

## **Cytoarchitectonics of the Rolandic operculum: morphofunctional ponderings**

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**Abstract**

Constantin von Economo (1876–1931) had a long-standing interest in the cellular structure of the human cerebral cortex. In the present article I highlight a historical paper that von Economo published in 1930 on the cytoarchitectonics of the Rolandic operculum, an English translation of which I provide as supplementary material. I further discuss some morphofunctional aspects of the human opercular cortex from a modern perspective, as well as the clinical relevance to language dysfunctions, the operculum syndrome, and epilepsy.

**Keywords:** Cerebral cortex; Cytoarchitectonics; Frontoparietal operculum; History of neuroscience; Constantin von Economo (1876–1931)

## **Introduction**

In 1925, Constantin von Economo (1876–1931) and Georg N. Koskinas (1885–1975) published their monumental atlas of cytoarchitectonics of the adult human cerebral cortex, which represented an enormous intellectual and technical effort (von Economo and Koskinas 2008; Triarhou 2007a). These two classical neuroanatomists took Korbinian Brodmann's studies (Brodmann 1909) to a new zenith, by defining 54 'ground', 76 'variant' and 107 'modification' areas, as opposed to Brodmann's 44 areas for the human cerebral cortex.

The cytoarchitectonic studies of the cerebral cortex made by von Economo and Koskinas are not just of major significance for the history of neuroscience, but they also provide a source of useful data for contemporary studies of the human cerebral cortex, currently used and reused in vivid and lively manners by neuroanatomists (e. g., García-Cabezas et al. 2020) and neuroimaging researchers alike (e. g., Scholtens et al. 2018; Zhang et al. 2020).

In 1930, von Economo founded and directed the Department of Brain Research in Vienna within the premises of the University Neuropsychiatric Clinic that was at the time chaired by Otto Pötzl (1877–1962), successor to Nobel laureate Julius Wagner-Jauregg (1857–1940). One paper in a series of cytoarchitectonic studies derived from the new Department was on the Rolandic operculum (von Economo 1930) (Fig. 1), an English translation of which I provide herein as Supplementary material.

In that article, von Economo (1930) discusses the relationships between the sulcal and areal distribution patterns in the Rolandic operculum, as well as individual macroscopic anatomical variations. The article is structured into four main subsections: a general introductory paragraph, a section on the cytoarchitectonics of the Rolandic operculum, a 'peculiar' case with an unusual ventral extension of the central sulcus, and a concluding comment with his position regarding the neuronal underpinnings of language and mental acts.

## **Cortical type**

The 'cortical type' is a paramount contribution of von Economo, and a key concept for our understanding of the cerebral cortex. It is based on 'the constant variations that one observes in each of the layers in different regions' (von Economo and Koskinas 1925, 2008; von Economo 1927, 2009). It is interesting to note that Santiago Ramón y Cajal attributed great relevance and importance to the concept of cortical type, to the point that he included

the famous figure of von Economo's types in the chapter devoted to the nervous system (under the epigraph 'Regional variations of the cerebral cortex') of the later editions of his textbook of general histology for medical students (see the English translation: Ramón y Cajal 1933).

The concept of cortical type is more meaningful and practical than the concept of cortical area, like the areas of Brodmann. If one knows the cortical type of a given area, then one can predict several key structural, connectional, and functional features of this area. For instance, modern tract-tracing techniques allowed to realise that cortical types are related to laminar patterns of cortico-cortical connections and, therefore, to cortical hierarchies. Thus, cortical types predict the laminar patterns of cortico-cortical connections according to the Structural Model of Helen Barbas (Barbas and Rempel-Clower 1997). But cortical types also predict the spread of cortico-cortical projections from one area across fewer or more areas. Actually, this has been shown in the frontal operculum by Morecraft et al. (2015); in that paper, figure 15 summarises the wide spreading of cortico-cortical connections of frontal opercular areas: areas with simpler laminar architecture (agranular and dysgranular cortical types), like dysgranular insula and opercular ProM areas, have widespread projections to many cortical areas, while areas with a progressively more complex laminar cytoarchitecture (eulaminate I, II, and III cortical types), like ventral premotor and ventral primary motor areas, project to fewer areas.

These two features of cortico-cortical connections (laminar patterns and spreading of projections from one area across fewer or more areas) are key for distributing cortical areas across cortical hierarchies and for calibrating the extent of influence of a given area onto the rest of the cerebral cortex. Cortical type is also related to synaptic plasticity: the expression of markers related to synaptic plasticity is higher in cortical areas with a simpler, and lower in areas of a more complex laminar cytoarchitecture (García-Cabezas et al. 2017). And all these structural, connectional, and functional features of cortical areas are predicted by cortical type, a concept that we owe to von Economo.

Cortical type gradations in the frontal operculum have been described in macaques (Barbas and Pandya 1987) and in humans (Sanides 1970; García-Cabezas et al. 2020). In his article, von Economo (1930) mentions three different types of neighbouring areas that converge on the Rolandic operculum.

## **Anatomy**

The operculum is formed by the adjoining of three lobes, which determine its four main regions: the frontal (premotor) operculum, the parietal operculum, the temporal operculum and the Rolandic operculum. The operculum covers the underlying insular gyri. The superior wall of the lateral (Sylvian) fissure is formed by the frontal operculum anteriorly and by the parietal operculum posteriorly. The inferior wall of the Sylvian fissure is created by the temporal operculum. The Rolandic operculum, also known as the subcentral gyrus or the central/basal operculum, is the part located on the precentral and postcentral gyri, on either side of the central sulcus of Rolando. Histologically, the subcentral area (Brodmann area 43) is a transition region of the frontoparietal operculum (Tonkonogy and Puente 2009; Catani and Thiebaut de Schoten 2012).

The term frontoparietal operculum refers to the parts of the frontal and the parietal lobe that overlie the dorsal surface of the insula. It is composed of the frontal operculum rostrally and the parietal operculum caudally. It constitutes the superior bank of the lateral fissure and is separated from the insula by the superior limiting sulcus (Braininfo 2020). The frontoparietal operculum (Fig. 2) is characterised by a V-shaped convolution consisting of the pars triangularis of the inferior frontal gyrus ( $F_3$ ), located just superiorly to the anterior Sylvian point, and usually containing a descending branch of the inferior frontal sulcus. The three following U-shaped convolutions are composed of the pars opercularis of  $F_3$ , which is always intersected by the inferior part of the precentral sulcus; the Rolandic operculum, composed of the inferior connection of the precentral and postcentral gyri enclosing the inferior part of the central sulcus; the connection arm between the postcentral and supramarginal gyri that contains the inferior part of the postcentral sulcus; and, finally, the C-shaped convolution constituted by the connection of the supramarginal and superior temporal ( $T_1$ ) gyri that encircles the posterior end of the Sylvian fissure. The precentral and postcentral gyri are consistently united inferiorly by the subcentral gyrus or Rolandic operculum (Ribas 2011).

Regarding the morphology of the Rolandic operculum and its adjacent cortex, the lateral segment of the anterior subcentral sulcus continues ventrally into the opercular cortex, which is hidden within the lateral fissure. The anterior ascending ramus of the lateral fissure extends dorsally from the lateral fissure, often traversing  $F_3$  at a slight anterior incline. A small gyral bridge separates the lateral segment of the anterior subcentral sulcus from the

opercular segment of the anterior subcentral sulcus, which extends medially along the entire width of the frontal operculum until it reaches the circular insular sulcus (Eichert et al. 2020).

The frontal operculum is formed by the pars opercularis of  $F_3$ . Occasionally, the diagonal sulcus of Eberstaller (1884) may divide it into two parts (ten Donkelaar 2020). Eberstaller (1890) described the sulcus diagonalis as dividing the pars opercularis of  $F_3$  into a posterior component, the pars basilaris, and an anterior component, the pars ascendens. The sulcus diagonalis stops short within the frontal operculum. Brodmann (1909) described this sulcus as separating an anterior opercular area from a posterior opercular area (Sprung-Much and Petrides 2018). Brodmann area 43, which Brodmann (1909) included in the operculum, was not considered an independent area by von Economo and Koskinas (2008), but rather a transitional formation or mixing of the caudal postcentral area *PD* and the supramarginal area *PF*, which they denoted as area *PFD* or supramarginal area, caudal postcentral transition (Goldstein 1927; von Bonin 1950; von Economo 2009).

The central sulcus usually does not reach the lateral sulcus; it is separated from the lateral sulcus by the Rolandic operculum and delimited by the anterior and posterior subcentral sulci (Déjerine and Déjerine-Klumpke 1895). Nonetheless, von Economo (1930) described the expansion of the oral postcentral area *PB* in one case characterised by the peculiarity of the central sulcus not ending at the cerebral convexity on the surface of the operculum, but extending further ventrally, by crossing the operculum and giving the impression that it ran into the lateral fissure. By unfolding the Sylvian fossa, the central sulcus, coursing over the convexity of the operculum, also carved its ventral surface at a 1-cm depth, where the Sylvian fossa faced the lower surface of the operculum. With such an extension of the central sulcus ventrally, it still represented the sharp boundary between the parietal and the frontal regions. Both the motor precentral area *FA* and the oral postcentral area *PB* ended early at the dorsal parts of the operculum, as it happens in most cases, about 1.5 cm away from the dorsal lip of the Sylvian fissure in the depths of the central sulcus. By such a downward extension of the central sulcus, the giant pyramidal postcentral area *PA* actually appeared to extend ventrally, whereas that extension did not affect the precentral area *FA* and the oral postcentral area *PB*. The agranular frontal area *FB* and the intermediate postcentral area *PC* expanded normally into the basal surface of the operculum, without being affected by that extension of the central sulcus. Moreover, the central sulcus formed the boundary between the parietal and the frontal cortex, advancing itself into the

operculum somewhat frontally in a further expansion, all the way to its end on the lower surface of the operculum. From that peculiar extension of the central sulcus ventrally, von Economo (1930) concluded that neither an extension of the motor nor the sensory regions occurred. There was most likely an extension of the giant pyramidal postcentral area PA, which reached further ventrally.

### **Connections**

In the rhesus macaque monkey, the anteriormost part of the inferior parietal lobule (supramarginal area PF) projects to the ventral Brodmann area 6, including the caudal bank of the lower branch of the arcuate sulcus, to the ventral Brodmann area 46 below the sulcus principalis, and to the cortex of the rostral and pericentral frontal operculum (Petrides and Pandya 1984; Morecraft et al. 2015). Studies have specified that area PF is primarily connected with somatosensory areas and with parietal and frontal face– and arm–related areas, thus offering new insight into the possible role of the inferior parietal lobule in space perception and motor control (Rozzi et al. 2006). The anatomical connections of anterior and posterior cingulate areas and the adjacent somatomotor and somatosensory areas have been summarised in figure form by Morecraft et al. (2004, 2012), also showing connections to opercular areas.

In the human brain, the Rolandic operculum receives a transcallosal projection from the posterior cingulate cortex. Ipsilateral afferents are distributed in the temporal and frontal lobes, in particular from the middle and posterior cingulate cortices, the dorsomesial prefrontal cortex and the anterior insula and posterior cingulate, and with the postcentral gyrus, the paracentral lobule and the temporo-parieto-occipital junction. It sends efferent fibres to the parietal lobe, as well as to the ipsilateral frontal, temporal and occipital lobes. The strongest projections are to the postcentral gyrus, the superior parietal lobule, the fusiform gyrus, and the inferior temporal gyrus. As a part of the primary gustatory cortex, the Rolandic operculum is located anterior to the cortical somatic tongue representation. Its connectivity supports a role in feeding behaviour and speech production. The Rolandic operculum shows a complex connectivity pattern with the infrasyllian level (parahippocampal gyrus; temporal operculum; fusiform gyrus; amygdala; temporal pole; and superior, middle and inferior temporal gyri) thought to have a role in sensory–auditory integration, which is essential for speech production (Măliia et al. 2018).

The precentral gyrus, in addition to its superior and inferior connections with the postcentral gyrus via the superior (paracentral lobule) and inferior frontoparietal fold (Rolandic operculum or subcentral gyrus), is also usually connected to the postcentral gyrus via a transverse gyrus that lies along the bottom of the central sulcus and constitutes the so-called Broca's middle frontoparietal *pli de passage* (Ribas 2011).

## Functions

The varieties of cortical types across opercular areas (Table 1) likely underlie and help to explain the complex connectivity pattern and the complex functions of the operculum: from limbic agranular and dysgranular areas, involved in emotional processing, to multimodal and unimodal eulaminate areas, to primary sensory koniocortices (Mesulam 1998; Barbas 2015; García-Cabezas et al. 2019). Thus, the complex functions of the operculum include sensory, motor, autonomic, cognitive processing and language, all of which are implemented by highly specialised neuronal populations and their widespread connections.

Electrical stimulation experiments in humans have implicated the operculum and the insula in gustation (Penfield and Jasper 1954) and in the induction of vocalisation (Penfield and Roberts 1959). Besides its role in emotion processing, the Rolandic operculum functions as the sensory system for gustatory and visceral sensation along with the cingulate cortical network (Eickhoff et al. 2006b). In the human parietal operculum, based on measurements of the 'grey level index' (an indicator of the volume fraction of neuron somata), Eickhoff et al. (2006a, c) identified four distinct heterogeneous cytoarchitectonic areas, OP1–OP4, as the anatomical correlates of the secondary somatosensory cortex (S2). Area OP4 is similar in location to Brodmann area 43 and to von Economo–Koskinas area *PFD*, because it contains large pyramidal cells in cortical layers IIIc and Va. Topographically, OP1 corresponds to S2, while OP4 is similar to the parietal ventral area. OP3 may be the human homologue of the ventral somatosensory area in non-human primates (Eickhoff et al. 2006a, c).

The functionally-defined S2 was localised in the parietal operculum, within the Sylvian fissure. Penfield and Jasper (1954) provided the first description for the human brain in their neurosurgical stimulation studies. Brodmann areas 40 and 43 extend into the parietal operculum and are candidates for S2 on topographic grounds; they partially correspond, respectively, to the opercular modification  $PF_{op}$  and to the von Economo–Koskinas subcentral area *PFD* (Table 1). Area  $FCD_{op}$  (opercular intermediate granular frontal area)

denotes a transitional variant between the opercular intermediate frontal area  $FC_{op}$  and the granular frontal area in operculum  $FD_{op}$  (Triarhou 2007b).

The frontal operculum (Broca's area) is involved in cognitive/motor sequence production and imitation as well as singing tasks, including musical imitation and vocal learning. Strong activations in the right frontal operculum are observed when human subjects are asked to imagine continuations of the opening fragments of familiar songs without words. Activation of the frontal operculum during covert singing tasks provides further support for a key role of this area in the human song-control system, and, conceivably, instrumental performance as well. Moreover, the frontal operculum is activated during tasks that involve the processing of rhythm and time-intervals in addition to the processing of pitch. The use of complex and novel melodies enables the identification of the roles of two regions of the 'musical brain', namely the superior part of the temporal pole (Brodmann area 38) and the pars opercularis of  $F_3$  (Brodmann area 44/6). The latter may be part of a mirror system involved in audiovocal template matching for both pitch and rhythm, thus transcending in its functional role the purely motor aspects of vocalisation (Brown et al. 2004).

There are prominent changes within the central opercular region and the posteroventral insula, possibly related to the long-lasting encoding of haptic information, which results from experimental tasks requiring memory (recurring and missing stimulus identification). By using positron emission tomography, those studies investigated the neural systems involved in the memory processing of experiences through touch while the human subjects performed tasks that involved different levels of tactual memory (Bonda et al. 1996).

An extensive region located at the junction of the anterior insula and the frontal operculum, at the intersection of the circular insular sulcus and the frontal operculum, is an integral part of the performance monitoring network (Amiez et al. 2016).

The midventrolateral prefrontal region (Brodmann areas 47/12 and 45) is involved in active controlled retrieval processing necessary for the disambiguation of vibrotactile information in short-term memory. This particular part of the prefrontal cortex functionally interacts with the secondary somatosensory areas in the parietal operculum and the rostral inferior parietal lobule during controlled processing for the retrieval of specific tactile information (Kostopoulos et al. 2007).

The Rolandic operculum processes integrated exteroceptive–interoceptive signals that

are necessary for interoceptive awareness as well as bodily self-consciousness. Bilateral Rolandic operculum contiguous to the insula is not only involved in the processing and awareness of interoceptive signals, but also in bodily self-consciousness-related processes based on cardiovisual stimulation (Blefari et al. 2017).

### **Clinical relevance**

The anatomy and physiology of the frontoparietal operculum is important in clinical neurology, because it is involved in speech and language disorders as well as epilepsy and the operculum syndrome (Fusco and Vigeveno 1991).

### *Speech and language*

Early experimental physiology studies showed that the function of the operculum is in direct relation to its development in children, whose aptitude for exteriorising their ideas by means of speech increases as the texture of the cerebral cortex matures (Jakob 1906).

The processing of local transitions is subserved by the left frontal operculum, a region that is phylogenetically older than Broca's area and specifically responsible for the computation of hierarchical dependencies. There seems to be a functional differentiation between the two phylogenetically and cytologically different cortical areas in the left frontal lobe. The evaluation of transitional dependencies in sequences generated by a finite-state primitive grammar (known to be learnable by non-human primates) activates a phylogenetically older cortex, the deep frontal operculum. On the other hand, the computation of hierarchical dependencies in sequences generated according to the more complex phrase-structure grammar (which characterises human language) additionally recruits a phylogenetically younger cortex, namely the surface portion of Broca's area (Brodmann area 44/45 or von Economo–Koskinas magnocellular agranular intermediate frontal area  $FCB_m$  and triangular granular frontal area  $FD_r$ ) (Friederici et al. 2006).

The areas in and around the lower ends of the central gyri and the Rolandic operculum are related to the central control of the oral and larynx movements involved in articulation, the third stage of speech production. It seems that a lesion around the Rolandic operculum, probably in Broca's area, also underlies central level word-finding and sentence production disturbances (Tonkonogy and Puente 2009).

The Rolandic operculum (Brodmann area 43) is often destroyed in Broca's aphasia

(Henschen 1922; Nielsen 1946; Hécaen and Consoli 1973; Mohr et al. 1978; Tonkonogy 1986). Niessl von Meyendorf (1930) underlined the importance of lesions in the Rolandic operculum in the development of an articulation disorder in global aphasia with a large infarction in the anterior and posterior language areas of the left cerebral hemisphere, including the Rolandic operculum, while Broca's area was unaffected. Kleist (1934) also suggested a lesion in the Rolandic operculum as a pathogenetic factor in aphasic dysarthria.

Lesions crucial for the development of oral apraxia are located in the left frontal and the Rolandic opercula, the adjacent areas of T<sub>1</sub> and the anterior portion of the insula (Tognola and Vignolo 1980). Pierre Marie (1906) emphasised the critical role of subcortical lesions in the causation of aphasia; he attributed the development of anarthria to a lesion of the lenticular zone, including the caudate-putamen, globus pallidus, internal and external capsule, insula, Rolandic operculum and supramarginal gyrus on the inner side of the lateral fissure (Tonkonogy and Puente 2009).

Lecours and Lhermitte (1976) reported an isolated lesion in the Rolandic operculum, verified by autopsy, in articulation aphasia. In the case of a patient with expressive speech disorder (Tonkonogy and Goodglass 1981), there was a transient, predominantly articulatory difficulty, which was thought to be associated with an ischemic necrotic lesion in the lower part of the left motor strip and a lesion of the anterior part of the Rolandic operculum. Thus, articulatory disorders (i.e. articulation causing a cortical dysarthria – slowness and dysprosodic alteration of speech-melody with stuttering and poor control of pitch) may be associated with lesions of the Rolandic operculum, whereas transient word-finding difficulties have been reported in cases with lesions of the posterior part of F<sub>3</sub>.

Transcortical motor aphasia or dynamic aphasia may be considered to be a type of frontal lobe aphasia representing an important, often overlooked, part of the frontal lobe syndrome. However, in cases of Broca's aphasia, the frontal portion of the posterior part of F<sub>3</sub> only represents the anterior part of the lesion, which extends posteriorly to the Rolandic operculum, the insula and subcortical structures (Tonkonogy and Puente 2009).

In global aphasia, an extensive cerebral infarction in the left hemisphere occupies the cortex and underlying white matter around the left lateral fissure, extending from Broca's area, the Rolandic operculum and the insula, through the supramarginal gyrus and anterior and middle parts of T<sub>1</sub>, to the angular gyrus (Tonkonogy 1986).

### *Foix–Chavany–Marie syndrome*

Bilateral destruction of the Rolandic operculum caused by perisylvian infarctions may result in the bilateral anterior opercular or Foix–Chavany–Marie syndrome (Foix et al. 1926; Alajouanine et al. 1959; Garde et al. 1961; Rebutti et al. 1964; Mariani et al. 1980).

A left hemisphere lesion confined to the Rolandic operculum and sparing Broca’s area is not associated with a linguistic impairment of speech; rather, it is associated with a more peripheral deficit of speech articulation. The destruction of the lower motor strip (with the Rolandic operculum) exclusively affects articulatory abilities without involving language organisation. In a patient who suffered two successive, right and left, strokes that damaged the Rolandic operculum on both sides, the clinical picture was characterised by selective impairment of volitional facio-pharyngo-glosso-masticatory movements with a sparing of automatic and reflex motor activity. The deficit in speech articulation was much severer than the cortical dysarthria, and though completely speechless, the patient was not aphasic: because the left Rolandic operculum lesion was superimposed on pre-existing right hemisphere damage, including the right Rolandic operculum, the typical clinical pattern of Foix–Chavany–Marie syndrome developed, with a complete inability to vocalise (Villa and Caltagirone 1984).

Intense psychological symptoms, such as high apathy, depression, anxiety and perceived stress, may be associated with lesions of the right Rolandic operculum (part of Brodmann area 43) in post-stroke patients (Sutoko 2020).

### *Epilepsy*

The circuminsular fibre tracts to the Rolandic operculum described above (under the subheading ‘Connections’) are one of the commonest patterns of ictal spreading from temporal to extratemporal locations (Măliia et al. 2018).

Oroalimentary automatisms are produced by a synchronised spread of discharge to the Rolandic operculum in mesial temporal lobe epilepsy. In insulo-opercular epilepsy, the Rolandic operculum is the symptomatogenic zone of the facial tonic and clonic contractions. Seizure propagation to the Rolandic operculum generates different semiologies owing to the varying synchronisation frequencies and energies of the sub-bands, depending on the site of seizure origin (Wang et al. 2020).

In a bilingual patient with left low-grade glioma involving the Rolandic operculum and a

history of increasing seizures, Espadaler and Conesa (2011) detected cortical areas crucial for Spanish using preoperative navigated transcranial magnetic stimulation; the repetitive navigated transcranial magnetic stimulation showed language areas for Spanish in the pars opercularis and pars triangularis.

### **Concluding remark: mentality from neurons**

In the latter part of his article, von Economo (1930) rebutted a point raised by the philosopher–neuropsychiatrist Erwin Niessl von Mayendorf (1873–1943). Niessl von Mayendorf was a pupil of Paul Flechsig (1847–1929) and Carl Wernicke (1848–1905) and a pioneer of aphasia and the localisation of language in the brain (Steinberg 2009). He pursued an approach that stood in contrast to both localisationism and antilocalisationism, the theories that predominated in the early 20th century, and took the stance that cognitive processes were the result of association (Frauenlob et al. 2012). Niessl von Mayendorf (1930) attributed mental functions specifically to the typical giant-size pyramidal cells of layer IIIc in Broca’s area, which he called ‘von Economo speech cells’ (*Economos Sprachzellen*).

By and large, von Economo (1930) did not agree with the ascription of mental functions or their localisation to specific cytoarchitectonic areas or to a particular neuron type. Instead, he explained that mental processes are complex and also involve subcortical areas in addition to the cerebral cortex. The so-called brain centres *participate* in the emergence of mental functions, rather than *being* the brain centres of mental functions *sensu stricto*, while the physiological functions of any neuron may include conduction, facilitation, inhibition, excitation and sensitisation and not a direct mental process.

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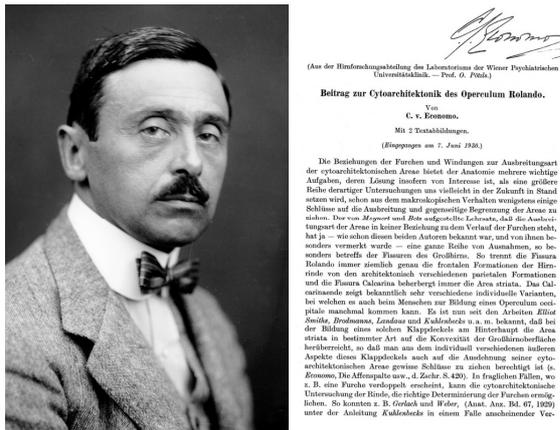
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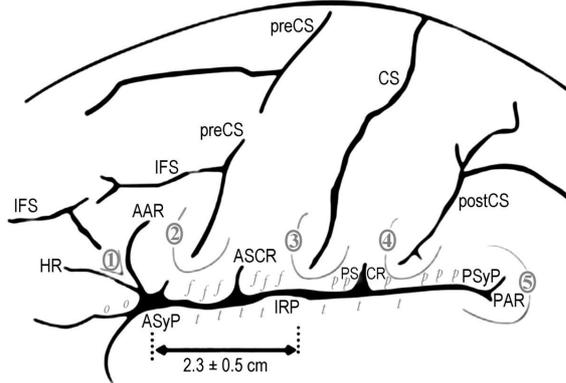
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## Figures



**Figure 1** The title page of von Economo's original article on the cytoarchitectonics of the Rolandic operculum, right (von Economo 1930). Signature from the author's private archive. Portrait of Constantin von Economo by Max Schneider, Vienna. Courtesy of Austrian National Library. Used by permission and protected by Copyright Law. Copying, redistribution or retransmission without the author's express written permission is prohibited.



**Figure 2** A modern schematic drawing to depict the sulcal and gyral morphology around the frontoparietal operculum (from Ribas 2011). Abbreviations: (1) pars triangularis of the inferior frontal gyrus ( $F_3$ ); (2) pars opercularis of  $F_3$ ; (3) Rolandic operculum or subcentral gyrus; (4) connection arm between the postcentral and supramarginal gyri; (5) C-shaped convolution; AAR, anterior ascending ramus of the lateral (Sylvian) fissure; ASCR, anterior subcentral ramus of the lateral fissure; ASyP, anterior Sylvian point; CS, central sulcus of Rolando; *f*, frontal operculum; HR, horizontal ramus of the lateral fissure; IFG,  $F_3$ ; IFS, inferior frontal sulcus; IRP, inferior Rolandic point, projection of the central sulcus in the lateral fissure; *o*, orbital operculum; *p*, parietal operculum; PAR, posterior ascending ramus of the lateral fissure; postCS, postcentral sulcus; preCS, precentral sulcus; PSCR, posterior subcentral ramus of the lateral fissure; PSyP, posterior Sylvian point; *t*, temporal operculum.

Supplementary material

## **Contribution to the cytoarchitectonics of the Rolandic operculum \***

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## **Introduction**

The relationship between the sulci and gyri to the mode of distribution of cytoarchitectonic areas presents several important problems in anatomy. The solution of those problems is of interest because future research may let us draw at least certain conclusions about the distribution of the areas and the demarcation of their boundaries, simply based on the macroscopic pattern. The principle established by Meynert (1868, 1872) and Betz (1874, 1881) that the mode of distribution of the cortical areas bears no relationship whatsoever to the course of the sulci in the cerebral hemispheres has several exceptions. Both Meynert and Betz were aware of such exceptions, and they took their studies further. Thus, the central sulcus of Rolando consistently separates, more or less, the frontal formations of the cerebral cortex from the various parietal cytoarchitectonic formations, and the calcarine sulcus always enlaces the striate area. The calcarine end is known to present noticeable individual variations; occasionally, one may even observe an occipital operculum in humans. It is now known – through the work of Elliot Smith (1904, 1907), Brodmann (1903, 1909), Landau (1923), Kuhlenbeck (1928) and others – that, in the formation of such a cap on the occipital pole, the striate area stretches in a certain way on the convexity of the cerebral hemispheric surface, such that one might draw some conclusions from the individually differing external aspects of that cap and the expansion of its cytoarchitectonic areas (von Economo 1930). In questionable cases where, for example, a sulcus appears doubled, cortical cytoarchitectonics allows the correct determination of the sulci. For example, Gerlach and Weber (1929), guided by Hartwig Kuhlenbeck, showed in one case a clear doubling of the central sulcus. Such an apparent duplication was not associated with any enlargement of the motor cortex. Indeed, the anterior segments of those two sulci simply constituted the boundary between the precentral and the postcentral areas, thus corresponding to the correct central sulcus.

## **Cytoarchitectonics of the Rolandic operculum**

One field that shows many individual variations, not only in its gross anatomical relationships but also with regard to the demarcation of its areas, is the Rolandic operculum; von Economo and Koskinas (1925) previously provided a schematic depiction of several types of the anatomical boundaries of this field, which I reproduce here (Fig. S1). In this drawing, one can see that the sensory tactile sphere *PB* (the oral postcentral area) with its granulous

koniocortex, which occupies the larger part of the rear wall of the central sulcus in its entire dorsoventral course, ends even somewhat earlier – that is, while still dorsal to the shallow ventral end of the central sulcus and inside it – whereas the agranular motor precentral area FA either ends concomitantly with the central sulcus or passes over only with a small segment ventral to the end of the operculum. On the other hand, the agranular frontal area FB occupies the entire remaining anterior half of the surface of the convexity of the operculum and extends across its lower surface, from which it faces the Sylvian fissure, and from where it continues further into its surface underneath, turning into its small insular surface inside the depths of the Sylvian fossa. The formation PA (giant pyramidal postcentral area), which extends into the valley of the central sulcus from the cortical brink to the operculum, slightly ascends to the shallow ventral end of the central sulcus somewhat to the surface of the operculum, where it extends, in the shape of a leaf – though in a very small mass – to the expansion of the remaining free space between the intermediate postcentral area PC and the agranular frontal area FB. By contrast, the magnocellular intermediate postcentral area PC, which encases the dome of the postcentral gyrus, beginning from the cortical brink and ending lower, also occupies the entire caudal half of the Rolandic operculum. The sensory tactile sphere PB (oral postcentral area) is thus the only one among these areas that does *not* reach the surface of the operculum, while it remains hidden inside the depths of the central sulcus and its ending.

### **An unusual case**

At this point, it is of interest to investigate the behaviour of the expansion of the oral postcentral area PB in a brain in which the central sulcus does not end at the cerebral convexity on the surface of the operculum, but extends further ventrally by passing through the operculum, such that it appears as if it runs into the Sylvian fissure. In the examined brain (specimen no. 10) with this peculiarity, one could see, by unfolding the Sylvian fossa, that the central sulcus of Rolando, which courses over the convexity of the operculum, also carves its ventral surface at a 1-cm depth, where the Sylvian fossa faces the lower surface of the operculum. Therefore, it was interesting to investigate whether, with such an extension of the central sulcus in the ventral direction, the sensory tactile sphere would also eventually extend further ventrally than usual. Fig. S2a shows the gross anatomical landmarks in a semi-schematic form, with the ventral surface of the operculum also depicted. Fig. S2b shows the

spread of the individual areas as they were traced in serial sections; the area boundaries are herein marked with the various dotted lines. One can see in Fig. S2b that the central sulcus – together with its continuation into the ventral surface of the operculum and with its imaginary extension in the same direction further medially – represents the sharp boundary between the parietal and frontal formations. However, neither the motor precentral area FA nor the sensory tactile sphere PB (oral postcentral area) reach the central sulcus through this extension nor expand further ventrally or even on the roof of the Sylvian fossa; rather, they both end early, as it happens in most other cases, at the dorsal parts of the operculum, about 1.5 cm away from the dorsal lip of the Sylvian fissure in the depths of the central sulcus. By contrast, the narrow giant pyramidal postcentral area PA, which lies between the precentral area FA and the oral postcentral area PB, extends as far as they do into the depths of the central sulcus, further ventrally into the lower surface of the operculum; in the Sylvian fossa it even projects out a bit to the end of the central sulcus and the basal surface of the operculum. Thus, by this extension of the central sulcus downwards, the giant pyramidal postcentral area PA actually appears to extend ventrally, whereas such an extension, as already mentioned, does not affect the precentral area FA and the oral postcentral area PB. The superficial areas FB (agranular frontal area) and PC (intermediate postcentral area) expand as usual into the basal surface of the operculum, without being otherwise affected by this extension of the central sulcus. Furthermore, the latter constitutes the boundary between the parietal and frontal cortices, preventing (or at least deferring) the tendency of the parietal intermediate postcentral area PC (Fig. S1) and advancing itself into the operculum somewhat frontally in a further expansion – indeed, all the way to its end on the lower surface of the operculum.

Accordingly, from an abnormal extension of the central sulcus ventrally, we cannot conclude that an extension of either the motor or the sensory sphere exists; there is most likely an extension of the giant pyramidal postcentral area PA that reaches further ventrally. This finding completes our knowledge of this area – which exhibits numerous gross anatomical individual variations – and of the relationship between the sulcal and areal distribution variants.

### **On the neuronal substrate of mental acts**

In addition to the foregoing, allow me to revisit a publication by Niessl von Mayendorf

(1930), which cites my description of Broca's area, hence, the part lying immediately rostral to the Rolandic operculum. I drew attention, as Brodmann (1909) did before me, to the point that the foot of the inferior frontal gyrus ( $F_3$ ) has a peculiar structure, which is very distinctive: on the one hand, the anteriorly located pars triangularis of the granular frontal area ( $FD_7$ ) is clad in a typical granular cortex; on the other hand, although not so sharply defined, one can nonetheless recognise, at least sufficiently, the cortex of the caudally located Rolandic operculum, such that it becomes evident that it must constitute an independent area. Niessl von Mayendorf (1930) cited my words correctly: 'In any case, this peculiar formation justifies the identification of this area as an individual area – particularly with regard to the physiology of this field'. This area is distinguished from others in particular because it contains unique giant-size cells, the pyramidal cells of layer IIIc. (I also emphasised the fact that those giant cells may not be sufficiently well developed in certain cases). Niessl von Mayendorf (1930) interprets my claim, as if I would attribute a special importance for language to these giant cells, and he calls them 'von Economo speech cells' (*Economos Sprachzellen*). That could lead to the erroneous view that I identify the cytoarchitectonic areas with the centres of localisation of our mental functions, and as if I would consider several of those functions as bound to special cells. It is quite incomprehensible to me how one could impute such an opinion to myself, despite the fact that I have always held the view, based on my experience with encephalitis lethargica, that mental processes and functions are much more complex than generally assumed, and that they cannot even be linked to the cerebral cortex alone, but, in addition, to subcortical centres, which, in the order of events, often have a decisive role. To clarify my position on this matter with precision, I cite below a passage from my work on the cellular structure of the cerebral cortex and progressive cerebration (von Economo 1929):

Indeed it is highly unlikely (apart from the purely singular motor effect and the purely singular sensory stimulus) that what we presently call a mental or a nervous physiological function always corresponds to the influence of one of these particular cerebral cortical fields (i.e., the cytoarchitectonic areas); it is much more likely that what is necessary for each of these apparently unique functions is the effect and cooperation of absolutely definite groups of such cerebral fields, whereby each one, regrouped in another arrangement, finds a use in triggering other *functions*. In other words, I emphasise the current overall effect of the cerebral cortex and

the deeper parts of the cerebral hemispheres, in which the peculiar group effect of certain individual anatomical cerebral fields leads, by giving a predominant tone and direction, to a particular physiological end result, which leads to a physiological nervous function from the impression of a unit. Therefore, it would be correct, instead of talking about brain centres of certain functions, to simply speak of centres, whose participation is especially important for the emergence of certain functions. This is how I would like to be understood, were we henceforth to talk exactly about centres, or about the localisation of certain functions.

Of course, it occurred even less likely to me to either view any particular cells – or even the so-called ‘special cells’ – as the point of departure or localisation of any so-called mental act, like certain authors did previously, and like Niessl von Mayendorf (1930) probably thought I did. I never spoke of ‘speech cells’. Regarding this point, I would like to clarify my precise position, in what must have eluded Niessl von Mayendorf (von Economo and Koskinas 1925, p. 68, footnote 1):

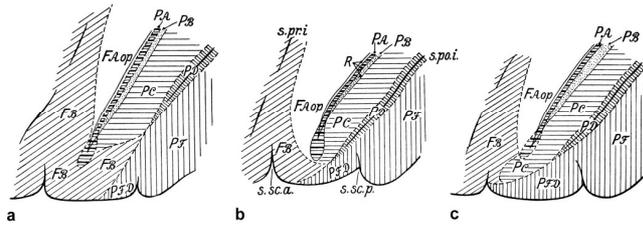
A specific mental function is often attributed to cells in general, and to special cells in particular, and one may speak, as we saw, e.g., of specific visual cells, auditory cells, and so forth. Of course, such a claim only seems permissible to us in a *metaphorical* sense, i.e., only insofar as stating that one encounters such cells in the visual area, in the auditory area, et cetera, but not in the sense that the specific mental quality of the corresponding modality would have its seat in that cell! This quality is much too complicated to imagine that its material substrate would be bound to a single cell or a single cell type. Moreover, for now, if we wish to stick to solid data, we can only ascribe a physiological function to cells, such as conduction, facilitation, inhibition, possibly the storage of excitations or sensitisation, and so on. If we conceivably speak of motor or sensory cells insofar as they are directly connected to receptive or efferent organs, then we must keep in mind, at present, that we do this merely in a *metaphorical* sense and only as a manner of speaking. The best of course would be to refrain from such designations altogether.

Thus, I think that Niessl von Mayendorf’s error has been satisfactorily rebutted.

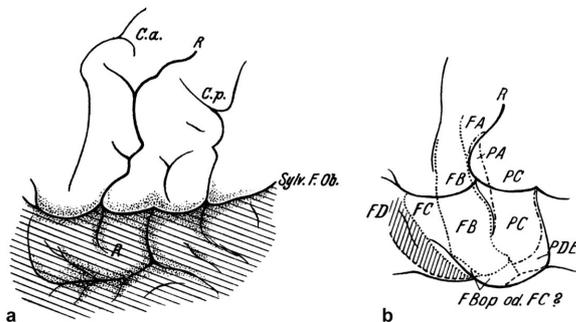
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## Figures



**Figure S1** The schematic drawings **a**, **b** and **c** depict three different types of neighbouring areas that converge on the Rolandic operculum, and the anatomical area demarcation at a region with many individual variations. The sensory tactile domain *PB* (oral postcentral area), with its granulous *koniocortex* – which occupies the largest part of the rear wall of the central sulcus of Rolando (*R*) in its entire dorsoventral extent – terminates somewhat anteriorly, i.e., dorsal from the shallow ventral extreme of the central sulcus but still within it. On the other hand, the agranular motor precentral area *FA* either ends concomitantly with the sulcus or reaches across with only a small segment, ventral to the sulcus end, yet still within the operculum. Abbreviations: *s.po.i.*, inferior postcentral sulcus; *s.pr.i.*, inferior precentral sulcus; *s.sc.a.*, anterior subcentral sulcus; *s.sc.p.*, posterior subcentral sulcus; *FB*, agranular frontal area; *FA<sub>op</sub>*, opercular precentral area; *PA*, giant pyramidal postcentral area; *PB*, oral postcentral area; *PC*, intermediate postcentral area; *PD*, caudal postcentral area; *PF*, supramarginal area; *PDF*, transitional area between the two latter formations.



**Figure S2 a** A semi-schematic illustration of the gross anatomical relations, with the ventral surface of the operculum shown as well **b** The extent of individual areas and their boundaries, marked by dotted lines, as determined from serial sections. The central sulcus of Rolando (*R*) includes its continuation on the ventral surface of the operculum and an imaginary prolongation in the same direction further medially, representing a sharp boundary between the parietal and frontal structures. Abbreviations: *C.a.*, precentral gyrus; *C.p.*, postcentral gyrus; *Sylv.F.Ob.*, surface area of the lateral (Sylvian) fissure.