passage gyral. Un autre sillon, le sillon central postérieur transverse, se prolonge en parallèle avec le sillon central postérieur sur la partie ventrale du gyrus central postérieur. Le sillon central postérieur transverse peut être considéré comme la partie inférieure du complexe sulcal central postérieur car sa présence dans le cerveau coïncide avec une longueur totale plus courte du sillon central postérieur et dans certains cas il chevauche avec la fin de la partie ventrale du sillon central postérieur.

La seconde étude examine le sillon interpariétal et un sillon étroitement associé avec celui-ci, à savoir le sillon de Jensen dans 40 volumes d'IRM cérébrales. Le cortex du sillon intrapariétal, est toujours impliqué dans les études de transformations visuo-motrices de coordonnées et de l'orientation visuelle du mouvement dans l'espace. Cependant, les connaissances actuelles de la variabilité interpersonnelle dans la morphologie du sillon intrapariétal est insuffisante pour identifier le sillon intrapariétal avec précision dans les hémisphères cérébraux des sujets individuels ce qui complique l'établissement de relations cohérentes structure-fonction dans le lobe pariétal postérieur. Les résultats démontrent, le plus souvent, que le sillon intrapariétal peut être divisé en deux branches, la partie antérieure et postérieure du Rami, par un pont gyral, immergé ou visible de la surface du cerveau. Le sillon de Jensen est situé à proximité de ce pont gyral entre les deux branches du sillon intrapariétal et il forme un certain nombre de modèles avec le sillon intrapariétal, survenant le plus fréquemment en tant que branche latérale du sillon intrapariétal ou un sillon peu profond qui lui est associé. Généralement, la terminaison ventrale du sillon de Jensen est située entre la première et seconde branche caudale du sillon temporal supérieur se terminant dans le lobe pariétal inférieur, mais dans un petit nombre d'hémisphères, il peut fusionner superficiellement avec la première branche caudale du sillon temporal supérieur.

La troisième étude applique les conclusions morphologiques de la première étude afin de démontrer une relation entre la structure du sillon central postérieur et les représentations sensori-motrices des différentes parties du corps dans le lobe pariétal antérieure. Dans cette étude, les mouvements des membres inférieurs (pied et jambe), membre supérieur (bras et main) et le visage (le clignement des yeux, les mouvements de la bouche et de la langue) produit par les sujets dans le scanner (IRM), suscitent des changements de l'activité fonctionnelle dans la région centrale et dans la limite postérieure des groupes d'activités fonctionnelles dans le gyrus postérieur sont liées à la position des segments distincts du sillon central postérieur sur une base participant-par-participant. Les résultats ont démontré que le bord postérieur de la représentation sensori-moteur d'une partie spécifique du corps est formé par un segment spécifique du sillon central postérieur. Ainsi, la morphologie du lobe pariétal antérieur est fortement liée aux modèles d'activation de fonctions sensori-motrice.

Les résultats de l'examen morphologique du cortex pariétal dans l'espace stéréotaxique MNI, présentés dans cette thèse, peuvent être utilisés pour relier les changements fonctionnels spécifiques de l'activité obtenus dans les études de neuro-imagerie aux détails de l'anatomie des sillons et circonvolutions chez les sujets individuels. Nos résultats expérimentaux ont déjà clarifié l'organisation fonctionnelle du lobe pariétal antérieur en établissant une relation forte entre les représentations sensori-motrices des différentes parties du corps et les segments distincts du sillon central postérieur. De plus, sur la base de l'examen de la littérature disponible, la possible pertinence fonctionnelle de la structure anatomique du sillon intrapariétal et le sillon de Jensen a été discuté et doit être étudié de manière explicite dans les sujets individuels dans de futures recherches, maintenant que les détails de morphologie de ces sillons pariétaux ont été fournis.

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## **Statement of Originality**

The studies presented in Chapters Two, Three, and Four, provide novel findings about the morphology of the postcentral sulcus, the intraparietal sulcus and the sulcus of Jensen in the parietal lobe of the human brain, and the relation of the postcentral sulcus morphology to the functional organization of sensorimotor representations. These studies have all been prepared in manuscript format and submitted for publication in peer-reviewed journals. The study in Chapter Two has been published in the Journal of Comparative Neurology and the study in Chapter Three has been published in the Proceedings of the Royal Society: Biological Sciences. The study in Chapter Four has been submitted for publication to the European Journal of Neuroscience and is currently under consideration (at the "revise and resubmit" stage).

These studies were also presented at the following international conferences: Annual Meeting of the Canadian Association for Neuroscience, Montreal (2008), Annual Meeting of the Society for Neuroscience, New Orleans (2012), and Annual Meeting of the Canadian Association for Neuroscience, Montreal (2014).

## **Contribution of Authors**

The experiments were designed with Dr. Petrides. I conducted the experiments and carried out the data analysis, and the findings were discussed and interpreted together with Dr. Petrides. The manuscripts were then co-authored with Dr. Petrides.

Dr. Celine Amiez is a co-author in the study presented in Chapter Four. The functional Magnetic Resonance Imaging data used in that study were acquired and processed with Statistical Parametric Mapping software by Dr. Amiez. The experiment was designed together with Dr. Petrides and I performed the individual subject analysis, which involved examination of the morphology of the postcentral sulcal complex and the transverse postcentral sulcus based on the findings of the morphological study presented in Chapter Two, identification of the local functional activity maxima, and relating these functional foci to the morphology of the postcentral sulci.

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## **Chapter One**

#### **1. General Introduction**

The parietal lobe of the human brain is an anatomically complex and functionally heterogeneous region. The somatosensory cortex in the anterior part of the parietal lobe contains an orderly arrangement of representations of different body parts and processes information related to touch, proprioception, pain and temperature (e.g., Penfield and Rasmussen, 1950; Bushnell et al., 1999; Timmermann et al., 2001; Iwamura, 2007; Rolls, 2010; Moulton et al., 2012; Frot et al., 2013). The posterior part of the parietal lobe participates in visual-motor coordinate transformations (e.g., Culham and Valyear, 2006; Vingerhoets, 2014), visual-spatial attentional processing (e.g., Corbetta et al., 1998; Simon et al., 2002; Astafiev et al., 2003; Thiel et al., 2004), perceptual mental rotation and mental transformation (e.g., Alivisatos and Petrides, 1997; Vingerhoets et al., 2002; Mohr et al., 2006; Champod and Petrides, 2007, 2010; Weiss et al., 2009), mathematical operations (e.g., Dehaene et al., 2003; Delazer et al., 2003) and, in the left hemisphere of the brain, in certain aspects of language processing (e.g., Binder et al., 2009; Price, 2010; Segal and Petrides, 2013; Seghier, 2013; Petrides, 2014). Since the development of Positron Emission Tomography (PET) and functional Magnetic Resonance Imaging (fMRI), a large number of studies is conducted each year attempting to understand the functional roles played by different parts of the parietal lobe. In these studies, the location of functional changes in activity is commonly expressed as average coordinates of group data in a standard proportional stereotaxic space (see section 1.2 " Standard proportional stereotaxic space" below), which allows establishing an approximate location of the cortical areas participating in specific cognitive operations and determining the general large-scale functional topography of the parietal region. Unfortunately, due to the fact that the variability in morphology of sulci and gyri remains substantial in the brains registered in a standard stereotaxic space, the distinct functional regions, which are located close to each other in space but differ in function are likely to have similar average stereotaxic coordinates (e.g. Amiez et al., 2006). As a result, the average stereotaxic coordinates fail to discriminate between the adjacent functionally-distinct loci of activity. In contrast, in the brains of individual subjects the location of these functionally-distinct regions can be described with precision with respect to particular aspects of the local sulcal and gyral morphology (Amiez et al., 2006). For instance, a functional change in activity may be described as dorsal or ventral to one sulcus, anterior or posterior to another sulcus, or at the junction between the two sulci. It follows then that a detailed analysis of the morphological

features of the sulci of the cerebral cortex and their patterns formed with the nearby sulci is necessary if detailed relations between morphology and function are to be established (Petrides, 2012). Previous research in our laboratory has uncovered several structure-function relations in the brains of individual subjects, when the sulcal patterns of a particular region were well defined, and it also differentiated between adjacent activity clusters, which could not be distinguished in the average group data (e.g., Amiez et al., 2006; Amiez and Petrides, 2009, 2014; Amiez et al., 2013; Segal and Petrides, 2013). For instance, Amiez et al. (2006) were able to establish the relation of specific parts of the superior precentral sulcus to the frontal eye field and the adjacent premotor hand region because the details of the morphology of the sulci in this region and their variability had been examined (Germann et al., 2005). More recently, Amiez and Petrides (2014) were able to identify in the human brain the three cingulate motor areas and establish their relations to the sulcal patterns in the cingulate region based on a subject-persubject analysis in which the anatomical variability was not treated as noise but rather as critical information to be related to function. This research demonstrated that examination of the sulci and their variability in a given region of the cerebral cortex is indispensable to a proper examination of detailed structure-function relations.

In spite of an abundance of neuroimaging research, there is still a lack of systematic anatomical investigation of the variability of the sulci in the parietal lobe of the human brain. This thesis provides a detailed morphological study of the parietal sulci by examining them in a large sample of MRI brain volumes of neurologically normal subjects. The anatomical findings of this research are used further to establish an important structure-function relationship in the anterior part of the parietal lobe in an fMRI study. In this functional neuroimaging experiment the local sulcal and gyral morphology is related to the somatomotor representations in the anterior parietal cortex of individual subjects. The results suggest that the local morphology of the anterior parietal lobe may predict functional sensorimotor activation patterns in the individual subjects.

The introduction of this thesis provides a brief review of the available literature about the morphology of the parietal lobe, its cytoarchitecture and functional organization. It also draws attention to different features of the postcentral sulcus, intraparietal sulcus and the sulcus of Jensen, as described in the existing anatomical sources, and poses a number of experimental questions which are addressed in the studies reported in Chapters Two, Three and Four of this thesis. The introduction concludes with a brief summary of the studies which comprise the thesis.

# 1.1 Morphology of the main sulci on the lateral surface of the parietal lobe in the human brain

The parietal lobe occupies an intermediate position between the frontal, occipital and temporal lobes (see Figure 1.1). On the lateral surface of the brain it extends from the superior longitudinal fissure medially to the lateral fissure laterally. The central sulcus marks the anterior border and the extension of the parieto-occipital fissure onto the lateral surface of the hemisphere demarcates the posterior border of the parietal lobe. The two most prominent sulci on the lateral aspect of the parietal lobe are the postcentral sulcus and the intraparietal sulcus, which subdivide it into large functional zones. The postcentral sulcus forms a separation between the anterior parietal lobe, involved in somatosensory information processing and the posterior parietal lobe, which performs higher-order integration of somatosensory, motor, visual and auditory information, and spatial information processing for action.

The prominent systematic investigations of the primate brain morphology go back to the 19th century, when the brains of lower primates were compared with the brains of great apes and humans. Relative to the brains of monkeys, which have only one major sulcus in the parietal lobe, namely the intraparietal sulcus, the morphology of the human parietal lobe has been difficult to understand due to an increase in the number of major sulci and their inter-individual variability on the surface of the brain. Initially, the main features of the postcentral and intraparietal sulci, which concern their location, orientation, continuity and patterns with one another, were established by means of visual inspection of these structures on the outer surface of the brain as no specialized technology existed at that time which would allow the systematic study of the human brain anatomy in three-dimensions.

As early as the end of the 19th century it was established that, in the human brain, the postcentral sulcus is a prominent structure, which extends from the superior longitudinal fissure to the lateral fissure and forms the posterior boundary of the postcentral gyrus (e.g. Cunningham, 1892; Duvernoy et al., 1991; Petrides, 2012; see Figure 1.1). The anatomical atlases are not consistent with respect to the number of segments of the postcentral sulcus and illustrate the postcentral sulcus either as a single continuous sulcus (e.g. Smith, 1907; Economo and Koskinas, 1925) or a sulcal complex composed of two to three sulcal segments (e.g. Eberstaller, 1890; Retzius, 1896; Sarkissov et al., 1955). In addition, an association between the postcentral sulcus and the anterior extent of the intraparietal sulcus is described to vary significantly from one individual hemisphere to the next. In some subjects, the two sulci merge on the surface of the

brain (Eberstaller, 1890; Retzius, 1896; Brodmann, 1909; Economo and Koskinas, 1925; Sarkissov et al., 1955; Ono et al., 1990; see Figures 1.2-1.3), while in others, a narrow gyral passage separates the postcentral sulcus from the anterior intraparietal sulcus (Retzius, 1896; Smith, 1907; Ono et al., 1990).

Unlike the postcentral sulcus, which exists as a shallow indentation or a set of dimples in the brain of macaque monkeys, the intraparietal sulcus is a prominent sulcus present in both human and non-human primate species (Petrides, 2012; see Figures 1.1-1.4). In the brain of macaque monkeys, the intraparietal sulcus extends obliquely across the parietal region in a simple manner and it is frequently the only prominent sulcus in the parietal lobe (Brodmann, 1905; Paxinos et al., 2000; see Figure 1.4). The basic primate pattern formed by the intraparietal sulcus in the monkeys becomes more complex in the great apes and reaches its highest complexity in the human brain (Cunningham, 1892).

In the human brain, the intraparietal sulcus is located directly posterior to the postcentral sulcus and it divides the posterior parietal lobe into the superior and inferior parietal lobules. The superior parietal lobule is the cortical region located posterior to the bifurcation of the dorsal end of the superior postcentral sulcus and the callosomarginal (cingulate) sulcus and anterior to the projection of the parieto-occipital fissure onto the lateral surface of the brain (Petrides, 2012; see Figure 1.1). The sulcus of Brissaud, the paroccipital sulcus and the medial ramus of the transverse occipital sulcus form the lateral boundary of the arcus parieto-occipitalis, which surrounds the termination of the parieto-occipital fissure on the medial edge of the hemisphere and the lateral surface (Petrides, 2012; see Figure 1.1). The anterior part of the inferior parietal lobule contains the supramarginal gyrus, which surrounds the ascending termination of the lateral fissure (Economo and Koskinas, 1925; Petrides, 2012; see Figures 1.1, 1.3). The angular gyrus is located posterior to the supramarginal gyrus and it occupies the remainder of the inferior parietal lobule. The angular gyrus abuts the third caudal termination of the superior temporal sulcus (Economo and Koskinas, 1925; Petrides, 2012; see Figures 1.1, 1.3) and surrounds the central (second) caudal termination of the superior temporal sulcus (Segal and Petrides, 2012b). The intraparietal sulcal complex consists of the horizontal segment or the intraparietal sulcus proper located anteriorly and the occipital segment, referred to as either the paroccipital segment of the intraparietal sulcus or the paroccipital sulcus located posteriorly (Petrides, 2012; see Figure 1.1).

Examination of the anatomical sources has produced a number of questions arising from a lack of systematic investigation of the sulci in the posterior parietal lobe. For instance, in anatomical references the intraparietal sulcus is frequently represented diagrammatically as a single continuous horizontally-oriented sulcus (Economo and Koskinas, 1925; Duvernoy et al., 1991; see Figure 1.3). In contrast, observation of parietal lobes of post-mortem and digitized human brain specimen suggests that the intraparietal sulcus may be instead a complex of sulcal segments of varying lengths and orientations, including the vertical orientation (Cunningham, 1892; Retzius, 1896; Connolly, 1950). Interestingly, some anatomical references suggest that the intraparietal sulcus may consist of two segments which have a consistent relationship with one another (Cunningham, 1892).

A poorly known sulcus, the anterior intermediate parietal sulcus of Jensen (Petrides, 2012; see Figure 1.1), also referred to as the sulcus intermedius (Jensen, 1870) or sulcus intermedius primus of Jensen (Economo and Koskinas, 1925; see Figure 1.3) is associated with the intraparietal sulcus in the inferior parietal lobule. The anterior intermediate parietal sulcus of Jensen (Petrides, 2012) is a short sulcus which emerges out of the inferior bank of the intraparietal sulcus and runs for some distance at the posterior edge of the supramarginal gyrus between the first and second caudal branches of the superior temporal sulcus, which invade the inferior parietal lobule (Petrides, 2012; see Figure 1.1). There is no systematic information concerning the relation of the anterior intermediate parietal sulcus of Jensen to the intraparietal sulcus or its various segments. For instance, is the sulcus of Jensen an independent sulcus which merges with the intraparietal sulcus or it is a side-branch of the intraparietal sulcus. Furthermore, lack of information about the relationship between the anterior intermediate parietal sulcus of Jensen and the caudal terminations of the superior temporal sulcus may lead to considerable confusion in its identification. Specifically, when the anterior intermediate parietal sulcus of Jensen approaches the first caudal termination of the superior temporal sulcus and appears to merge with it, it may be classified as a much longer caudal branch of the superior temporal sulcus and not an independent sulcus.

From the onset and almost until the end of the 20th century the study of morphology of the parietal sulci was restricted to the photographic images and/or physical examination of the brain tissue, which provided small access to the interior of the sulci, as every precaution was taken not to damage the valuable post-mortem brain specimen. The number of brains, in which the sulci were opened up significantly to visualize the entire banks and the fundus was, likely,

insufficient to conduct a systematic study. The outer cortical examination could help establish the general features of the sulcal morphology in the parietal region, for instance, the location and orientation of the sulci, but in view of high inter-individual variability it could not help us identify the sulci with confidence and investigate their shape below the cortical surface in detail. The development of magnetic resonance imaging (MRI) technology makes it possible now to visualize the brains of living subjects non-invasively at a high resolution and in a short period of time. In order to advance our understanding of the sulcal morphology and address the questions raised earlier, in all studies, presented in this thesis, a systematic examination of the postcentral, intraparietal and their neighbouring sulci was performed in a series of two-dimensional sections (coronal, horizontal and sagittal) of MRI brain scans of individual subjects and the continuity of the sulci was assessed from different angles along their entire extent. Similar method was successfully used in previous investigations of the precentral (Germann et al., 2005), orbital (Chiavaras et al., 2001), occipital (Iaria et al., 2008), superior temporal (Segal and Petrides, 2012b) and collateral (Huntgeburth and Petrides, 2012) sulcal complexes in our laboratory. This systematic approach allowed addressing the inter-subject variability in morphology of the abovementioned parietal sulci on the surface of the brain and establishing the fundamental sulcal patterns occurring repeatedly in different subjects.

#### **1.2 Standard proportional stereotaxic space**

The purpose of a standardized reference system is to describe the position of different structures and functional activity peaks in any brain. The coordinate space of the Talairach and Tournoux atlas (Talairach et al., 1967; Talairach and Tournoux, 1988) uses two sets of sections (coronal and sagittal) from two cerebral hemispheres of one post-mortem 60-year-old female brain as its reference (Collins, in Petrides, 2012, pp. 11-17). The origin of the coordinate system employed by the Talairach and Tournoux atlas is located on the medial surface of the hemisphere at the dorsal-anterior aspect of the anterior commissure (Talairach and Tournoux, 1988). Three axes, such as medio-lateral, anterior-posterior and dorso-ventral originate in the anterior commissure and provide coordinates for localizing areas of interest in the brain (Talairach et al.,1967; Talairach and Tournoux, 1988). The medio-lateral (left-right) axis is represented by the x coordinate (positive values are anterior to the anterior commissure), and the dorso-ventral (superior-inferior) axis by the z coordinate (positive values are anterior to the anterior commissure), and the dorso-ventral (superior-inferior) axis by the z coordinate (positive values are superior to a line drawn through

the dorsal-anterior aspect of the anterior commissure and the inferior aspect of the posterior commissure; Talairach and Tournoux, 1988). Initially, the boundaries of the Talairach and Tournoux standardized space were established by the smallest box that completely enclosed the post-mortem template brain and the produced brain volume was divided into 12 sub-volumes. In order to match a new subject's brain to the atlas brain, corresponding anterior and posterior commissures needed to be aligned and the sub-volumes were scaled linearly via piecewise linear transformation to approximate the shape and size of the subject's brain to the atlas template (Collins et al., 1994). Currently used automatic techniques have simplified the process of linear transformation of a subject's brain into the Talairach and Tournoux standardized space (for discussion see Collins, in Petrides, 2012, pp. 11-17).

It is important to recognize that anatomical normalization of individual brains to the Talairach and Tournoux template brain has several important limitations. Since the Talairach and Tournoux atlas is based on a single brain of an older subject, it is not representative of a large population of younger subjects who normally participate in neuroimaging research (Collins, in Petrides, 2012, pp. 11-17). In addition, the template based on a specific brain cannot account for the significant variability that exists between shapes and locations of brain structures in different brains. As a result, linear transformation of individual brains cannot match completely the Talairach and Tournoux template brain (Collins, in Petrides, 2012, pp. 11-17). While there is a relatively accurate alignment of deep brain structures with little inter-subject variability close to the anterior and posterior commissures, there is less correspondence for cortical regions located further away from the commissures and the areas that show asymmetry between the hemispheres (Mazziotta et al., 1995). Moreover, a direct comparison between the Talairach and Tournoux brain template and the standard brains transformed into the Talairach and Tournoux stereotaxic space shows that the transformed brains of normal subjects are slightly bigger in size (they are higher, deeper and longer), so that the differences between the corresponding brain structures are expected to get more noticeable as we get from the middle of the brain towards the outside (Penhune et al., 1996).

As the majority of clinical and neuroimaging studies are performed on large populations of subjects, it is important to take into account high inter-individual variability of brain structures when designing the coordinate space (Collins et al., 1994). The Montreal Neurological Institute stereotaxic space (MNI space) is a modification of the Talairach and Tournoux standardized space and it has been developed on the basis of the MRI brain volumetric data of several hundred

young neurologically-normal subjects (for discussion see Collins, in Petrides, 2012, pp. 11-17). The origin of the MNI space is in a vicinity of the anterior commissure and it uses the same principles for defining the medio-lateral (x-axis; positive values in the right hemisphere), anterior-posterior (y-axis; positive values in the anterior direction) and dorso-ventral (z-axis; positive values in the superior direction) axes as the Talairach and Tournoux atlas (Collins, in Petrides, 2012, pp. 11-17).

Throughout the years several models of the MNI space have been created (i.e. these models define the same MNI stereotaxic space), including Average250 T1 model, Average305 T1 model and ICBM152 models, which implemented successive improvements in the MRI technique (Collins, in Petrides, 2012, pp. 11-17). The above-mentioned models represent the average brain anatomy (e.g. average brain size and shape, average position and shape of sulci, gyri and ventricles) of multiple subjects and, hence, can be used successfully as targets for registration of individual MRI brain scans, acquired in the native space, to one standard proportional stereotaxic space. The most recent ICBM152 T1 model is characterized by 1-mm isotropic resolution and an improved cortical definition and level of detail (due to higher gray matter-white matter contrast) compared with the earlier models of the MNI space and there is an improved alignment of cortical features between any normal brain and the ICBM152 template as opposed to the Talairach and Tournoux template (Collins, in Petrides, 2012, pp. 11-17). Furthermore, ICBM152 is a standard MNI template which is currently used by many neuroimaging data analysis programs. The main advantage of the MNI stereotaxic space is that it is representative of the population of brain volumes and, thus, it may be used for precise communication and comparison of specific clinical and experimental data obtained in large populations of subjects (Chiavaras and Petrides, 2000).

Unlike the previous anatomical investigations of the parietal cortical region in postmortem human brain specimen, in the studies presented in this thesis, the postcentral sulcus, the intraparietal sulcus and their patterns with the neighboring sulci were examined in the MRI brain volumes transformed in the MNI proportional stereotaxic space. Hence, the anatomical and functional data acquired in our research are presented in the most commonly used by the neuroimaging community stereotaxic reference system.

#### 1.3 Anterior parietal lobe: somatosensory cortex

On the postcentral gyrus of the primate brain, there is an orderly arrangement of somatic sensory representations of the various parts of the body. Using electrical stimulation during brain surgery in human patients, Penfield and colleagues (Penfield and Boldrey, 1937; Penfield and Rasmussen, 1950) determined the general dorsal to ventral sequence of bodily representations in the postcentral gyrus with the toes and feet lying most dorsally and followed, in a ventral direction, by the legs, trunk, arm, hand, and orofacial region. The classic schematic diagram containing the approximate location, relative size and sequence of body representations in the postcentral gyrus of the human brain is known as the sensory "homunculus" of Penfield and Rasmussen (1950). More recently, this somatosensory topography was confirmed in a large number of neuroimaging studies in which the subjects produced movements of body parts or sensory stimulation was applied to the surface of body regions (e.g., Fink et al., 1997; Nakamura et al., 1998; Boling et al., 2002; McGlone et al., 2002; Nihashi et al., 2002; Iannetti et al., 2003; Fabri et al., 2005; Miyamoto et al., 2006; Nevalainen et al., 2006; Blatow et al., 2007; Huang and Sereno, 2007; Kapreli et al., 2007; Stoeckel et al., 2007; Kopietz et al., 2009; Lin et al., 2010; Sakamoto et al., 2011; Huang et al., 2012).

Microscopic examination of the histological brain sections in primates demonstrated that on the basis of variations in structural neuronal properties (e.g. differences in cell shape, size and density in gray matter lamina), the cortex of the postcentral gyrus could be divided into four cytoarchitectonic regions, 3a, 3b, 1 and 2, occupying specific locations and characterized by distinct patterns of connectivity with other areas of the brain (Vogt and Pandya, 1978; Pons and Kaas, 1986; Morecraft et al., 2004, 2012; Petrides, 2014). In the human brain, area 3a occupies the fundus and the lowermost part of the posterior bank of the central sulcus and it is followed by area 3b in the posterior bank of the central sulcus (Geyer et al., 1997, 1999; Petrides, 2014). Area 1 is located in the anterior part of the crown of the postcentral gyrus (Brodmann, 1909; Geyer et al., 1997, 1999; Petrides, 2014) and area 2 extends from the posterior part of the postcentral gyrus into the anterior bank of the postcentral sulcus in the human brain (Brodmann, 1909; Grefkes et al., 2001; Petrides, 2014). In an observer-independent quantitative cytoarchitectonic study of 10 human post-mortem brains, Grefkes et al. (2001) established that area 2 was always located in the anterior bank of the postcentral sulcus. The anterior border of area 2 could extend as far anterior as the crown of the postcentral gyrus and the posterior border could be found on the posterior bank of the postcentral sulcus when this sulcus was shallow (less than 0.5 cm deep;

Grefkes et al., 2001). Using the observer-independent approach, Caspers et al. (2006, 2008) identified cytoarchitectonic area PFt in the dorsal-anterior part of the supramarginal gyrus, which extends on the posterior bank of the postcentral sulcus and borders area 2 posteriorly in the majority of hemispheres.

Based on the relatively gross electrical stimulation parameters used by Penfield and colleagues (Penfield and Boldrey, 1937; Penfield and Rasmussen, 1950) in the surgical operating room to explore the somatosensory region, it was believed that there was only one somatosensory representation on the postcentral gyrus, which was referred to as SI, namely the primary somatosensory cortex (Penfield and Rasmussen, 1950). However, microstimulation mapping in non-human primates showed that there are four distinct somatosensory representations on the postcentral gyrus that correlate with cytoarchitectonic areas 3a, 3b, 1, and 2 (Whitsel et al., 1971; Merzenich et al., 1978; Kaas et al., 1979; Kaas, 1983). Evidence that these cytoarchitectonic areas contribute to specific aspects of the processing of somatosensory information receives support from their specialized inputs from different types of receptors. Area 3a is activated robustly by the stimulation of deep mechanoreceptors, mainly muscle spindles, during the movements of the foot, leg, arm and hand (Merzenich et al., 1978; Kaas, 1983, 1993; Moore et al., 2000). Areas 3b and 1 receive inputs from the rapidly and slowly adapting cutaneous receptors with some input coming from the deep tissues or proprioceptors (Merzenich et al., 1978; Kaas, 1983). These areas are activated prior to and as part of the movement of different body regions, and they play a role in a movement adjustment by means of feed-forward and feed-back connections (Merzenich et al., 1978; Kaas, 1983, 1993; Moore et al., 2000). Area 2 inputs originate mostly from the deep receptors in joints (Merzenich et al., 1978; Kaas, 1983). A number of recent neuroimaging studies provide evidence that there are several representations of the hand, more specifically the digits and the palm, in the human somatosensory cortex, which could be assigned to different cytoarchitectonic subdivisions in the postcentral gyrus (Gelnar et al., 1998; Kurth et al., 2000; Moore et al., 2000; Blankenburg et al., 2003; Overduin and Servos, 2004; van Westen et al., 2004; Nelson and Chen, 2008). Although there is only some evidence for multiple representations of the other body regions (Miyamoto et al., 2006), the findings nonetheless suggest that similar to the non-human primate, in the human brain, there may be topographically-organized representations of the body regions in each cytoarchitectonic subdivision of the somatosensory cortex, areas 3a, 3b, 1 and 2.

Previously, the location of representations of the different body parts on the postcentral gyrus was expressed with respect to the relative distance from the lateral and superior longitudinal fissures in individual subjects (Penfield and Rasmussen, 1950; Woolsey et al., 1979; Hari et al., 1993), which did not allow performing precise comparisons of these findings between individual brains. In modern functional neuroimaging studies, the location of the sensory representation of each body region is determined by averaging functional activity across multiple subjects in a standard proportional stereotaxic space. However, as the postcentral gyrus demonstrates notable inter-individual variability in morphology in the stereotaxic space, the functional activity of interest is likely to be observed in a somewhat different stereotaxic location in each individual subject (Martuzzi et al., 2014) and, moreover, the activity peaks sharing the same stereotaxic location in different subjects can, instead, be located in different parts of the somatosensory cortex. Thus, the local variability in function cannot be addressed successfully in a group-level analysis and it demands a subject-per-subject examination. Importantly, such subject-per-subject analysis has already provided morphological landmarks for both motor and cognitive processes in different parts of the frontal (Boling et al., 1999; Amiez et al., 2006; Amiez and Petrides, 2009, 2014; Derrfuss et al., 2012; Amiez et al., 2013) and posterior parietal cortex (Segal and Petrides, 2013) and produced precise anatomical-functional targets that are subject specific. Motivated by the detailed findings of the systematic morphological exploration of the postcentral gyrus and the postcentral sulcus in the MNI stereotaxic space, presented in Chapter Two, the relationship between the local sulcal and gyral morphology and somatomotor representations was examined in an fMRI study in the anterior parietal cortex on a participantper-participant basis. This work in presented in Chapter Four of this thesis.

#### **1.4 Posterior parietal lobe**

On the lateral surface of the brain, the posterior parietal region is composed of the superior and inferior parietal lobules. The cortex on the lateral surface of the superior parietal lobule consists of cytoarchitectonic area PE (Economo and Koskinas, 1925; area 7 of Brodmann, 1909; area 7 of Sarkissov et al., 1955; area 7 of Scheperjans et al., 2008a, 2008b; see Figures 1.2, 1.3) with local variants being recognized (Economo and Koskinas, 1925; Scheperjans et al., 2008a, 2008b). Anteriorly, area PE borders dorsal-medial area PA<sub>2</sub> (Economo and Koskinas, 1925; area 5 of Brodmann, 1909; area 75 of Vogt, 1911; area 5L of Scheperjans et al., 2005; see Figures 1.2, 1.3), which follows the marginal branch of the cingulate sulcus (callosomarginal

sulcus) from the medial surface of the brain to the dorsal-posterior part of the postcentral gyrus and the superior parietal lobule (Economo, 2009), and may be located within the dorsal termination of the postcentral sulcus (Scheperjans et al., 2005). The anterior and lateral borders of area PA<sub>2</sub> are with area 2 (Brodmann, 1909; Grefkes et al., 2001; Petrides, 2014; area PD of Economo and Koskinas, 1925; see Figures 1.2, 1.3). According to Economo and Koskinas (1925; see Figure 1.3), the fundus and the banks of the intraparietal sulcus are largely occupied by a regional variant of the superior parietal area, referred to as area PE(D).

The supramarginal gyrus, surrounding the ascending termination of the lateral fissure in the anterior part of the inferior parietal lobule, is occupied by area PF (Economo and Koskinas, 1925; area B of Smith, 1907; area 40 of Brodmann, 1909; area 40 of Sarkissov et al., 1955; area PF of Eidelberg and Galaburda, 1984; see Figures 1.2, 1.3) with local variants (Economo and Koskinas, 1925; Caspers et al., 2006, 2008). Anteriorly, area PF (or its local variant, area PFt, according to Caspers et al., 2006, 2008) borders area 2 (Brodmann, 1909; Grefkes et al., 2001; Petrides, 2014) within the inferior part of the postcentral sulcus. The angular gyrus, enclosing the central caudal branch of the superior temporal sulcus in the posterior part of the inferior parietal lobule, is occupied by area PG (Economo and Koskinas, 1925; area A of Smith, 1907; area 39 of Brodmann, 1909; area 39 of Sarkissov et al., 1955; area PG of Eidelberg and Galaburda, 1984; area PG of Caspers et al., 2006, 2008; see Figures 1.2, 1.3) with local variants being recognized (Economo and Koskinas, 1925; Sarkissov et al., 1955; Caspers et al., 2006, 2008). A transitional cytoarchitectonic area PFm (Economo and Koskinas, 1925; area PFm of Caspers et al., 2006, 2008; area PFG of Eidelberg and Galaburda, 1984; see Figures 1.3) is described at the boundary between the supramarginal and angular gyri.

Insight into the numerous functions of the posterior parietal lobe first comes from case studies of neurological patients presenting with visuospatial and visuoperceptual disorders (Gerstmann, 1940; Critchley, 1953), impaired numerical judgements (Gerstmann, 1940; Benton, 1961; Dehaene and Cohen, 1997), impaired use of everyday tools and objects (Geschwind and Kaplan, 1962; Goldenberg et al., 2003) and language difficulties, including writing and reading (Dejerine, 1892, 1914; Auerbach and Alexander, 1981; Damasio and Geschwind, 1984; Cipolotti et al., 1991; Dronkers and Wilkins, 2004) due to brain tumours and cerebro-vascular accidents or diseases, which disrupt the integrity of the parietal cortex. Unfortunately, the large and variable extent of lesions, including underlying white matter damage, and variability in the pattern of impairments observed in these patients do not let determine the functionally distinct regions that

are critically important for the impaired behavioural and cognitive processes or relate the neuropsychological symptoms to specific anatomical landmarks in the parietal region in a reliable manner. More recently, functional neuroimaging studies have begun to study the functional specialization in the posterior parietal lobe in healthy right-handed subjects and demonstrated that the same cortical regions, e.g. the angular gyrus, contribute to a variety of experimental tasks and cognitive processes. For instance, tasks involving number comparison and calculation (addition, subtraction and multiplication) produce changes in activity in the intraparietal sulcus and the angular gyrus, with the left hemisphere predominance (Dehaene et al., 1999; Pinel et al., 2001; Simon et al., 2002; for review see Dehaene et al., 2003; Nieder and Dehaene, 2009; Seghier, 2013). In addition, in the left hemisphere of the brain of right-handed individuals, the angular gyrus is involved in different aspects of semantic processing, such as comprehension of spoken and written individual words and sentences (Segal and Petrides, 2013; for reviews see Binder et al., 2009; Price, 2010; Seghier, 2013). The process of writing involves the anterior part of the superior parietal lobule in the dominant left hemisphere, which interacts with the angular gyrus when the process of writing is closely preceded by reading (Segal and Petrides, 2012a). In the left hemisphere of the brain, the anterior part of the intraparietal sulcus and the cortex extending into the adjacent supramarginal gyrus, the anterior angular gyrus and the ventral superior parietal lobule are involved in viewing, planning, pantomiming and executing tool gestures, irrespective of the hand used (Johnson-Frey et al., 2005; for review see Lewis, 2006; Creem-Regehr, 2009; Vingerhoets, 2014), as well as naming of tools (Chao and Martin, 2000), viewing of pictures depicting various tools (Valyear et al., 2007; Peeters et al., 2009; Chouinard and Goodale, 2012; Mruczek et al., 2013) and observing the use of tools vs. hand actions (Peeters et al., 2009). The available evidence implicates the superior parietal lobule in visual-motor coordinate transformations necessary for planning and guiding motor behaviour in space, including reaching arm movements, pointing hand movements and saccadic eye movements, as well as visual-spatial attentional processing (for review see Culham and Valyear, 2006; Vingerhoets, 2014).

In the early cytoarchitectonic maps of the human brain and the guenon monkey brain (genus Cercopithecus, i.e. Old World monkeys), created in the beginning of the 20th century, Brodmann (1909, 2006 English translation) raised the issue of inter-species structural homology (see Figures 1.2, 1.4). According to Brodmann, in the anterior part of the parietal lobe, both the monkey and the human contained cytoarchitectonically homologous areas 3, 1 and 2 (Brodmann,

1909, 2006 English translation; see Figures 1.2, 1.4). In contrast, the cytoarchitectonic organization of the posterior parietal cortex of the guenon monkey appeared to be significantly different from that of the human. Specifically, in the cytoarchitectonic map of the human brain, Brodmann (1909) used the term area 7 to refer to the superior parietal lobule and areas 40 (area PF of Economo and Koskinas, 1925) and 39 (area PG of Economo and Koskinas, 1925) to the inferior parietal lobule (see Figure 1.2). In the brain of guenon monkey, however, Brodmann (1909) used the term area 7 to refer both to the caudal superior parietal lobule and the inferior parietal lobule (see Figure 1.4), although he considered area 7 to be an "undifferentiated precursor zone for all parietal areas (apart from area 5)" in the human brain, including areas 40 and 39 (Brodmann, 1909, 2006 English translation, p. 133). Despite the fact that Brodmann warned against drawing absolute homologies on the basis of his initial research (Brodmann, 2006 English translation), the schematic representation of cytoarchitectonic area 7 in the inferior parietal lobule of the monkey led researchers to believe that the monkey does not have the structural and functional homologue of the inferior parietal lobule (the supramarginal and angular gyri) of the human brain. Based on this early conclusion, the behavioural lesion studies in the monkey tested the effect of large posterior parietal cortical lesions (encompassing both the superior and inferior parietal lobules) on learning and retention in somatosensory discrimination tasks (e.g. perception of the shape of objects by palpation with a hand, performed in the dark or out of sight). These findings were not consistent or conclusive with respect to the role of the posterior parietal cortex in tactile discrimination in the monkey (Pribram and Barry, 1956; Wilson, 1957; Ettlinger and Wegener, 1958; Ettlinger and Kalsbeck, 1962; Ridley and Ettlinger, 1975). The possibility that the inferior parietal lobule in the monkey may, in fact, correspond functionally to the inferior parietal lobule in the human brain was addressed by Petrides and Iversen (1979). These investigators studied the effect of lesions restricted to the inferior parietal lobule of the macaque monkey on a visuo-spatial task and showed that, similar to the human brain, the inferior parietal lobule is involved in the analysis of spatial relations (Petrides and Iversen, 1979). The single-cell recording studies of Hyvarinen and Poranen (1974) and Mountcastle et al. (1975) also demonstrated the involvement of the inferior parietal lobule in the monkey in spatial information processing. These pioneering electrophysiology and behavioural lesion studies, which provided early evidence of homology between the inferior parietal lobule of the monkey and the human, were followed by a detailed examination of the anatomical organization of the entire posterior parietal cortex in the monkey (the superior and inferior

parietal lobules) and the patterns of its connectivity (Pandya and Seltzer, 1982; Petrides and Pandya, 1984, 2009; Seltzer and Pandya, 1984, 1986; Neal et al., 1987, 1990; Cavada and Goldman-Rakic, 1989; Andersen et al., 1990; Neal, 1990; Preuss and Goldman-Rakic, 1991; Lewis and Van Essen, 2000a, 2000b; Gregoriou et al., 2006).

The existing comparative anatomical research strongly suggests that the posterior parietal cortex preserves the cytoarchitectonic organization across the primate species, despite its significant expansion in the human brain and substantial inter-species differences in sulcal morphology (for discussion see Petrides and Pandya, 2002; Iacobini, 2006). The main cytoarchitectonic areas of the parietal lobe in the human brain have cytoarchitectonically comparable areas showing a similar topographic arrangement in the macaque monkey brain (for instance, compare Seltzer and Pandya, 1986, with Economo and Koskinas, 1925; Petrides and Pandya, 2002 and unpublished studies; Petrides, 2014), which suggests their similarity in function (Petrides and Iversen, 1979). As a result, well-controlled single-cell recording experiments in monkeys can offer us an insight into the fundamental roles played by the neural precursors of the corresponding cytoarchitectonic areas in the human brain and describe the neural metrophysiological mechanisms involved in spatial operations in the parietal region.

The neuroimaging research is motivated to establish functional homologies between the regions in the monkey and human posterior parietal cortex by employing similar experimental paradigms in the human subjects (for instance, see Bremmer et al., 2001; Koyama et al., 2004). In the macaque monkey, the location of functional regions is usually described with respect to only one principal sulcus of the parietal lobe, the intraparietal sulcus. In contrast, the human parietal lobe has several major sulci and so in order to describe the location of specific functional activity in the human brain with precision, it is necessary to relate the activity clusters to the underlying sulcal and gyral morphology. As discussed above, in many studies location of the functional activity with respect to spatial aspects of movement of the eyes, arm and hand is commonly reported as the group-average coordinates in a standard proportional stereotaxic space. Typically, no relation of the activity peaks to the underlying sulcal anatomy is made in individual subjects and this may be attributed, in part, to substantial variability of the segments of the intraparietal sulcus in a standard proportional stereotaxic space and difficulty in their identification in individual participants. Due to varying methodologies, different neuroimaging studies, which investigate the same functional process of interest (e.g. functional activity of the putative homologue of the lateral intraparietal area LIP), are likely to report somewhat different

average stereotaxic coordinates of the activity foci with non-marginal standard deviations. When such average stereotaxic coordinates acquired in different studies are projected onto the brain of the same subject or a group of subjects, registered in a standard stereotaxic space, they inadvertently point to different anatomical structures. For instance, even a small difference of several millimetres between the average (mean) coordinates in the x-, y- and z-axes would determine if an activity peak is positioned in the postcentral sulcus or the anterior intraparietal sulcus, within the intraparietal sulcus versus the superior or inferior parietal lobules. Thus, in the absence of accurate information about the location of the putative homologues of the macaque monkey areas in the human brain can only remain approximate. As a result, an important issue of homology between the monkey and human posterior parietal regions remains under debate. A brief discussion of several functional areas identified within the intraparietal sulcus of the macaque monkey and their putative homologues in the posterior parietal cortex of the human brain, as proposed in the existing neuroimaging literature, is provided below.

Early knowledge about the neurophysiological mechanisms involved in the spatial guidance of arm, hand and eye movements in the posterior parietal cortex comes from electrophysiology recordings in non-human primates. Following the single-cell recording study of Mountcastle and colleagues (1975) functional organization of the cortex submerged within the intraparietal sulcus was studied thoroughly in a number of fundamental single-cell recording studies, which subdivided it into the anterior, lateral, caudal, ventral and medial intraparietal areas (for review, see Grefkes and Fink, 2005). The anterior intraparietal area (AIP), lateral intraparietal area (LIP) and caudal intraparietal area (CIP) are marked in the lateral bank of the intraparietal sulcus on the basis of electrophysiology recordings and these functional areas succeed each other in the anterior-to-posterior direction (Grefkes and Fink, 2005; Durand et al., 2007; Evangeliou et al., 2009; see Figure 1.4). Area AIP is located directly posterior to the hand region of the somatosensory cortex in the anterior part of the lateral bank of the intraparietal sulcus in the macaque monkey (Gallese et al., 1994; Sakata et al., 1995; Murata et al., 2000) and it is involved in grasping hand movements (Gallese et al., 1994; Sakata et al., 1995; Murata et al., 2000; Baumann et al., 2009). Area AIP contains populations of neurons, which discharge when a monkey fixates its eyes upon a specific object of specific shape, size and axial orientation and/ or manipulates it with the hand (Sakata et al., 1995; Murata et al., 2000). A micro-injection of Muscimol, an agonist of the inhibitory neurotransmitter GABA, into area AIP produces a

temporary impairment in hand preshaping, i.e. forming an appropriate hand configuration for grasping an object (Gallese et al., 1994), which emphasizes a critical role of area AIP in grasping. Grasping deficits are observed in patients who have lesions in the anterior part of the intraparietal sulcus, suggesting that this is a critical region for prehensile action in the human brain (Binkofski et al., 1998). Similarly, a transient disruption of neural activity in the anterior intraparietal sulcus by means of transcranial magnetic stimulation (TMS) disturbs the performance of grasping movements (Tunik et al., 2005; Rice et al., 2006). Functional neuroimaging studies provide additional evidence that the anterior part of the intraparietal sulcus, close to its junction with the postcentral sulcus, is involved in visually-guided grasping and tactile manipulation of objects hidden from sight (Binkofski et al., 1999; Jancke et al., 2001; Culham et al., 2003; Frey et al., 2005; Shikata et al., 2008; Cavina-Pratesi et al., 2010; Jacobs et al., 2010; Marangon et al., 2011; for review, see Culham et al., 2006; Vingerhoets, 2014), suggesting this region to be a putative homologue of the monkey area AIP in the human brain.

Area LIP is situated on the lateral bank of the intraparietal sulcus in the macaque monkey (Andersen et al., 1987; Gnadt and Andersen, 1988; Blatt et al., 1990; Barash et al., 1991a, 1991b; Eskandar and Assad, 2002) and it borders area AIP anteriorly and area CIP posteriorly (Durand et al., 2007; Evangeliou et al., 2009; see Figure 1.4). Neuronal populations in area LIP demonstrate visual-, auditory- and memory-guided saccadic activity related to ongoing and intended eye movements in the preferred direction (Barash et al., 1991a, 1991b; Stricanne et al., 1996). The purpose of saccadic eye movements is to bring a salient stimulus into the fovea (Bremmer, 2011). It has been suggested that area LIP participates in a higher level spatial planning of saccadic eye movements rather than the low level sensory-motor control over the production of these movements (Barash et al., 1991a). Thus, reversible inactivation of area LIP with Muscimol has no influence on the execution of saccades, including their latency and amplitude. but it impairs the selection of appropriate spatial targets (Wardak et al., 2002). Furthermore, neuronal activity in area LIP is enhanced by the behaviourally relevant stimuli suggesting the involvement of this area in visual-spatial attentional processing (Colby et al., 1996; Gottlieb et al., 1998; Bisley and Goldberg, 2003). Functional neuroimaging studies conducted in human subjects implicate the cortical region within the posterior part of the intraparietal sulcus and extending into the superior parietal lobule in the preparation and execution of saccadic eye movements in the pro- and anti-saccade tasks, and also memory- and visually-guided saccade tasks (Corbetta et al., 1998; Connolly et al., 2000; Heide et al., 2001;

Simon et al., 2002; Astafiev et al., 2003; Medendorp et al., 2003, 2005, 2006; Brown et al., 2004; Curtis and Connolly, 2008; Beurze et al., 2009; Hinkley et al., 2009; Jamadar et al., 2013; for review, see Culham et al., 2006; Vandenberghe and Gillebert, 2009). The same cortical region shows a functional change in activity during the covert orientating and re-orienting of visual-spatial attention to peripheral visual stimuli (Corbetta et al., 1998; Simon et al., 2002; Astafiev et al., 2003; Thiel et al., 2004), suggesting a possible link between the preparation of saccadic eye movements and covert shifts of attention (Corbetta et al., 1998; Astafiev et al., 2003). TMS applied to the posterior part of the intraparietal sulcus and the adjacent angular gyrus produces errors in target-accuracy of saccadic eye movements (Vesia et al., 2010). Moreover, reduced accuracy and slower response time on a memory-guided saccade task are demonstrated by the patients with unilateral cortical lesions in the superior angular gyrus and the adjoining areas (Pierrot-Deseilligny et al., 1991), suggesting that the posterior part of the intraparietal sulcus and the neighbouring regions may be homologues to the macaque area LIP.

Area CIP is found posterior to area LIP in the posterior part of the lateral bank of the intraparietal sulcus in the macaque monkey (see Figure 1.4) and its visually responsive neurons are involved in coding orientation of a longitudinal axis and surface features of threedimensional objects in space, such as surface orientation, width and depth (Shikata et al., 1996; Taira et al., 2000; Tsutsui et al., 2001, 2002; for review see Sakata et al., 1998, 2005; Tsutsui et al., 2005). Temporary inactivation of area CIP with Muscimol produces an impairment in surface discrimination of three-dimensional stimuli (Tsutsui et al., 2001). Neural processing in area CIP is likely to contribute to our perception of three-dimensional object structure and be useful during visual skilled hand-object interactions, such as an online adjustment of the hand orientation when grasping an object (Shikata et al., 1996; for review see Sakata et al., 1998). The putative homologue of area CIP in the human brain is located within the posterior part of the intraparietal sulcal complex and it is involved in coding of orientation of the principal axis (Faillenot et al., 2001) and visual discrimination of surface orientation on the basis of texture (Shikata et al., 2001, 2003, 2008).

The ventral intraparietal area (VIP), which is located ventral to area LIP in the fundus and extends slightly into the adjacent banks of the intraparietal sulcus in the macaque monkey (Maunsell & Van Essen, 1983; Colby et al., 1993; see Figure 1.4) is involved in motion processing of visual (Colby et al., 1993), somatosensory (Duhamel et al., 1998), vestibular

(Bremmer et al., 2002b; Schlack et al., 2002; Klam and Graf, 2003) and auditory stimuli (Schlack et al., 2005) mainly in a close within-reach space of the animal ("near-extra-personalspace", p. 818 in Bremmer, 2011). Neurons in area VIP demonstrate preference for the direction of motion of visual, somatic and vestibular stimuli (Bremmer et al., 2002a) and may have smooth pursuit (slow eye movement) related activity (Colby et al., 1993; Schlack et al., 2003), which maintains these motion stimuli in the fovea (Bremmer, 2011). The suggested location of the putative homologue of area VIP in the human brain includes the depth of the anterior intraparietal sulcus and the adjacent superior parietal lobule and the superior branch of the postcentral sulcus (Lewis et al., 2000; Bremmer et al., 2001; Sereno and Huang, 2006; also see Sereno and Huang, 2014). Functional neuroimaging research implicates this cortical region in processing and integration of motion information produced by moving visual, auditory and tactile stimuli close to the subject's face or body (Griffiths et al., 1998; Lewis et al., 2000; Bremmer et al., 2001; Kitada et al., 2003; Sereno and Huang, 2006; for review, see Grefkes and Fink, 2005).

In the macaque monkey, the medial intraparietal area (MIP) is situated postero-medial to area LIP in the medial bank of the intraparietal sulcus (Colby and Duhamel, 1991; see Figure 1.4) and it is a part of the parietal reach region (PRR), which is involved in planning and execution of reaching arm movements (Snyder et al., 1997; Batista et al., 1999; for review see Cohen & Andersen, 2002). Neurons in area MIP demonstrate direction selectivity with respect to movements of the hand (Eskandar & Assad, 1999) and also movements of a behaviourallyrelevant visual stimulus (Eskandar & Assad, 2002), and they discharge prior to and during hand movements (Eskandar & Assad, 1999, 2002). Both the PRR and LIP are proposed to encode locations of sensory targets (e.g. visual, auditory) in the eye-centred frame of reference in order to coordinate efficiently the reaching arm movements with the saccadic eye movements (Batista et al., 1999: Cohen & Andersen, 2000: for review see Cohen & Andersen, 2002). Functional neuroimaging research suggests that the homologue of PRR in the human brain may involve, as in the macaque monkey, the superior parietal lobule, including the adjacent cortex in the intraparietal sulcus and the parieto-occipital fissure (Connolly et al., 2000; Astafiev et al., 2003; Bernier and Grafton, 2010; Beurze et al., 2010; Leoné et al., 2014; for review, see Vesia and Crawford, 2012; Vingerhoets, 2014). Impairements in visually-guided reaching movements are observed in neurological patients with lesions to the posterior superior parietal lobule, the posterior intraparietal sulcus and, less frequently, the posterior inferior parietal lobule (Perenin

and Vighetto, 1988). Vesia and Crawford (2012) suggest that the direction of reaching movements is encoded in the medial posterior intraparietal sulcus and the adjacent angular gyrus, whereas the target of reaching movements is processed by the posterior intraparietal sulcal complex (i.e. the paroccipital sulcus) in the vicinity of the parieto-occipital fissure.

In order to clarify the functional topography in the posterior parietal cortex in the human brain, future neuroimaging studies will need to examine explicitly the detailed relations between the location of the putative homologues of areas AIP, LIP, CIP, VIP and MIP, on the one hand, and the local morphology of the intraparietal sulcal complex at the level of individual subjects, on the other. The goal of the morphological study presented in Chapter Three of this thesis is to provide the foundation for such structure-function studies. Specifically, our investigation aimed to determine the major subdivisions of the intraparietal sulcus and the types of association they form with each other and with the adjacent parietal sulci. This study also clarified the relation between the intraparietal sulcus and the paroccipital sulcus. In the anatomical atlases, the paroccipital sulcus is frequently joined with the intraparietal sulcus and other possible types of association are rarely discussed. Finally, our anatomical study provided a thorough examination of the sulcus of Jensen in the inferior parietal lobe and described the patterns of its association with the subdivisions of the intraparietal sulcus and the caudal branches of the superior temporal sulcus. In future neuroimaging studies, the putative homologues of areas AIP, LIP, CIP, VIP and MIP can be related to various subdivisions of the intraparietal sulcus and the sulcus of Jensen on the basis of information presented in our study.

#### 1.5 Aims and overview

In the parietal lobe of the human brain there are two main sulcal landmarks of high structural and functional importance, the postcentral sulcus and the intraparietal sulcus. The postcentral sulcus separates the anterior parietal lobe involved in processing somatosensory information from the posterior parietal lobe involved with visual-motor and visual-spatial properties. The intraparietal sulcus marks the boundary between two main subdivisions of the posterior parietal cortex, the superior parietal lobule involved in spatial guidance of movement from the inferior parietal lobule implicated in spatial, linguistic, and numeric processing. The anterior intermediate parietal sulcus of Jensen is always joined with the intraparietal sulcus on the surface of the inferior parietal lobule, complicating accurate identification of each sulcus. Both the postcentral sulcus and the intraparietal sulcus are not simple continuous sulci, but
complexes of sulcal branches that require precise identification and description of their patterns. Such critical anatomical information is not yet available for researchers, despite the fact that, at present, it is difficult to find a single neuroimaging study of the parietal lobe which would not attempt to report the findings in relation to the postcentral sulcus or the intraparietal sulcus. Insufficient knowledge about the inter-individual variability in morphology and patterns formed by the postcentral sulcus, intraparietal sulcus and the anterior intermediate parietal sulcus of Jensen in a standard proportional stereotaxic space is a major hurdle in the establishment of precise structure-function relations in the somatosensory and posterior parietal cortical region. The objective of the studies presented in Chapters Two and Three is to provide detailed morphological descriptions of the basic sulcal units (segments or branches) composing the postcentral and intraparietal sulci in the MNI stereotaxic space in order to facilitate their identification in future anatomical and neuroimaging studies. On the basis of the systematic exploration of morphology of the postcentral sulcus, presented in Chapter Two, a strong structure-function relationship between the local variability in morphology of the postcentral sulcus and the subdivisions in the sensorimotor cortex is established in the anterior parietal lobe in Chapter Four.

More specifically, in Chapter Two of this thesis, the postcentral sulcus is investigated systematically in the continuous series of coronal, horizontal and sagittal sections of 80 human cerebral hemispheres scanned with MRI and registered in the MNI standard proportional stereotaxic space. This study identifies the major subdivisions of the postcentral sulcus and provides the stereotaxic coordinates of their endpoints in the MNI space. In addition, it characterizes the patterns formed by the postcentral sulcus with the neighbouring sulci, including the superior longitudinal fissure, lateral fissure, the anterior intraparietal sulcus and the marginal branch of the cingulate sulcus. Lastly, it discusses a previously poorly known sulcus, the transverse postcentral sulcus.

Chapter Three of this thesis provides a detailed exploration of the intraparietal sulcus, paroccipital sulcus and the anterior intermediate parietal sulcus of Jensen in the coronal, horizontal and sagittal sections of the MRI scans of 80 cerebral hemispheres registered in the MNI stereotaxic space. This work describes the main subdivisions of the intraparietal sulcus and their relation to each other and the paroccipital sulcus. Importantly, the patterns of the sulcus of Jensen, which is frequently misidentified in the literature, are described with the superior temporal sulcus and the subdivisions of the intraparietal sulcus.

Chapter Four of this thesis examines the relationship between the structure of the postcentral sulcus and representations of different body parts in the sensorimotor cortex. This study identifies the major subdivisions of the postcentral sulcus in individual subjects and explores whether the location of activation foci recorded on the postcentral gyrus in a functional neuroimaging study in which these subjects produced movements of different body parts relates to the specific subdivisions of the postcentral sulcus.

## **1.6 Figures**



Figure 1.1. Schematic representation of the sulci in the parietal, posterior temporal and occipital lobes on the lateral surface of the human brain. Reproduced from Petrides (2012) with permission. Abbreviations: aipsJ, anterior intermediate parietal sulcus of Jensen; alocs, accessory lateral occipital sulcus; AnG, angular gyrus; aocs-v, anterior occipital sulcus, ventral ramus (ascending limb of the inferior temporal sulcus); aplf, ascending posterior ramus of the lateral fissure; ascs, anterior subcentral sulcus; cs, central sulcus (sulcus of Rolando); csts1, caudal superior temporal sulcus, first segment; csts2, caudal superior temporal sulcus, second segment (angular sulcus); csts3, caudal superior temporal sulcus, third segment (anterior occipital sulcus); dplf, descending posterior ramus of the lateral fissure; eccs, external calcarine sulcus (sulcus calcarinus externus of Cunningham); iocs, inferior occipital sulcus; iprs-p, inferior precentral sulcus, posterior ramus; iprs-s, inferior precentral sulcus, superior ramus; ips, intraparietal

sulcus; ips-po, intraparietal sulcus, paroccipital segment (paroccipital sulcus); lf, lateral fissure; locs, lateral occipital sulcus (prelunate sulcus); lus, lunate sulcus; pips, posterior intermediate parietal sulcus; POA, parieto-occipital arcus (arcus parietooccipitalis, parieto-occipital arch); PoG, postcentral gyrus; pof, parieto-occipital fissure; PrG, precentral gyrus; pscs, posterior subcentral sulcus; sB, sulcus of Brissaud; sfs-p, superior frontal sulcus, posterior segment; SmG, supramarginal gyrus; sms, supramarginal sulcus; spcs, superior postcentral sulcus; SPL, superior parietal lobule; sprs, superior precentral sulcus; sps, superior parietal sulcus; STG, superior temporal gyrus; sts, superior temporal sulcus (parallel sulcus); tocs-l, transverse occipital sulcus, lateral ramus; tocs-m, transverse occipital sulcus, medial ramus.



Figure 1.2. Cytoarchitectonic map of the left hemisphere of the human brain by Brodmann (1909).



Figure 1.3. Cytoarchitectonic map of the left hemisphere of the human brain by Economo and Koskinas (1925).



Figure 1.4. (**a**) Cytoarchitectonic map of the lateral surface of the monkey brain by Brodmann (1905). (**b**) Cytoarchitectonic subdivisions of the superior and inferior parietal lobules in the left hemisphere of one rhesus macaque monkey brain. Reproduced from Figure 1 in Pandya and Seltzer (1982) with permission. (**c**) Approximate position of areas AIP, LIP, CIP on the lateral bank, area VIP in the fundus and area MIP on the medial bank of the opened intraparietal sulcus, schematically represented in red. Abbreviations: AS, arcuate sulcus; CS, central sulcus; IOS, inferior occipital sulcus; IPS, intraparietal sulcus; LF, lateral fissure; LS, lunate sulcus; PS, principal sulcus; STS, superior temporal sulcus.

# **Chapter Two**

# 2. Morphological Patterns of the Postcentral Sulcus in the Human Brain

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## 2.1 Abstract

The morphological structure of the postcentral sulcus and its variability were investigated in 40 structural magnetic resonance images of the human brain registered to the Montreal Neurological Institute (MNI) proportional stereotaxic space. This analysis showed that the postcentral sulcus is not a single sulcus, but rather a complex of sulcal segments separated by gyri which merge its banks at distinct locations. Most of these gyri are submerged deep within the sulcus and can be observed only by examining the depth of the sulcus, although a small proportion may be observed from the surface of the brain. In the majority of the examined cerebral hemispheres (73.75%), the postcentral sulcus is separated into two or three segments, and less frequently into four or five segments (12.5%) or remains continuous (13.75%). Examination of the in-depth relationship between the postcentral sulcus and the intraparietal sulcus revealed that these two sulci may appear to join on the surface of the brain, but they are in fact always separated by a gyrus in the cortical depth. In 32.5% of the examined hemispheres, a dorso-ventrally oriented sulcus, the transverse postcentral sulcus, is located anterior to the postcentral sulcus on the lower part of the postcentral gyrus. Systematic examination of the morphology of the postcentral sulcus in the proportional stereotaxic space which is used in functional neuroimaging studies is the first step towards the establishment of anatomical-functional correlations in the anterior parietal lobe.

#### **2.2 Introduction**

The postcentral gyrus, which forms the anterior part of the parietal lobe, is delimited by the central sulcus, anteriorly, and the postcentral sulcus, posteriorly (Figure 2.1). Pioneer studies using electrical stimulation during brain surgery established that, as in nonhuman primates, the postcentral gyrus of the human brain is the somatosensory cortex and that there is an orderly arrangement of sensory representations of the different parts of the body along its dorsoventral extent (Penfield and Rasmussen, 1952; Woolsey et al., 1979). More recently, the organization of the somatosensory cortex along the postcentral gyrus of the human brain has been examined and confirmed with functional neuroimaging (Nakamura et al., 1998; Boling et al., 1999, 2002; Fabri et al., 2005). The postcentral sulcus, which separates the postcentral gyrus from the posterior parietal cortex, is traditionally described as a prominent sulcus extending from the superior aspect of the hemisphere to the lateral fissure (e.g. Ono et al., 1990; Duvernoy et al., 1991). It is sometimes illustrated as a single continuous sulcus (e.g. Smith, 1907; Economo and Koskinas, 1925) or divided into two or three segments which are superior and inferior to each other (e.g. Eberstaller, 1890; Retzius, 1896; Brodmann, 1909; Sarkissov et al., 1955; Ono et al., 1990). The dorsal end of the postcentral sulcus is often depicted as a V-shaped structure consisting of two branches coming together at one point (Brodmann, 1909; Economo and Koskinas, 1925; Sarkissov et al., 1955). A simple single branch termination of the dorsal postcentral sulcus is less frequently described (Eberstaller, 1890; Smith, 1907; Ono et al., 1990).

Various patterns of how the postcentral sulcus relates to neighbouring sulci have been reported. In some cases, a continuous postcentral sulcus or one of its segments merges with the horizontal intraparietal sulcus (Eberstaller, 1890; Retzius, 1896; Brodmann, 1909; Economo and Koskinas, 1925; Sarkissov et al., 1955; Ono et al., 1990). In other cases, the postcentral sulcus and the intraparietal sulcus appear to be separated by a narrow, often submerged, gyrus (Retzius, 1896; Smith, 1907; Ono et al., 1990). With regard to the cingulate sulcus, when its marginal ramus is visible on the lateral surface of the brain, it is often shown to terminate between the two branches of a bifurcated dorsal end of the postcentral sulcus (Brodmann, 1909; Economo and Koskinas, 1925; Ono et al., 1990).

The existing studies of the morphological variations of the border between the postcentral gyrus (somatosensory cortex) and the posterior superior and inferior parietal lobules, which is formed by the postcentral sulcus, namely the focus of the present investigation, were largely based on visual inspection of the outer cortical surface of post-mortem human brain specimens.

The general features of the sulcal and gyral morphology of this region were established, such as the general location and orientation of the superior and inferior postcentral sulci. However, the limitations of such an approach are evident as shown by the fact that, in a large number of brains, the superior and inferior postcentral sulci may appear to merge superficially with each other and the intraparietal sulcus (i.e. the sulci cannot be differentiated on the outer cortical surface) and yet they may be distinct entities if one were to examine their shape below the surface of the cortex. Similarly, little attention was given in the past to small sulci adjacent to the postcentral sulcus which may have an important role as anatomical/ functional landmarks. Thus, there are limits to how precisely the substantial variability of cortical folding patterns exhibited both between individual human brains and between the two hemispheres of a single brain can be studied with traditional visual inspection. Furthermore, there has been no quantitative examination of these sulci and the patterns they form in a standard stereotaxic space, which is the space within which modern anatomical and functional studies of the human brain are conducted.

The development of neuroimaging technologies at the end of the 20<sup>th</sup> century provided a new effective methodology for the systematic study of the morphology of the gyri and sulci of the human brain. Appropriate neuroimaging software permits the simultaneous examination of an anatomical feature of interest in several two-dimensional planes, such as coronal, sagittal and horizontal, permitting the accurate charting of the depth and continuity of a particular sulcus from different sections at each point along its length (e.g. Germann et al., 2005). It is particularly important to follow the course of each sulcus from its appearance on the surface of the brain to the fundus because a prominent sulcus which may look continuous on the surface of the brain may be segmented into several major subunits in its depth by submerged gyri that form bridges between the banks of this sulcus (Regis et al., 2005). These bridging gyri have been called "plis de passage" (crossing folds) by Gratiolet or "annectant gyri" by Cunningham and Horsley (Germann et al., 2005; Huttner et al., 2005; Regis et al., 2005). When a specific pli de passage (annectant gyrus) is visible from the surface of the brain, a particular sulcus may be judged by visual inspection as discontinuous and it can be marked as several separate (and sometimes unrelated) sulci on certain anatomical maps, but if the pli de passage is not visible from the surface, the same sulcus may be marked as continuous and its branches not recognized. Moreover, unusual sulcal patterns may originate when segmented portions of the main sulci merge with each other on the cortical surface. Regis et al. (2005) argue that there is a good correspondence between the interruptions of the main sulci described in the literature and the

positions of submerged plis de passage. Thus, it may be possible to classify large inter-individual variability of sulcal structures observed in the human brain into simpler sulcal patterns by considering the basic sulcal subunits in the deepest fundal region (Huttner et al., 2005; Regis et al., 2005).

The importance of the careful study of the local morphological variability of sulci in the human brain was recently highlighted in our laboratory when it was shown that a major controversy could be resolved by examining functional activity in relation to the variations in local sulcal and gyral morphology (Amiez et al., 2006). A frequent approach in functional neuroimaging studies is to average activity observed in a number of subjects in the standard proportional stereotaxic space to determine stereotaxic coordinates of the brain region involved in a specific sensory or motor process. In such cases, any relation of activity in individual subjects to variations in sulcal and gyral morphology is obscured. While this approach does not pose major problems when an approximate location of a functional activity is searched for, functional activities related to two distinct processes but located close to each other cannot be resolved by examination of the average activity peaks. We have shown that examining functional activity in relation to the local sulcal variability can provide important insights into structure/function relations that are impossible when activity is averaged (Amiez et al., 2006). For instance, when the functional activations in dorsal posterior frontal cortex during a visuomotor hand conditional task and a saccadic eye movement task are averaged across brains, the resulting average activation peaks cannot be differentiated, but a subject-by-subject analysis demonstrates separate locations for the two functional peaks and a clear relationship between a specific type of functional activity and the local sulcal morphology (Amiez et al., 2006). Visuomotor hand conditional activity related to the hand premotor cortical region is localized in the dorsal branch of the superior precentral sulcus, while the saccadic eye movement activity occupies the ventral branch of the superior precentral sulcus (Amiez et al., 2006). It is clear, then, that in order to study functional organization of the cerebral cortex in detail, we must be fully aware of the extent to which the sulcal and gyral morphology differs between individual brains, as well as to be able to identify those anatomical patterns which are common among individuals. Systematic examination of the postcentral sulcus in the standard proportional stereotaxic space employed in functional neuroimaging studies is the first step towards establishment of anatomical-functional correlations in the anterior parietal lobe.

The goal of the present study was to examine the morphological variability of the postcentral sulcus by following its course from the surface of the brain to the fundus in magnetic resonance imaging (MRI) scans. The aim was to provide a detailed examination of the morphology and variability in the morphology of the postcentral sulcus in the two hemispheres of the human brain to aid in the investigation of functional activity related to complex somatomotor function since the postcentral sulcus forms the border of the postcentral gyrus (somatosensory cortex) with the anterior parts of both the superior and inferior parietal lobules which are known to play important roles in the control of action, including action related to writing (for review, see Petrides and Pandya, 2002). We consider two types of gyri, submerged in the fundal depth and extending from the fundus to the cortical surface as they separate individual sulcal segments. The aim was to determine the patterns formed by the postcentral sulcus with the rest of sulci in the anterior parietal lobe by considering true connections in the fundal depth. In addition, accessory sulci and their relation to the main postcentral branches, which have not been previously described, are examined so that a complete understanding of the morphology of the postcentral sulcus can emerge. In the present study the postcentral sulcus was examined in MRI brain volumes transformed in the Montreal Neurological Institute (MNI) proportional stereotaxic space (Evans et al., 1992; Mazziotta et al., 1995a,b), which is a further development of the stereotaxic space of Talairach and Tournoux (1988). The standardized proportional stereotaxic space provides a common quantitative framework and it is used for accurate communication, comparison and correlation of specific clinical and experimental data obtained in various neuroimaging studies (Chiavaras et al., 2000).

## 2.3 Materials and methods

#### Subjects

MRI scans of 40 human brains were randomly selected from the population of brain scans in the International Consortium for Brain Mapping (ICBM) database (Mazziotta et al., 1995a, 1995b). The examined sample consisted of 24 males (mean age 23.4 years, SD 3.18) and 16 females (mean age 24.6 years, SD 4.33). All subjects were right-handed, had a negative history of neurological and/or psychiatric disorders, and gave informed consent.

## Magnetic Resonance Imaging

All MRI scans were performed on a Philips Gyroscan 1.5T superconducting magnet system. By means of a fast-field echo 3-D acquisition sequence, 160 contiguous 1-mm T<sub>1</sub>weghted images ( $T_r = 18$  msec,  $T_e = 10$  msec, flip angle 30 degrees) were collected in the sagittal plane. Each acquired MRI volume was transformed into the MNI standard proportional stereotaxic space using an automated registration program with a three-dimensional (3D) crosscorrelation approach to match the single MRI volume with the intensity average of 305 brain volumes previously aligned into standardized stereotaxic space (Evans et al., 1992; Collins et al., 1994). This transformation was necessary to normalize and correct the MR images for interindividual differences in gross brain size. The transformed brain volumes were then resampled on a 1-mm<sup>3</sup> isotropic grid (1mm x 1mm x 1mm voxel size). The thickness of obtained coronal, sagittal and horizontal slices was 1 mm.

The anterior commissure serves as the origin of the MNI stereotaxic space (x = 0, y = 0, z = 0) where the coordinates are given in millimetres. The medio-lateral (left-right) axis is represented by the x coordinate (positive values represent the right hemisphere), the rostro-caudal (anterior-posterior) axis by the y coordinate (positive values are rostral to the anterior commissure), and the dorso-ventral (superior-inferior) axis by the z coordinate (positive values are superior to a horizontal line drawn through the anterior and posterior commissures).

## Segmentation of intrasulcal gray matter

An interactive 3D imaging software package DISPLAY (MacDonald, 1996) was used to mark the parietal sulci on individual MRI brain scans. DISPLAY allows the scans to be viewed simultaneously in the coronal, horizontal and sagittal planes of section. When the cursor, controlled by the mouse, was moved to any location in a given section, the sections in the other two planes were automatically updated to show the corresponding views of the location of interest. The movement of the cursor was also observed on a 3-D reconstruction of the brain surface.

The overall intensity of sections and gray-white matter contrast were adjusted in DISPLAY, so that each sulcus could be clearly observed from the surface of the brain to its fundus. The cerebrospinal fluid voxels between the banks of individual sulci were manually selected by 'coloring' them with the 'mouse-brush' tool. Each sulcus of interest was identified using a specific color label to mark the space within its banks along its entire course. The sulci of

interest were examined in 1-mm steps in all planes of section to determine their direction and extent, as well as to establish at which point they terminate i.e. they may no longer be observed in either one of three corresponding slices.

## Surface renderings

Three-dimensional surface renderings of individual brains were acquired using two different types of software. Initially, an automatic, model-based, surface deformation algorithm was used to reconstruct 40 brain volumes already existing in the MNI stereotaxic space into three-dimensional objects and visualize the labelled sulci on the outer surface of individual volumes (MacDonald et al., 1994). After the sulcal labels were marked on contiguous two-dimensional sections (coronal, horizontal and sagittal), they were projected to and viewed on the three-dimensional reconstructions of 40 MRI brain volumes. In addition, Caret v.5.5 software was used to reconstruct the same 40 MRI brain volumes placed in the MNI space in three dimensions and slightly 'inflate' them to reveal the deep or submerged parts of sulci, not commonly seen from the surface of the brain (Van Essen, 2005). Such slight "inflation" retained the characteristic shape of the sulci of a given brain volume but allowed inspection of their depth.

After 40 structural MRI brain volumes were imported into Caret 5.5, they were upregistered to the Washington University stereotaxic coordinate space 711-2B-111, which is a version of the Talairach stereotaxic space with an origin at the anterior commissure (Van Essen, 2005). Following registration, the brain volumes were re-sampled on an isotropic grid with 1mm<sup>3</sup> voxel size. Volume segmentation and initial surface reconstruction were done using SureFit algorithm, which is a part of Caret 5.5 software. Topological errors produced during segmentation were corrected using an automated processing sequence and manual editing in order to remove various irregularities. A segmentation boundary created using SureFit processing sequence was approximately equidistant from the inner and outer limits of the cortical gray matter (cortical layer 4). Initial 'raw' surface generated along the segmentation boundary was 'smoothed' to produce a 'fiducial'' surface which is an improved representation of the 3D cortical surface. The quality of cortical segmentation produced with Caret 5.5 was evaluated by visual examination of the generated 3D surfaces and their comparison with the 3D renderings created using an automated algorithm developed by MacDonald and colleagues (1994). Threedimensional surface reconstructions of 40 brain volumes generated with two different types of software showed the same external surface features of sulcal and gyral morphology in corresponding volumes. In the final step Caret 5.5 software was used to inflate the surface of brain volumes using up to two smoothing iterations and an inflation factor equal to 1.02. This operation created an effect of opening up the sulci of interest and revealing the submerged parts of sulcal anatomy. Slightly inflated 3D surface reconstructions produced with Caret 5.5 were used to emulate the external surface view of postmortem brains. The procedure for segmentation of T1-weighted structural MRI volumes is described in detail in "Caret 5 Tutorial: segmentation, flattening and registration" available from Van Essen Lab Wiki Home Page (http://brainvis.wustl.edu).

# Stereotaxic coordinates of the submerged gyri (submerged plis de passage) of the postcentral sulcus

Stereotaxic coordinates of the midpoints (centers) of the submerged gyri of the postcentral sulcus were determined manually on horizontal sections of the MRI brain volumes. All horizontal sections belonging to a volume were examined at 1 mm intervals. When a section which contained two segments of the postcentral sulcus separated by a submerged gyrus was encountered, it was examined to determine whether one of the segments of the postcentral sulcus was at its deepest and most ventral fundal point i.e. no sections ventral to the current section contained the same sulcal segment. Once the section of interest was found, the stereotaxic coordinates of the central point of the submerged gyrus between the two segments were determined manually. Given the small size of submerged gyri in the examined sections, the error in determining their central point is expected to be less than 2-3 mm in the anterior-posterior (y) and medial-lateral (x) axes. There is little to no error in the dorso-ventral (z) coordinate of the midpoints of submerged gyri because the midpoints were determined in the sections containing the deepest fundal regions of sulcal segments and the sulcal segments were not observed in the sections immediately ventral to the sections of interest. Although the current values of the stereotaxic coordinates of four submerged gyri are estimates of their actual central points, the estimated coordinates always fall within the larger regions of the submerged gyri and therefore are still indicative of their location.

## 2.4 Results

#### Postcentral sulcus

The present examination of the postcentral sulcus in 80 hemispheres of human MRI brain scans revealed that the postcentral sulcus can either remain continuous or it may be separated into segments by gyri, which merge its banks. Some of the gyri, which divide the postcentral sulcus into segments, may be visible from the surface of the brain, while others are hidden deep within the sulcus (submerged gyri; Figures 2.2-2.10). Submerged gyri separate the postcentral sulcus into segments by merging its banks at specific locations close to the fundus. Submerged gyri can be identified only in serial sections. Gyri visible from the surface of the brain, i.e. non-submerged gyri, merge two banks of the postcentral sulcus both in depth and on the surface. They are identified equally well on three-dimensional reconstructions of MRI brain volumes and cross-sections.

In the present paper, submerged gyri are called submerged plis de passage and nonsubmerged gyri are called visible gyri. Additionally, terms submerged plis de passage and visible gyri are combined under a more broad term interrupting gyri, i.e. gyri which divide the postcentral sulcus into segments.

In some hemispheres both types of interrupting gyri were present, submerged plis de passage and visible gyri (17.5% of all hemispheres). In the majority of hemispheres only one type of interrupting gyri was present, either submerged plis de passage (42.5% of hemispheres) or visible gyri (26.25% of hemispheres). In the rest of hemispheres (13.75%), no interrupting gyri could be identified.

The results show that the postcentral sulcus can be divided into five segments by four submerged plis de passage and/or visible gyri. In the majority of examined brains, the postcentral sulcus contained less than five segments and less than four interrupting gyri were observed in each individual hemisphere.

The postcentral sulcus was continuous and could be followed without any interruption from its dorsal end to the ventral end in 13.75% of all hemispheres (see Table 2.1). Most frequently, however, the postcentral sulcus consisted of either 2 segments (46.25% of all hemispheres) or 3 segments (27.5% of all hemispheres). In a small number of cases, the postcentral sulcus contained 4 to 5 segments (Table 2.1).

The averaged estimates of the stereotaxic coordinates were established for four submerged plis de passage, described as the first, second, third and fourth submerged plis de passage (see Methods; Table 2.2). The first submerged pli de passage is most dorsal and the fourth submerged pli de passage is most ventral with respect to the rest of submerged plis de passage.

The stereotaxic coordinates could not be found for the visible gyri because of their relatively large size and continuity. However, in the MNI stereotaxic space, the locations of four visible gyri were found to correspond generally to locations of four submerged plis de passage. Therefore, in order to describe spatial location of a visible gyrus a reference will be made to a specific submerged pli de passage, whose estimated stereotaxic coordinates fall within the cortical region occupied by the visible gyrus.

In 47.5% of all examined hemispheres both types of interrupting gyri, i.e. submerged plis de passage and visible gyri, occurred at the stereotaxic location of the third submerged pli de passage. Interrupting gyri at the location of the first, second and fourth submerged plis de passage were observed in 37.5%, 22.5% and 25% of all hemispheres respectively (see Table 2.3 and Figure 2.2).

The majority of gyri located at the stereotaxic location of the third and fourth submerged plis de passage in the left and right hemispheres were submerged gyri, whereas most of the gyri located next to the first submerged pli de passage were visible on the surface of the brain (see Table 2.3).

Both submerged plis de passage and visible gyri were more frequently found in the left hemisphere than in the right hemisphere.

## *Hemisphere differences*

There were hemispheric differences in the segmentation of the postcentral sulcus in the forty MRI brain volumes examined (see Table 2.1). On average, in the right hemisphere, the postcentral sulcus consisted of fewer segments than in the left hemisphere. More specifically, the postcentral sulcus was continuous or consisted of two segments in a larger number of right hemispheres (72.5%) than left hemispheres (47.5%). The postcentral sulcus consisting of three, four and five segments was located more often in the left hemisphere (52.5%) than the right hemisphere (27.5%). The left hemisphere contained more interrupting gyri at the stereotaxic coordinates of the first, third and fourth submerged plis de passage (see Table 2.3). Interrupting gyri at the location of the second submerged pli de passage were distributed approximately equally between the left and right hemispheres.

#### Segmentation patterns comparison between two hemispheres of individual brains

When two hemispheres of the same brain were compared to each other with regard to the number of segments of the postcentral sulcus, it was observed that in approximately one fourth of all brains (27.5% or 11 brains) the postcentral sulcus showed the same type of segmentation. In 15% of all brains both hemispheres contained the postcentral sulcus consisting of two segments and in 10% of the brains the postcentral sulcus was divided into 3 segments in both hemispheres of the same brain.

In 55% of the brains (22 brains) the postcentral sulcus showed a certain number of segments in one hemisphere and had this number increased by one (i.e. contained one extra segment or +1 pattern) in the other hemisphere of the same brain. For instance, the postcentral sulcus contained 2 segments in the right hemisphere and 3 segments in the left hemisphere. The majority of brains demonstrated a less segmented pattern in the right hemisphere and a more segmented +1 pattern in the left hemisphere.

In 17.5% of the brains (7 brains) the postcentral sulcus showed +2, +3 or +4 levels of segmentation in the opposite hemisphere. As an example, the postcentral sulcus consisted of 2 segments in the right hemisphere and 4 segments in the left hemisphere. Alternatively, the postcentral sulcus could be continuous in the right hemisphere and contain 3, 4 or 5 segments in the left hemisphere. In these cases, the left hemisphere was always associated with a more segmented postcentral sulcus and the right hemisphere with a less segmented postcentral sulcus.

#### Surface view vs. cross-section view

In order to characterize the postcentral sulcus and its segments earlier investigators frequently used visual observation of the external brain surface, which contained sulci and nonsubmerged (visible) gyri. As a result, the postcentral sulcus was often described as a continuous sulcus or a set of two to three sulci which cross the brain surface in a dorso-ventral direction. The present investigation, which considers the postcentral sulcus in its depth, suggests that the postcentral sulcus may consist of up to five segments separated by submerged and nonsubmerged gyri.

In order to see how two methodologies compare, we applied both methods to the same population of 40 human MRI brain volumes. First, we identified and followed the postcentral sulcus and its segments in horizontal, sagittal and coronal sections. Next, we identified and described the postcentral sulcus in 3D Caret reconstructions of the same brain volumes. The results were compared with each other. In only 25% of cases when the postcentral sulcus was characterized as continuous using surface-based methodology, was it also described as continuous when using cross sections to examine the depth (Figure 2.2a). In 57% of hemispheres where the postcentral sulcus was determined to consist of 2 segments using surface-based methodology, it was also determined to contain 2 sulcal segments by means of cross section analysis (Figures 2.2b, 2.3-2.6). In the remaining 43% of hemispheres described as containing the postcentral sulcus with 2 segments through surface observation, the postcentral sulcus was found to consist of three to five segments in cross sections (Figure 2.2e). Using surface-based methodology, the postcentral sulcus was found to consist of 3 segments in only 6% of all hemispheres (Figure 2.2d), whereas cross-section analysis found that 27.5% of all hemispheres contained the postcentral sulcus with three segments. Only cross-section analysis and not the surface-based descriptions of the postcentral sulcus found that it may consist of four to five sulcal segments. Therefore, although there is a partial overlap between results obtained with 2 different methods, the surface-based analysis can not be used as an accurate predictor of submerged morphology of the postcentral sulcus.

## Dorsal end of the postcentral sulcus

Analysis of the postcentral sulcus in horizontal sections revealed that the most frequent type of dorsal termination of the sulcus was bifurcation (68.75% of all hemispheres) followed by a standard straight line (23.75%; see Table 2.4 and Figure 2.11). Least often the postcentral sulcus terminated with 3 short extensions or branches (7.5%; Figure 2.11e). Comparison between two hemispheres showed that bifurcation of the dorsal end more often occurred in the left hemisphere, while a straight line end was more common in the right hemisphere (see Table 2.4).

## Patterns of the postcentral sulcus

## Connection with the lateral fissure

Surface observation of the postcentral sulcus shows that, in some brains, it appears to merge with the lateral fissure i.e. the separating gyrus between the two sulci is too small to be detected visually. We identified a similar pattern in 3D surface reconstructions of 40 MRI brain volumes and correlated it with the number of segments of the postcentral sulcus, which were determined using cross-section analysis. Our findings show in a third of all hemispheres (30%) the postcentral sulcus forms a superficial connection with the lateral fissure (see Table 2.5 and

Figure 2.11a,c). Additionally, the greater the number of segments the postcentral sulcus has, the more often it seems to merge with the lateral fissure in 3D reconstructed images. Thus, in 62.5% of all hemispheres with 4 segments of the postcentral sulcus, 43.5% of hemispheres with 3 segments of the postcentral sulcus, and 21.6% of all hemispheres with 2 segments of the postcentral sulcus, the postcentral sulcus appeared to merge with the lateral fissure. In contrast, only 9% of hemispheres with the continuous postcentral sulcus showed a surface connection with the lateral fissure.

As analyzed with the surface-based and cross-section methodology, a larger proportion of brains in which the postcentral sulcus seemed to merge with the lateral fissure contained a bifurcated dorsal termination of the postcentral sulcus (36.4%) as opposed to a regular straight line termination (21.1%).

## Same brain differences with regards to the postcentral sulcus connection with the lateral fissure

The results show that when the postcentral sulcus does not appear to merge with the lateral fissure in one hemisphere of the brain, then it does not form a superficial connection with the lateral fissure in the other hemisphere in 71.4% of all brains. Conversely, when the postcentral sulcus merges with the lateral fissure in one hemisphere of the brain, then it merges with the lateral fissure in the other hemisphere in only 33% of all brains. In other words, when the postcentral sulcus appears to merge with the lateral fissure in one hemisphere, it is two times more likely not to merge with the lateral fissure in the other hemisphere.

## Connection with the superior longitudinal fissure

In approximately one third of all hemispheres (28.75%) the postcentral sulcus reached the superior longitudinal fissure (see Table 2.4 and Figure 2.11b,d). However, it did not extend to the medial surface, but remained on the lateral surface very close to the superior longitudinal fissure. There were no differences between the left and right hemispheres with regards to this pattern (see Table 2.4).

## Connection with the intraparietal sulcus

The intraparietal sulcus, also identified as the horizontal segment of the intraparietal sulcus, is located posterior to the postcentral sulcus and it has a more or less horizontal or anterior-posterior orientation. Examination of the intraparietal sulcus both in 3D surface

reconstructions of brain volumes and cross sections showed that the anterior end of the intraparietal sulcus is located at the same dorso-ventral level as the superior frontal sulcus.

External surface-based analysis of the connection between the postcentral sulcal complex and the anterior part of the intraparietal sulcus in 40 reconstructed MRI brain volumes showed that the anterior intraparietal sulcus was separated from all segments of the postcentral sulcus simultaneously by a visible (non-submerged) gyrus in 40% of all hemispheres (see Table 2.6 and Figure 2.12). Less frequently the anterior intraparietal sulcus was determined to merge superficially with the continuous postcentral sulcus (31.25% of all hemispheres). In 20 % of all hemispheres the intraparietal sulcus connected superficially with the inferior segment of the postcentral sulcus and it was separated by a visible gyrus from the superior segment of the postcentral sulcus. In a small number of cases the anterior intraparietal sulcus appeared to merge with the superior (6.25% of all hemispheres) or middle (2.5% of all hemispheres) segment of the postcentral sulcus and it was separated by a gyrus from the rest of the segments of the postcentral sulcus and it was separated by a gyrus from the rest of the segments of the postcentral sulcus and it was separated by a gyrus from the rest of the segments of the postcentral sulcul complex (see Table 2.6 and Figure 2.12).

Anterior intraparietal sulcus appeared to merge with the middle or inferior postcentral sulcus more often in the left hemisphere than in the right hemisphere, while it connected superficially with the superior segment of the postcentral sulcus mainly in the right hemisphere (see Table 2.6).

Investigation of the connection between the anterior intraparietal sulcus and the postcentral sulcal complex (which included all postcentral sulcal segments) in horizontal sections showed that the two sulci are always separated by a submerged or visible gyrus (100% of all cases). Therefore, in spite of the superficial connection, the intraparietal and postcentral sulci always have separate origins.

#### Patterns with the ascending/marginal branch of the cingulate sulcus

Analysis of the ascending branch of the cingulate sulcus in cross sections showed that it terminated anterior to or between the two branches of a bifurcated ("V") dorsal end of the postcentral sulcus in the majority of cases (71.25% of hemispheres; see Table 2.7). Less common was a termination posterior to the dorsal end of the postcentral sulcus (28.75% of hemispheres). Figure 2.13 shows examples of patterns formed by the ascending branch of the cingulate sulcus and the dorsal termination of the postcentral sulcus.

The ascending branch of the cingulate sulcus terminated anterior to or between the branches of a bifurcated dorsal termination of the postcentral sulcus in a larger number of left than right hemispheres (see Table 2.7). At the same time, termination posterior to the dorsal end of the postcentral sulcus was more common for the right hemispheres.

Surface-based analysis showed that in 41.25% of all hemispheres the ascending branch of the cingulate sulcus extended to and could be clearly seen on the lateral surface of 3D reconstructions of human brain volumes. This pattern occurred more frequently in the left hemisphere than in the right hemisphere.

#### Sulci dorsal to the postcentral sulcus

The results of cross-section and surface-based analyses revealed a frequent occurrence of sulci located directly dorsal to the postcentral sulcus. These sulci could be classified into two categories: i) short sulci which remained on the lateral surface of the brain and occurred in approximately one tenth of all hemispheres (11.25%), and ii) somewhat longer sulci which extended to the medial surface of the brain by crossing the superior longitudinal fissure in about one third of all hemispheres (33.75%; see Table 2.8). Two types of sulci are illustrated in a diagrammatic form in Figure 2.14.

Both types of sulci were usually located superior to the first submerged pli de passage and they had a horizontal (anterior-posterior) or diagonal orientation. The non-vertical (i.e. or non-dorso-ventral) orientation of the dorsal sulci and their superior position on the lateral surface were the main reasons why the dorsal sulci were not considered to be segments of the postcentral sulcus.

Dorsal sulci which extended to the medial surface of the brain (type ii) were more often observed in the left hemisphere, while the sulci which remained on the lateral surface and did not extend to the medial surface (type i) were more commonly found in the right hemisphere (see Table 2.8).

Analysis of two hemispheres of the same brain showed that when one hemisphere of the brain contained sulci which were located dorsal to the postcentral sulcus and extended to the medial surface (type ii), then there was a 22% chance that the opposite hemisphere of the same brain would also contain comparable sulci. The probability to find similarly placed sulci in the opposite hemisphere of the same brain was smaller (11%) for the dorsal sulci which remained on the lateral surface and did not extend to the medial surface (type i). Therefore, in the majority of

brains, only one hemisphere contained sulci which were located directly dorsal to the postcentral sulcus.

It seems possible that in some specimen the postcentral sulcus joins with the sulci located dorsal to it at the level of their fundus deep inside the brain, such that the individual origins of sulci cannot be detected in cross sections. In this case, the postcentral sulcus would be considered to extend to the dorso-medial edge of the hemisphere and make a connection with the superior longitudinal fissure.

## Sulcal patterns on the inferior postcentral gyrus

In this paper a portion of the postcentral gyrus located ventral to the second submerged pli de passage of the postcentral sulcus is referred to as the inferior postcentral gyrus. In 45% of all hemispheres, there were no sulci located on the inferior postcentral gyrus (see Table 2.9). In one third of all hemispheres (32.5%) we observed a sulcus of variable length which was located anterior to the postcentral sulcus on the inferior postcentral gyrus (Figure 2.15). It had a vertical dorso-ventral orientation and it was often placed in parallel with the postcentral sulcus (Figure 2.15). This sulcus was named the transverse postcentral sulcus.

Occasionally, the transverse postcentral sulcus could appear to connect with the lateral fissure on the surface of reconstructed 3D brain volumes, but cross-section analysis confirmed that the transverse postcentral sulcus was always separated from the lateral fissure by a gyrus. The length of the transverse postcentral sulcus varied from brain to brain. The transverse postcentral sulcus was most often seen in combination with the postcentral sulcus which contained 2 segments (50%) and less often with the continuous postcentral sulcus (27%) or the postcentral sulcus consisting of 3 segments (19%; also Figure 2.15).

As verified with the surface-based analysis, the transverse postcentral sulcus was present in hemispheres where the postcentral sulcus did not merge superficially with the lateral fissure (96.2%). The transverse postcentral sulcus was more often present in the right hemisphere of the brain (61.5%) than in the left hemisphere (38.5%; see Table 2.9).

Averaged data show that in the hemispheres where the transverse postcentral sulcus was absent, the postcentral sulcus terminated ventral to the fourth submerged pli de passage. In the hemispheres with the transverse postcentral sulcus, the postcentral sulcus terminated close to the stereotaxic coordinates corresponding to the third submerged pli de passage, while the transverse postcentral sulcus started at the stereotaxic location of the second submerged pli de passage. We suggest that the transverse postcentral sulcus belongs to the postcentral sulcal complex and it may be considered an inferior part of the postcentral sulcus on the basis of the following evidence: i) the transverse postcentral sulcus appears around the base of the second submerged pli de passage in horizontal sections; ii) the transverse postcentral sulcus is mostly present when the postcentral sulcus consists of 2 segments; iii) the transverse postcentral sulcus is located anterior to the postcentral sulcus and it often overlaps with the ventral end of the postcentral sulcus; iv) the transverse postcentral sulcus is present in the brains with a shorter length of the postcentral sulcus and does not appear in the brains where the postcentral sulcus merges superficially with the lateral fissure.

It is possible that in some of the brains examined in the present study the transverse postcentral sulcus merged with the postcentral sulcus in the fundus and it did not appear as an independent sulcus anterior to the postcentral sulcus. In those brains the transverse postcentral sulcus was likely to be identified as an integral part of the postcentral sulcus.

In addition to the transverse postcentral sulcus, there were other types of sulci which were observed on the inferior postcentral gyrus. In 53.5% of all hemispheres, sulci which originated on the upper lip of the lateral fissure also extended onto the lateral surface of the brain (e.g. posterior subcentral sulcus, sulcus transverses operculi parietalis primus and secondus, using terminology of Economo and Koskinas, 1925; see Table 2.9 and Figures 2.3-2.10, 2.11b,d). These sulci appeared as branches of the lateral fissure in 3D surface reconstructions of MRI brain volumes. Sulci from the parietal operculum were much more frequently observed on the inferior postcentral gyrus in the left hemisphere of the brain than in the right hemisphere.

#### Examples of sulcal features and patterns in two MRI brain volumes

A number of features and patterns of the postcentral sulcus are demonstrated in two hemispheres taken from two different brains within the sample of MRI brain volumes used in this study. Figures 2.3-2.6 show cross sections taken from the left hemisphere of an MRI brain volume (case 1). The postcentral sulcus consists of 2 segments which are separated at the first submerged pli de passage by a visible/ non-submerged gyrus (Figures 2.4c-e, 2.5i). Both surfacebased and cross-section analyses show the same segmentation pattern of the postcentral sulcus. The postcentral sulcus does not form a superficial connection with the lateral fissure (Figure 2.6l-m). It does not reach the superior longitudinal fissure either. The dorsal termination of the postcentral sulcus is a bifurcation and it has a V- shape (Figure 2.4a-c). There are no sulci located dorsal to the postcentral sulcus. The ascending branch of the cingulate sulcus is seen on the lateral surface of the brain (Figures 2.3, 2.51-m; also see the same hemisphere on Figure 2.2b). It terminates inside the V-end/ bifurcation of the postcentral sulcus (see Figure 2.4a-c). Surface-based analysis shows that the intraparietal sulcus merges with the inferior segment of the postcentral sulcus (in addition to Figure 2.3 see Figure 2.2b). Cross-section analysis shows a submerged gyrus between the intraparietal sulcus and the postcentral sulcus (Figure 2.4i-j). The transverse postcentral sulcus is located anterior to the postcentral sulcus on the inferior postcentral gyrus and its origin is close to the second submerged pli de passage (see Figures 2.4g-p, 2.5a-f, 2.6k-m). There are no other sulci on the inferior postcentral gyrus.

Figures 2.7-2.10 show a number of features of the postcentral sulcus in serial sections taken from the right hemisphere of an MRI brain volume (case 2). On the 3D surface of the brain the postcentral sulcus appears as a continuous sulcus. Analysis of the postcentral sulcus in cross sections reveals that it consists of 3 segments (superior, middle and inferior) separated by the third and fourth submerged plis de passage (Figures 2.8i-k, 2.10g, 2.10l-o). The postcentral sulcus forms a superficial connection with the lateral fissure (Figure 2.10m-o) and it reaches the superior longitudinal fissure (Figures 2.8a-b, 2.9k-o). Dorsal end of the postcentral sulcus is bifurcated and the ascending branch of the cingulate sulcus terminates inside the bifurcation (Figure 2.8c-e). There are sulci located directly dorsal to the postcentral sulcus, which cross the superior margin of hemisphere (Figure 2.8b-d). The postcentral sulcus does not merge with the intraparietal sulcus (Figure 2.8i). There are no sulci on the inferior postcentral gyrus.

## **2.5 Discussion**

The present investigation established that the postcentral sulcus is a complex of sulcal segments located directly posterior to the central sulcus, extending from the dorsal aspect of the hemisphere close to the midline to the lateral fissure. The postcentral sulcus was examined systematically in two-dimensional serial sections of 40 MRI brain volumes in the MNI stereotaxic space. This approach permitted us to characterize the submerged structure of the postcentral sulcus and describe in-depth relationships between the postcentral sulcus and its neighboring sulci. It should be noted that the patterns formed by the main sulci deep within the fundus are less variable among individuals than the appearance of sulci on the surface of the brain and the sulcal variability increases, in general, towards the outer cortical surface (Lohmann and Cramon, 2000; Regis et al., 2005). In addition, the presence of submerged gyri within

individual sulci can partition the sulci into basic sulcal units and clarify sulcal patterns on the external cortical surface (Huttner et al., 2005; Regis et al., 2005). The present results show that, in the majority of hemispheres, the postcentral sulcus is separated into two (46.25%) or three (27.50%) segments by gyri that join its banks (Figure 2.2; Table 2.1). Less frequently, the postcentral sulcus consists of four or five segments (12.5%) or remains continuous (13.75%). The majority of gyri which divide the postcentral sulcus into segments are submerged deep within the sulcus (submerged plis de passage) and can be observed only in brain sections, while a smaller proportion of gyri may be seen from the surface of the brain (visible gyri; see Table 2.3). Submerged plis de passage and visible gyri occur in four distinct locations of the MNI stereotaxic space and the locations of the corresponding submerged plis de passage and visible gyri overlap (Table 2.2).

Cunningham (1892) describes deep annectant gyri which divide the superior and inferior segments of the postcentral sulcus into smaller units. These basic sulcal units appear as small depressions in the fetal brain and unite into larger structures as the brain continues its prenatal and postnatal development (Connolly, 1950). Cunningham's deep annectant gyri are akin to the submerged gyri described in the current study. It may be suggested, that the four submerged plis de passage (submerged gyri) separate five original postcentral sulcal units which appear early in the development of the fetal brain and have specific functional relevance (see below). Cunningham (1892) also mentions the common occurrence of a deep gyrus (the anterior deep annectant gyrus of Eberstaller) which marks the separation between the horizontal segment of the intraparietal sulcus and the inferior postcentral sulcus. This is consistent with the findings of the current study which demonstrated that the postcentral and intraparietal sulci can appear to join on the surface of the brain, but they are in fact always separated by a gyrus in the cortical depth (Figure 2.4i-j).

Several studies suggest that there may be a relationship between the development of cortical convolutions and the architectonic, functional, and connectional specialization of cortical regions (Connolly, 1950; Welker, 1990; Toro and Burnod, 2005). The position of the main sulci is thought to reflect the underlying cortical organization and be a result of interactions between genetic factors, cytoarchitectonic differentiation, mechanical tension produced by the thalamocortical and cortico-cortical fibers, modulatory influence of the afferent fibers on cortical growth, and the initial geometry of the cortex and its asymmetries (Connolly, 1950; Welker, 1990; Van Essen, 1997; Toro and Burnod, 2005). Despite considerable inter-individual variability in sulcal

and gyral morphology, the main sulci demonstrate relatively constant topographical relationships with each other. Although there may not be a simple correspondence between the cytoarchitectonic boundaries and the sulcal fundi (Geyer et al., 1999), structural components of individual sulci (fundus, walls) and gyri (crown, banks) can serve as landmarks which identify the approximate locations of specific architectonic areas in MRI images or real-life brain specimens. At present, accurate borders of cytoarchitectonic areas can be determined only under light microscopy in histological brain sections and not in the MRI images. To address this problem, probability maps reflecting the variability of cytoarchitectonic areas in the standard stereotaxic space have been created for several cortical areas (Geyer et al., 2000; Grefkes et al., 2001; Eickhoff et al., 2006). The probability maps can be used with individual MRI brain volumes to assess the location of functional activations with respect to the averaged locations of cytoarchitectonic areas.

Influential cytoarchitectonic maps subdivided the anterior parietal lobe into several cortical areas. According to Brodmann (1909), the postcentral gyrus may be parcellated into three main architectonic areas: area 3 (the rostral postcentral area which occupies the posterior bank of the central sulcus), area 1 (the intermediate postcentral area which is located on the anterior lip of the postcentral gyrus), and area 2 (the caudal postcentral area that occupies the posterior part of the postcentral gyrus and which extends into the anterior bank of the postcentral sulcus). Brodmann (1909) also pointed out that the granular cortex on the posterior bank of the central sulcus is separated from the agranular motor cortex on the anterior bank of this sulcus by a narrow transitional area in its fundus that has the characteristics of both the agranular and granular areas. Later on, this transitional zone was named area 3a, and Brodmann's area 3 was now referred to as area 3b (Kaas, 1983; Geyer et al., 1999). The cytoarchitectonic map of Sarkissov and colleagues (1955) also shows areas 3, 1 and 2. Economo and Koskinas (1925) provided detailed descriptions of the features of the cytoarchitectonic areas of the postcentral region and corresponding high quality photographic images. The following main areas and their subdivisions were identified in the anterior parietal lobe: PA (PA1, PA2), PB (PB1, PB2), PC and PD. Area PA<sub>1</sub> (which corresponds to area 3a of Brodmann) occupies the fundus and the lowermost part of the posterior wall of the central sulcus. It extends from the ventral end of the central sulcus, where it can be seen slightly on the lateral surface of the brain to the dorsal end of the central sulcus and the surrounding region on the medial surface of the brain (Economo, 2009). Area PA<sub>2</sub> follows the ascending branch of the cingulate sulcus from the paracentral lobule to the dorsal-posterior part of the postcentral gyrus and the superior parietal lobule (Economo, 2009). On the lateral surface of the brain area  $PA_2$  is located posterior to the dorsal extent of area PC. Economo and Koskinas' area PB occupies the upper two-thirds of the posterior wall of the central sulcus and extends in parallel to area  $PA_1$  from the ventral end of the central sulcus to its dorsal end on the paracentral lobule. Subdivisions PB1 and PB2 reflect inhomogeneity in granularity within area PB; they form strips and islets throughout this area. Area PB corresponds to area 3 of Brodmann that subsequently came to be referred to as area 3b in order to distinguish it from the transitional zone, area 3a. Area PC forms a wide strip posterior to area PB (Economo and Koskinas, 1925) and occupies the visible part of the postcentral gyrus (the crown and the lips) and it extends from the parietal operculum to the paracentral lobule. Area PC may correspond, in part, to areas 1 and 2 of Brodmann. Area PD of Economo and Koskinas occupies the walls and the fundus of the postcentral sulcus along its entire length (Economo, 2009). A recent investigation examined the extent of Brodmann area 2 in 10 post-mortem human brains using two types of analysis, observer-dependent (analysis of histological sections under the light microscope) and observer-independent (analysis of histological sections using a computer algorithm) (Grefkes et al., 2001). The findings showed that area 2 was always located within the anterior wall of the postcentral sulcus and the position of its borders varied between the individual brains (Grefkes et al., 2001). The anterior boundary of area 2 could reach the crown of the postcentral gyrus and the posterior boundary could extend slightly caudal to the fundus of the postcentral sulcus. The dorsal and ventral boundaries of area 2 were located within several millimeters of the dorsal and ventral terminations of the postcentral sulcus. In the brains with the segmented postcentral sulcus, area 2 traversed the dividing gyral bridges without any interruptions in its continuity (Grefkes et al., 2001).

The present results demonstrate that, in approximately two thirds of the examined hemispheres, the postcentral sulcus has a bifurcated dorsal termination, which resembles the shape of the letters Y and V (Table 2.4). In the rest of the hemispheres, the postcentral sulcus has a single dorsal ending similar to the letter I (see Figures 2.11 and 2.13; Table 2.4). The architectonic maps of Brodmann (1909), Economo and Koskinas (1925) and Vogt (1911) show an architectonically distinct area located between the branches of the dorsal termination of the postcentral sulcus and extending onto the medial surface of the brain (area 5 of Brodmann, 1909; area PA<sub>2</sub> of Economo and Koskinas, 1925; area 75 of Vogt, 1911). In the study by Scheperjans et al. (2005) Brodmann area 5 was found to consist of one lateral (5L) and two medial (5M and

5Ci) subareas. The lateral subdivision of area 5 (5L) was located within the dorsal end of the postcentral sulcus near the superior longitudinal fissure. Area 5L extended from the anterior wall to the posterior wall of the dorsal termination of the postcentral sulcus or approached the ascending branch of the cingulate sulcus on the lateral surface of the brain. Area 5L was located posterior and medial to area 2 and it replaced area 2 in the anterior wall of the dorsal end of the postcentral sulcus (Scheperjans et al., 2005). The most dorsal part of lateral area 5 could be observed occasionally on the cortical surface of neighboring gyri, including the crown of the postcentral gyrus or between the branches of the postcentral sulcus. In the monkey, area 5 receives proprioceptive information from the postcentral somatosensory cortex and appears to play an important role in the encoding of arm postures and movement in space within a bodycentered reference frame. It is believed to participate in the coordinate transformation and sensorimotor guidance of motor behavior (Kalaska, 1996; Wenderoth et al., 2004). Neuroimaging research on human subjects implicates area 5 in the performance of directional goal-directed hand movements under somatosensory control (Wenderoth et al., 2004) and performance of movements under proprioceptive control without visual feedback (Grefkes et al., 2004). Stereotaxic coordinates of functional activations localized in putative Brodmann area 5 in the above neuroimaging studies are x = -26, y = -36, z = 74 (Grefkes et al., 2004) and x = -12, y z = -50, z = 70; x = 18, y = -46, z = 74; and x = 20, y = -46, z = 72 (Wenderoth et al., 2004). These coordinates tend to place area 5 activations close to the point of bifurcation of the dorsal end of the postcentral sulcus, adjacent to the dorsalmost end of the single dorsal termination of the postcentral sulcus and dorsal to both of these structures, as established in the present study in the MNI stereotaxic space.

Neurophysiological work on non-human primates discovered a set of areas located along the intraparietal sulcus. Of particular interest for the present investigation is the most anterior of these areas, the anterior intraparietal area (AIP), which is located in the anterior part of the lateral bank of the intraparietal sulcus in the monkey brain (Gallese et al., 1994; Sakata et al., 1995). In the monkey, AIP is involved in grasping movements, which depend on the shape of an object to be manipulated (Gallese et al., 1994; Sakata et al., 1994; Sakata et al., 1994; Sakata et al., 2009). In the human, the presumed homologue of AIP is activated by visual and tactile tasks, which involve three-dimensional attributes of objects, such as shape, size and orientation (Binkofski et al., 1998; Grefkes et al., 2002; Frey et al., 2005; Zhang et al., 2005). Based on the currently available, yet limited knowledge of the anatomo-functional organization of the intraparietal sulcus in the

human, the following two possibilities can be entertained regarding the putative location of the human homologue of monkey area AIP. According to one view, the human homologue of AIP may be located in the anterior part of the horizontal segment of the intraparietal sulcus or in a cortical region at the intersection between the postcentral and intraparietal sulci. For example, Binkofski et al. (1999) reported the location of the human homologue of AIP at x = -40, y = -40, z = 40, and Shikata et al. (2001) reported the location of the human AIP at x = -37, y = -40, z =47 (for review of the coordinates of the human AIP in the anterior intraparietal sulcus see Frey et al., 2005, and Shikata et al., 2008). According to the findings of the present study, the postcentral and intraparietal sulci can appear to merge on the surface of the brain, but they are in fact always separated by a gyrus in the cortical depth (Figure 2.4i-j). In relation to our study, the stereotaxic coordinates of the human area AIP, as reported in the neuroimaging studies of Binkofski et al. (1999) and Shikata et al. (2001), place the human AIP at the gyrus between the postcentral and intraparietal sulci. However, there is another possibility that must also be entertained. The inferior segment of the postcentral sulcus, which has also been described as the vertical (ascending) part of the intraparietal sulcus (Cunningham, 1892), may relate to area AIP. We believe that this hypothesis must be entertained because area AIP in the monkey is located between the somatosensory area 2 and the most anterior part of the inferior parietal lobule. If the general anatomo-functional structure of the intraparietal sulcus is conserved between the monkey and the human, then the human homologue of the monkey area AIP may be expected at the transition between somatosensory area 2 and the most rostral part of the inferior parietal lobule, which is defined by the inferior part of the postcentral sulcus. There is one functional neuroimaging study by Simon et al. (2002) that reported tentative coordinates for the human AIP at x = -60, y = -32, z = 36. These coordinates correspond to the inferior part of the postcentral sulcus in the current study.

In the human brain, the somatosensory cortical region extends from the superior longitudinal fissure to the lateral fissure and its boundaries are formed by the central sulcus, anteriorly, and the postcentral sulcus, posteriorly. As mentioned above, this somatosensory region is subdivided into cytoarchitectonic areas 3a, 3b, 1 and 2 (Brodmann, 1909; Geyer et al., 1999; Grefkes et al., 2001). Area 3b (area PB) is classified as the granulous koniocortex, while areas 1 and 2 belong to the homotypic isocortex. Although sometimes all of the postcentral gyrus somatosensory region is referred to as SI (primary somatosensory region), because the classical stimulation research in patients and monkeys did not have the resolution to distinguish effects due to the stimulation of different architectonic areas (Penfield and Rasmussen, 1952; Woolsey et al., 1979), in fact only the granulous cortical area 3b should be referred to as the primary somatosensory cortex (Kaas, 1983). In addition to their difference in cytoarchitecture, areas 3a, 3b, 1 and 2 receive inputs from different submodalities (Merzenich et al., 1978; Kaas, 1983). Area 3a receives afferents from deep subcutaneous receptors, primarily muscle spindles. Area 3b receives inputs from rapidly and slowly adapting cutaneous receptors and area 1 afferents from rapidly adapting cutaneous receptors. Area 2 receives inputs from deep receptors in joints (Merzenich et al., 1978; Kaas, 1983). Physiological studies in monkeys have established that each architectonic area within the somatosensory cortex contains an orderly arranged representation of the various parts of the body (Whitsel et al., 1971; Merzenich et al., 1978; Kaas, 1983).

The estimated dorsal to ventral arrangement of bodily representations in the human postcentral somatosensory cortex, based on the functional neuroimaging literature, is the following: toes, ankle, knee, midline trunk, hand, lips and teeth, tongue. We compared the stereotaxic coordinates of sensory representations of different parts of the body (see Table 2.10) with the averaged estimates of the stereotaxic coordinates of the four submerged plis de passage of the postcentral sulcus based on the present study (see Table 2.2) in order to examine a functional-anatomical relationship between the bodily representations and their posterior boundaries that are formed by the segments of the postcentral sulcus. Sensorimotor representations of the toes, ankle, knee and the entire foot are located on the postcentral gyrus above the first submerged pli de passage of the postcentral sulcus, anterior to the dorsal part of the first segment of the postcentral sulcus. Their representative locations approach the superior longitudinal fissure on the lateral and medial brain surface (see Tables 2.2 and 2.10). Activation peaks of sensory representations of the midline trunk are located close to the first submerged pli de passage of the postcentral sulcus and between the first and second segments of the postcentral sulcus. Sensory representations of the fingers and the hand are located between the first and second submerged plis de passage, anterior to the second segment of the postcentral sulcus. The lips, teeth and tongue are represented in the sensory cortex anterior to the third segment of the postcentral sulcus, between the second and third submerged plis de passage. The tip of the tongue is represented between the third and fourth submerged plis de passage, anterior to the fourth segment of the postcentral sulcus (see Tables 2.2 and 2.10).

In nearly half of all examined hemispheres (47.5%) both types of interrupting gyri, i.e. submerged plis de passage and visible gyri, occurred at the stereotaxic location of the third submerged pli de passage, which separates somatosensory representation of the hand dorsally from the representation of the face ventrally. Visible gyri occurred more often at the location of the first submerged pli de passage, which separates somatosensory representations of the toes, knee and ankle dorsally from the representation of the representation of the hand ventrally.

In one third of all hemispheres examined, there was a sulcus of variable length located anterior to the postcentral sulcus on the most ventral part of the postcentral gyrus (Figure 2.15). We refer to this sulcus as the transverse postcentral sulcus because it appears to correspond to the sulcus postcentralis (retrocentralis) transversus of Eberstaller (see Cunningham, 1892). Cunningham calls the sulcus postcentralis transversus the lowermost part of the postcentral sulcus, which may join superficially the inferior postcentral sulcus, but always remains separated from it by a deep annectant gyrus. In the brains examined in the current study, the transverse postcentral sulcus had a vertical dorso-ventral orientation and it was often placed in parallel with the postcentral sulcus. It was most frequently located in hemispheres where the postcentral sulcus terminated around the third submerged pli de passage. In these hemispheres, the transverse postcentral sulcus originated next to the second submerged pli de passage. In those brains where the postcentral sulcus terminated close to the fourth submerged pli de passage or ventral to it, the transverse postcentral sulcus was absent. Thus, we suggest that the transverse postcentral sulcus is an inferior segment of the postcentral sulcus which may or may not merge with the postcentral sulcus deep inside the fundus. Since the transverse postcentral sulcus is located next to the somatosensory face area, it may separate an anterior part of the postcentral gyrus from a posterior part of the postcentral gyrus that may play a different functional role related to the orofacial region of the body. Analysis of the stereotaxic coordinates of somatosensory representations of the lips, teeth and tongue (see Table 2.10) always placed them anterior to the transverse postcentral sulcus, which was determined from the anatomical observation of this sulcus in 40 human MRI brain volumes (unpublished observation). Therefore, it is suggested that the transverse postcentral sulcus is a morphological landmark separating the sensorimotor representation of the face from the posterior parietal cortex.

The present study investigated, in the MNI proportional stereotaxic space, the morphological structure of the postcentral sulcus and its relationship with the neighboring sulci. The results of this anatomical work may be used to relate specific functional activations acquired in neuroimaging studies and registered to the standardized proportional stereotaxic space to details of sulcal and gyral anatomy of the anterior parietal lobe in the same stereotaxic space. A clear relationship between a specific type of functional activity and the local sulcal morphology can help clarify the functional organization of the cerebral cortex.

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### 2.8 Abbreviations

#### Sulci and gyri

**aIPS**, anterior part of the horizontal segment of the intraparietal sulcus CS, central sulcus **CingS**, ascending (marginal) branch of the cingulate sulcus dS, sulcus located dorsal to the PoCS G-1st, gyrus which divides PoCS into 2 segments, superior and inferior PoCS. This gyrus is visible on the surface and in the fundus. It is located at the first submerged pli de passage. **iPoCS**, inferior postcentral sulcus iPrS, inferior precentral sulcus **IPS**, intraparietal sulcus (horizontal segment and its branches) LF, lateral fissure LuS, lunate sulcus mPoCS, middle postcentral sulcus **OpS**, sulcus located on the parietal operculum (upper lip of the lateral fissure) sFS, superior frontal sulcus sPoCS, superior postcentral sulcus **POF**, parieto-occipital fissure posc, posterior subcentral sulcus sPrS, superior precentral sulcus SLF, superior longitudinal fissure STS, superior temporal sulcus TrS, transverse postcentral sulcus

#### Submerged plis de passage

- 3, third submerged pli de passage
- 4, fourth submerged pli de passage
- 1s, submerged gyrus at location of the first submerged pli de passage
- 1v, visible gyrus at location of the first submerged pli de passage
- 2s, submerged gyrus at location of the second submerged pli de passage
- 2v, visible gyrus at location of the second submerged pli de passage

3s, submerged gyrus at location of the third submerged pli de passage
3v, visible gyrus at location of the third submerged pli de passage
4s, submerged gyrus at location of the fourth submerged pli de passage
spdp, submerged pli de passage

## 2.9 Tables

Table 2.1. Incidence and distribution of segments of the postcentral sulcus (PoCS) among the left (LH) and right (RH) hemispheres of 40 MRI brain volumes

<b>Type of PoCS</b>	LH+RH		LH		RH	
Segmentation	Total # % 80		Total #	% 40	Total #	% 40
	LH+RH	LH+RH	LH	LH	RH	RH
Continuous	11	13.75	3	7.5	8	20
Two segments	37	46.25	16	40	21	52.5
Three segments	22	27.50	12	30	10	25
Four segments	9	11.25	8	20	1	2.5
Five segments	1	1.25	1	2.5	0	0

	Average MNI coordinates									
Structure	Left	t hemisph	ere	Right hemisphere						
	X	У	Z	X	У	Z				
First submerged pdp*	-28	-34	54							
Second submerged pdp	-38	-31	43	36	-32	43				
Third submerged pdp	-41	-27	35	45	-25	34				
Fourth submerged pdp	-55	-18	28	52	-16	29				

Table 2.2. Averaged stereotaxic coordinates of four submerged plis de passage (submerged pdp) in the MNI proportional stereotaxic space

Note: \* There were not enough data to determine the stereotaxic coordinates of the first submerged pli de passage in the right hemisphere.

Table 2.3. Incidence of the presence of submerged and visible gyri in the distinct locations of four submerged plis de passage (spdp) in the left (LH) and right (RH) hemispheres of 40 MRI brain volumes

		LH		RH			LH-	+RH	
Location	Total	% 40	% Total	Total	% 40	% Total	Total #	% Total	
	# LH	LH	LH+RH	# RH	RH	LH+RH	LH+RH	LH+RH	
Submerged g	gyri								
1st spdp	6	15	85.71	1	2.5	14.29	7	8.75	
2nd spdp	6	15	54.55	5	12.5	45.45	11	13.75	
3rd spdp	18	45	60	12	30	40	30	37.5	
4th spdp	10	25	62.5	6	15	37.5	16	20	
Visible gyri									
1st spdp	16	40	69.57	7	17.5	30.43	23	28.75	
2nd spdp	2	5	28.57	5	12.5	71.43	7	8.75	
3rd spdp	5	12.5	62.5	3	7.5	37.5	8	10	
4th spdp	2	5	50	2	5	50	4	5	
Interrupting	gyri (col	mbined si	ubmerged ar	nd visible	e gyri)				
1st spdp	22	55	73.33	8	20	26.67	30	37.5	
2nd spdp	8	20	44.44	10	25	55.56	18	22.5	
3rd spdp	23	57.5	60.53	15	37.5	39.47	38	47.5	
4th spdp	12	30	60	8	20	40	20	25	

Type of dorsal end of PoCS	LH+RH		LH		RH	
	Total #	% 80	Total #	% 40	Total #	% 40
	LH+RH	LH+RH	LH	LH	RH	RH
Dorsal end is regular	19	23.75	7	17.5	12	30
Dorsal end is bifurcated	55	68.75	31	77.5	24	60
Dorsal end has three branches	6	7.5	2	5	4	10
PoCS reaches the superior longitudinal fissure	23	28.75	11	27.5	12	30

Table 2.4. Types of dorsal termination of the postcentral sulcus (PoCS) and their incidence in the left (LH) and right (RH) hemispheres of the human brain

PoCS relative to LF	LH+RH		LH		RH	
	Total #	% 80	Total #	% 40	Total #	% 40
	LH+RH	LH+RH	LH	LH	RH	RH
PoCS superficially merges	24	30	13	32.5	11	27.5
with LF (i.e. gyrus separating the						
sulci is submerged)						
PoCS does not superficially	56	70	27	67.5	29	72.5
merge with LF (i.e. gyrus separating the						
sulci is visible)						

Table 2.5. Patterns formed by the postcentral sulcus (PoCS) and the lateral fissure (LF) and their incidence in the left (LH) and right (RH) hemispheres of the human brain

PoCS and anterior IPS	LH-	-RH	LH		RH	
(surface-based analysis)	Total #	% 80	Total #	% 40	Total #	% 40
	LH+RH	LH+RH	LH	LH	RH	RH
IPS merges with	25	31.25	10	25	15	37.5
continuous PoCS						
IPS merges with	5	6.25	0	0	5	12.5
superior PoCS						
IPS merges with	16	20	11	27.5	5	12.5
inferior PoCS						
IPS merges with	2	2.5	2	5	0	0
middle PoCS						
IPS merges with superior	0	0	0	0	0	0
and inferior PoCS						
IPS is separated from	32	40	17	42.5	15	37.5
all segments of PoCS						
by a visible gyrus						

Table 2.6. Patterns formed by the postcentral sulcus (PoCS) and the anterior part of the horizontal segment of the intraparietal sulcus (IPS) on the surface of the brain

PoCS and CingS	LH+	LH+RH LH		RH		
	Total #	% 80	Total #	% 40	Total #	% 40
	LH+RH	LH+RH	LH	LH	RH	RH
CingS is seen on the	33	41.25	19	47.5	14	35
lateral surface						
CingS terminates anterior	57	71.25	31	77.5	26	65
to PoCS or inside a						
bifurcation of PoCS						
CingS terminates posterior to PoCS	23	28.75	9	22.5	14	35

Table 2.7. Patterns formed by the postcentral sulcus (PoCS) and the ascending branch of the cingulate sulcus (CingS) in the left (LH) and right (RH) hemispheres of the human brain

Table 2.8. Types of sulci which are located dorsal to the postcentral sulcus (PoCS) and their patterns with the superior longitudinal fissure (SLF) in the left (LH) and right (RH) hemispheres of the human brain

Types of sulci located	LH+RH		LH		RH	
dorsal to PoCS	Total # % 80		Total #	% 40	Total #	% 40
	LH+RH	LH+RH	LH	LH	RH	RH
Sulci dorsal to PoCS which reach SLF	27	33.75	17	42.5	10	25
Sulci dorsal to PoCS which <i>do not</i> reach SLF	9	11.25	3	7.5	6	15

Types of sulci on	LH-	-RH		LH			RH	
infPoCG	Total #	% 80	Total #	% 40	% 80	Total #	% 40	% 80
	LH+RH	LH+RH	LH	LH	LH+RH	RH	RH	LH+RH
Transverse post-	26	32.5	10	25	38.5	16	40	61.5
central sulcus								
No sulci on	36	45	16	40	44.4	20	50	55.6
infPoCG								
All other sulci								
(posterior	43	53.5	26	65	60.5	17	42.5	39.5
subcentral sulcus,								
opercular sulci)								

Table 2.9. Types of sulci located on the inferior postcentral gyrus (infPoCG) and their incidence in the left (LH) and right (RH) hemispheres of the human brain

Study	Brain	Left	t hemisph	ere	<b>Right hemisphere</b>			
	region	stereot	axic coord	linates	stereot	axic coord	inates	
	-	X	У	Z	X	У	Z	
Kapreli et al. 2007*	Toes	- 6.1	- 42.9	72.3	6.1	- 39.2	71.8	
	Ankle	- 6.8	-41.3	70.9	6.4	- 38.3	70.1	
	Knee	- 9.9	- 39.6	68.4	10.1	- 36.7	68.8	
Ferretti et al. 2004	Foot	- 4	- 42	59				
Fabri et al. 2005	Lateral midline				30	- 33	55	
	trunk							
	Posterior				32	- 33	53	
	midline trunk							
	Anterior				34	- 25	53	
	midline trunk							
Fabri et al. 2005	Hand				41	- 25	54	
Ferretti et al. 2004	Hand	- 34	- 35	50				
Blatow et al. 2007	Fingers	- 49	-21	46	49	- 19	46	
Kapreli et al. 2007*	Finger	- 38.7	-26.5	53.6	38.5	-23.7	50.4	
Blatow et al. 2007	Lips	- 56	- 17	36	52	- 14	38	
Lotze et al. 2000	Lip pursing	- 52	- 16	38	54	- 6	38	
Miyamoto et al.	Rostral lip	- 55.5	- 11.3	41.7				
2006	Middle lip	- 58.3	- 16.0	39.4				
	Caudal lip	- 58.0	-21.2	39.1				
	Rostral tooth	- 55.8	- 11.0	40.4				
	Middle tooth	- 57.6	- 16.1	39.4				
	Caudal tooth	- 56.7	-22.2	40.8				
	Rostral tongue	- 57.1	- 9.8	38.5				
	Middle tongue	- 58.1	- 15.4	38.2				
	Caudal tongue	- 57.9	-21.1	39.1				
Lotze et al. 2000	Tip of tongue	- 52	2	32	66	- 2	24	

Table 2.10. Representation of different body regions in the contralateral primary somatosensory cortex

Note: \* In Kapreli et al. (2007) representations are shown for the primary sensorimotor cortex.

# 2.10 Figures



Figure 2.1. Schematic representation of the main sulci on the lateral surface of the human brain.



Figure 2.2. Segmentation of the postcentral sulcus on the surface of the brain and in the fundus. This figure illustrates 7 different types of interaction between the surface-based and cross-section analyses with regard to segmentation patterns of the postcentral sulcus. All panels show 3D reconstructions of MRI brain volumes used in this study. In (a), (b) and (d) the postcentral sulcus is found to contain one, two and three segments, respectively, using both methodologies. In (c), (e), (f) and (g) the cross section analysis determined that the postcentral sulcus is divided into a larger number of segments in the fundus than on the surface of the brain. In (a) the postcentral sulcus is continuous both in the fundus and on the surface. In (b) the postcentral sulcus is divided into two segments by a visible gyrus located at the  $1^{st}$  submerged pli de passage [1v]. In (c) the postcentral sulcus is continuous on the surface of the brain, but it is divided into two segments by a submerged gyrus located at the 3rd submerged pli de passage [3s]. In (d) the postcentral sulcus consists of 3 segments separated by two visible gyri at the 2nd and 3rd submerged plis de passage [2v; 3v]. In (e) the postcentral sulcus appears to consist of two segments on the surface of the brain, but it is divided into three segments in the fundus. The first interrupting gyrus at the 3rd submerged pli de passage is submerged [3s] and the second interrupting gyrus at the 3rd submerged pli de passage is visible on the brain surface [3v]. In (f) the postcentral sulcus appears continuous on the surface of the brain, but it is divided into four segments by submerged gyri in its fundus. The submerged gyri are located at the 2nd, 3rd and 4th submerged plis de passage [2s; 3s; 4s]. In (g) the postcentral sulcus appears continuous on the surface of the brain, but it is divided into five segments by submerged gyri in its fundus. The submerged gyri are located at the 1st, 2nd, 3rd and 4th submerged plis de passage [1s; 2s; 3s; 4s].



Figure 2.3. Three-dimensional reconstruction of the left hemisphere of the MRI brain volume (case 1) used in the current study. Horizontal sections are shown in Figure 2.4, coronal sections in Figure 2.5 and sagittal sections in Figure 2.6.



Figure 2.4. Horizontal sections from the left hemisphere of the MRI brain volume (case 1) with the sulci of interest identified. The level in the dorso-ventral dimension (z coordinate) is given in millimetres for each section.



Figure 2.5. Coronal sections from the left hemisphere of the MRI brain volume (case 1) with the sulci of interest identified. The level in the rostro-caudal dimension (y coordinate) is given in millimetres for each section.



Figure 2.6. Sagittal sections from the left hemisphere of the MRI brain volume (case 1) with the sulci of interest identified. The level in the medio-lateral dimension (x coordinate) is given in millimetres for each section.



Figure 2.7. Three-dimensional reconstruction of the right hemisphere of the MRI brain volume (case 2). Horizontal sections are shown in Figure 2.8, coronal sections in Figure 2.9 and sagittal sections in Figure 2.10.



Figure 2.8. Horizontal sections from the right hemisphere of the MRI brain volume (case 2) with the sulci of interest identified. The level in the dorso-ventral dimension (z coordinate) is given in millimetres for each section.



Figure 2.9. Coronal sections from the right hemisphere of the MRI brain volume (case 2) with the sulci of interest identified. The level in the rostro-caudal dimension (y coordinate) is given in millimetres for each section.



Figure 2.10. Sagittal sections from the right hemisphere of the MRI brain volume (case 2) with the sulci of interest identified. The level in the medio-lateral dimension (x coordinate) is given in millimetres for each section.



e



Figure 2.11. Dorsal termination of the postcentral sulcus (PoCS). Superficial connection of the postcentral sulcus with the lateral fissure (LF) and the superior longitudinal fissure (SLF).



Figure 2.12. Patterns formed by the postcentral sulcal complex (PoCS) and the horizontal segment of the intraparietal sulcus (IPS) on the surface of the brain. In (**a**) a visible gyrus separates a continuous PoCS from IPS. IPS and PoCS do not merge. In (**b**) a gyrus between PoCS and IPS is submerged. IPS merges with the continuous PoCS on the surface of the brain only. In (**c**) a gyrus between sPoCS, iPoCS and IPS is visible on the surface of the brain. IPS and PoCS do not merge. In (**d**) a gyrus between sPoCS and IPS is visible on the surface of the brain. A gyrus between iPoCS and IPS is submerged. IPS merges with the iPoCS on the surface of the brain. A gyrus between iPoCS and IPS is visible on the surface of the brain. A gyrus between iPoCS and IPS is visible on the surface of the brain. A gyrus between iPoCS and IPS is visible on the surface of the brain. A gyrus between sPoCS and IPS is visible on the surface of the brain. A gyrus between sPoCS and IPS is visible on the surface of the brain. A gyrus between sPoCS and IPS is visible on the surface of the brain. A gyrus between sPoCS and IPS is submerged. IPS merges with the sPoCS on the surface of the brain only. In (**f**) a gyrus between mPoCS and IPS is submerged. mPoCS merges with IPS on the surface of the brain only.



Figure 2.13. Patterns formed by the ascending branch of the cingulate sulcus (CingS) and the postcentral sulcus (PoCS). In (**a**) CingS terminates anterior to PoCS or inside a bifurcated dorsal end of PoCS. In (**b**) CingS terminates posterior to PoCS.





Figure 2.14. Sulci located dorsal (dS) to the postcentral sulcus (PoCS) on the lateral surface of the brain which cross (**a-d**) and do not cross (**c-f**) the superior margin of hemisphere. Ascending branch of the cingulate sulcus (CingS) is not visible on the lateral surface of the brain.


Figure 2.15. The transverse postcentral sulcus (TrS). In (**a**) the postcentral sulcus (PoCS) is divided into two segments, the superior and inferior postcentral sulci (sPoCS and iPoCS) by a submerged gyrus. The dorsal end of TrS is located at the 2nd submerged pli de passage. In (**b**) PoCS is continuous. The dorsal end of TrS is at the level of the 1st submerged pli de passage. In (**c**) PoCS is continuous. The dorsal end of TrS is located at the 2nd submerged pli de passage. In (**d**) PoCS is divided into 2 segments (sPoCS and iPoCS) by a submerged gyrus. The dorsal end of TrS is at the level of the 3rd submerged pli de passage.

# **Chapter Three**

# 3. Morphological Patterns of the Intraparietal Sulcus and the Anterior Intermediate Parietal Sulcus of Jensen in the Human Brain

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# 3.1 Prelude

In the first anatomical study (Chapter Two), the morphology of the postcentral sulcus, which provides the posterior boundary of the anterior parietal lobe was investigated systematically in a large sample of human brains. The results demonstrated that the postcentral sulcus is composed of distinct sulcal segments, which are separated by gyral passages in the depth of the brain (Figures 2.2, 2.8j-k). Most commonly, the postcentral sulcus has a bifurcated dorsal termination and the marginal branch of the cingulate sulcus terminates anterior to it or between its branches (Figures 2.11, 2.13). The findings of our morphological study presented in Chapter Two demonstrated a frequent occurrence of a previously poorly known sulcus, named the transverse postcentral sulcus, anterior to the postcentral sulcus on the inferior postcentral gyrus (Figure 2.15) and suggested that it belongs to the postcentral sulcal complex. Despite a commonly observed association between the postcentral sulcus and the anterior intraparietal sulcus on the surface of the brain, these two sulci are always separated by a gyral passage in the fundus (Figure 2.4i-j). The aim of the second anatomical study (Chapter Three) was to examine in detail the variability of the sulcal segments that make up the intraparietal sulcus and the relation of these sulcal segments to a less well known sulcus that is related to the intraparietal sulcus, namely the anterior intermediate parietal sulcus of Jensen. The intraparietal sulcus and the anterior intermediate parietal sulcus of Jensen were studied thoroughly in the coronal, horizontal and sagittal sections in 80 human hemispheres scanned with MRI scanner. In addition, the patterns formed by the intraparietal sulcus, the anterior intermediate parietal sulcus of Jensen and the three caudal branches of the superior temporal sulcus, that enter the inferior parietal lobule and approach the intraparietal sulcus, were examined on an individual subject basis.

#### **3.2 Abstract**

Distinct parts of the intraparietal sulcal cortex contribute to sensorimotor integration and visual spatial attentional processing. A detailed examination of the morphological relations of the different segments of the complex intraparietal sulcal region in the human brain in standard stereotaxic space, which is a prerequisite for detailed structure-to-function studies, is not available. This study examined the intraparietal sulcus (IPS) and the related sulcus of Jensen in magnetic resonance imaging brain volumes registered in the Montreal Neurological Institute stereotaxic space. It was demonstrated that the IPS is divided into two branches: the anterior ramus and the posterior ramus of the IPS, often separated by a submerged gyral passage. The sulcus of Jensen emerges between the anterior and posterior rami of the IPS and its ventral end is positioned between the first and second caudal branches of the superior temporal sulcus. In a small number of brains, the sulcus of Jensen may merge superficially with the first caudal branch of the superior temporal sulcus. The above morphological findings are discussed in relation to previously reported functional neuroimaging findings and provide the basis for future exploration of structure-to-function relations in the posterior parietal region of individual subjects.

#### **3.3 Introduction**

The intraparietal sulcus (IPS), the main sulcus on the lateral surface of the posterior parietal lobe, was first described in the middle of the nineteenth century by Turner (1866). In the human brain, it is a complex sulcus and its functional organization is not well understood. By contrast, in the monkey, it is a relatively simple furrow and its functional organization has been clarified by elegant single neuron recording studies. The anterior intraparietal sulcal cortex (area AIP) has been shown to be involved in complex sensorimotor integration (Taira et al., 1990; Sakata et al., 1995; Murata et al., 2000; Baumann et al., 2009), while its more central and caudal parts (lateral, medial and caudal intraparietal areas) play critical roles in visuo-spatial and attentional processing (Blatt et al., 1990; Barash et al., 1991a, 199b; Shikata et al., 1996; Snyder et al., 1997; Batista et al., 1999; Tsutsui et al., 2001, 2003; Eskandar and Assad, 2002; Bisley and Goldberg, 2003). More recently, there have been several attempts to explore the functional organization of the intraparietal sulcal cortex in the human brain using functional neuroimaging methods (Binkofski et al., 1998; Corbetta et al., 1998; Connolly et al., 2000; Astafiev et al., 2003; Koyama et al., 2004; Frey et al., 2005; Shikata et al., 2008; Cavina-Pratesi et al., 2010; Marangon et al., 2011; for reviews see Culham and Valyear, 2006; Medendorp et al., 2011; Vesia and Crawford, 2012). Such studies face a major problem, namely the fact that, in the human brain, the sulcal segments of the IPS exhibit considerable variability. It is clear that understanding the morphological variability and relationships between the various intraparietal segments and the patterns formed with the nearby sulci is critical for detailed exploration of structure-to-function relations in the parietal region of the human brain, especially in individual brains. Several studies have now demonstrated that detailed understanding of the local sulcal morphology and its variability across brains is a pre-requisite for the establishment of precise relations between cortical representations and the specific sulcal anatomy in individual subjects (Amiez et al., 2006; Segal and Petrides, 2013; Amiez and Petrides, 2014). Structure-to-function relations that remained obscure from functional neuroimaging studies reporting only the average location of functional activity in standard stereotaxic space were uncovered when activity was examined in individual subjects following a detailed understanding of the local morphological variability (Amiez et al., 2006; Segal and Petrides, 2013; Amiez and Petrides, 2014).

Although the IPS is frequently represented diagrammatically as a single continuous horizontally-oriented sulcus, even a brief examination of the posterior parietal region in the human brain reveals a collection of sulci of varying lengths and orientations indicating that the

IPS is a complex of sulcal segments (Cunningham, 1892; Retzius, 1896; Connolly, 1950; Petrides, 2012). Furthermore, there is a poorly studied short sulcus, the anterior intermediate parietal sulcus of Jensen (Petrides, 2012), also referred to as the sulcus intermedius (Jensen, 1870) or sulcus intermedius primus of Jensen (Economo and Koskinas, 1925), which appears to emerge out of the inferior bank of the IPS and may have important functional implications. The limited information available about the structure of the IPS complex and its inter-individual variability, as well as the sulcus of Jensen, is based on visual inspection of the sulci on the surface of the brain (Ono et al., 1990). In order to advance understanding of the IPS patterns, it is necessary to examine the depth of the sulci in a continuous series of two-dimensional sections. Such an approach reveals discontinuities by gyral passages located in the sulcal depth and, therefore, not visible from surface inspection of the brains (Zlatkina and Petrides, 2010). This study examined the morphology of the intraparietal sulcal region in continuous serial twodimensional sections in order to establish the details of the morphological variations of the IPS and clarify the relationship between its segments, the sulcus of Jensen, and the nearby sulci, such as the three caudal branches of the superior temporal sulcus that enter the inferior parietal lobule and approach the IPS. The Magnetic Resonance Imaging (MRI) brain volumes used were registered in the Montreal Neurological Institute (MNI) proportional stereotaxic space which is the most frequently used framework to describe the location of structural and functional neuroimaging findings.

#### 3.4 Materials and methods

The methodology is similar to that in the study of Zlatkina and Petrides (2010). The data are based entirely on the examination of continuous series of sections in the region of interest. The three-dimensional surface reconstructions provided in this article are examples of a small number of cases in which the submerged gyral passages were large enough to be visualized by "inflating" the brain volumes and, as such, could be used to provide the reader with the outward appearance of these discontinuities that are most often found in the depth of the IPS. Note also that the paroccipital sulcus, which is sometimes discussed in relation to the IPS, is not examined in this study as it is considered an independent sulcus found in the occipital region of the brain (Petrides, 2012).

# Subjects

The sample consisted of 24 male (mean age 23.3 years, SD 4.05) and 16 female (mean age 24.6 years, SD 5.6) MRI brain volumes obtained from the International Consortium for Brain Mapping (ICBM) database (www.loni.usc.edu/ICBM; Mazziotta et al., 1995a, 1995b, 2001). The ICBM project, which is supported by the National Institute of Biomedical Imaging and Bioengineering, is the result of efforts of co-investigators from University of California, Los Angeles (UCLA), MNI, University of Texas at San Antonio and the Institute of Medicine, Juelich/Heinrich Heine University—Germany. The identification numbers of the brain volumes used in this article are the following: mni\_0100–mni\_0103, mni\_0107–mni\_0112, mni\_0114–mni\_0121,mni\_0123, mni\_0125, mni\_0131, mni\_0133, mni\_0135, mni\_0137–mni\_0141, mni\_0144, mni\_0146, mni\_0148–mni\_0153, mni\_0200, mni\_0201, mni\_0203, mni\_0204.

#### Magnetic Resonance Imaging

The MRI scans were performed on a Philips Gyroscan 1.5T superconducting magnet system. A three-dimensional spoiled gradient echo acquisition sequence was used to collect 178 contiguous sagittal T<sub>1</sub>-weghted images (TR=18 ms, TE=10 ms, flip angle=30°, 256 x 256 matrix, 256 mm FOV, voxel size isotropic 1 mm3) covering the head from ear to ear. The intensity correction for non-uniformity was performed with the help of the N3 program (Sled et al., 1998). The mritotal program from the mni\_autoreg package was applied to estimate the 9 parameter linear transformation required to map the MRI data into the MNI stereotaxic space (Collins et al., 1994). Each MRI volume was resampled using a tri-linear kernel onto a 1-mm grid in the stereotaxic space.

## Segmentation of intrasulcal gray matter and surface renderings

The postcentral sulcus, the intraparietal sulcus, the anterior intermediate parietal sulcus of Jensen, the sulcus of Brissaud and the paroccipital sulcus were identified and traced manually on individual MRI brain volumes with the help of an interactive imaging software package DISPLAY (MacDonald, 1996). The sulci of interest were examined in coronal, horizontal, and sagittal sections at 1-mm intervals in order to determine their direction, extent, and patterns formed with each other.

Three-dimensional surface renderings of individual brains were acquired using two different types of software. CIVET image processing pipeline version 1.1.12 available via the

CBRAIN interface (http://mcin-cnim.ca/neuroimagingtechnologies/cbrain/) was used to extract the cortical surfaces from the MINC files containing the individual MRI brain scans (Ad-Dab'bagh et al., 2006). Additionally, Caret v.5.5 software available at <a href="http://brainvis.wustl.edu/was">http://brainvis.wustl.edu/was</a> used to produce three-dimensional reconstructions of the same individual brains and slightly 'inflate' them (2 smoothing iterations, inflation factor equal to 1) to reveal the deep or submerged parts of sulci, not commonly seen from the surface of the brain (Van Essen, 2005).

# Conversion of stereotaxic space coordinates

In some of the functional neuroimaging studies, Talairach and Tournoux (1988) stereotaxic space coordinates were provided rather than MNI coordinates. In these cases, the Talairach and Tournoux coordinates were converted to MNI space coordinates using the Signed Differential Method provided at <u>http://www.sdmproject.com/</u>. The obtained MNI space coordinates of the region of interest were projected onto an average brain template (ICBM152 non-linear 6th generation model available from <u>http://www.bic.mni.mcgill.ca</u>; Grabner et al., 2006).

#### Supplementary Material

Supplementary Material consisting of Tables and Figures is provided in Appendix B of this thesis.

# **3.5 Results**

It is important to note that, in this article, the IPS does not include the paroccipital sulcus which is an independent sulcus that has sometimes been referred to as a posterior extension of the IPS (see Petrides, 2012).

# Rami of the intraparietal sulcus and their connection with the paroccipital sulcus

The IPS extends posterior to the postcentral sulcal complex as far as the sulcus of Brissaud and the anterior part of the paroccipital sulcus (Figure 3.1). Investigation of the IPS in continuous serial two-dimensional sections demonstrated that, in the majority of hemispheres, it could be divided, by a gyral passage, into two main branches, the anterior ramus and the posterior ramus (60% of the left hemispheres and 67.5% of the right hemispheres; Figures 3.2bd, 3.3; supplementary material, Figures S1b,d, S2, S4). This gyral passage is either submerged (Figures 3.2b-c, 3.3a; supplementary material, Figures S1d, S2, S4) or visible from the surface of the brain (Figure 3.2d). Much less frequently, the IPS was composed of three rami (10% of the left hemispheres and 7.5% of the right hemispheres). In a number of cases, the subdivisions of the IPS could not be determined and it was, therefore, treated as a single uninterrupted sulcus (30% of the left hemispheres and 25% of the right hemispheres; Figure 3.2a; supplementary material, Figures S1a,c,e, S5-S8).

In general, the gyral passages separating the IPS into rami by linking its banks were most frequently submerged and not visible from the reconstructed brain surface (84.4% of all passages in the left and 63.6% of all passages in the right hemisphere; Figure 3.3a; supplementary material, Figures S1d, S4). When present, these submerged gyral passages were generally more pronounced on the inferior bank of the IPS in close proximity to the dorsal terminations of the caudal superior temporal sulcus (supplementary material, Figure S2). In a smaller proportion of cases, the gyral passages were of considerable size and connected the banks of the IPS from the fundus to the surface, resulting in several disconnected and isolated sulcal units (15.6% of all passages in the left and 36.4% of all passages in the right hemisphere; Figure 3.2d).

In 50% of the left hemispheres and 65% of the right hemispheres, the posterior end of the IPS was separated from the paroccipital sulcus by a gyral passage visible from the reconstructed brain surface (Figure 3.2a,b; supplementary material, Figure S1b,e). In the remainder of the hemispheres, the posterior part of the IPS appeared to merge with the paroccipital sulcus on the surface of the brain, but these two sulci were still separated by a small gyral passage in the sulcal depth (Figure 3.3a-c; supplementary material, Figure S4). Superficial connection between the posterior ramus of the IPS and the paroccipital sulcus was sometimes completed with the help of a small tertiary sulcus (15% of the left and 7.5% of the right hemispheres).

A previous investigation of the IPS complex from the surface of the brain by Ono et al. (1990) reported that the IPS complex is continuous in 72% of the left and 28% of the right hemispheres, and it is separated into two segments in 28% of the left and 68% of the right hemispheres (p. 67 in Ono et al., 1990). However, it should be noted that the two segments in the Ono et al. (1990) study refer to the IPS proper (examined here) and the paroccipital sulcus, an independent sulcus that is sometimes treated as a component of the IPS complex. Thus, the two rami of the IPS reported here (and their percentages) refer to the IPS proper and not the IPS and the paroccipital sulcus.

The supramarginal sulcus was observed in the majority of left and right hemispheres on the supramarginal gyrus (87.5% of the left and 85% of the right hemispheres). It was either present as a set of dimples or a slightly more pronounced sulcus (Figures 3.2, 3.3a-c; supplementary material, Figures S1, S4, S5, S7).

#### Anterior intermediate parietal sulcus of Jensen

The anterior intermediate parietal sulcus of Jensen (also, the sulcus of Jensen) is a short sulcus which emerges out of the inferior bank of the IPS at the posterior end of the supramarginal gyrus. Systematic examination of continuous serial two-dimensional sections demonstrated the sulcus of Jensen in 67.5% of the left and 80% of the right hemispheres.

In 40% of the left and 70% of the right hemispheres examined, the sulcus of Jensen emerged from the main stem of the IPS as a deep inferiorly-directed side-branch with no separation between the main stem and the side-branch (i.e. with no gyral passage separating them; Figure 3.2a; supplementary material, Figures S1a, S3a). In cases in which the sulcus of Jensen was underdeveloped, it appeared as a notch on the surface of the brain (12.5% of the left and 5% of the right hemispheres; Figure 3.2b; supplementary material, Figures S1b, S3b).

In a smaller number of cases, the sulcus of Jensen consisted of a shallow sulcus which was attached to the main stem of the IPS, and the connection between the two sulci was observed in a number of horizontal sections (15% of the left and 5% of the right hemispheres; Figures 3.2c, 3.3; supplementary material, Figures S1c-d, S3c, S4-S8).

Frequently, the sulcus of Jensen was located between the first and second caudal branches of the superior temporal sulcus (57.5% of the left and 62.5% of the right hemispheres; Figure 3.2a-c; supplementary material, Figures S1a-d, S3a-c). In a smaller number of cases, the sulcus of Jensen merged superficially with the first caudal branch of the superior temporal sulcus (7.5% of the left and 17.5% of the right hemispheres; Figure 3.2d; supplementary material, Figures S1e, S3d). However, the two sulci were separated in the depth by a submerged gyral passage. Only in 2.5% of the left hemispheres, the sulcus of Jensen was located anterior to the first caudal branch of the superior temporal sulcus.

In 42.5% of the left hemispheres, the sulcus of Jensen and both rami of the IPS could be clearly identified. In 32.5% of these left hemispheres, the sulcus of Jensen was associated with the anterior ramus of the IPS. In 55% of the right hemispheres, both rami of the IPS and the sulcus of Jensen were observed. In these cases, the sulcus of Jensen was associated with either

the anterior (27.5% of the right hemispheres; Figure 3.2d; supplementary material, Figure S1d) or the posterior ramus of the IPS (27.5% of the right hemispheres; Figure 3.2b,c; supplementary material, Figure S1b). When the sulcus of Jensen was associated with the posterior ramus of the IPS, it was located posterior to the gyral passage separating the anterior ramus from the posterior ramus of the IPS.

Note that, in a few of the 80 hemispheres examined (5% of the left and 7.5% of the right hemispheres), the classification of the sulcus of Jensen was ambiguous, and therefore these cases were excluded when calculating the percentage of occurrence of this sulcus. In over a quarter of all examined hemispheres a shallow sulcus or a set of dimples not connected with the IPS were observed between the first and second caudal branches of the superior temporal sulcus (27.5% of the left and 37.5% of the right hemispheres; Figure 3.2a,d; supplementary material, Figure S1e).

#### **3.6 Discussion**

This study investigated the morphological variations of the IPS and the sulcus of Jensen, as well as how the latter sulcus relates to the three caudal branches of the superior temporal sulcus that invade the inferior parietal lobule and approach the IPS. Examination of the depth of the sulci based on a continuous series of sections demonstrated a number of novel facts. First, despite notable inter-individual variability, the IPS can be clearly divided into two main parts (an anterior and a posterior ramus) by a gyral passage that is either submerged (Figures 3.2b, c, 3.3a; supplementary material, Figures S1d, S2, S4) or visible from the surface of the brain (Figure 3.2d) in the majority of cerebral hemispheres. This subdivision of the IPS proper into two rami should not be confused with the distinction made by Ono et al. (1990) between the IPS proper and the paroccipital sulcus (e.g. see Figure on p.67 in Ono et al., 1990; see also Results section of this article). The paroccipital sulcus is an independent sulcus that is sometimes referred to as a branch of the IPS (Petrides, 2012). As demonstrated here, in over half of all cases the posterior ramus of the IPS and the paroccipital sulcus are clearly separated by a gyral passage visible from the surface of the brain (Figure 3.2a,b; supplementary material, Figure S1b,e). Second, this study demonstrated three main patterns of the relation between the sulcus of Jensen and the IPS. The sulcus of Jensen emerges out of the inferior bank of the IPS, most frequently, as a deep inferiorly-directed branch of the IPS (Figure 3.2a; supplementary material, Figures S1a, S3a); less frequently, it appears as a notch (Figure 3.2b; supplementary material, Figures S1b, S3b) or a shallow sulcus merging with the IPS (Figures 3.2c, 3.3; supplementary material, Figures S1c,d,

S3c, S4-S8). Third, the relationship of the sulcus of Jensen with the three caudal branches of the superior temporal sulcus that invade the inferior parietal lobule and approach the IPS was defined. Most commonly the sulcus of Jensen is located between the first and second caudal branches of the superior temporal sulcus but in some hemispheres it connects superficially with the termination of the first caudal branch of the superior temporal sulcus (7.5% of the left and 17.5% of the right hemispheres; Figure 3.2d; supplementary material, Figures S1e, S3d). In such cases, failure to examine continuous serial sections in detail and identify the first caudal branch of the superior temporal sulcus in the inferior parietal lobule (for instance, see p. 16 in Ono et al., 1990) can lead to confusion of the caudalmost part of the first branch of the superior temporal sulcus of Jensen (for instance, see Figure 9.10C on p.71 in Ono et al., 1990), which might have important functional consequences. Finally, the availability of the anatomical data in the MNI stereotaxic space has allowed us to relate the morphological findings to functional neuroimaging data, which is impossible to do with data that are not presented in the standard stereotaxic space (Ono et al., 1990). The functional significance of the main morphological findings of this study is discussed below.

# The anterior and the posterior rami of the IPS may be the homologues in the human brain of areas AIP and LIP/PRR originally defined in the macaque monkey brain

A major finding of this study has been the demonstration that, in the majority of cases, the IPS consists of two main rami and, furthermore, that the anterior ramus extends anterior to the sulcus of Jensen, whereas the posterior ramus extends posterior to it. In the macaque monkey, electrophysiological studies have identified a number of functional regions on the banks and fundus of the IPS, which are often referred to as the anterior, lateral and caudal intraparietal areas (Grefkes and Fink, 2005). The anterior intraparietal area (AIP) is located in the anterior part of the IPS and its neuronal activity has been linked to grasping with the hand (Sakata et al., 1995; Murata et al., 2000; Baumann et al., 2009). By contrast, neurons in the lateral intraparietal area (LIP), which is located on the lateral bank of the IPS posterior to area AIP, have saccade-related activity, including ongoing and anticipated saccades, and their activity is modulated by visual attention (Blatt et al., 1990; Barash et al., 1991a, 1991b; Snyder et al., 1997; Eskandar and Assad, 2002; Bisley and Goldberg, 2003). The parietal reach region (PRR) is located postero-medial to area LIP in the medial bank of the IPS, it includes the medial intraparietal area (MIP) anteriorly and it is involved in reaching arm movements (Snyder et al., 1997; Batista et al.,

1999). The limited available evidence suggests that the border between the AIP and LIP regions in the macaque monkey may be placed at the same antero-posterior level as the border between areas PF/PFG and PG (or area 7b, corresponding to PF/PFG, and area 7a, corresponding to area PG, in an older terminology used in macaque monkey studies) on the free surface of the inferior parietal lobule (Andersen et al., 1990; Durand et al., 2007; Gharbawie et al., 2011; Nelissen and Vanduffel, 2011). A systematic investigation combining single-cell recording in areas AIP and LIP with cytoarchitectonic analysis conducted in the same animals would be necessary to confirm this relation.

In the human brain, the cortex within the anterior ramus of the IPS, which lies anterior to the sulcus of Jensen and forms the medial border of areas PF/PFG of the supramarginal gyrus (Economo and Koskinas, 1925), may be the homologue of area AIP. By contrast, the posterior ramus, which lies posterior to the sulcus of Jensen and forms the medial border of area PG (Economo and Koskinas, 1925), may be the homologue of area LIP. The human homologue of area PRR may include the cortical region medial to the posterior ramus of the IPS, extending as far as the parieto-occipital fissure. Thus, the sulcus of Jensen may be an important division of the anterior intraparietal sulcal cortex, processing information related to high-level sensorimotor control and the cortex within the posterior IPS contributing to visuo-spatial attentional processing. The available functional neuroimaging data discussed below are consistent with the above proposal.

The issue of the cortical topography of the homologues of areas AIP, PRR and LIP in the human brain has been addressed in functional neuroimaging studies investigating activation foci in the parietal cortex during the performance of hand movements (grasping, reaching, or pointing), saccadic eye movements and visuo-spatial attentional processes (Binkofski et al., 1998; Corbetta et al., 1998; Connolly et al., 2000; Sereno et al., 2001; Astafiev et al., 2003; Medendorp et al., 2003; Koyama et al., 2004; Frey et al., 2005; Shikata et al., 2008; Peeters et al., 2009; Bernier and Grafton, 2010; Beurze et al., 2010; Cavina-Pratesi et al., 2010; Jacobs et al., 2010; Gallivan et al., 2011; Marangon et al., 2011; for reviews, see Culham and Valyear, 2006; Medendorp et al., 2011; Vesia and Crawford, 2012; also see supplementary material, Tables S1-S3). We projected the average coordinates of the putative AIP, LIP and PRR activity reported in these functional neuroimaging studies onto an average brain template (ICBM152 non-linear 6th generation model; Grabner et al., 2006) and examined the location of the peaks with respect to the IPS morphology as established in this study. Functional activity related to

saccadic eye movements and attentional processing, reflecting putative area LIP, and activity related to pointing and reaching hand movements in the putative area PRR were observed in the posterior ramus of the IPS that lies caudal to the sulcus of Jensen. By contrast, activity related to grasping hand movements, reflecting putative area AIP, was located in the anterior ramus of the IPS (anterior to the sulcus of Jensen) and close to the junction of the IPS with the postcentral sulcus, not only in the average-group data (Jacobs et al., 2010; Marangon et al., 2011; also see Table 1 in Frey et al., 2005; and see Table 1 in Shikata et al., 2008), but also consistently observed in the individual subjects (see Figure 4 in Frev et al., 2005; Shikata et al., 2008; Cavina-Pratesi et al., 2010). Shikata et al. (2008) localize the AIP homologue in the human brain at x = -39.6, y = -40.1, z = 44.7 and x = 41.2, y = -40.6, z = 50.2 (MNI space), and similar coordinates have been provided by Marangon et al. (2011), x = -42.2, y = -43.1, z = 51.7 and x =38.7, y = -35.7, z = 44.8. These coordinates place the activity close to the gyral passage separating the postcentral sulcus from the anterior ramus of the IPS (Zlatkina and Petrides, 2010). If the narrow gyral passage is visible from the surface of the brain (Figure 3.2b-d), then the activity appears to be located within the inferior branch of the postcentral sulcus, located ventral to the IPS and the anterior ramus of the IPS. When this gyral passage is submerged (Figure 3.2a), the functional activity may be found at the intersection of the postcentral sulcus and the IPS, and may extend antero-ventrally into the inferior branch of the postcentral sulcus. Thus, it remains for future research to establish whether parts of the homologue of area AIP in the human brain may extend to the cortex within the inferior branch of the postcentral sulcus.

Of particular interest is a neuroimaging experiment (Koyama et al., 2004) that used the same saccade paradigm both in humans and macaque monkeys, namely the species in which area LIP has been defined physiologically. The results suggested a functional correspondence between the dorsal subdivision of area LIP in the monkey with the posterior IPS region in the human brain (Koyama et al., 2004). When we projected the MNI space coordinates reported by Koyama et al. (2004) in the human subjects (x = -22, y = -62, z = 60 and x = 22, y = -62, z = 60) onto an average brain template (ICBM152 non-linear 6th generation model; Grabner et al., 2006), we observed that this putative homologue of area LIP in the human brain occurs close to the posterior ramus of the IPS near the inferior termination of the superior parietal sulcus. Other neuroimaging investigations consistently point to the posterior ramus of the IPS (i.e. posterior to the sulcus of Jensen) in the vicinity of the ventralmost point of the superior parietal sulcus as the locus of activation related to saccades, potentially reflecting putative area LIP (Corbetta et al.,

1998; Sereno et al., 2001; Astafiev et al., 2003; Medendorp et al., 2003; Shikata et al., 2008; see also supplementary material, Tables S1, S2). However, we must emphasize here that the detailed relations between sulcal morphology and LIP and PRR can only be understood from future studies that should explicitly examine such relations at the individual subject level in the context of individual morphological variation (Amiez et al., 2006; Segal and Petrides, 2013; Amiez and Petrides, 2014). The anatomical findings of this study are a necessary pre-requisite for such an examination.

Functional neuroimaging research suggests that the homologue of PRR in the human brain may involve, as in the macaque monkey, the superior parietal lobule, including the adjacent cortex in the IPS and the parieto-occipital fissure (Connolly et al., 2000; Astafiev et al., 2003; Bernier and Grafton, 2010; Beurze et al., 2010; Leoné et al., 2014; for review, see Vesia and Crawford, 2012; also see supplementary material, Tables S2, S3). There is evidence that on the lateral surface of the posterior parietal cortex neural networks involved in planning and execution of saccades (putative area LIP homologue) and reaching and pointing hand movements (putative PRR homologue) overlap significantly, suggesting the absence of distinct effectorspecific regions (see supplementary material, Table S2 and compare supplementary material, Tables S1, S3). Based on the descriptions and stereotaxic space coordinates provided in the literature (see supplementary material, Tables S2, S3), the human homologue of PRR may be located on the medial bank of the posterior ramus of the IPS and also medial to it in the superior parietal lobule. Although the individual-subject analysis by Bernier and Grafton (2010) and Medendorp et al. (2003) demonstrated that the putative homologue of PRR is located "within a small sulcus running medially from the intraparietal sulcus" (p. 6211 in Medendorp et al., 2003) or "slightly dorsal to the medial branch of IPS" (p. 778 in Bernier and Grafton, 2010), future morphological examination of the superior parietal region is necessary to establish whether the sulcus the authors are referring to is an independent sulcus, such as the superior parietal sulcus, or a part of the IPS complex extending into the superior parietal lobule.

The available evidence in the monkey suggests that the posterior border of area LIP with area CIP is located in the most posterior part of the IPS before it merges with the lunate and parieto-occipital sulci (Tsutsui et al., 2001, 2003). In the human brain, Shikata et al. (2008) localize the intraparietal region involved in saccadic eye movements (putative area LIP) at x = -25.6, y = -57, z = 58.4 and x = 26.1, y = -59.4, z = 57.6. These MNI space coordinates would place LIP in the posterior ramus of the IPS as defined in this study. Area CIP in the human brain

has been placed by Shikata et al. (2008; pp. 416, 419) in a so-called "side branch of the posterior intraparietal sulcus" anterior to the parieto-occipital fissure. The MNI space coordinates (x = -15.5, y = -66.3, z = 58.4 and x = 21, y = -65.7, z = 55.9) and Figure 2 (p. 415) provided by Shikata et al. (2008) allowed us to interpret the "side branch of the posterior intraparietal sulcus" as the sulcus of Brissaud. This sulcus appears at the intersection of the posterior end of the IPS and the paroccipital sulcus, and therefore the available information localizes the putative area CIP in the human brain to this intersection of the posterior end of the IPS with the paroccipital sulcus (Figure 3.1). We therefore interpret the data provided by Shikata et al. (2008) for the human homologue of area LIP to be the posterior ramus of the IPS until its connection with the paroccipital sulcus. Beyond this point starts the CIP region. This is consistent with the suggestion by Orban et al. (2006) that the human LIP homologue lies in the IPS until its confluence with the parieto-occipital fissure, and therefore, according to the current morphological findings, it would consist of the posterior ramus of the IPS and its confluence with the paroccipital sulcus.

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#### **3.8 Data accessibility**

Human MRI brain scans from the International Consortium for Brain Mapping (ICBM) database used in the current article are disseminated by the Laboratory of Neuro Imaging at the University of Southern California (http://www.loni.usc.edu/). The identification numbers of the MRI scans are provided in the Methods section of this article.

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# 3.10 Figures



Figure 3.1. Schematic representation of the parietal sulci of interest on the lateral surface of the human brain. Abbreviations: aipsJ, anterior intermediate parietal sulcus of Jensen; CingS, marginal branch of the cingulate sulcus on the lateral surface of the brain; CS, central sulcus; cSTS1, first caudal branch of the superior temporal sulcus; cSTS2, second caudal branch of the superior temporal sulcus; cSTS3, third caudal branch of the superior temporal sulcus; iPoCS, inferior branch of the postcentral sulcus; IPS, intraparietal sulcus (main horizontal part of the intraparietal sulcus); IPS-PO, paroccipital sulcus, often considered as the paroccipital part of the intraparietal sulcus; LF, lateral fissure; pips, posterior intermediate parietal sulcus; POF, parieto-occipital fissure; sB, sulcus of Brissaud; SmgS, supramarginal sulcus; sPoCS, superior branch of the postcentral sulcus; STS, superior temporal sulcus; STS, superior temporal sulcus.



Figure 3.2. Demonstration of the anterior intermediate parietal sulcus of Jensen (aipsJ) in the hemispheres of different subjects. (**a**) aipsJ is clearly a downward branch of the intraparietal sulcus (IPS); (**b**) aipsJ is a simple notch; (**c**) aipsJ is a shallow sulcus merging with the IPS; (**d**) aipsJ connects superficially with the first caudal branch of the superior temporal sulcus (cSTS1). Abbreviations: aipsJ, anterior intermediate parietal sulcus of Jensen; CS, central sulcus; cSTS1, first caudal branch of the superior temporal sulcus; cSTS2, second caudal branch of the superior

temporal sulcus; cSTS3, third caudal branch of the superior temporal sulcus; iPoCS, inferior branch of the postcentral sulcus; IPS, intraparietal sulcus (main horizontal part of the intraparietal sulcus); IPSa, anterior ramus of the horizontal part of the intraparietal sulcus; IPSp, posterior ramus of the horizontal part of the intraparietal sulcus; IPS-PO, paroccipital sulcus, often considered as the paroccipital part of the intraparietal sulcus; LF, lateral fissure; PoCS, postcentral sulcus; POF, parieto-occipital fissure; SmgS, supramarginal sulcus; sPoCS, superior branch of the postcentral sulcus.



Figure 3.3. Horizontal and coronal sections from the right hemisphere of one subject showing two rami of the intraparietal sulcus (IPS) and the anterior intermediate parietal sulcus of Jensen (aipsJ). (**a-c**) Horizontal sections. The level in the dorso-ventral dimension (*z* coordinate) is provided in millimetres for each section; (**d-f**) Coronal sections. The level in the anterior-posterior dimension (*y* coordinate) is provided in millimetres for each section; (**d-f**) Coronal sections. The level in the anterior-posterior dimension (*y* coordinate) is provided in millimetres for each section. Abbreviations: aipsJ, anterior intermediate parietal sulcus of Jensen; CS, central sulcus; cSTS1, first caudal branch of the superior temporal sulcus; cSTS2, second caudal branch of the superior temporal sulcus; iPSa, anterior ramus of the horizontal part of the intraparietal sulcus; IPSp, posterior ramus of the horizontal part of the intraparietal sulcus, often considered as the paroccipital part of the

intraparietal sulcus; PoCS, postcentral sulcus; POF, parieto-occipital fissure; SmgS, supramarginal sulcus; SPS, superior parietal sulcus.

# **Chapter Four**

# 4. The Postcentral Sulcal Complex and the Transverse Postcentral Sulcus and their Relation to Sensorimotor Functional Organization

Zlatkina, V., Amiez, C., & Petrides, M. (2015). The postcentral sulcal complex and the transverse postcentral sulcus and their relation to sensorimotor functional organization. The manuscript has been submitted to the *European Journal of Neuroscience* and it is currently under review (at the "revise and resubmit" stage).

# 4.1 Prelude

The postcentral sulcus lies at the boundary between the anterior somatosensory region of the parietal lobe, investigated in detail in the first study on the morphology of the postcentral gyrus (Chapter Two), and the posterior part of the parietal lobe that is explored in our second study on the morphology of the intraparietal sulcal region (Chapter Three). In Chapter Two, we have shown that the postcentral sulcus is a complex of distinct sulcal segments, which extend from the medial edge of the hemisphere to the lateral fissure (Figures 2.2) and form the posterior border of the topographically organized sensorimotor cortex. We have conducted a functional Magnetic Resonance Imaging study (Chapter Four) in order to explore a possible relationship between the somatomotor representations and the specific segments of the postcentral sulcal complex. In this study, movements of the foot, leg, arm, hand, tongue and mouth, and eye blinking performed by subjects during functional MRI scanning elicited changes in activity in the central region and the location of activity peaks was related to the position of the segments of the postcentral sulcus in the MNI space on a subject-per-subject basis. In addition, the location of functional activity elicited by the oral (mouth and tongue) movements was related to the location of the transverse postcentral sulcus. The aim of our neuroimaging study was to explore the possibility that the arrangement of somatomotor representations in the anterior parietal lobe may be predicted from the local sulcal morphology in individual subjects.

#### 4.2 Abstract

It has been demonstrated that the postcentral sulcus, which forms the posterior boundary of the sensorimotor region, is a complex of distinct sulcal segments. Although the general somatotopic arrangement in the human sensorimotor cortex is relatively well known, we do not know whether the different segments of the postcentral sulcus relate in a systematic way to the sensorimotor functional representations. Participants were scanned with functional magnetic resonance imaging while they made movements of different body parts and the location of functional activity was examined on a subject-by-subject basis with respect to the morphological features of the postcentral sulcus. The findings demonstrate that the postcentral sulcus of each subject may be divided into five segments and there is a tight relationship between sensorimotor representations of different body parts and specific segments of the postcentral sulcus. The results also addressed the issue of the transverse postcentral sulcus, a short sulcus that is present within the ventral part of the postcentral gyrus in some brains. It was shown that, when present, this sulcus is functionally related to oral (mouth and tongue) sensorimotor representation. When this sulcus is not present, the inferior postcentral sulcus which is also related to the oral representation is longer. Thus, the sulcal morphology provides an improved framework for functional assignments in individual subjects.

### **4.3 Introduction**

In the human and non-human primate brains, the sensorimotor cortex extends along the central sulcus with the different parts of the body represented in an orderly topographic manner (e.g., Penfield and Boldrey, 1937; Penfield and Rasmussen, 1950; Whitsel et al., 1971; Merzenich et al., 1978; Woolsey et al., 1979; Nelson et al., 1980; Kaas, 1983; Wu and Kaas, 2003; Chen et al., 2005, 2007). The electrical-stimulation research of Penfield and colleagues during brain surgery has established the general dorsal to ventral sequence of the cortical motor and somatic sensory body representations in the precentral and postcentral gyri of the human brain, respectively, with the toes and feet lying most dorsally and medially, followed, in a ventral direction, by the legs, trunk, arm, hand, and the orofacial region (e.g., Penfield and Rasmussen, 1950). More recently, functional neuroimaging has confirmed this general somatotopic arrangement (Nakamura et al., 1998; Boling et al., 2002; Ianetti et al., 2003; Fabri et al., 2005; Miyamoto et al., 2006; Nevalainen et al., 2006; Blatow et al., 2007; Huang and Sereno, 2007; Kapreli et al., 2007; Stoeckel et al., 2007; Kopietz et al., 2009; Sakamoto et al., 2010; Stringer et al., 2011; Huang et al., 2012).

A recent study of the morphology of the postcentral sulcus, which forms the posterior boundary of the central sensorimotor region in the human brain, has shown that it is a complex of distinct sulcal segments (Zlatkina and Petrides, 2010), raising the question whether these segments relate to the sensorimotor representations of different body parts. It should be noted here that several recent studies have shown that functional activations can often be linked to specific morphological features of the sulci and gyri of the human brain when the functional data are examined in individual subjects, providing better understanding of structure-to-function relationships (e.g., Amiez et al., 2006, 2013; Amiez and Petrides, 2009, 2014; Derrfuss et al. 2012; Segal and Petrides, 2013). With regard to sensorimotor representations, there is evidence that the hand representation in the motor cortex relates to a specific morphological feature of the central sulcus, referred to as the "hand knob" (*pli de passage moyen* of Broca) (Yousry et al., 1997; Boling et al., 1999; Alkadhi and Kollias, 2004). The latter finding suggests that relations between the segments of the postcentral sulcus and sensorimotor representations of body parts may also exist.

In addition, there is the question of the transverse postcentral sulcus. This small sulcus is observed in a significant number of hemispheres in the ventral part of the postcentral gyrus and, when it is not present, the most ventral branch of the postcentral sulcus extends further ventrally (Zlatkina and Petrides, 2010). Is there a functional significance to these observations? The present functional neuroimaging study was designed to examine the above questions, namely whether there is a relationship between the different segments of the postcentral sulcal complex and the representations of different body parts and the functional meaning of the presence or absence of the transverse postcentral sulcus.

#### 4.4 Materials and methods

The methodology will be described here briefly because it was presented in detail in the study by Amiez and Petrides (2014) who investigated the representation of the different parts of the body in the cingulate motor cortex on the medial surface of the hemisphere in the same group of subjects.

# Subjects

Twelve healthy right-handed volunteers (8 females and 4 males, mean age = 29 years  $\pm$  6.6 standard deviation) participated in this fMRI study. All participants gave informed consent. The study was conducted according to the institutional guidelines established by the Ethics Committee of the Montreal Neurological Hospital and Institute.

#### Paradigms

In order to establish the location of representations of the different body parts in the cortical region of interest (the central sulcus, postcentral gyrus and postcentral sulcus), the subjects performed movements of the foot, leg, arm, hand, mouth, tongue, and blinking of the eyes.

During the instruction period, which commenced each trial, a sentence was presented in the middle of the screen for 1.5 s, which specified to the subjects the type of movement they will be required to perform in this trial. Specifically, the sentence read: "move your left foot", "move your right foot", "move your left leg", "move your right leg", "move your left arm", "move your right arm", "move your left hand", "move your right hand", "move your tongue", "move your mouth" and "do eye blinking". Following a delay period (4 - 6 s), a fixation point was presented in the center of the screen for 5 s and it required the participants to produce the movement indicated in the instruction period while maintaining an ocular fixation. The subjects were instructed to end the movement upon disappearance of the fixation dot. During the movements of

the foot, leg, arm and hand, the subjects were required to keep their limbs straight (no movements of the toes in the foot condition, ankles in the leg condition, wrist in the arm condition and fingers in the hand condition were allowed) and perform up and down small amplitude movements (maximum 10s° for the arm and leg, and 20s° for the hand and foot). The participants were required to make circular tongue movements with the mouth closed in the condition "move your tongue", and produce circular mouth movements with the mouth closed in the condition "move your mouth". The subjects continuously blinked their eyes when instructed to "do eye blinking". Each movement was practiced thoroughly in the MR scanner prior to the scanning session. In the control condition, the participants were required to sustain fixation on the central fixation point for 22.5 s. An inter-trial period lasted between 8 and 10 s. The sequence of visual stimuli was presented with the help of E-prime 1.2 (Psychology Software Tools Inc.).

#### Region of interest and contrasts

The cortical region of interest included both banks and fundus of the central sulcus, the crown of the postcentral gyrus and both banks and fundus of the postcentral sulcal complex. The dorsal boundary was the superior longitudinal fissure and the ventral boundary was the upper lip of the lateral fissure (parietal operculum).

Functional changes in activity in the region of interest were estimated by comparing the blood oxygen level-dependent (BOLD) signal during the performance of foot, leg, arm, hand, mouth, tongue and eye blinking movement trials (experimental condition) with the ocular fixation trials (control condition). The contralateral changes in activity were examined in response to the movements of the right foot, right leg, right arm, right hand and left foot, left leg, left arm and left hand. Both contralateral and ipsilateral changes in activity were examined for the orofacial type of movements, namely movements of the tongue, mouth, and eye-lids (blinking).

#### MRI acquisition

Scanning of the participants was performed on a 3-T Siemens Magnetom TrioTim MRI Scanner (Siemens AG, Erlangen, Germany). Following a high-resolution T1 anatomical scan (whole head, 1 mm<sup>3</sup> isotropic resolution), 7–8 runs of 170 images each (30 horizontal T2\* gradient echo-planar images (EPI), base resolution matrix = 128, voxel size =  $2 \times 2 \times 2$  mm,

repetition time = 2.1 s, echo time = 30 ms, flip angle = 90°) were acquired. The participants observed the screen through a mirror which was mounted directly above their eyes and had a 45-degree incline. The subjects completed 5 - 7 scanning sessions (1 subject completed 5 sessions, 3 subjects completed 6 sessions and 8 subjects completed 7 experimental sessions), each one lasting approximately 7 min. The following blocks of trials were presented randomly during each experimental session: 5 s mouth movements (i.e. about 5 rotations), 5 s tongue movements (i.e. about 5 rotations), 5 s left leg movements (i.e. about 8 up and down movements), 5 s right leg movements (i.e. about 8 up and down movements), 5 s left arm movements (i.e. about 8 up and down movements), 5 s left arm movements (i.e. about 8 up and down movements), 5 s right arm movements (i.e. about 8 up and down movements), 5 s right hand movements (i.e. about 8 up and down movements), 5 s right hand movements (i.e. about 8 up and down movements), 5 s right hand movements (i.e. about 8 up and down movements), 5 s right hand movements (i.e. about 8 up and down movements), 5 s right hand movements (i.e. about 8 up and down movements), 5 s right hand movements), 5 s ocular fixation. The onset of each instruction sentence was synchronized with the scanner acquisition via a trigger signal generated by the scanner.

# Data analysis

Data preprocessing and analysis were performed with Statistical Parametric Mapping software (SPM8b; Wellcome Department of Cognitive Neurology, University of College London, London, United Kingdom; http://www.fil.ion.ucl.ac.uk/spm) and Matlab 7.9 (www.mathworks.com). The detailed description can be found in Amiez and Petrides (2014).

As pointed out above, the region of interest in our study included the motor and sensory responses in the central sulcus, postcentral gyrus and postcentral sulcus produced by movement of the various parts of the body. Examination of the morphological structure of the central sulcus and the postcentral sulcal complex in each individual subject preceded the examination of the location of the activation peaks with respect to the sulci. In each individual subject, *t* statistical maps of the contrasts of interest, produced by subtracting the ocular fixation control condition from each experimental condition involving movement of different body parts, were superimposed on the anatomical MRI volume. The relationship between the stereotaxic location of the functional activity peaks, identified as the voxels with the highest *t* value within a cluster of functional activity, and the postcentral sulcal segments was examined on a subject-per-subject basis. The highest activity peaks were used instead of the centers of gravity because they do not
depend on the diameter of a smoothing kernel during data pre-processing and they are not influenced by the statistical threshold (Stoeckel et al., 2007).

The gray matter volume covered by the slices was 600 cm<sup>3</sup>. A region of interest (ROI) analysis was conducted at the level of individual subjects. The estimated ROI included both banks of the central sulcus, the crown of the postcentral gyrus and both banks of the postcentral sulcus. The ROI was reported to have a volume of 11.61 cm<sup>3</sup> and 10.05 cm<sup>3</sup> in the left and right hemispheres, respectively (gray matter volume of both banks of the central sulcus = 3.61 cm<sup>3</sup> in the left hemisphere and 3.49 cm<sup>3</sup> in the right hemisphere; volume of the postcentral gyrus = 4.20 cm<sup>3</sup> in the left hemisphere and 3.56 cm<sup>3</sup> in the right hemisphere; gray matter volume of both banks of the postcentral sulcus = 3.79 cm<sup>3</sup> in the left hemisphere and 3.01 cm<sup>3</sup> in the right hemisphere; Goldberg et al., 2013). The threshold t-value for reporting a peak as significant (p<0.05) was t = 3.77, when the peaks were predicted in the ROI. In addition, a predicted cluster of voxels with a t-value > 2.5 was significant (p<0.05) when its threshold extent was > 308.67 mm<sup>3</sup> (corrected for multiple comparisons using the method of Friston et al., 1995).

# Conversion of stereotaxic space coordinates

Because several earlier functional neuroimaging studies referred to in the Discussion section of the present article had provided functional activity peak coordinates in the stereotaxic space of Talairach and Tournoux (1988), which differs somewhat from the MNI stereotaxic space, these coordinates were converted to MNI space coordinates using the Signed Differential Method provided at http://www.sdmproject.com/ and projected onto an average brain template (ICBM152 non-linear 6th generation model; Grabner et al., 2006). This was necessary to permit direct comparison of coordinates across studies.

## 4.5 Results

#### Anatomical observations of the postcentral sulcal complex and the transverse postcentral sulcus

Examination of the morphological features of the postcentral sulcal complex and the transverse postcentral sulcus in the individual subjects preceded the examination of the sensorimotor activity with respect to the sulci. In an earlier anatomical study, we had demonstrated that, in most brains, the postcentral sulcus is not a continuous structure but rather a complex of dorso-ventrally oriented sulcal segments (Zlatkina and Petrides, 2010; also see Figures 4.1-4.13 in the present study). The postcentral sulcus is separated into segments by

submerged gyral bridges ("plis de passage") which are frequently small in size and link the anterior and posterior banks of the sulcus at specific locations (see Figures 4.2, 4.5 and 4.7). The gyral bridges may be pronounced and visible from the surface of the brain, as can be seen, for example, in the gyral passage between the second and third segments in Figure 4.5, and the gyral passages between the first and second segments, and the second and third segments in Figure 4.7. In our earlier anatomical study, we had identified in total four submerged gyral bridges (*plis de* passage) on the MRI scans of the subjects, with the first pli de passage being most dorsal and the fourth *pli de passage* being most ventral, and provided their average stereotaxic coordinates in the MNI standard stereotaxic space (Zlatkina and Petrides, 2010). It should be pointed out that, in our earlier anatomical study, we had adopted a conservative approach, namely only those *plis de passage* which were 2 mm or more in depth were considered, and the stereotaxic coordinates of the identified *plis de passage* were never compared between the subjects or used for identification of the *plis de passage* in any of the subjects in order to avoid bias in the examination of the data (Zlatkina and Petrides, 2010). Because of this conservative approach less than four *plis de passage* were identified in the majority of subjects and the postcentral sulcus was divided into two to three segments, on average (Zlatkina and Petrides, 2010). The present study provides a refinement of the former anatomical study. Based on our acquired expertise, we were able to identify smaller *plis de passage* which were only 1 mm in depth. Furthermore, in cases in which specific segments of the postcentral sulcus had an unusual shape (i.e. the sulcus curved in an unexpected manner), the average MNI space coordinates of the *plis de passage* (published in Zlatkina and Petrides, 2010) were used to help identify the corresponding *plis de* passage and end-points of such segments. Thus, we were able to identify four plis de passage in all the subjects, leading to the subdivision of the postcentral sulcus into five segments in the MRI scan of each subject in the present study.

In each individual subject, the superior branch of the postcentral sulcus, which is located dorsal to the intersection with the intraparietal sulcus, and the inferior branch of the postcentral sulcus, which is located ventral to this intersection were identified. The superior branch of the postcentral sulcus comprises the first and second segments of this sulcus and the inferior branch comprises the third, fourth and fifth segments. Figures 4.1-4.13 demonstrate five segments of the postcentral sulcus on the lateral surface of the brain of three individual subjects (Figures 4.2, 4.5, 4.7), in serial two-dimensional sections of the individual subjects (Figures 4.3-4.4, 4.6, 4.8-4.9),

and the average brain template (ICBM152 non-linear 6th generation model; Figures 4.10-4.13; Grabner et al., 2006).

In the current study, the transverse postcentral sulcus, which is located anterior to the postcentral sulcus in the inferior postcentral gyrus, was present in 2 left hemispheres (e.g. see Figures 4.5-4.6) and 3 right hemispheres. The occurrence of the transverse postcentral sulcus did not affect the subdivision of the postcentral sulcus into segments. The postcentral sulcus was divided into five segments in all hemispheres regardless of whether the transverse postcentral sulcus was present or absent. However, the presence of the transverse postcentral sulcus was related to the ventral position of the inferior branch of the postcentral sulcus. In the hemispheres in which the transverse postcentral sulcus was *absent*, the inferior branch of the postcentral sulcus was located much more ventral and approached the lateral fissure. The average coordinates of its ventralmost end-point were  $x = -63.1 \pm 1.2$ ,  $y = -24.6 \pm 4.6$ ,  $z = 20.3 \pm 3.3$ (average for 10 left hemispheres) and  $x = 60.2\pm4.2$ ,  $y = -18.9\pm6.3$  and  $z = 22.0\pm6.4$  (average for 9 right hemispheres). In the hemispheres of five subjects in which the transverse postcentral sulcus was *present*, the ventralmost end-point of the inferior branch of the postcentral sulcus was located more dorsally and further away from the lateral fissure at  $x = -63.0 \pm 1.4$ ,  $y = -31.5 \pm 12.0$ ,  $z = 29.0 \pm 1.4$  (average for 2 left hemispheres) and  $x = 62.7 \pm 1.2$ ,  $y = -22.3 \pm 13.7$  and  $z = 31.3 \pm 6.4$ (average for 3 right hemispheres), and the ventralmost end-point of the transverse postcentral sulcus was located at x =  $-52.5\pm3.5$ , y =  $-21\pm2.8$ , z =  $13\pm1.4$  (average for 2 left hemispheres) and  $x = 63 \pm 1.0$ ,  $y = -15.7 \pm 2.1$  and  $z = 25.0 \pm 5.3$  (average for 3 right hemispheres). However, as an exception, in two right hemispheres, in which the transverse postcentral sulcus was absent, the ventral end-point of the inferior branch of the postcentral sulcus was located relatively dorsal at x = 61, y = -24, z = 34 and x = 61, y = -6 and z = 30, perhaps the result of an atypically elongated ascending limb of the lateral fissure.

#### **Functional observations**

As expected from previous functional neuroimaging studies involving movement of different parts of the body, clusters of activity were observed both in the precentral (motor) and postcentral (somatic sensory) gyri, including both banks of the central sulcus (e.g. Fink et al., 1997; Moore et al., 2000; Meier et al., 2008). These peri-central functional activity clusters that were related to specific body parts extended anterior and posterior to the central sulcus in a nearly symmetrical manner. In other words, the dorsal and ventral boundaries of different body

part representations were similar in the precentral and postcentral gyri, as well as within the central sulcus. It was, therefore, possible to address the primary question of the present study, namely the relationship between sensorimotor functional activations and the five segments of the postcentral sulcal complex, including the transverse postcentral sulcus when present. In the presentation of the results, the cortical region along the central sulcus which includes both banks and extends into the precentral and postcentral gyri will be referred to as the *pericentral sensorimotor region* or simply *the pericentral region*.

The stereotaxic space coordinates of the functional activity peaks were recorded in the pericentral sensorimotor region in the individual subjects and averaged across all subjects. Table 4.1 lists the average coordinates of the functional activity peaks recorded in the central sulcus. Table 4.2 reports the average coordinates of the activity peaks recorded in the postcentral sulcus and the findings in Table 4.2 are discussed mainly for those experimental conditions (e.g. the hand movements), in which at least 50% of all subjects demonstrated a functional change in activity in the same segment or a point of separation between two segments of the postcentral sulcus.

# Lower extremity region (foot and leg)

The foot and leg were commonly represented in the dorsomedial part of the pericentral region and the clusters extended onto the most dorsal lateral surface of the hemisphere. On the horizontal sections, the foot and leg were represented anterior to the first segment of the postcentral sulcus, when it approached the medial edge of the hemisphere, or anterior-dorsal to it, when the postcentral sulcus was located further away from the midline (Table 4.1, Figures 4.2, 4.3a-b, 4.10a-b). In addition, the subject-per-subject analysis demonstrated that the foot and leg were also represented within the first segment of the superior branch of the postcentral sulcus (Table 4.2, Figures 4.7, 4.8a-b, 4.12b).

Hence, the first segment of the postcentral sulcus formed the posterior boundary of the foot and leg sensorimotor activity. The additional foot and leg representations were observed within the first segment of the postcentral sulcus in the majority of subjects.

# Upper extremity region (arm and hand)

Both the arm and hand sensorimotor activity was represented in the pericentral region anterior to the second segment of the postcentral sulcus (Table 4.1, Figures 4.2, 4.3c-d, 4.10c-d)

and, in some subjects, the functional activity extended anterior to the gyral passage separating the second segment from the first segment. The second segment of the postcentral sulcus was located posterior to and at the same dorso-ventral level as the "hand knob" region of the central sulcus, the site of hand representation in the primary motor cortex (i.e., x = -37, y = -22, z = 57, and x = 40, y = -23, z = 56 in MNI space according to Boling et al., 1999; also see Yousry et al., 1997 and Alkadhi and Kollias, 2004).

The findings also demonstrated the arm and hand functional activity clusters within the superior and inferior branches of the postcentral sulcus (Table 4.2, Figures 4.7, 4.8c-e, 4.9a-c, 4.12c-e, 4.13a-c). In the superior branch, in the left hemisphere, the hand and arm were represented in the first segment and also in the second segment of the postcentral sulcus (Figures 4.7, 4.8c-d, 4.9a-b, 4.12c-d, 4.13a-b). In the superior branch, in the right hemisphere, the arm and hand were represented mainly at the gyral passage separating the first and second segments of the postcentral sulcus and also in the second segment of the postcentral sulcus. In the inferior branch of the postcentral sulcus, both in the left and right hemispheres, the arm and hand were represented within the fourth segment of the postcentral sulcus and the functional activity extended slightly into the third (Table 4.2, Figures 4.7, 4.8e, 4.9c) and fifth segments.

Therefore, the second segment of the postcentral sulcus formed the posterior boundary of the sensorimotor activity of the arm and hand. In addition, the arm and hand representations were observed in three distinct loci within the postcentral sulcus, namely the first segment (or at the gyral passage separating the first and second segments), the second segment and the fourth segment of the postcentral sulcus.

#### *Upper face region (blinking)*

In about one half of all subjects, changes in activity related to eye-blinking were observed in the pericentral region anterior to the ventralmost part of the third segment of the postcentral sulcus near its junction with the fourth segment (Table 4.1, Figures 4.2, 4.3e). Hence, the ventralmost part of the third segment formed the posterior boundary of the blinking sensorimotor activity.

#### *Lower face region (mouth and tongue)*

The fourth and fifth segments belong to the inferior branch of the postcentral sulcus and they are located below its intersection with the horizontal part of the intraparietal sulcus. The fourth and fifth segments were usually shorter than the more dorsal segments, and the separation between the fourth and fifth segments was not well defined in the majority of subjects in this study. For this reason, the localization of the mouth and tongue representations with respect to the inferior segments of the postcentral sulcus was less well defined. Most frequently the mouth and tongue movements produced one to two functional activity clusters in the pericentral region anterior to the fourth segment of the postcentral sulcus and, in some subjects, the functional activity extended slightly dorsally and/or ventrally i.e. the activity extended anterior to the gyral passages separating the fourth segment from the third and fifth segments of the postcentral sulcus (Table 4.2, Figures 4.2, 4.4a-c).

In two right hemispheres, in which the transverse postcentral sulcus was absent and the ventral end-point of the inferior branch of the postcentral sulcus was located relatively dorsal at x = 61, y = -24, z = 34 and x = 61, y = -6, z = 30 (see 'Anatomical observations' section above), the clusters of functional activity associated with the tongue movements were observed anterior to the fifth segment of the postcentral sulcus and not anterior to the ventralmost part of the fourth segment.

In the hemispheres of subjects in which the transverse postcentral sulcus existed the sensorimotor activity elicited by movements of the mouth and tongue did not spread beyond the transverse postcentral sulcus (Figures 4.5, 4.6a-b). In the brains without the transverse postcentral sulcus, the functional activity associated with the mouth and tongue movements extended as far posteriorly as the inferior branch of the postcentral sulcus (Figure 4).

In addition, the functional activity related to tongue movements was observed within the fourth segment of the postcentral sulcus (Figures 4.7, 4.9d) and, in some subjects, it extended slightly into the third (Figure 4.13d) and fifth segments.

In four out of five hemispheres in which the transverse postcentral sulcus was present, the functional activity peaks corresponding to the representation of the tongue were observed in the transverse postcentral sulcus (Figures 4.5, 4.6c). In two of these hemispheres, the activity peaks were recorded in the central, the inferior branch of the postcentral and transverse postcentral sulci. In the other two hemispheres, the functional peaks were observed in the central and transverse postcentral sulci (Figures 4.5, 4.6c).

To summarize, when the transverse postcentral sulcus was absent, the fourth segment of the postcentral sulcus formed the posterior boundary of the sensorimotor activity of the mouth and tongue. In the hemispheres, in which the transverse postcentral sulcus was present, the oral sensorimotor activity did not extend beyond the transverse postcentral sulcus. The tongue activity was also observed within the fourth segment of the postcentral sulcus.

#### 4.6 Discussion

The present research examined the relation between the representations of different body parts and the segments of the postcentral sulcus and the transverse postcentral sulcus. During scanning, the subjects performed simple movements of different body parts which elicited an expected change in activity in the central sulcus and the precentral and postcentral gyri (e.g. Fink et al., 1997; Moore et al., 2000; Meier et al., 2008; Gazzola and Keysers, 2009). The peak movement representations were located in the central sulcus and the functional activity extended onto the precentral and postcentral gyri in a nearly symmetrical manner, such that the dorsal and ventral boundaries of the different body-part representations in the precentral and postcentral gyri were very similar (e.g. see Moore et al., 2000).

#### *Relations between the segments of the postcentral sulcus and sensorimotor representations*

The anatomical component of the present investigation, which is a refinement of the former anatomical study (Zlatkina and Petrides, 2010), demonstrated that the postcentral sulcus can be divided into five segments in each hemisphere of the human brain. The individual subject analysis showed, for the first time, tight relationships between certain segments of the postcentral sulcus and sensorimotor functional activity corresponding to different body parts. These segments of the postcentral sulcus were located consistently at the posterior border of the pericentral sensorimotor representations of particular body parts (Table 4.1, Figures 4.3-4.4). By pericentral sensorimotor representations we refer to the activity that extends around the central sulcus and involves the precentral and postcentral gyri. The findings showed that the local sulcal morphology of the postcentral sulcus is a reliable reference for mapping the somatotopic organization of the sensorimotor representation was previously only hinted at by the well-known relation of the primary motor representation of the hand to a particular morphological feature of the central sulcus, the well-known "hand knob" (Yousry et al., 1997; Boling et al., 1999; Alkadhi and Kollias, 2004).

The present results demonstrated that, in general, the foot and leg sensorimotor representations were located in the pericentral region anterior to the first segment of the

postcentral sulcus and that the foot/leg functional activity extended medially into the paracentral lobule (Table 4.1, Figures 4.2, 4.3a-b). The arm and hand were represented most frequently in the pericentral region anterior to the second segment of the postcentral sulcus (Table 4.1, Figures 4.2, 4.3c-d). Interestingly, the second segment of the postcentral sulcus was located posterior to and at the same dorso-ventral level as the "hand knob" region of the central sulcus, namely the known site of hand representation in the primary motor cortex. The functional activity produced by eye blinking was consistently observed anterior to the ventralmost part of the third segment of the postcentral sulcus (Table 4.1, Figures 4.2, 4.3e). Commonly, the mouth and tongue were represented in the pericentral region anterior to the fourth segment of the postcentral sulcus with the functional activity extending slightly anterior to the adjacent segments (Table 4.1, Figures 4.2, 4.4a-c).

Movement of the above-mentioned body parts did not produce sensorimotor activity in the pericentral region anterior to the third and fifth segments of the postcentral sulcus. It is suggested here that sensorimotor related activity of the body parts not examined in the current study, such as the forehead, brow or nose (upper face), may lie anterior to the third segment, whereas functional activity related to the teeth, gums, jaw, pharynx and larynx (lower face and upper gastrointestinal tract) may lie in the pericentral region anterior to the fifth segment of the postcentral sulcus.

In addition to the functional activity observed in the pericentral region, i.e. the precentral and postcentral gyri, as summarized above, single-subject analysis demonstrated activity related to various body parts *within* the distinct segments of the superior and inferior branches of the postcentral sulcus (Figures 4.7-4.9). Note that the cytoarchitecture of the cortex that occupies the banks of the postcentral sulcus, namely Brodmann area 2, is very different from that of the cortex that occupies the crown of the postcentral gyrus, namely Brodmann area 1 (Brodmann, 1909; Grefkes et al., 2001; Petrides, 2014). Importantly, the arrangement of arm and hand representations within the postcentral sulcus differed significantly from the general dorso-ventral sequence of such representations in the pericentral region.

The foot and leg representations were located in the first segment (Figures 4.7, 4.8a-b), while the tongue representation was observed in the fourth segment of the postcentral sulcus (Figures 4.7, 4.9d). Unlike these representations of the lower limb and the tongue region, which were observed in one location only, the arm/hand activity clusters were recorded in three distinct locations within the postcentral sulcus. In the superior branch of the postcentral sulcus, the

activity clusters related to movement of the arm and hand were recorded within the first segment (Figures 4.7, 4.8c, 4.9a) and the second segment (Figures 4.7, 4.8d, 4.9b). In the inferior branch of the postcentral sulcus, the arm and hand representations were observed within the fourth segment with the activity extending slightly into the adjacent segments (Figures 4.7, 4.8e, 4.9c). Previous studies had not examined activity specifically in relation to the five segments of the postcentral sulcus, but more generally in relation to a superior branch and an inferior branch. Our findings are consistent with the general results of these earlier functional neuroimaging studies which reported activity in the superior branch of the postcentral sulcus during both motor (general sensorimotor) and sensory stimulation of the lower body, arm, and hand (fingers) (Kurth et al., 2000; Stoeckel et al., 2007; Huang et al., 2012; Martuzzi et al., 2014) and in the inferior branch of the postcentral sulcus during stimulation of the hand (fingers), lips and tongue (Blankenburg et al., 2003; Watanabe et al., 2004; Stoeckel et al., 2007; Nelson and Chen, 2008; Sakamoto et al., 2010; Huang et al., 2012, see their supplementary information Figures S4-S5). In addition, changes in functional activity in the superior and inferior branches of the postcentral sulcus are observed in complex hand movement tasks, including writing, controlling a joystick, and texture and shape encoding (Stephan et al., 1995; Grefkes et al., 2004; Miquee et al., 2008; Gazzola and Keysers, 2009; Segal and Petrides, 2012; Kaas et al., 2013).

The representation of the arm and hand in multiple segments of the postcentral sulcus that was observed in the present study may reflect a higher level of sensorimotor integration and therefore less distinct somatotopy within the postcentral sulcus in comparison with the pericentral region (Blankenburg et al., 2003; Miyamoto et al., 2006; Iwamura, 2007). Non-human primate recording studies have shown that, in comparison with Brodmann area 3 in the most anterior part of the postcentral gyrus, Brodmann area 2 in the posterior part of the postcentral somatosensory region exhibits an increase in the size and complexity of neuronal receptive fields and, also, an increase in the number of neurons with complex receptive fields covering multiple fingers (Sur et al., 1980; Iwamura et al., 1983, 1993; Pons et al., 1985; Iwamura, 2007). Thus, Brodmann area 2, which in the human brain is located in the postcentral sulcus, appears to integrate sensory representations from different body parts. Future research will be necessary to establish the specific contributions made by the cortical regions located within the first and second segments of the superior branch of the postcentral sulcus and the fourth segment of the inferior branch of the postcentral sulcus to different types of simple and skilled arm/hand movements.

The transverse postcentral sulcus is related to the mouth and tongue sensorimotor region

An important contribution of the current investigation is clarification of the functional role of the transverse postcentral sulcus, a sulcus that appears in some brains in the ventral part of the postcentral gyrus. The transverse postcentral sulcus is a relatively deep more or less vertically-oriented sulcus of variable length that courses anterior and in parallel to the inferior branch of the postcentral sulcus (Zlatkina and Petrides, 2010). In this study, the transverse postcentral sulcus was present in approximately one fifth of all hemispheres (21% of 24 hemispheres), which is somewhat lower than its frequency of occurrence in our previous study that was based on a larger number of subjects (32.5% of 80 cerebral hemispheres examined by Zlatkina and Petrides, 2010). Note that the presence of the transverse postcentral sulcus in the brain did not affect the subdivision of the postcentral sulcus into five segments. When the transverse postcentral sulcus was present in a hemisphere, the inferior branch of the postcentral sulcus did not reach as far ventrally and the transverse postcentral sulcus was functionally related to the mouth and tongue region (Figures 4.5, 4.6a-b). When the transverse postcentral sulcus was absent, the inferior branch of the postcentral sulcus extended ventrally towards the lateral fissure and activity related to the sensorimotor mouth and tongue regions was observed in relation to this sulcus (Figure 4). These novel findings strongly suggest that the transverse postcentral sulcus is a part of the postcentral sulcal complex and, when present, it includes cortex that relates functionally to the oral region of the sensorimotor cortex. The dynamic relation between the presence and absence of the transverse postcentral sulcus and functional activity in the most ventral part of the inferior postcentral sulcus should be explored in the future.

Another interesting issue concerns the relation of the transverse postcentral sulcus to cytoarchitectonic areas on the inferior postcentral gyrus, namely Brodmann areas 1 and 2, and the nearby Brodmann area 40 (area PF of Economo and Koskinas, 1925; Brodmann, 1909; Geyer et al., 1997, 1999; Grefkes et al., 2001; Caspers et al., 2006, 2008). One possibility may be that the transverse postcentral sulcus is related to the location of the border between somatosensory Brodmann areas 1 and 2. Alternatively, it may be related to Brodmann area 2 and nearby Brodmann area 40. The relation of the transverse postcentral sulcus and the inferior postcentral sulcus in hemispheres with and hemispheres without the transverse postcentral sulcus to cytoarchitectonic Brodmann areas 1, 2, and 40 should be examined in future studies.

There have been several hypotheses with respect to the origin of the transverse postcentral sulcus. For instance, Cunningham (1892) considered the transverse postcentral sulcus

to be a distinct sulcus which developed in the 8<sup>th</sup> month of gestation (also see Tables 20 and 30 in Retzius, 1896), while Connolly (1950) proposed that the transverse postcentral sulcus is derived directly from the bifurcated inferior portion of the postcentral sulcus, which detached in the course of development and formed a separate sulcus below the main inferior postcentral branch. Functional significance of the transverse postcentral sulcus as a marker of the oral (mouth and tongue) sensorimotor region and its compensatory relation with the inferior branch of the postcentral sulcus (Connolly, 1950) support the suggestion that the transverse postcentral sulcus belongs to the postcentral sulcul complex.

# General comments on the organization of the sensorimotor region and variability of cerebral sulci

Certain aspects of motor control depend on primary motor cortex (Brodmann area 4) that covers the anterior bank of the central sulcus and a variable part of the precentral gyrus, while somatic sensory aspects involve the posterior bank of the central sulcus covered by Brodmann area 3 and the adjacent Brodmann area 1 on the crown of the postcentral gyrus and Brodmann area 2 in its most posterior part continuing into the postcentral sulcus (Brodmann, 1909; Vogt and Vogt, 1919; Zilles et al., 1995; Gever et al., 1997, 1999; Grefkes et al., 2001; Petrides, 2014). The cortico-cortical feedforward and feedback projections joining the precentral and postcentral gyri integrate the sensory and motor components during the performance of movement (Pons and Kaas, 1986; Morecraft et al., 2004, 2012). Microelectrode mapping in nonhuman primates demonstrated a distinct somatotopic representation of the contralateral body surface in the motor cortex and in each of the three cytoarchitectonic areas of the somatosensory cortex (Woolsey et al., 1952; Whitsel et al., 1971; Merzenich et al., 1978; Kaas et al., 1979; Kaas, 1983; Donoghue et al., 1992; Tokuno and Tanji, 1993). Clearly, the movements performed by the subjects in the present study involved multiple architectonic areas of the pericentral region since they would be expected to activate a diversity of peripheral receptors, including deep receptors in joints and muscles (e.g. Golgi tendon organs and muscle spindles), as well as rapidly and slowly adapting cutaneous mechanoreceptors (Merzenich et al., 1978; Kaas, 1983; Matthews, 1988). In addition, a segregation of function with respect to effectors in the medial-tolateral direction, such as the hindlimb, forelimb, upper face and lower face was clearly demonstrated in the current study and it is consistent with the general somatotopic organization of both the motor cortex and the somatosensory cortex in the human brain (Penfield and Boldrey, 1937; Penfield and Rasmussen, 1950; Hari et al., 1993; Fink et al., 1997; Nakamura et al., 1998; Moore et al., 2000; Disbrow et al., 2003; Blatow et al., 2007; Kapreli et al., 2007; Eickhoff et al., 2008; Meier et al., 2008; Gazzola and Keysers, 2009; Kopietz et al., 2009; Huang et al., 2012).

The mouth and tongue movements produced frequently two functional activity clusters in the pericentral region. The peak voxels of these clusters were located in the central sulcus and the clusters overlapped considerably in the medial-lateral axis (Figure 4.2, 4.4). It is possible that the mouth and tongue movements could not be produced in isolation or independently from one another in their respective experimental conditions and the combination of the mouth and tongue representations was frequently observed. The studies conducted both in the monkey (Cure and Rasmussen, 1954; McGuinness et al., 1980; Murray and Sessle, 1992; Hatanaka et al., 2005; Morecraft et al., 2014) and human subjects (Penfield and Rasmussen, 1950; Woolsey et al., 1979; Nakamura et al., 1998; Rödel et al., 2003; Miyamoto et al., 2006) strongly suggest that the dorsal cluster is more likely to be representative of mouth movements and the ventral cluster of tongue movements. There is also evidence of the existence of both ipsilateral and contralateral representations of the oral structures, specifically the mouth and tongue, in the somatosensory cortex of human (Disbrow et al., 2003; Ianetti et al., 2003; Nevalainen et al., 2006; Blatow et al., 2007) and non-human primates (Ogawa et al., 1989; Manger et al., 1995, 1996; Jain et al., 2001; Iwamura, 2007). The topographic arrangement of the ipsilateral and contralateral oral sensorimotor activity clusters is not clear at the moment and needs further investigation.

The source of inter-subject and inter-hemispheric variability in the morphology of the cerebral sulci is not well understood at present. A prominent hypothesis, the tension-based hypothesis, proposes that the formation of sulci is driven by mechanical tension along the axonal projections that connect adjacent cortical areas and suggests a topographic relation between the location of sulci and inter-areal boundaries (Van Essen, 1997). Similarly, Sanides (1972) had earlier proposed that, in the process of cortical expansion, sulci may be formed at the junction between "two areas of different cortical thickness and/or density" (Sanides, 1972, p. 351) and observed that the boundaries of many architectonic areas are located within the sulci. For instance, the thick agranular Brodmann area 4 occupies the anterior bank of the central sulcus while the thin and hyper-granular Brodmann area 3 lies in its posterior bank (see Figure 28 in Petrides, 2014). Other sulci are axial folds around which particular areas are located, such as the calcarine fissure both banks of which are occupied by Brodmann area 17, i.e. the primary visual cortex (Sanides, 1972). Recently, Mota and Herculano-Houzel (2015) demonstrated that in the

mammalian brain the level of cortical folding is related to the entire cortical surface area and cortical thickness rather than the total number of neurons, and, hence, any abnormalities in neuronal migration are likely to affect the degree of folding. The variability of sulcal patterns may then be linked to the time of appearance of the cerebral sulci and the incidence of their occurrence (Armstrong et al., 1995; Tamraz and Comair, 2006) and may thus depend on a variety of genetic, epigenetic, ontogenetic, and environmental prenatal factors which contribute to cortical folding (Goldman-Rakic and Rakic, 1979; Rakic, 1988, 2004; Welker, 1990; Dehay et al., 1996; Sur and Rubenstein, 2005; Kochunov et al., 2010). Specifically, the primary sulci, which appear prior to the 30th week of gestational development in every neurologically healthy individual, are significantly less variable than the secondary and tertiary sulci, which form later in gestation in some healthy individuals but not others (Chi et al., 1977; Armstrong et al., 1995; Chiavaras et al., 2001; Tamraz and Comair, 2006). For instance, our findings demonstrate that, while the postcentral sulcus (the primary sulcus) is present in every hemisphere, the transverse postcentral sulcus (a non-primary sulcus) is observed only in a subset of hemispheres (Zlatkina and Petrides, 2010). The results of this study which show that the length of the postcentral sulcal segments in the inferior postcentral gyrus is related to the presence of the transverse postcentral sulcus suggest a dynamic interplay during development. It is important to note that the absence of specific secondary or tertiary sulci does not reflect an absence of cytoarchitectonic areas but rather reflects the folding pattern of nearby sulci (e.g. length or depth of such sulci). Future research about the sources of sulcal variability is likely to benefit from knowledge of the variability of the existing sulcal patterns in adult brains and their relation to cytoarchitectonic and functional organization.

# Conclusions

The current study demonstrated that the location of sensorimotor representations in the central region and within the postcentral sulcus is tightly linked with the morphology of the postcentral sulcus. The segments of the postcentral sulcus provide a reliable structural framework which may be used to interpret activation sites in the sensorimotor cortex and in the postcentral sulcus on an individual subject basis. The transverse postcentral sulcus and the most ventral part of the inferior postcentral sulcus when the transverse postcentral sulcus is not present may be considered a morphological landmark marking the border zone between the mouth and tongue region of the postcentral gyrus and the most anterior part of the inferior parietal lobule.

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### 4.9 Tables

Table 4.1. The average MNI stereotaxic space coordinates of functional activity peaks located within the central sulcus of the contralateral hemisphere and related to foot, leg, arm, hand, mouth, tongue and eye-blinking movements. The activity peaks are based on the comparison of the BOLD signal in the experimental condition (foot, leg, arm, hand, mouth, tongue and eye-blinking movement) vs. the ocular fixation trials in each individual subject and averaged across the subjects. Posterior boundary of the sensorimotor representations of the foot, leg, arm, hand, mouth, tongue and eye-blinking movements is formed by distinct segments of the postcentral sulcus (PoCS).

Body	Posterior	Left Hemisphere				Right Hemisphere			
Part	Boundary	MNI coordinates (± SD)			N of subjects	MNI coordinates (± SD)			N of
								subjects	
Foot	s1 and	-6.00	-31.00	73.29	11/12	10.14	-27.86	75.14	7/12
	dorsal to	(± 3.21)	(± 6.10)	(± 4.20)		(± 4.02)	(± 4.71)	(± 2.27)	
	PoCS								
Leg	s1 and	-9.00	-28.82	72.47	12/12	12.44	-28.33	70.44	8/12
	dorsal to	(± 3.87)	(± 6.42)	(± 5.36)		(± 3.13)	(± 3.97)	(± 4.67)	
	PoCS								
Arm	s2	-30.94	-24.31	65.25	11/12	31.31	-23.56	64.75	11/12
		(± 5.58)	(± 6.41)	(± 7.79)		(± 4.00)	(± 4.05)	(± 6.40)	
Hand	s2	-33.64	-23.43	66.43	11/12	32.93	-22.73	64.27	11/12
		(± 5.06)	(± 6.69)	(± 4.78)		(± 3.79)	(± 4.45)	(± 7.67)	
Blinking	ventral	-42.67	-12.33	46.00	5 (+1)/12	49.00	-5.67	49.33	7/12
	part of s3	(± 5.28)	(± 5.32)	(± 7.38)		(± 5.39)	(± 2.45)	(± 6.48)	
Mouth	s4	-51.23	-11.69	38.46	12/12	52.93	-6.87	40.13	12/12
		(± 5.57)	(± 2.90)	(± 4.01)		(± 6.11)	(± 4.45)	(± 7.23)	
Tongue	s4	-54.79	-8.36	35.50	11/12	52.57	-6.62	43.90	11/12
		(± 7.75)	(± 4.13)	(± 5.13)		(± 7.18)	(± 4.99)	(± 11.89)	

Note: The number (N) of subjects in which the sensorimotor activity was observed in indicated in "N of subjects" field. The number in brackets in the "N of subjects" field indicates the number of subjects in which the functional activity was present below the statistical threshold. For instance, 5 (+1)/12 signifies that in the left hemisphere, the eye-blinking activity reached

significance in five subjects and it was present below the statistical threshold in one subject. Abbreviations: dorsal to PoCS, the functional activity cluster is located dorsal-and-anterior to the postcentral sulcus; PoCS, the postcentral sulcus; s1, the first segment of the postcentral sulcus; s2, the second segment of the postcentral sulcus; s3, the third segment of the postcentral sulcus; s4, the fourth segment of the postcentral sulcus. Table 4.2. The average MNI stereotaxic space coordinates of functional activity peaks located within the postcentral sulcus of the contralateral hemisphere and related to movement of the foot, leg, arm, hand, mouth, and tongue, as well as eye-blinking. The activity peaks are based on the comparison of the BOLD signal in the experimental condition (foot, leg, arm, hand and tongue movements) vs. the ocular fixation trials in each individual subject and averaged across the subjects.

Body	Location		Left He	misphere	Right Hemisphere				
Part		MNI coordinates (± SD)			N of	MNI coordinates (± SD)			N of
					subjects				subjects
Foot	s1	-21.25	-43.50	64.00	4/12	15.00	-38.29	73.14	7/12
		(± 7.68)	(± 1.91)	$(\pm 0.00)$		(± 5.20)	(± 1.60)	(± 4.14)	
Leg	s1	-16.57	-42.43	64.86	7/12	16.71	-39.43	70.57	6/12
		(± 3.74)	(± 2.76)	(± 5.64)		(± 5.12)	(± 5.56)	(± 5.86)	
Arm	s1	-21.43	-42.43	69.71	5/12				
		(± 3.21)	(± 6.60)	(± 6.16)					
	gyral passage					26.50	-38.17	64.00	6/12
	between s1-s2					(± 3.89)	(± 2.56)	(± 4.73)	
	s2	-36.63	-35.75	65.00	6/12	32.25	-35.25	64.00	4/12
		(± 4.90)	(± 5.06)	(± 3.21)		(± 5.68)	(± 3.77)	(± 5.89)	
	s4	-52.43	-24.14	45.57	7 (+2)/12	53.25	-19.25	40.00	4/12
		(± 5.26)	(± 2.97)	(± 5.53)		(± 10.24)	(± 5.38)	(± 4.32)	
Hand	s1	-17.71	-46.14	66.00	6/12				
		(± 5.44)	(± 4.60)	(± 5.77)					
	gyral passage					24.71	-37.43	67.43	7/12
	between s1-s2					(± 3.77)	(± 2.30)	(± 6.50)	
	s2	-35.14	-37.86	61.71	6/12	30.80	-35.80	60.40	4/12
		(± 5.43)	(± 4.26)	(± 3.15)		(± 4.60)	(± 2.05)	(± 5.37)	
	s4	-50.73	-25.64	44.55	8 (+1)/12	52.75	-19.50	46.75	8/12
		(± 6.17)	(± 3.67)	(± 6.64)		(± 5.68)	(± 4.75)	(± 6.41)	
Tongue	s4	-53.71	-25.71	42.57	6 (+1)/12	58.00	-16.25	44.50	4(+2)/12
		(± 5.31)	(± 6.21)	(± 7.19)		(± 1.63)	(± 7.18)	(± 7.19)	

Note: The number of subjects in which the sensorimotor activity was observed in indicated in "N of subjects" field. A number in brackets in the "N of subjects" field indicates the number of subjects in which the functional activity was present below the statistical threshold. For instance,

6 (+1)/12 signifies that in the left hemisphere, the tongue movement activity reached significance in six subjects and it was present below the statistical threshold in one subject. Abbreviations: s1, the first segment of the postcentral sulcus; s2, the second segment of the postcentral sulcus; s4, the fourth segment of the postcentral sulcus.

# 4.10 Figures



Figure 4.1. Schematic representation of the segments of the postcentral sulcus and the transverse postcentral sulcus in the parietal lobe of the human brain. Abbreviations: CingS, cingulate sulcus; CS, central sulcus; cSTS1, first caudal branch of the superior temporal sulcus; cSTS2, second caudal branch of the superior temporal sulcus; cSTS3, third caudal branch of the superior temporal sulcus; iPreCS, inferior precentral sulcus; IPS, intraparietal sulcus; LF, lateral fissure; s1, first segment of the postcentral sulcus; s2, second segment of the postcentral sulcus; s3, third segment of the postcentral sulcus; s4, fourth segment of the postcentral sulcus; s5, fifth segment of the postcentral sulcus; SFS, superior frontal sulcus; SPS, superior parietal sulcus; STS, superior temporal sulcus; TrS, transverse postcentral sulcus.



Figure 4.2. Reconstruction of the left hemisphere of one typical subject with the segments of the postcentral sulcus (s1-s5) identified. Arrowheads indicate the points of separation between the segments of the postcentral sulcus. The activation foci for the leg, foot, arm, hand, blinking of the eyes, mouth and tongue representations are projected schematically onto the central sulcus. There are two peaks in the mouth (mouth1 and mouth2) and tongue (tongue1 and tongue2) experimental conditions. Horizontal, coronal and sagittal sections displaying the location of activity peaks in the left hemisphere of this subject are provided in Figure 3 (leg, foot, hand, arm and eye blinking conditions) and Figure 4 (mouth and tongue conditions). Abbreviations: CS, central sulcus; IPS, intraparietal sulcus; LF, lateral fissure; mouth1, activity peak 1 in the mouth condition; mouth2, activity peak 2 in the mouth condition; PoCS, postcentral sulcus; s1, first segment of the postcentral sulcus; s4, fourth segment of the postcentral sulcus; s5, fifth segment of the

postcentral sulcus; sPreCS, superior precentral sulcus; SPS, superior parietal sulcus; tongue1, activity peak 1 in the tongue condition; tongue2, activity peak 2 in the tongue condition.



**B** Foot









C Hand



















E Blinking









Figure 4.3. Functional maps of the contrasts of interest, namely the leg (**a**), foot (**b**), hand (**c**), arm (**d**) and blinking of the eyes (**e**; blinking) movements versus the ocular fixation condition, are shown in the horizontal, coronal and sagittal sections of the left hemisphere in one typical subject. Location of activity peaks is marked in the corresponding sections with a yellow asterisk. The reconstructed view of the left hemisphere of the same subject is shown in Figure 1. The postcentral sulcus segments (s1-s5) are outlined in different colors. The level in the dorsoventral dimension (z coordinate) and the anterior-posterior dimension (y coordinate) is provided in millimeters for each section in the MNI standard proportional stereotaxic space. The color scale represents the range of t-values. Abbreviations: CS, central sulcus; IPS, intraparietal sulcus; s1, first segment of the postcentral sulcus; s4, fourth segment of the postcentral sulcus; s5, fifth segment of the postcentral sulcus.
## A Mouth peak 1





































Figure 4.4. Functional maps of the contrasts of interest, namely the mouth (**a-b**) and tongue (**c-d**) movements versus the ocular fixation condition, are shown in the horizontal, coronal and sagittal sections of the left hemisphere in one typical subject. Location of activity peaks is marked in the corresponding sections with a yellow asterisk. There are two activity peaks in the mouth (**a-b**) and tongue (**c-d**) conditions. The reconstructed view of the left hemisphere of the same subject is shown in Figure 1. The postcentral sulcus segments (s1-s5) are outlined in different colors. The level in the dorso-ventral dimension (z coordinate) and the anterior-posterior dimension (y coordinate) is provided in millimeters for each section in the MNI standard proportional stereotaxic space. The color scale represents the range of t-values. Abbreviations: CS, central sulcus; IPS, intraparietal sulcus; s3, third segment of the postcentral sulcus; s4, fourth segment of the postcentral sulcus; s5, fifth segment of the postcentral sulcus.



Figure 4.5. Reconstruction of the left hemisphere of one typical subject with the transverse postcentral sulcus and the segments of the postcentral sulcus (s1-s5) identified. Arrowheads indicate the points of separation between the segments of the postcentral sulcus. There are two peaks in the tongue experimental condition, one in the central sulcus (tongue1) and another one in the transverse postcentral sulcus (tongue2). The activation peaks and borders of functional activity clusters for the mouth and tongue representations are projected schematically onto the surface of the central sulcus, transverse postcentral sulcus and the postcentral gyrus. Horizontal, coronal and sagittal sections displaying the location of activity peaks in the mouth and tongue experimental conditions in the left hemisphere of this subject are provided in Figure 6. Abbreviations: CS, central sulcus; IPS, intraparietal sulcus; LF, lateral fissure; PoCS, postcentral sulcus; s1, first segment of the postcentral sulcus; s4, fourth segment of the postcentral sulcus; s5, fifth segment of the postcentral sulcus; sPreCS, superior precentral sulcus; SPS, superior parietal

sulcus; tongue1, activity peak 1 in the tongue condition; tongue2, activity peak 2 in the tongue condition; TrS, transverse postcentral sulcus.

## A Mouth









**B** Tongue peak 1



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Figure 4.6. Functional maps of the contrasts of interest, namely the mouth (**a**) and tongue (**b-c**) movements versus the ocular fixation condition, are shown in horizontal, coronal and sagittal sections of the left hemisphere of one typical subject, which contains the transverse postcentral sulcus. Location of activity peaks is marked in the corresponding sections with an asterisk.

Yellow asterisk marks the peaks in the central sulcus (**a-b**) and red asterisk indicates the peak in the transverse postcentral sulcus (**c**). The reconstructed view of the left hemisphere of the same subject is shown in Figure 5. The postcentral sulcus segments (s2-s5) are outlined in different colors. The level in the dorso-ventral dimension (z coordinate) and the anterior-posterior dimension (y coordinate) is provided in millimeters for each section in the MNI standard proportional stereotaxic space. The color scale represents the range of t-values. Abbreviations: CS, central sulcus; s2, second segment of the postcentral sulcus; s3, third segment of the postcentral sulcus; s4, fourth segment of the postcentral sulcus; s5, fifth segment of the postcentral sulcus; TrS, transverse postcentral sulcus.



Figure 4.7. Reconstruction of the left hemisphere of one typical subject with the segments of the postcentral sulcus (s1-s5) identified. Arrowheads indicate the points of separation between the segments of the postcentral sulcus. The activation peaks for the leg, foot, arm, hand and tongue representations are projected schematically onto the surface of the postcentral sulcus. There are three activity peaks in the arm condition (arm1, arm2 and arm3) and three peaks in the hand condition (hand1, hand2 and hand3). Horizontal, coronal and sagittal sections displaying the location of activity peaks in the left hemisphere of this subject are provided in Figure 8 (leg, foot and hand conditions) and Figure 9 (arm and tongue) conditions. Abbreviations: arm1, arm activity peak 1; arm2, arm activity peak 2; arm3, arm activity peak 3; CS, central sulcus; hand1, hand activity peak 1; hand2, hand activity peak 2; hand3, hand activity peak 3; IPS, intraparietal sulcus; LF, lateral fissure; PoCS, postcentral sulcus; s1, first segment of the postcentral sulcus; s4, fourth segment of the postcentral sulcus; s5, fifth segment of the postcentral sulcus; sPreCS, superior precentral sulcus.

### A Leg



**B** Foot



C Hand peak 1



**D** Hand peak 2



## E Hand peak 3



Figure 4.8. Functional maps of the contrasts of interest, namely the leg (**a**), foot (**b**) and hand (**c**-**e**) movements versus the ocular fixation condition, are shown in the horizontal, coronal and sagittal sections of the left hemisphere in one typical subject. The leg (**a**) and foot (**b**) activity peaks are located in the first segment of the postcentral sulcus. The hand activity peaks are located in the first segment (**c**; hand peak 1), the second segment (**d**; hand peak 2) and in the dorsalmost part of the fourth segment of the postcentral sulcus (**e**; hand peak 3). Location of activity peaks is marked in the corresponding sections with an asterisk. The reconstructed view of the left hemisphere of the same subject is shown in Figure 7. The postcentral sulcus segments (s1-s5) are outlined in different colors. The level in the dorso-ventral dimension (*z* coordinate) and the anterior-posterior dimension (y coordinate) is provided in millimeters for each section in the MNI standard proportional stereotaxic space. The color scale represents the range of t-values. Abbreviations: CS, central sulcus; IPS, intraparietal sulcus; s1, first segment of the postcentral sulcus; s4, fourth segment of the postcentral sulcus; s5, fifth segment of the postcentral sulcus.

## A Arm peak 1



## **B** Arm peak 2



C Arm peak 3



# **D** Tongue



Figure 4.9. Functional maps of the contrasts of interest, namely the arm (**a**-**c**) and tongue (**d**) movements versus the ocular fixation condition, are shown in the horizontal, coronal and sagittal sections of the left hemisphere in one typical subject. The arm activity peaks are located in the first segment (**a**; arm peak 1), the second segment (**b**; arm peak 2) and the gyral passage separating the third and fourth segments of the postcentral sulcus (**c**; arm peak 3). (**d**) The tongue activity peak is located in the fourth segment of the postcentral sulcus. Location of activity peaks is marked in the corresponding horizontal and coronal sections with an asterisk. The reconstructed view of the left hemisphere of the same subject is shown in Figure 7. The postcentral sulcus segments (s1-s5) are outlined in different colors. The level in the dorso-ventral dimension (z coordinate) and the anterior-posterior dimension (y coordinate) is provided in millimeters for each section in the MNI standard proportional stereotaxic space. The color scale represents the range of t-values. Abbreviations: CS, central sulcus; IPS, intraparietal sulcus; s1, first segment of the postcentral sulcus; s4, fourth segment of the postcentral sulcus; s5, fifth segment of the postcentral sulcus.



**B** Foot







C Hand





 $\mathbf{V}^{=}$ 



**D** Arm



Figure 4.10. MNI coordinates of the activity peaks averaged across subjects in the leg (**a**), foot (**b**), hand (**c**) and arm (**d**) experimental conditions are displayed as star-filled spheres in the central sulcus in the sagittal, coronal and horizontal sections of an average brain template (ICBM152 non-linear 6th generation model). The postcentral sulcus segments are outlined in color. The level in the medial-lateral dimension (x coordinate), anterior-posterior dimension (y coordinate) and the dorso-ventral dimension (z coordinate) is provided in millimeters for each section in the MNI standard proportional stereotaxic space. Abbreviations: 1-2psp, a point of separation between the first and second segments of the postcentral sulcus; CS, central sulcus; CingS, cingulate sulcus; IPS, intraparietal sulcus; LF, lateral fissure; s1, first segment of the postcentral sulcus; s2, second segment of the postcentral sulcus; STS, superior temporal sulcus.

# A Blinking



**B** Mouth



C Tongue



Figure 4.11. MNI coordinates of the activity peaks averaged across subjects in the blinking of the eyes (**a**; blinking), mouth (**b**) and tongue (**c**) experimental conditions are displayed as star-filled spheres in the central sulcus in the sagittal, coronal and horizontal sections of an average brain template (ICBM152 non-linear 6th generation model). The postcentral sulcus segments (s2-s5) are outlined in color. The level in the medial-lateral dimension (x coordinate), anterior-posterior dimension (y coordinate) and the dorso-ventral dimension (z coordinate) is provided in millimeters for each section in the MNI standard proportional stereotaxic space. Abbreviations: CS, central sulcus; IPS, intraparietal sulcus; LF, lateral fissure; s2, second segment of the postcentral sulcus; s3, third segment of the postcentral sulcus; STS, superior temporal sulcus.



Figure 4.12. MNI coordinates of the activity peaks averaged across subjects in the leg (**a**) foot (**b**) and hand (**c-e**) experimental conditions are displayed as star-filled spheres in the postcentral sulcus (**b**, **c-e**) and medial to it (**a**) in the sagittal, coronal and horizontal sections of an average brain template (ICBM152 non-linear 6th generation model). (**a**) The leg activity peak is located medial to the first segment of the postcentral sulcus. (**b**) The foot activity peak is located within the first segment of the postcentral sulcus. (**b**) The foot activity peak is located within the first segment of the postcentral sulcus. The hand activity peaks are located in the first segment (**c**; hand peak 1), the second segment near the ventral endpoint of the first segment (**d**; hand peak 2) and in the ventral part of the third segment of the postcentral sulcus (**e**; hand peak 3). The postcentral sulcus segments (s1-s3) are outlined in color. The level in the medial-lateral dimension (x coordinate), anterior-posterior dimension (y coordinate) and the dorso-ventral dimension (z coordinate) is provided in millimeters for each section in the MNI standard proportional stereotaxic space. Abbreviations: CS, central sulcus; IPS, intraparietal sulcus; LF,

lateral fissure; s1, first segment of the postcentral sulcus; s2, second segment of the postcentral sulcus; s3, third segment of the postcentral sulcus; SPS, superior parietal sulcus; STS, superior temporal sulcus.

### A Arm peak 1











CS

C Arm peak 3



**ÙF** 

STS

**D** Tongue



Figure 4.13. MNI coordinates of the activity peaks averaged across subjects in the arm (**a-c**) and tongue (**d**) experimental conditions are displayed as star-filled spheres in the postcentral sulcus in the sagittal, coronal and horizontal sections of an average brain template (ICBM152 non-linear 6th generation model). The arm activity peaks are located in the first segment (**a**; arm peak 1), the second segment (**b**; arm peak 2) and in the ventral part of the third segment of the postcentral sulcus and at the point of separation between the third and fourth segments of the postcentral sulcus. The postcentral sulcus segments (s1-s4) are outlined in color. The level in the medial-lateral dimension (x coordinate), anterior-posterior dimension (y coordinate) and the dorso-ventral dimension (z coordinate) is provided in millimeters for each section in the MNI standard proportional stereotaxic space. Abbreviations: CS, central sulcus; IPS, intraparietal sulcus; s3, third segment of the postcentral sulcus; s4, fourth segment of the postcentral sulcus; SPS, superior parietal sulcus; STS, superior temporal sulcus.

### **Chapter Five**

### 5. General Discussion

The development of neuroimaging technologies in the end of last century made it possible to study the organization of the parietal brain region non-invasively and perform systematic comparisons of distinct anatomical and functional features in a large number of individuals. The accuracy of such inter-subject comparisons of experimental data depends on the precision and consistency with which the anatomical structures, i.e. the sulci and gyri, are identified in different brain scans. Our current knowledge about the main parietal sulci was acquired, mainly, by studying the sulci on the surface of the brain, and it is not sufficient to address the substantial variability of structures commonly observed between different brains and even between different hemispheres of the same brain. There is evidence to suggest that the variability in cortical folding diminishes noticeably towards the fundus (Lohmann and Cramon, 2000; Regis et al., 2005) and, hence, examination of the in-depth view of the sulci can lead to decreased ambiguity in their identification and allow us to acquire a more complete understanding of their morphology (Germann et al., 2005; Huntgeburth and Petrides, 2012; Segal and Petrides, 2012b; Amiez and Petrides, 2014).

The first goal of this thesis was to conduct a systematic investigation of the morphology of three main sulci in the parietal lobe of the human brain, namely the postcentral sulcus (Chapter Two), the intraparietal sulcus and the anterior intermediate parietal sulcus of Jensen (Chapter Three), by examining them in their entirety, from the surface of the brain to the fundus, in continuous series of two-dimensional sections in a large sample of human brain scans. The findings demonstrated that the postcentral sulcus, the intraparietal sulcus and the sulcus of Jensen form a limited number of recognizable and repeating patterns in their depth, which merge and become distorted on the surface of the brain. The results of this morphological study can help researchers exploring the functional organization of the parietal region to identify these sulci in individual subjects with an increased accuracy and relate their functional findings to the local sulcal and gyral morphology in a consistent manner.

The second goal of this thesis was to examine a relationship in the anterior part of the parietal lobe between the sensorimotor representations of different body parts and five distinct segments of the postcentral sulcus, which form their posterior boundary (Chapter Four). In addition, our fMRI study presented in Chapter Four investigated a functional significance of the presence or absence of the transverse postcentral sulcus and its relation to the sensorimotor

representations in the ventral part of the postcentral gyrus. Such structure-function relationships, already demonstrated in other regions of the brain (e.g. Amiez et al., 2006; Amiez and Petrides, 2009, 2014; Amiez et al., 2013; Segal and Petrides, 2013), have a strong predictive value in that an accurate identification of a sulcus can indicate the functional specialization of an adjacent cortical region. Being able to determine the body region representation on the postcentral gyrus in the absence of an fMRI scan will provide useful information for researchers and clinicians.

#### 5.1 Morphological investigation of the anterior parietal lobe

Our morphological study of the postcentral sulcus presented in Chapter Two builds upon and advances the previous morphological examinations of the anterior parietal region in two ways. First, it investigates the variability in morphology and patterns of the postcentral sulcus with the neighbouring sulci in the continuous series of coronal, horizontal and sagittal sections instead of the surface of the reconstructed brain volumes in order to observe the complex cortical shape submerged in the sulcal depth. Second, the anatomical findings of this research conducted in a large sample of human MRI brain scans are reported in the MNI standard proportional stereotaxic space in order to make them available for use by the neuroimaging community. An important observation of this study concerns a frequent occurrence of small submerged gyral passages which separate the postcentral sulcus into distinct segments and, also, intervene between the end-points of the postcentral sulcus and the marginal branch of the cingulate sulcus, lateral fissure and the anterior intraparietal sulcus when they approach one another in the depth. Importantly, the position of these submerged gyral passages in the anterior parietal lobe in the MNI stereotaxic space is not random as they are encountered repeatedly in the similar stereotaxic locations in different brains (see Table 2.2) resulting in a small number of reoccurring and easily recognizable sulcal patterns.

Previous anatomical investigations identified up to three segments of the postcentral sulcus, which were separated by prominent gyral passages on the surface of the adult human brain (Eberstaller, 1890; Retzius, 1896; Smith, 1907; Economo and Koskinas, 1925; Sarkissov et al., 1955; Ono et al., 1990; Duvernoy et al., 1991). The main morphological finding of Chapter Two is refined in Chapter Four and it shows that the postcentral sulcal complex may be divided reliably into five sulcal segments in individual MRI brain scans, when the small gyral passages submerged deep within the sulcus are taken into account. Our anatomical data demonstrate that the two branches of the postcentral sulcus, which are located superior and inferior to its

intersection with the horizontally oriented intraparietal sulcus, have a consistent relationship with respect to the segments of the postcentral sulcus. The superior branch of the postcentral sulcus is composed of the first and second segments of the postcentral sulcus and it marks the anterior border of the superior parietal lobule, while the inferior branch consists of the third, fourth and fifth segments of the postcentral sulcus at the anterior border of the inferior parietal lobule. This information about the composition of the superior and inferior branches of the postcentral sulcus may become important in those cases in which the intraparietal sulcus does not have an oblique orientation, but it is vertical in its course and, hence, does not indicate the boundary between the functionally distinct cortical regions of the superior and inferior parietal lobules. Future functional (e.g. neuroimaging, clinical studies examining lesion effects in patients) and structural (e.g. cytoarchitectonic) research is necessary to determine whether the separation between the second and the third segments of the postcentral sulcus may estimate the anterior dorso-ventral (horizontal) border between the superior and inferior parietal lobules in the hemispheres in which the intraparietal sulcus has a vertical direction.

Anatomical analysis of the postcentral sulcus in serial sections demonstrated that, in the majority of hemispheres, its dorsal termination is bifurcated i.e. it is shaped as the letter Y or V, and in about a quarter of all cases it has a single, almost straight line termination, shaped as the letter I (see Table 2.4 and Figure 2.11). In over two-thirds of all hemispheres the marginal branch of the cingulate sulcus terminates anterior to or between the two branches of the bifurcated dorsal termination, and in the remaining cases it lays posterior to the dorsal termination of the postcentral sulcus (see Table 2.7 and Figure 2.13). It may be suggested that the layout of cytoarchitectonic areas, which perform different types of processing in the superior postcentral gyrus, namely areas PC, PD and PA<sub>2</sub> (Economo and Koskinas, 1925), is reflected in the local variability in morphology and patterns of the postcentral sulcus and the marginal branch of the cingulate sulcus. By establishing the position of borders between the cytoarchitectonic areas with respect to the different types of the dorsal termination of the postcentral sulcus and its relation with the marginal branch of the cingulate sulcus in histological brain sections, it becomes possible to use these sulci as landmarks to determine the approximate locations of specific architectonic areas in the MRI brain slices of individual subjects. Hence, our findings about the in-depth association and patterns of the postcentral sulcus and the marginal branch of the cingulate sulcus form the basis for subsequent cytoarchitectonic investigations of the superior postcentral gyrus.

Our morphological investigation of the relation between the postcentral sulcus and the anterior intraparietal sulcus in the human brain shows that these sulci have separate origins or "sulcal roots" (Regis et al., 2005). In all cases in which the postcentral sulcus and the intraparietal sulcus form a superficial association on the surface of the brain (60% of all hemispheres; see Table 2.6 and Figure 2.12), a submerged gyral bridge disconnects them in the depth. In the remaining cases, the postcentral sulcus is separated from the intraparietal sulcus by a noticeable gyral passage both on the surface of the brain and in the fundus (40% of all hemispheres; see Table 2.6 and Figure 2.12). As a result, the intraparietal and postcentral sulci are always separated below the surface of the brain and so they represent different sulcal units. The independent gestational development of the intraparietal sulcus and the inferior branch of the postcentral sulcus is also described in the literature (Cunningham, 1892; Retzius, 1896; Jefferson, 1913). Our anatomical finding has a direct functional relevance. In the human brain, the putative homologue of monkey area AIP, which is involved in grasping hand movements (e.g. Murata et al., 2000), is commonly described to be located *approximately* at the junction of the postcentral sulcus and the intraparietal sulcus (e.g. Culham et al., 2003; Frey et al., 2005; Shikata et al., 2008; Jacobs et al., 2010; Cavina-Pratesi et al., 2010; Marangon et al., 2011) and, based on the results of our morphological analysis, it would include the gyral passage between the postcentral sulcus and the intraparietal sulcus, submerged or visible from the surface of the brain. Additional functional neuroimaging evidence indicates that the location of area AIP may also include the adjacent cortex within the anterior ramus of the intraparietal sulcus and/or the cortex within the inferior branch of the postcentral sulcus (e.g. see Figure 4 in Frey et al., 2005). Furthermore, the limited anatomical data in the monkey brain suggest that the lateral border of area AIP is formed by cytoarchitectonic area PF (Andersen et al., 1990; Durand et al., 2007; Gharbawie et al., 2011; Nelissen and Vanduffel, 2011) and, if a similar relation holds place in the human brain, then the putative homologue of area AIP may be located in the inferior postcentral sulcus or the anterior intraparietal sulcus, which border area PF antero-medially (Economo and Koskinas, 1925). Future research should examine directly the location of the putative area AIP functional activity with respect to the anterior ramus of the intraparietal sulcus and the inferior branch of the postcentral sulcus on an individual subject basis.

An important novel finding of the morphological study presented in Chapter Two is an occurrence of a previously poorly-known sulcus, referred to as the transverse postcentral sulcus in our study, on the ventral part of the postcentral gyrus in about one third of all hemispheres

(see Table 2.9 and Figure 2.15). One of the first descriptions of the transverse postcentral sulcus was made by Eberstaller (1890) who referred to it as the sulcus retrocentralis (postcentralis) transversus and considered it to be the lowermost part of the postcentral sulcus. Connolly (1950) argued that the sulcus retrocentralis transversus is derived directly from the bifurcated inferior portion of the postcentral sulcus, which detached in the course of development and formed a separate sulcus below the main inferior postcentral branch. The transverse postcentral sulcus courses in a dorso-ventral direction anterior to the postcentral sulcus and the two sulci are separated by a gyral passage visible from the surface of the brain. It is suggested that the transverse postcentral sulcus may belong to the postcentral sulcal complex on the basis of at least two morphological observations. First, the presence of the transverse postcentral sulcus is associated with a shorter ventral extension of the postcentral sulcus i.e. further distance of the inferior termination of the postcentral sulcus from the lateral fissure. The transverse postcentral sulcus is not observed in the hemispheres in which the postcentral sulcus forms a superficial association with the lateral fissure. And second, the transverse postcentral sulcus is a deep sulcus and its dorsal end overlaps often with the inferior end of the postcentral sulcus. Given the location of the transverse postcentral sulcus in the ventral postcentral gyrus, how does this sulcus relate to the arrangement of cytoarchitectonic areas PC, PD and PF (Economo and Koskinas, 1925) at the border with the posterior parietal cortex? The observed relation between the presence of the transverse postcentral sulcus and the more dorsal termination of the inferior postcentral sulcus suggests that the transverse postcentral sulcus forms a structural continuation of the postcentral sulcus and, consequently, it may mark the border between areas PD and PF (Economo and Koskinas, 1925). The functional significance of the transverse postcentral sulcus is investigated in the fMRI study presented in Chapter Four of this thesis and it is discussed further on

### 5.2 Morphological investigation of the posterior parietal lobe

Our research presented in Chapter Three of this thesis is the first known systematic investigation of the morphology and variability in the morphology of the intraparietal sulcus in serial two-dimensional sections in a large number of human brains registered in the MNI stereotaxic space. The objective of this study is to provide the clinical and functional researchers of the parietal lobe, who consistently refer to the intraparietal sulcus either as a region of interest, locus of functional activity or an anatomical landmark, with the knowledge necessary to address the variability of the intraparietal sulcus in individual subjects. The reason why the study of variability in morphology is important is because in contrast to a common text-book perception of the intraparietal sulcus as an oblique-oriented and continuous sulcus, in a real human brain it is a complex of sulcal segments or branches of varying lengths and orientations (both oblique and vertical), which may be displaced towards the medial edge of the hemisphere or the dorsal boundary of the temporal lobe. However, by studying the branches of the intraparietal sulcus in the serial sections with respect to the adjacent sulci, such as the postcentral sulcus, the superior parietal sulcus, the anterior intermediate parietal sulcus of Jensen, the superior temporal sulcus and the paroccipital sulcus, it becomes possible to view the variability as a combination of representative sulcal patterns, which can be recognized in different subjects. The significance of research presented in Chapter Three lies in the fact that it identifies the main branches of the intraparietal sulcus and the patterns with the neighbouring sulci in the MNI stereotaxic space, and this information forms the basis for accurate identification of the intraparietal sulcus in future neuroimaging studies.

The anatomical study of the intraparietal sulcus demonstrated that in the majority of cases it can be divided into two main branches, the anterior and posterior rami of the intraparietal sulcus, by a gyral passage, submerged or visible from the surface of the brain (Figures 3.2b-d, 3.3; Appendix B, Figures S1b,d, S2, S4). Less frequently, the gyral passage between the branches of the intraparietal sulcus cannot be detected in the serial sections and the intraparietal sulcus is treated as a single continuous sulcus (Figure 3.2a; Appendix B, Figures S1a,c,e, S5-S8). Cytoarchitectonic studies established a relation between the supramarginal and angular gyri and, correspondingly, areas PF and PG (Economo and Koskinas, 1925) of the inferior parietal lobule. This raises a question about whether the cortical regions within the anterior and posterior rami of the intraparietal sulcus, which are found medial to the supramarginal gyrus and angular gyrus, may also have different cytoarchitecture, such that the cortex submerged within the anterior ramus of the intraparietal sulcus may be composed of another type of architectonic area.

A major result of our morphological investigation of the posterior parietal cortex in serial sections is the clarification of an association between the intraparietal sulcus and the anterior intermediate parietal sulcus of Jensen, which veers at the dorsal-posterior edge of the supramarginal gyrus. The sulcus of Jensen occurs in the majority of cerebral hemispheres as a deep inferiorly-directed side-branch of the intraparietal sulcus, which may be long (Figure 3.2a;

Appendix B, Figures S1a, S3a) or short (Figure 3.2b; Appendix B, Figures S1b, S3b). Less frequently it exists as a shallow sulcus attached to the main stem of the intraparietal sulcus on the surface of the brain and separated from it by a gyral bridge in the depth (Figures 3.2c, 3.3; Appendix B, Figures S1c-d, S3c, S4-S8). The sulcus of Jensen may be associated with the anterior ramus or the posterior ramus of the intraparietal sulcus in which case it is located posterior to the gyral passage separating the anterior ramus from the posterior ramus of the intraparietal sulcus.

At present, the structural (e.g. cytoarchitectonic) and functional significance of the sulcus of Jensen is completely unknown and a number of interesting hypotheses can be proposed on the basis of the morphological findings of the current study. First, it may be possible that the position of the sulcus of Jensen near the gyral passage separating the anterior ramus from the posterior ramus of the intraparietal sulcus may correspond to the boundary between the two cytoarchitectonically-different cortical regions within the anterior and posterior rami of the intraparietal sulcus, as proposed above. Second, a possible relation may exist between the lateral prolongation of the sulcus of Jensen onto the convexity of the inferior parietal lobule at the posterior edge of the supramarginal gyrus and the position of the border between areas PF and PG (Economo and Koskinas, 1925). Lastly, different levels of development achieved by the sulcus of Jensen, from a small notch to a deep side-branch of the intraparietal sulcus, may have a functional significance. For instance, in a neuroimaging study, the distribution of functional activity peaks in the inferior parietal lobule of one subject, in which the sulcus of Jensen is long, may differ from another subject, in which the sulcus of Jensen exists as a notch or is absent.

An important finding concerns the main patterns of relation between the sulcus of Jensen and the caudal branches of the superior temporal sulcus approaching it in the inferior parietal lobule. Most frequently, the sulcus of Jensen is located between the first and second caudal terminations of the superior temporal sulcus (Figure 3.2a-c; Appendix B, Figures S1a-d, S3a-c). Occasionally, however, the first caudal branch of the superior temporal sulcus connects with the sulcus of Jensen on the surface of the hemisphere, appearing as a long continuous structure (Figure 3.2d; Appendix B, Figures S1e, S3d). The possibility of a superficial association between the sulcus of Jensen and the first caudal superior temporal sulcus is alerting because a failure to examine these sulci in serial sections can result in their misidentification, as well as the misinterpretation of the functional and structural data in the supramarginal gyrus.

Neuroimaging studies suggest that, in the human brain, the cortex within the intraparietal sulcus and in the posterior part of the superior parietal lobule, extending medially into the precuneus, may correspond to several functional regions within the intraparietal sulcus of the macaque monkey, namely areas AIP, VIP, LIP and PRR (for reviews see Culham and Valyear, 2006; Medendorp et al., 2011; Vesia and Crawford, 2012). The location of the putative homologue of area AIP in the human brain, as discussed earlier, may correspond to the junction of the postcentral and intraparietal sulci (Culham et al., 2003; Frey et al., 2005; Shikata et al., 2008; Cavina-Pratesi et al., 2010; Jacobs et al., 2010; Marangon et al., 2011) and extend into the inferior branch of the postcentral sulcus and/or the anterior ramus of the intraparietal sulcus. The homologue of monkey area VIP, involved in polymodal motion processing, is suggested to be located adjacent to area AIP in the depth of the anterior ramus of the intraparietal sulcus and the superior branch of the postcentral sulcus (Lewis et al., 2000; Bremmer et al., 2001; Sereno and Huang, 2006; also see Sereno and Huang, 2014). Notably, at present, the putative homologues of areas AIP and VIP are the only two regions, whose location may be predicted purely on the basis of sulcal landmarks in the human brain, possibly because it is relatively easy to identify the intersection between the postcentral sulcus and the anterior intraparietal sulcus in different subjects. In contrast, the issue of homology between the macaque monkey area LIP, involved in saccadic eye movements and attention processing, and PRR, participating in reaching arm movements (for review see Grefkes and Fink, 2005), and their counterparts in the human brain has not yet been resolved, despite the fact, that the researchers use similar experimental tasks in both species. Part of the reason why the location of the homologues of area LIP and PRR has not been defined consistently in the human brain relates to the method of identification and description of this putative location. Commonly, the location of functional activity with respect to saccadic eye movements and reaching arm movements is reported in the group-average stereotaxic space coordinates and described in general anatomical terms, such as the "middle part" or the "posterior part" of the intraparietal sulcus, or the "superior parietal lobe", which leads to difficulty in sharing and comparing such findings by the researchers. If, instead, the location of the putative LIP and PRR activity were to be examined explicitly in individual subjects with respect to specific anatomical landmarks then the results could be compared across multiple subjects and many studies with relative ease. The morphological findings presented in Chapter Three, which include the subdivision of the intraparietal sulcus into two rami and their relation with the sulcus of Jensen, are an essential pre-requisite for such investigations.

On the basis of the average coordinates of the putative LIP and PRR activity reported in the literature it may be proposed that the cortex within the posterior ramus of the intraparietal sulcus and its medial extension into the superior parietal lobule may include the homologues of areas LIP and PRR. Two neuroimaging studies, which performed the individual subject analysis, related the location of the putative homologues of LIP and PRR to a sulcus connected with the intraparietal sulcus in the superior parietal lobule (Medendorp et al., 2003; Bernier and Grafton, 2010), but it remained unknown whether the sulcus the authors referred to was an independent sulcus, such as the superior parietal sulcus, or a part of the intraparietal sulcal complex. Indeed, examination of the posterior parietal region demonstrated that the superior parietal sulcus, which is commonly located between the superior branch of the postcentral sulcus and the sulcus of Brissaud and may merge superficially with the intraparietal sulcus, may be confused with an actual side-branch of the intraparietal sulcus, which extends medially into the superior parietal lobule. Hence, accurate identification in individual subjects of the anterior and posterior rami of the intraparietal sulcus, including their medial extension, and the superior parietal sulcus becomes a requirement for establishing the location of LIP and PRR homologues in the human brain.

The morphological study of the posterior extent of the intraparietal sulcus demonstrated a gyral passage separating it from the paroccipital sulcus in all cases examined. In over a half of the cerebral hemispheres, this gyral bridge was well-developed and visible from the surface of the brain (Figure 3.2a,b; Appendix B, Figure S1b,e), and in the remaining cases it was submerged in the depth (Figure 3.3a-c; Appendix B, Figure S4). The existence of this intervening gyral passage is significant as it may indicate that, in the human brain, the intraparietal sulcus and the paroccipital sulcus develop independently from one another i.e. from different "sulcal roots" (Wilder, 1886; Cunningham, 1892; Jefferson, 1913; Regis et al., 2005) and, furthermore, it may mark the separation between the functionally different cortical regions within the posterior ramus of the intraparietal sulcus and paroccipital sulcus. As discussed earlier, the cortex in the posterior ramus of the intraparietal sulcus may be involved in visualspatial and attentional information processing (Heide et al., 2001; Astafiev et al., 2003; Curtis and Connolly, 2008; for review see Vandenberghe and Gillebert, 2009; Vingerhoets, 2014), while the cortex of the paroccipital sulcus, which forms the lateral border of the parieto-occipital arch (Petrides, 2012), may participate in the higher-order extrastriate visual processing (e.g. visual processing of motion, three-dimensional shapes of objects; Sunaert et al., 1999; Wandell

et al., 2005, 2007; Orban et al., 2006; Swisher et al., 2007; Orban, 2011). The cytoarchitectonic organization of the cortex at the border between the intraparietal and paroccipital sulci has not been characterized in detail, but the limited evidence suggests the presence of transition from one cytoarchitectonic area to another (e.g. from area PEp to area PE $\gamma$  of Economo and Koskinas, 1925). On the basis of the study by Shikata et al. (2008) it may be concluded that the border between the putative homologues of area LIP and area CIP, which processes surface features of three-dimensional objects in space (for review see Grefkes and Fink, 2005), may be placed in the vicinity of the gyral passage separating the intraparietal sulcus from the paroccipital sulcus and the sulcus of Brissaud in the human brain.

#### 5.3 Structure-function relationships in the anterior parietal lobe

The sensorimotor cortex is located in the *pericentral region* in the human brain, which includes the precentral gyrus, central sulcus and the postcentral gyrus, and its posterior boundary is marked by the postcentral sulcus. Until now only one group of studies has demonstrated a reliable localization of the motor representation of one body part, namely the hand, to a specific morphologically-determined part of the central sulcus, referred to as the "hand knob" (*pli de passage moyen* of Broca; Yousry et al., 1997; Boling et al., 1999; Alkadhi and Kollias, 2004). The goal of our fMRI study presented in Chapter Four was to demonstrate that the localization of the hand to the "hand knob" region is not an isolated or a chance occurrence, but a regularity observed in the sensorimotor cortex and applicable to all three aspects of the body, namely the lower extremity, the upper extremity and the face.

Our results demonstrated, for the first time, a strong relationship between the sensorimotor representations of the foot, leg, arm, hand, eye-blinking, mouth and tongue, and the distinct segments of the postcentral sulcus, as identified in our first anatomical study in Chapter Two and refined in Chapter Four. A specific segment of the postcentral sulcus formed the posterior boundary of particular body-part representations in the pericentral region (Figures 4.2-4.4). In general, the functional activity produced by movements of the foot and leg was observed in the dorsomedial part of the pericentral region and anterior to the first segment of the postcentral sulcus. The arm and hand sensorimotor representations were located anterior to the second segment of the postcentral sulcus or anterior to the gyral passage separating the first segment from the second segment of the postcentral sulcus. The eye blinking functional activity was located in the pericentral region anterior to the ventralmost part of the third segment of the

postcentral sulcus. The sensorimotor representations of the oral region (mouth and tongue) were located in the pericentral region anterior to the fourth segment of the postcentral sulcus with the functional activity extending slightly anterior to the adjacent segments. Thus, the results of our study in Chapter Four showed that the somatotopic organization of the sensorimotor cortex relates to the local morphology of the postcentral sulcus in individual subjects in a reliable manner. It follows then that a careful examination of an anatomical MRI brain scan of a new subject may now estimate the location of representations of the lower body (foot and leg), upper body (arm and hand) and the face (eye-blinking, mouth and tongue) in the sensorimotor cortex based on the location of the segments of the postcentral sulcus.

Our findings also demonstrated that the circular movements of the mouth and tongue produced frequently two functional activity clusters in the pericentral region (Figures 4.2, 4.4). Owing to the inherent difficult in moving the mouth independently from the tongue and vice versa, the subjects were likely to elicit a change in functional activity in the mouth and tongue sensorimotor regions simultaneously. There are several reasons to suggest that the dorsal cluster was representative of the mouth movements and the ventral cluster of the tongue movements. First, microstimulation of the ventral motor and ventral premotor cortex in the monkey gives rise to movements of the upper face and lip dorsally and movements of the tongue and jaw ventrally (Cure and Rasmussen, 1954; McGuinness et al., 1980; Murray and Sessle, 1992; Hatanaka et al., 2005). Next, the injection of retrograde tract tracers in the ventral part of the motor face and head representation and not the dorsal part produces a heavy innervation of the hypoglossal motor nucleus in the brainstem, which projects to tongue musculature (Morecraft et al., 2014). In the human subjects, the findings produced by the electrical stimulation (Penfield and Rasmussen, 1950; Woolsey et al., 1979) and TMS of the precentral gyrus (Rödel et al., 2003), and Magnetoencephalography (Nakamura et al., 1998) and fMRI of the postcentral gyrus (Miyamoto et al., 2006) are consistent with the data acquired in the monkey and support the upright somatotopic arrangement of the face region in the ventral sensorimotor cortex.

The question may be asked, if the relationship between the morphological structure of the postcentral sulcus and the sensorimotor representations of different body parts is so consistent, then why it was not demonstrated earlier. After all, the topographic arrangement of sensorimotor representations in the pericentral region was explored previously (e.g., Fink et al., 1997; Nakamura et al., 1998; Lotze et al., 2000; Alkadhi et al., 2002; Boling et al., 2002; Iannetti et al., 2003; Fabri et al., 2005; Hanakawa et al., 2005; Miyamoto et al., 2006; Nevalainen et al., 2006;

Blatow et al., 2007; Huang and Sereno, 2007; Kapreli et al., 2007; Stoeckel et al., 2007; Kopietz et al., 2009; Sakamoto et al., 2010; Stringer et al., 2011; Huang et al., 2012) and our findings are consistent with the existing data. The first reason is that prior to our morphological examination of the postcentral sulcus, presented in Chapter Two, the postcentral sulcus was commonly partitioned into two branches only, namely the superior and inferior branches at the level of the anterior intraparietal sulcus, and further subdivisions were not performed. Furthermore, many of the previous studies reported the average stereotaxic space coordinates of group data for each body region representation in the sensorimotor cortex. In contrast, we conducted a subject-persubject analysis and recorded all functional activity peaks occurring in each experimental condition. Such approach allowed us to overcome the issue of inter-individual variability in morphology of the postcentral sulcal complex, which is present in a standard stereotaxic space and may influence the stereotaxic position of the relevant activity peaks, and study both the postcentral segments and the activity foci in the same subjects. As a result, the precise morphological-functional relations were identified in the anterior parietal lobe and they were subject-specific.

An important finding of our fMRI study is clarification of the role of the transverse postcentral sulcus, which was identified initially in the inferior postcentral gyrus in the morphological study presented in Chapter Two. The results showed that when the transverse postcentral sulcus is present in a hemisphere, it relates functionally to the representations of the mouth and tongue in the sensorimotor cortex (Figures 4.5-4.6). However, in the absence of the transverse postcentral sulcus, the postcentral sulcus extends further ventrally approaching the lateral fissure and forms the posterior border of the mouth and tongue sensorimotor cortex (Figure 4.4). It may be suggested that the transverse postcentral sulcus performs the role of the inferior branch of the postcentral sulcus in the inferior postcentral gyrus and it is proposed that the arrangement of cytoarchitectonic areas within the transverse postcentral sulcus may be similar to the cytoarchitectonic organization of the inferior postcentral sulcus. Both our structural and functional data, presented in Chapters Two and Four, support the hypothesis that the transverse postcentral sulcus belongs to the postcentral sulcal complex. Additional evidence may be provided by future cytoarchitectonic investigations of the inferior postcentral gyrus in the brains, which contain the transverse postcentral sulcus. At present, identification of the transverse postcentral sulcus in a structural MRI scan can be used by researchers to determine the position of representations of the mouth and tongue in the sensorimotor cortex.

In addition to the functional activity observed in the pericentral region, as discussed above, single-subject analysis of our fMRI study demonstrated activity related to various body parts representations within the postcentral sulcus in over half of all subjects (Figures 4.7-4.9). Dorsally, the highest activity peaks related to movement of the leg, foot and hand were recorded within the first segment of the postcentral sulcus, where the transition from dorsomedial area PA<sub>2</sub> to area PD of Economo and Koskinas (1925) occurs. In addition, the arm/hand representations were observed within the second segment of the postcentral sulcus in the left hemisphere and at the point of separation between the first and second segments of the postcentral sulcus in the right hemisphere, dorsal to the point of intersection between the postcentral and anterior intraparietal sulci. Cortex on the banks of the postcentral sulcus constitutes a transitional cytoarchitectonic area PD towards the cortical area PE of the superior parietal lobule (Economo and Koskinas, 1925). In the monkey, neurons located in the corresponding region, namely at the border between the somatosensory cortex of the postcentral gyrus and the cortex of the superior parietal lobule, demonstrate bilateral receptive fields in the forelimb (shoulder, arm and hand) and hindlimb (leg and foot) and respond to manipulation of joints and palpation of muscles (Iwamura et al., 1994, 2002; Taoka et al., 1998, 2000; Iwamura, 2007; Seelke et al., 2011). Functional neuroimaging studies conducted in the human subjects report changes in activity in the superior branch of the postcentral sulcus during sensory and motor stimulation of the lower body, arm and hand (fingers) regions (Kurth et al., 2000; Stoeckel et al., 2007; Huang et al., 2012; Martuzzi et al., 2014). In addition, changes in functional activity in the superior branch of the postcentral sulcus are observed in complex hand movement tasks (Gazzola and Keysers, 2009) involving bimanual directionally-incompatible drawing (Wenderoth et al., 2004), shape encoding (Miquee et al., 2008), writing (Segal and Petrides, 2012a) and joystick operation (Stephan et al., 1995; Grefkes et al., 2004), as well as planning and execution of hand and foot pointing movements (Heed et al., 2011). The present findings can help clarify in future neuroimaging studies the relationship between functional activation foci related to different types of hand movement and the local morphology of the postcentral sulcus at the individual subject level.

The analysis of arm/hand functional activity within the postcentral sulcus, provided in the fMRI study in Chapter Four, demonstrated that these representations were present not only in the superior branch of the postcentral sulcus, but also within the inferior branch of the postcentral sulcus (i.e. the fourth segment), indicating that the arrangement of somatomotor representations

within the postcentral sulcus differs from the general dorso-ventral sequence of such representations in the pericentral region. Furthermore, it may be expected that the cortical regions within the superior branch of the postcentral sulcus are responsible for a different aspect of sensorimotor integration during the arm/hand movement than the regions within the inferior branch of the postcentral sulcus. In the inferior branch of the postcentral sulcus, caudal postcentral area PD forms a transition towards the cortical area PF of the inferior parietal lobule (Economo and Koskinas, 1925). The role of the corresponding region at the border between the somatosensory cortex on the postcentral gyrus and the cortex of the inferior parietal lobule has not been determined in the monkey. The inferior part of the postcentral gyrus in the monkey brain is involved in processing the orofacial sensory information (Kaas, 1983; Pons et al., 1985; Iwamura et al., 2002; Padberg et al., 2007), while the cortex in the anterior part of the inferior parietal lobule may be implicated in specific goal-oriented and self-initiated actions involving the hand and/or the face of an animal, for instance, reaching, bringing an object to the mouth, grasping with the mouth or licking (Hyvarinen and Poranen, 1974; Leinonen and Nyman, 1979; Yokochi et al., 2003; Rozzi et al., 2008). The anterior part of the inferior parietal lobule in the monkey has a crude somatotopic organization (Hyvarinen, 1981; Andersen et al., 1990; Dong et al., 1994) and its neurons have large receptive fields situated on the hand, the face or both the hand and face (peri-mouth) regions (Hyvarinen and Shelepin, 1979; Hyvarinen, 1981; Robinson and Burton, 1980).

In our fMRI study, we observed the arm, hand and also the lower face/oral (tongue) representations within the fourth segment of the inferior branch of the postcentral sulcus with the clusters of activity extending into the adjacent segments (Figures 4.7-4.9). This observation finds additional support in the neuroimaging studies, which report a change in functional activity in the inferior branch of the postcentral sulcus during stimulation of the hand (fingers), lips and tongue (Blankenburg et al., 2003; Watanabe et al., 2004; Stoeckel et al., 2007; Nelson and Chen, 2008; Sakamoto et al., 2010; Huang et al., 2012, see their supplementary information Figures S4-S5). Similarly, the execution of complex hand movements, including writing, controlling a joystick, and texture and shape encoding (Stephan et al., 2013) produces a change in functional activity in the inferior branch of the postcentral sulcus. Future neuroimaging research should address the question about the functional roles played by different segments of the postcentral sulcus with regards to the same type of action, performed by the hand and arm (for instance,

writing or operating a joystick). Our study of the individual variability in morphology of the postcentral sulcus in the MNI stereotaxic space presented in Chapter Two and identification of three anatomically distinct sites within the postcentral sulcus in Chapter Four provide a basis for such investigations.

The process of gyral and sulcal formation in primates, which is not well understood at the moment, may be under the control of various genetic, epigenetic, ontogenetic and environmental prenatal factors and its proper development depends on the integrity of thalamo-cortical and cortico-cortical connections (Goldman-Rakic and Rakic, 1979; Rakic, 1988, 2004; Welker, 1990; Dehay et al., 1996; Sur and Rubenstein, 2005). The developmental hypotheses propose that the afferent cortical connections may be involved in guidance of the cortical folding process by means of mechanical tension exerted along the cortico-cortical fibers (Welker, 1990; Dehay et al., 1996; Van Essen, 1997; Hilgetag and Barbas, 2005, 2006; Herculano-Houzel et al., 2010), modulatory influence of afferent connections on the cortical growth (Goldman-Rakic, 1980) or difference in density of axonal terminations in the cerebral cortex (Nie et al., 2012). Experimental evidence suggests that the development of topography and somatotopic organization in the sensorimotor cortex of different species of mammals (e.g. rats, monkeys) also correlates with the development of thalamo-cortical projections (Welker, 1990; Killackey et al., 1995) and the distribution of discrete bundles of terminations of the thalamo-cortical afferents in the sensorimotor cortex is associated synaptically with the innervation density and relative location of different body regions (Killackey et al., 1995).

The relation between the anatomical landmarks (e.g. sulci, gyri, myelin-rich ovals and myelin-poor septa) and the somatic representations in the sensorimotor cortex of different orders/ infraclasses of mammals (e.g. carnivora, marsupialia, non-human primates) has been investigated in detail previously in the studies of comparative neurology (Connolly, 1950; Welker and Campos, 1963; Johnson, 1980; Welker, 1990). Specifically, in the sensorimotor cortex of several genera of carnivores, the cortical folds correspond to the boundaries between the physiologically defined representations of different body parts, which are not anatomically connected in the body (e.g. between the forelimb and hindlimb, forelimb and face, between the tips of adjacent fingers). For instance, in dogs, cats and raccoons, the head is represented in the coronal gyrus and the cortical region between the postcruciate and coronal sulci contains a sensory forelimb representation (Hamuy et al., 1956; Welker and Seidenstein, 1959; Welker and Campos, 1963; Johnson, 1980). In raccoons, the medial-lateral border between the hindlimb and forelimb

sensorimotor representations is located at the level of the postcruciate sulcus and the border between the forelimb and the face regions is formed by the coronal sulcus (Welker and Seidenstein, 1959). The digits and palm pads of the forelimb are separated by the branches of the tri-radiate sulcus and the adjacent spurs and dimples (Welker and Seidenstein, 1959). In some species of prosimian primates, distinct sulci form separation between the hindlimb and forelimb representations, and also the forelimb and the head/ face representations in the sensorimotor cortex (Radinsky, 1974; Carlson and Welt, 1981; Carlson and Fitzpatrick, 1982).

The sensory cortex of rodents and the New World (squirrel monkey, owl monkey, and marmoset monkey) and Old World (macaque monkey) monkeys contains no sulci between the somatotopic representations and the morphological markers of somatotopy are visualized histologically. In several species of rodents, the clusters of neurons called "barrels" represent individual mystacial vibrissae and pads of the feet and they are separated by cell-poor septa (Woolsey and Van der Loos, 1970; Johnson, 1980). In the somatosensory cortex of monkeys, myelin-poor horizontally-oriented septa separate representations of the forelimb and the face (Krubitzer and Kaas, 1990; Jain et al., 1998, 2008) and also lay between the individual digits representations, which exist as myelin-dense ovals (Jain et al., 1998; Qi and Kaas, 2004).

### **5.4 Conclusion**

The present morphological investigation of the parietal lobe has demonstrated that the postcentral sulcus and the intraparietal sulcus are not simple continuous structures, but rather complexes of sulcal segments separated by gyral passages. The available experimental evidence suggests that the patterns formed by the segments of the postcentral and intraparietal sulci with the neighbouring sulci of the parietal lobe may have cytoarchitectonic and functional significance, which needs to be studied in the future. The results of our systematic anatomical analysis, which addressed the issue of inter-individual variability of the sulci and their patterns in the MNI standard stereotaxic space, are a necessary prerequisite for such future investigations. Furthermore, our fMRI study established an important anatomical-functional relationship in the postcentral gyrus. These neuroimaging findings have demonstrated a link between representations of different body parts in the sensorimotor cortex and specific segments of the postcentral sulcus, which were identified on a subject-per-subject basis. More structure-function relations are expected to be discovered in the parietal lobe when the location of activation foci is

examined on a subject-per-subject basis with respect to the morphological features of the postcentral sulcus and the intraparietal sulcus.
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## Appendix A

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## **Appendix B**

### **Supplementary Material for Chapter Three:**

Zlatkina, V., & Petrides, M. (2014). Morphological patterns of the intraparietal sulcus and the anterior intermediate parietal sulcus of Jensen in the human brain. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1797), 20141493.

# Abbreviations used by the authors in the original articles that are cited in Supplementary

## Tables 1-3:

- AG, angular gyrus
- aIPR, anterior inferior parietal area
- aIPS, anterior intraparietal sulcus
- ant IPS, anterior intraparietal sulcus
- aSPL, anterior superior parietal lobule
- aSPR, anterior superior parietal area
- BA7, Brodmann area 7
- cIPS, caudal intraparietal sulcus
- hLIP, lateral intraparietal sulcus or lateral intraparietal area in the human
- IPs or IPS, intraparietal sulcus
- IPS1-5, intraparietal sulcus areas 1-5
- IPS hor, horizontal segment of the intraparietal sulcus
- LIP, lateral bank of the intraparietal sulcus or lateral intraparietal area
- LR2-3, left reach activation 2-3
- LS2-3, left saccade activation 2-3
- ISPR, lateral superior parietal area
- mid part of IPS, middle part of the intraparietal sulcus
- mIPR, middle inferior parietal area
- mIPS, medial area of the intraparietal sulcus, or medial intraparietal sulcus, or
  - midposterior intraparietal sulcus
- mPC, medial parietal cortex
- mSPR, medial superior parietal area
- pIPS, posterior intraparietal sulcus
- post IPS, posterior intraparietal sulcus

pSPR, posterior superior parietal area

**PPC**, posterior parietal cortex

rIPS, rostral intraparietal sulcus

retIPS, retinotopic intraparietal sulcus

**RS2-3**, right saccade activation 2-3

**RR5**, right reach activation 5

**SPG**, superior parietal gyrus

SPL, superior parietal lobule

SPL1, superior parietal lobule 1

Supplementary Table 1. List of studies with Talairach and Tournoux and MNI stereotaxic coordinates of activation foci related to saccadic eye movements or shifts of attention in the posterior parietal cortex

Task (Saccade or Attention)	Cortical Region, as identified	Left (LH) or Right (RH) Hemisphere	.H) orTalairach and(RH)Tournouxphere			MNI			
	by the authors		Х	Y	Ζ	Х	Y	Ζ	
	Asta	nfiev et al. 2003							
Saccade	pIPS/SPL	LH	-33	-63	54	-34	-60	62	
	Ĩ	RH	21	-63	46	25	-61	53	
	aIPS	LH	-31	-51	48	-32	-48	54	
		RH	31	-49	48	35	-46	53	
Attention	pIPS/SPL	LH	-25	-63	44	-25	-61	51	
		LH	-29	-61	52	-29	-58	60	
		LH	21	-65	52	25	-62	59	
	pIPS/SPL	RH	25	-59	44	29	-57	50	
		RH	31	-59	52	35	-56	59	
	aIPS	LH	-31	-51	46	-32	-48	52	
		RH	39	-53	54	44	-49	60	
	SPL	LH	-17	-65	48	-16	-63	56	
	Ben	der et al. 2013							
Saccade (cue period)	IPS	LH				-36	-46	42	
		RH				37	-57	42	
	SPG	LH				-26	-66	58	
	SPL	RH				26	-64	64	
Saccade (response period)	SPG	LH				-23	-69	59	
		RH				32	-58	52	
	IPS	LH				-35	-50	50	
		RH				35	-53	39	
	Brow	n et al. 2004 ***	k						
Memory > visual guided	rIPS	LH	-29	-50	36	-30	-48	41	
saccade		RH	34	-47	39	39	-44	43	
	cIPS	LH	-20	-71	42	-20	-70	50	
		RH	25	-62	42	29	-60	48	
Co	onnolly et al. 2000 *	*** (also see Cor	nolly et	al. 2002	)				

Antisaccade	mIPR	LH	-33	-62	34	-34	-61	40
		RH	33	-62	33	37	-61	38
	aIPR	LH	-41	-43	35	-43	-41	39
		RH	40	-48	36	45	-46	40
	Corl	betta et al. 1998	6		•		•	•
Saccade	ant IPS	LH	-23	-59	56	-23	-56	64
		RH	35	-57	54	40	-53	61
	post IPS	RH	13	-63	62	16	-59	70
Attention	ant IPS	LH	25	-59	56	29	-55	63
		RH	-25	-55	50	-25	-52	57
	post IPS	LH	17	-65	54	20	-62	62
		RH	-19	-63	60	-18	-59	69
	Curtis an	d Connolly 200	8 ***	•	•		•	•
Known cue/ saccade	aIPS	LH				-36.3	-47.3	47.3
		RH				39.4	-44.4	45.1
	pIPS	LH				-29.3	-65.6	44.4
		RH				26.9	-64.4	43.2
Known delay/ saccade	IPS	LH				-30.6	-63.9	37.5
Known response/ saccade	aIPS	LH				-39.1	-49.5	39.9
		RH				36.7	-42.5	43.3
	pIPS	RH				24.6	-63.9	39.6
	SPL	LH				-21.4	-68.7	52.8
		RH				16.1	-69.3	53.5
	DeS	ouza et al. 2003		•	•		•	•
Saccade	IPS	LH	-22	-60	50	-22	-57	57
		RH	23	-62	48	27	-59	55
	Gera	ardin et al. 2012	2					
Saccade	pIPS	LH	-13	-61	48	-12	-58	55
		RH	13	-63	49	16	-60	56
	mIPS	LH	-27	-54	47	-27	-51	54
		RH	31	-55	48	35	-52	54
	Hu a	nd Walker 201	1			I		
Saccade	PPC (PEF)	LH				-17	-65	56
		RH				20	-69	59
	Hin	kley et al. 2009	1	1	1	1	1	1
Saccade	LS2	LH	-25.6	-63.1	50.9	-26	-60	59
	RS2	RH	28.7	-59.9	50.1	33	-57	57

	LS3	LH	-14.7	-70.3	48.1	-14	-68	56		
	RS3	RH	17.9	-72.8	46.0	21	-71	54		
	Ja	ck et al. 2007			•	•				
Saccade	MIPS	LH	-30	-58	47	-30	-55	54		
		RH	27	-59	52	31	-56	59		
	Jama	adar et al. 2013	;							
Antisaccade (meta-analysis)	IPS	LH	-24	-62	46	-24	-60	53		
	IPS/precuneus	RH	26	-62	48	30	-59	55		
Prosaccade (meta-analysis)	IPS	RH	18	-68	50	21	-66	58		
		LH	-24	-62	40	-24	-60	47		
		RH	28	-52	44	32	-49	49		
	Kim	mig et al. 2001						1		
Saccade	SPL	LH	-31	-71	53	-31	-69	62		
		RH	26	-72	52	30	-70	60		
	Konen	and Kastner 2(	008	J		1	1	1		
Saccade	IPS1	LH, RH	± 25	-72	39	±29	-71	46		
	IPS2	LH, RH	± 24	-71	48	±28	-69	56		
	SPL1	LH, RH	± 18	-68	46	±21	-66	53		
Medendorp et al. 2006 (also see Medendorp et al. 2003, 2005)										
Saccade	retIPS	LH	-24.6	-61.4	44.7	-25	-59	52		
		RH	21.6	-59.4	46.1	25	-57	52		
Scl	luppeck et al. 2005	5 (also see Schlu	uppeck et	t al. 2006	5)	1	1	1		
Saccade	IPS1	LH, RH	± 21	-76	42	± 25	-75	49		
	IPS2	LH, RH	± 18	-71	52	± 21	-69	60		
	Shil	kata et al. 2008		J		1	1	1		
Saccade	mid part of IPS	LH				-25.6	-57	58.4		
		RH				26.1	-59.4	57.6		
	Van	Pelt et al. 2010	)							
Saccade	IPS	LH	-18	-59	49	-17	-56	56		
		RH	14	-61	52	17	-58	59		
	Sim	on et al. 2002						1		
Saccade	SPL	RH				16	-72	56		
	IPS hor.	RH				40	-48	48		
Attention	SPL	RH				24	-64	60		
	IPS hor	LH				-36	-60	60		
	Shul	man et al. 2003	; ;	1	1	1	1	<u>ı</u>		
Visual search/ attention	SPL	LH	-19	-63	44	-19	-61	51		

	IPs	LH	-27	-55	48	-27	-52	55			
		RH	27	-53	50	31	-50	56			
Thiel et al. 2004											
Reorienting of visuospatial	post IPS	RH	27	-60	45	31	-58	51			
attention	ant IPS	LH	-36	-45	42	-37	-42	47			
	Vos	ssel et al. 2012									
Dorsal attention network	IPS	LH				-29.4	-48.8	44.8			
		RH				29.0	-52.8	50.0			
Ventral attention network	IPS	LH				-29.0	-62.5	56.6			
		RH				38.6	-53.6	55.7			

Notes: The studies listed in Supplementary Table 1 provide coordinates of activation foci either in the Talairach and Tournoux (1988) space or in the MNI space. Since the goal was to project the stereotaxic coordinates onto an average brain template registered to the MNI space (ICBM152 non-linear 6th generation model; Grabner et al., 2006; see Discussion), the Talairach and Tournoux (1988) space coordinates reported in the listed studies were converted to the MNI space coordinates using the Signed Differential Method provided at http://www.sdmproject.com/ and both sets of coordinates were reported in Supplementary Table 1. The reader may also consider the additional references and stereotaxic coordinates provided in the review by Vandenberghe and Gillebert (2009; see Figure 3 on p. 174), which supplements the data presented in the current Table. \*\*\* indicates that only part of the data is presented in this table and the original articles must be consulted for a complete list of statistical contrasts.

Task (Saccade and Reaching, or	Cortical Region,	Left (LH) or	Talairach and Tournoux			MNI		
Saccade and Pointing)	and Pointing)as identifiedRight (RF)by the authorsHemisphe		Х	Y	Z	Х	Y	Z
	Beurze	et al. 2009						
Saccade and reach preparation	cIPS	LH	-24	-64	46	-24	-62	54
		RH	18	-70	43	21	-68	50
	Hagler	et al. 2007						
Saccade and pointing	IPS1	RH	20	-69	43	24	-67	50
	IPS2	RH	19	-64	51	23	-61	58
	IPS3	RH	23	-57	51	27	-54	57
	mPC	RH	11	-59	55	14	-56	62
	Leone	et al. 2014						
Saccade and hand pointing	mIPS	LH				-21	-63	60
Saccade and hand pointing	aSPL	LH				-24	-54	63
	Vesia et	al. 2010 **	-	-	•	-	•	-
Saccade and reach planning	mIPS	LH	-22.2	-64.8	41.8	-22	-63	49
		RH	23.8	-62.2	41.2	28	-60	47

Notes: The studies listed in Supplementary Table 2 provide coordinates of activation foci either in the Talairach and Tournoux (1988) space or in the MNI space. Since the goal was to project the stereotaxic coordinates onto an average brain template registered to the MNI space (ICBM152 non-linear 6th generation model; Grabner et al., 2006; see Discussion), the Talairach and Tournoux (1988) space coordinates reported in the listed studies were converted to the MNI space coordinates using the Signed Differential Method provided at http://www.sdmproject.com/ and both sets of coordinates were reported in Supplementary Table 2. \*\* indicates the region of interest that was defined by the authors prior to statistical analyses. Supplementary Table 3. List of studies with Talairach and Tournoux and MNI stereotaxic coordinates of the activation foci related to hand movements (reaching/ pointing) in the posterior parietal cortex

Task (Reaching or Pointing)	Cortical Region, as identified by the authors	Left (LH) or Right (RH) Hemisphere	Ta Ta	lairach an Fournoux Y	nd Z	X	MNI X Y Z				
Astafiev et al. 2003											
Pointing	pIPS/SPL	LH	-25	-63	46	-25	-61	53			
		RH	29	-59	46	33	-56	52			
	aIPS	LH	-35	-49	46	-36	-46	52			
		RH	35	-51	50	40	-47	55			
	SPL	LH	-11	-73	48	-10	-71	56			
		RH	15	-67	48	18	-65	55			
Bernier and Grafton 2010 ***											
Reach to visual:	SPL	LH				-32	-60	60			
gaze-centered (Table S1)		RH				22	-60	72			
Reach to proprioceptive :	IPS	LH				-26	-60	52			
gaze-centered (Table s1)		RH				30	-54	64			
	Be	urze et al. 2010			1		1	1			
Reach	cIPS	LH	-22	-63	49	-22	-61	57			
		RH	22	-64	49	26	-61	56			
	Blang	gero et al. 2009 **			1		1	1			
Meta-analysis and reach	precuneus area 7					21	-58	60			
	SPL area 7					-26	-54	62			
	precuneus area 7					-15	-76	53			
						18	-65	56			
Connolly et al. 2000											
Pro-pointing	pSPR	RH	17	-64	41	20	-62	47			
	aIPR	RH	38	-50	41	43	-47	45			
	ISPR	LH	-35	-49	33	-36	-47	38			
Anti-pointing	mIPR	LH	-29	-60	31	-30	-59	37			
		RH	29	-65	27	33	-65	32			
	aIPR	LH	-36	-49	39	-37	-47	44			
		RH	39	-50	41	44	-47	45			

	D	eSouza et al. 2000									
Pointing	rIPS	LH	-38	-49	44	-39	-46	50			
		RH	34	-46	41	39	-43	45			
	Ferna	ndez-Ruiz et al. 20	007								
Pointing	hLIP	LH	-26	-68	41	-26	-67	48			
	BA7	LH	-12	-60	57	-11	-71	52			
	AG	LH	-39	-65	40	-40	-64	47			
	G	refkes et al. 2004			1	1	1	1			
Joystick movement	IPS	LH				-28	-50	52			
(visuo-motor control)		RH				28	-56	50			
Joystick movement with	IPS	LH				-14	-62	56			
visual feedback		RH				16	-62	56			
Joystick movement with	IPS	LH				-28	-58	66			
no visual feedback		RH				30	-56	50			
	Н	linkley et al. 2009					1				
Reach-to-grasp	LR2	LH	-28.3	-57.3	49.0	-29	-55	56			
	LR3	LH	-6.4	-61.5	55.7	-5	-58	64			
	RR5	LH	27.1	-58.7	51.1	31	-56	58			
	Medendorp et al. 2003										
Pointing	IPS	LH	-19	-62	46	-19	-60	53			
		RH	22	-64	44	26	-62	50			
	S	Simon et al. 2002	1	1	1	1	1	1			
Pointing	SPL	RH				16	-68	52			
		RH	1			36	-48	56			

Notes: The studies listed in Supplementary Table 3 provide coordinates of activation foci either in the Talairach and Tournoux (1988) space or in the MNI space. Since the goal was to project the stereotaxic coordinates onto an average brain template registered to the MNI space (ICBM152 non-linear 6th generation model; Grabner et al., 2006; see Discussion), the Talairach and Tournoux (1988) space coordinates reported in the listed studies were converted to the MNI space coordinates using the Signed Differential Method provided at http://www.sdmproject.com/ and both sets of coordinates were reported in Supplementary Table 3. Figure 6 on p. 2905 by Konen et al. (2013) provides additional references and stereotaxic coordinates of the activity peaks produced by grasping and reaching movements. \*\* indicates the regions of interest defined by the authors prior to statistical analyses on the basis of earlier studies. \*\*\* indicates that only part of the data is presented in this table and the original articles must be consulted for a complete list of statistical contrasts.

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Supplementary Figure 1. Demonstration of the anterior intermediate parietal sulcus of Jensen (aipsJ) in the hemispheres of different subjects. (a) aipsJ is formed by a downward branch of the intraparietal sulcus (IPS); (b) aipsJ is a simple notch; (c-d) aipsJ is a sulcus merging with the IPS; (e) aipsJ connects superficially with the first caudal branch of the superior temporal sulcus (cSTS1). Abbreviations: aipsJ, anterior intermediate parietal sulcus of Jensen; CS, central sulcus; cSTS1, first caudal branch of the superior temporal sulcus; cSTS2, second caudal branch of the superior temporal sulcus; iPoCS, inferior branch of the postcentral sulcus; IPS, intraparietal sulcus (main horizontal part of the intraparietal sulcus); IPSa, anterior ramus of the horizontal part of the intraparietal sulcus; Sometimes considered as the paroccipital part of the intraparietal sulcus; Sometimes considered as the paroccipital part of the intraparietal sulcus; Sometimes considered as the paroccipital part of the intraparietal sulcus; Sometimes considered as the paroccipital part of the intraparietal sulcus; Sometimes considered as the paroccipital part of the intraparietal sulcus; Sometimes considered as the paroccipital part of the intraparietal sulcus; Sometimes considered as the paroccipital part of the intraparietal sulcus; Sometimes considered as the paroccipital part of the intraparietal sulcus; Sometimes considered as the paroccipital part of the intraparietal sulcus; Sometimes considered as the paroccipital part of the intraparietal sulcus; Sometimes considered as the paroccipital sulcus.



Supplementary Figure 2. Illustration of the gyral passage (1g) which separates the intraparietal sulcus (IPS) from the inferior branch of the postcentral sulcus (iPoCS) and gyral passage (2g) which subdivides the IPS into two rami: the anterior (IPSa) and posterior (IPSp) rami. Abbreviations: cSTS1, first caudal branch of the superior temporal sulcus; cSTS2, second caudal branch of the superior temporal sulcus; iPoCS, inferior branch of the postcentral sulcus; IPSa, anterior ramus of the horizontal part of the intraparietal sulcus; IPS-PO, paroccipital sulcus, sometimes considered as the paroccipital part of the intraparietal sulcus; LF, lateral fissure; POF, parieto-occipital fissure; sB, sulcus of Brissaud.



Supplementary Figure 3. Schematic representation of the anterior intermediate parietal sulcus of Jensen (aipsJ) in the human brain. (a) aipsJ is formed by a downward branch of the intraparietal sulcus (IPS); (b) aipsJ is a simple notch ; (c) aipsJ is a sulcus merging with the IPS; (d) aipsJ blends superficially with the first caudal branch of the superior temporal sulcus (cSTS1). Abbreviations: aipsJ, anterior intermediate parietal sulcus of Jensen; IPS, intraparietal sulcus (main horizontal part of the intraparietal sulcus); cSTS1, first caudal branch of the superior temporal sulcus.



Supplementary Figure 4. Three-dimensional reconstruction of the right hemisphere of one subject showing two rami of the intraparietal sulcus (IPS) and the anterior intermediate parietal sulcus of Jensen (aipsJ). The level of section is shown for horizontal sections (a-c) and coronal sections (d-f), displayed in Figure 3.3. Abbreviations: aipsJ, anterior intermediate parietal sulcus of Jensen; CS, central sulcus; cSTS1, first caudal branch of the superior temporal sulcus; cSTS2, second caudal branch of the superior temporal sulcus; cSTS3, third caudal branch of the superior temporal sulcus; IPSa, anterior ramus of the horizontal part of the intraparietal sulcus; IPSp, posterior ramus of the horizontal part of the intraparietal sulcus; LF, lateral fissure;

PoCS, postcentral sulcus; POF, parieto-occipital fissure; sB, sulcus of Brissaud; SmgS, supramarginal sulcus; SPS, superior parietal sulcus; STS, superior temporal sulcus.



Supplementary Figure 5. Three-dimensional reconstruction of the left hemisphere of one subject containing the anterior intermediate parietal sulcus of Jensen (aipsJ), which merges with the

intraparietal sulcus (IPS). The level of cut is shown for coronal sections (a-i) in Supplementary Figure S6, horizontal sections (a-g) in Supplementary Figure S7 and sagittal sections (a-h) in Supplementary Figure S8. Abbreviations: aipsJ, anterior intermediate parietal sulcus of Jensen; CS, central sulcus; cSTS1, first caudal branch of the superior temporal sulcus; cSTS2, second caudal branch of the superior temporal sulcus; cSTS3, third caudal branch of the superior temporal sulcus; iPoCS, inferior branch of the postcentral sulcus; IPS, intraparietal sulcus (main horizontal part of the intraparietal sulcus); IPS-PO, paroccipital sulcus, sometimes considered as the paroccipital part of the intraparietal sulcus; LF, lateral fissure; POF, parieto-occipital fissure; sB, sulcus of Brissaud; SmgS, supramarginal sulcus; sPoCS, superior branch of the postcentral sulcus; SPS, superior parietal sulcus.



Supplementary Figure 6. Coronal sections from the left hemisphere of one subject containing the anterior intermediate parietal sulcus of Jensen (aipsJ), which merges with the intraparietal sulcus (IPS). The level in the rostro-caudal dimension (y coordinate) is given in millimetres for each section. Three-dimensional reconstruction of the same hemisphere and the level of cut are shown in Supplementary Figure S5. Abbreviations: aipsJ, anterior intermediate parietal sulcus of Jensen; cSTS1, first caudal branch of the superior temporal sulcus; cSTS2, second caudal branch of the superior temporal sulcus; cSTS3, third caudal branch of the superior temporal sulcus; IPS, intraparietal sulcus (main horizontal part of the intraparietal sulcus); IPS-PO, paroccipital sulcus, sometimes considered as the paroccipital part of the intraparietal sulcus; LF, lateral fissure; PoCS, postcentral sulcus; POF, parieto-occipital fissure; SPS, superior parietal sulcus.





Supplementary Figure 7. Horizontal sections from the left hemisphere of one subject containing the anterior intermediate parietal sulcus of Jensen (aipsJ), which merges with the intraparietal sulcus (IPS). The level in the dorso-ventral dimension (z coordinate) is given in millimetres for each section. Three-dimensional reconstruction of the same hemisphere and the level of cut are shown in Supplementary Figure S5. Abbreviations: aipsJ, anterior intermediate parietal sulcus of Jensen; CS, central sulcus; cSTS1, first caudal branch of the superior temporal sulcus; cSTS2, second caudal branch of the superior temporal sulcus; cSTS3, third caudal branch of the superior temporal sulcus; IPS, intraparietal sulcus (main horizontal part of the intraparietal sulcus); IPS-PO, paroccipital sulcus; POF, parieto-occipital fissure; SmgS, supramarginal sulcus; SPS, superior parietal sulcus.



Supplementary Figure 8. Sagittal sections from the left hemisphere of one subject containing the anterior intermediate parietal sulcus of Jensen (aipsJ), which merges with the intraparietal sulcus (IPS). The level in the medio-lateral dimension (x coordinate) is given in millimetres for each section. Three-dimensional reconstruction of the same hemisphere and the level of cut are shown in Supplementary Figure S5. Abbreviations: aipsJ, anterior intermediate parietal sulcus of Jensen; CS, central sulcus; cSTS1, first caudal branch of the superior temporal sulcus; cSTS2, second caudal branch of the superior temporal sulcus; cSTS3, third caudal branch of the superior temporal sulcus; IPS, intraparietal sulcus (main horizontal part of the intraparietal sulcus); IPS-PO, paroccipital sulcus, sometimes considered as the paroccipital part of the intraparietal sulcus; LF, lateral fissure; PoCS, postcentral sulcus; SPS, superior parietal sulcus.