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Commentary

Cytoarchitecture of the cerebral cortex—More than localization

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The present paper reviews that macroanatomical landmarks are problematic for a reliable and sufficiently precise localization of clusters of activation obtained by functional imaging because sulcal and gyral patterns are extremely variable and macroanatomical landmarks do not match (in nearly all cases) architectonically defined borders. It argues that cytoarchitectonic probabilistic maps currently offer the most precise tool for the localization of brain functions as obtained from functional imaging studies. Finally, it provides some examples that cytoarchitecture is more than localization with respect to a particular brain region because it reflects the inner organization of cortical areas and, furthermore, functional principles of the brain.

Neuroanatomy achieved increasing attention in the human brain mapping community during the last years for relating brain function to its underlying structure. In this issue of *Neuroimage*, the paper of (Devlin and Poldrack, 2007) acknowledges this development, identifies problems in the current practice of applying neuroanatomical information in the context of functional imaging studies, and proposes converging on a common set of methods for reporting functional localization with respect to a common standard space and criteria for reporting activations in terms of Brodmann's areas (Brodmann, 1909).

Problems with macroanatomical landmarks

From its very beginning, architectonic research was not a pure anatomical effort, but the pioneers established structural–functional correlations by combined architectonic and neurophysiological observations in macaque and human brains (Brodmann, 1914; Vogt and Vogt, 1919). As shown with modern techniques, borders between cytoarchitectonic areas are functionally relevant. Combined electrophysiological and architectonic studies in experimental animals have demonstrated that response properties of neurons change at the border between two cytoarchitectonic areas (Luppino et al., 1991). The borders of architectonic areas in the cerebral cortex, however, are not reliably and precisely enough bound to macroanatomical landmarks (gyri and sulci), which are the recognizable anatomical structures – at least up to now – at the spatial resolution of magnetic resonance imaging (MRI) of the living human brain (Zilles et al., 1995, 1997; Amunts et al., 1999). Many cytoarchitectonic borders are located outside of a sulcus (e.g., major parts of the anterior border of area 4). Only the borders of a few architectonically defined areas show a sufficiently precise association with sulci, e.g., the posterior border of the primary motor to the somatosensory cortex which is located in the fundus of the central sulcus. However, the anterior border of the primary motor cortex shifts from a more rostral position to a more caudal position hidden in the central sulcus when moving on the brain surface in medio-lateral direction. The anterior border is not related either to the precentral or any other sulcus (Geyer and Zilles, 2005; Geyer et al., 1996). The primary visual cortex is always found in the calcarine sulcus, but its outer borders to V2 are not associated with a sulcus, and their positions may vary considerably among individuals (Amunts et al., 2000). The primary auditory cortex is always found on the Heschl gyrus, but its anterior border cannot be defined by a macroanatomical landmark (Morosan et al., 2001). Therefore, it may be sufficient to identify a gyrus or sulcus in order to define the localization of an activation in functional neuroimaging, but the underlying and functionally relevant structural segregation of an individual brain remains unknown unless the activation is registered on (cyto)-architectonic maps.

The relationship between cytoarchitectonic borders and surrounding sulci and gyri is even more loosely defined for most of secondary cortices and multimodal association areas. Here, sulci and gyri are extremely variable; reliable estimates of the localization of areal borders cannot be made on the basis of macroanatomical landmarks. For example, an activation restricted to the anterior intraparietal sulcus cannot be unambiguously attributed to either architectonic areas of the superior or inferior

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parietal lobule, or to such areas in the sulcus itself considering the spatial resolution of functional imaging and the structural variability of the intraparietal sulcus. The localization of functional activations on the basis of cytoarchitectonic maps provides here the best answer considering that many areas, with different cytoarchitecture, chemoarchitecture, and connectivity, share this location. Examples of areas in the region of the anterior intraparietal sulcus are areas hIp1, hIp2 of the anterior intraparietal sulcus (Choi et al., 2006), PF, Pfm of the inferior parietal (Caspers et al., 2006), hPe1 of the superior parietal lobule (Scheperjans et al., 2005), and Brodmann's area 2 at the postcentral gyrus (Grefkes et al., 2001).

Advantages and development of cytoarchitectonic probabilistic maps

Meanwhile, cytoarchitectonic probabilistic maps of this and other areas of the human brain have been introduced (http://www.fz-juelich.de/ime/index.php?index=51). Probabilistic cytoarchitectonic maps of cortical areas are based on (i) observer-independent definitions of areal borders (Schleicher et al., 1999) in cell body stained histological sections of ten, completely and serially sectioned post-mortem brains, (ii) 3D reconstruction of these sections using the MR data set of the same post-mortem brain prior to its embedding in paraffin and sectioning, and (iii) registration of these 3D data sets to a living standard reference brain as common reference space for cytoarchitectonic maps and functional imaging data (Zilles et al., 2002b; Amunts and Zilles, 2006).

Probabilistic maps of neighboring cortical areas may overlap to some extent due to their intersubject variability in size and location. Thus, the assignment of a cluster of activation to probabilistic maps of cytoarchitectonic areas may result in multiple areal associations. The probability with which a cluster belongs to either one or another area, however, is a quantitative measure, which can be used to weight the different interpretations against each other. Different methods have been proposed to compare cytoarchitectonic probabilistic maps with functional activations (Eickhoff et al., 2005, 2006). Some of them are implemented in the anatomy toolbox of SPM (http://www.fz-juelich.de/ime/spm_anatomy_toolbox). Toolboxes for other software systems will be available in the near future.

Presently, cytoarchitectonic maps do not cover the complete cerebral cortex. During this work in progress, only approximately 40% of the cortical surface has been mapped up to now. This is caused by the necessity to develop new methods for cytoarchitectonic mapping, 3D reconstruction of histological sections, and registration of post-mortem data to a reference space. Finally, the mapping itself is a time-consuming process, which requires approximately 1 person year for an area. Since the tools are now available, it is expected that cytoarchitectonic mapping will be finished within the next few years. Our strategy for the transitional period, during which probabilistic cytoarchitectonic maps are not available for the complete cortical surface, is to localize brain activations with respect to cytoarchitectonic maps whenever available or to identify the position of the activations according to the underlying individual or group macroanatomy and/or to stereotaxic coordinates in the unmapped regions.

The architectonic segregation of the cerebral cortex into cytoarchitectonic areas may provide information additional to that obtained in functional imaging studies when activations involve only parts of a cortical area, e.g., in cases of areas organized in a somatotopic manner. The hand region of the primary motor cortex (Brodmann's area 4), which is activated during finger tapping of the contralateral hand, may serve as an example. Cytoarchitecture encompasses the whole extent of Brodmann's area 4, not only the hand representation. That is, functional imaging alone would underestimate the extent of the area. In this case, both function and anatomy are necessary to understand the organization of the primary motor cortex. Moreover, for many/most of complex cognitive tasks it is not clear whether they activate a complete cytoarchitectonic area, several areas or only part of an area. Finally, the segregation of the cortex based on functional tasks may differ depending on the actual task. These "mismatches" between functional and cytoarchitectonic results are not a deficit of the combined functional/probabilistic architectonic approach, but rather a chance to understand the cortical organization more deeply.

Organizational principles of the cerebral cortex revealed through quantitative cytoarchitectonics

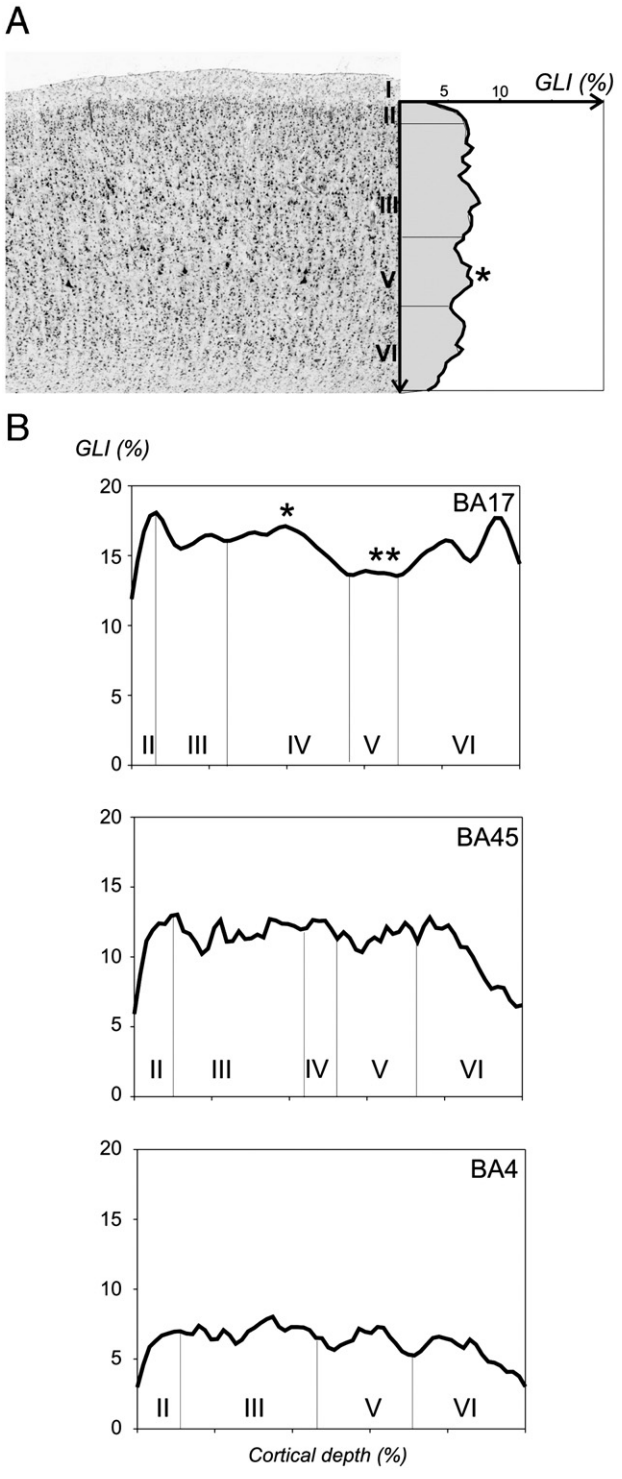
The cytoarchitectonic definition of a cortical area provides more than just a "label" for functional imaging studies. It contributes to our understanding of the organizational principles of the cerebral cortex through a quantitative analysis of cytoarchitecture. One way to do so is the analysis of parameter profiles, which quantify the cytoarchitecture of an area by capturing changes in the laminar structure from the surface of the cortex to the white matter border. Profiles sampled in different cortical areas differ between each other with respect to their shape parameters. Such parameter differences are the basis of an objective way of cortical analysis and mapping, in contrast to previous approaches of Brodmann and other researchers of that time, which were based on a pure visual inspection and verbal description. Examples of morphometric parameters are the gray level index (GLI) as a measure of the volume fraction of cell bodies (Schleicher and Zilles, 1990), cell size, and density.

GLI profiles of different brain regions differ between each other. The primary motor cortex (Brodmann's area 4) shows a characteristic cytoarchitecture which is reflected by GLI profiles (Fig. 1A). The low GLI value of area 4 indicates that the volume fraction of cell body is low but that the space between cell bodies, i.e., the neuropil, is larger than in any other cortical area. Furthermore, area 4 does not show a separate layer IV (agranular cortex), which results in a "smooth laminar pattern" (no pronounced local minima and maxima in the GLI profile).

The primary visual cortex, Brodmann's area 17 (V1), receives massive input from the lateral geniculate body. Layer IV can be subdivided into three sublayers (IVA, B and C) and further subsublayers, reflecting the complex organization of its connectivity (van Essen et al., 1981, 1986; Maunsell and van Essen, 1983; Shipp and Zeki, 1989; Fellemann and van Essen, 1991; Zilles and Clarke, 1997; Rockland, 2002). The cytoarchitecture of area 17 is well reflected by its GLI profile. It shows a high volume fraction of cell bodies throughout the cortical depth, and a broad and differentiated layer IV; layer V appears cell-sparse and the cortex shows a sharp border between layer VI and the white matter (Fig. 1B).

Although area 41 of the auditory cortex (Te1; (Morosan et al., 2001) is a primary sensory area as well, its cytoarchitecture differs from that of area 17. Fibers originating in the medial geniculate body of the metathalamus project mainly to layer IV. As a result, layer IV contains densely packed granular cells and is broad. However, it is not subdivided into sublayers as layer IV of area 17,

and it is less broad. The laminar organization of area 41 is reflected by a broad and distinct peak in the GLI profile. A similar organization can be found in the somatosensory areas 3a, 3b and 1, which also receive heavy projections from the thalamus, terminating in a well developed layer IV. Multimodal association areas, such as area 45 of the inferior frontal gyrus (Broca's region), show a different laminar organization. Area 45 has a broad layer III, which is highly differentiated (many local peaks in the GLI profile) and which can be subdivided into sublayers (Fig. 1B).



Differences in the shape of parameter profiles, therefore, reflect cytoarchitectonic similarities and dissimilarities. A profile can be interpreted as a frequency distribution, which enables extraction of features and the calculation of a feature vector. Schleicher and colleagues proposed the following features to describe the shape of a profile: the mean of the GLI profile, the first 4 statistical moments (standard deviation, center of gravity, skewness, and kurtosis), and the analogous parameters of the absolute of its first differential quotient (Schleicher and others, 1999). For example, a low mean GLI is an indicator of a low cell packing density (e.g., area 4), a high GLI is characteristic of the primary sensory areas, e.g., area 17 (Fig. 1). For a more detailed discussion of feature vectors, see also Zilles et al. (2002b).

The observer-independent mapping approach based on GLI profiles (Schleicher and others, 1999; Schleicher et al., 2005) has been applied for more than 40 areas of the human isocortex. The reliability and precision of the definition of cytoarchitectonic borders have been proven for each area, within one and the same brain, by an analysis of the position of borders in neighboring histological sections, and their comparison with borders revealed in neighboring myeloarchitectonic sections if available. In addition, cytoarchitectonic borders have been confirmed by independent receptor architectonic studies, where borders between cortical areas have been defined based on regional differences in the distribution of densities of receptor binding sites of various neurotransmitter systems, which have been compared with neighboring cytoarchitectonic sections (Geyer and others, 1996; Amunts et al., 2000; Zilles et al., 2002a; Geyer et al., 2005; Morosan et al., 2005).

If the borders of cortical areas have been defined, GLI profiles, sampled within different areas, can be used to quantify cytoarchitectonic differences between areas using multivariate statistical analysis. In subsequent analyses, samples of profiles from the delineated areas may contribute to an understanding of organizational principles and hierarchies of cortical areas since their similarities enable the generation of hierarchical trees of cortical areas.

Fig. 1. (A) Cytoarchitecture of the primary motor cortex, Brodmann's area 4, and corresponding GLI profile. The profile quantifies the laminar changes of the volume fraction of cell bodies from the border between layer I and II to the white matter border. Area 4 is characterized by a low cell density (i.e., a low mean GLI), the presence of giant pyramidal cells (Betz cells) in layer V (peak at the profile*), an un-sharp transition of layer II to III (no peak at the profile, but rather a transient increase in GLI from layer II to III, reaching a plateau in layer III), and a low cell density in layer VI with no sharp border to the white matter (GLI profile decreases towards the white matter). Roman numbers indicate cortical layers. (B) GLI profile of the primary motor cortex, area 4 in comparison to profiles of area 17 (primary visual cortex, V1), and area 45 (Broca's region). Note the differences in the overall cell packing density (GLI) which is maximal in area 17 and minimal in area 4. Thus, area 4 is characterized by a relatively high amount of neuropil, i.e., space for dendrites, and synapses between cell bodies. Area 45 shows a differentiated laminar pattern with many small peaks and local minima—a result of relatively large pyramidal cells, particularly in layers III and V, which project, among others, to cortical areas of the same and the contralateral hemisphere. The cytoarchitecture underlines the functional and connectional organization of the cortex—whereas area 4 is the primary motor area, dominated by heavy and long-distance output to subcortical nuclei and the brain stem, area 45 belongs to higher associative areas (involved in language processing) with a well developed layer III. Area 17 is an area which receives massive input from the lateral geniculate body in layer IV (*) and which projects to extrastriate areas. In contrast to area 4, layer V of area 17 has a low cell packing density and a low GLI (**).

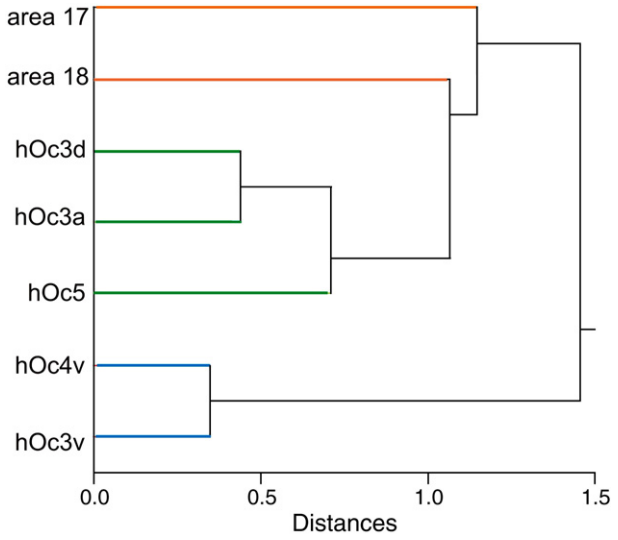


Fig. 2. Classification result of a cluster analysis (Euclidean distances, single linkage) in 7 occipital areas (striate and extrastriate) of ten human brains. The graph shows the dissimilarities (distances) between cytoarchitectonic areas as judged by their GLI profiles. Profiles were sampled in 3 histological sections per hemisphere, area, and brain. Features were extracted from these profiles, and the distance matrix was calculated as the input to a hierarchical cluster analysis. Note that the two "central" areas, area 17 and area 18, which occupy both sides of the calcarine sulcus, are most different from the other ones. The dorsally located extrastriate areas hOc3d, hOc3a (Kujovic et al., personal communication), and hOc5 (Malikovic and others, 2007) form a distinct cluster, and the ventrally located extrastriate areas hOc4v and hOc3v (Rottschy and others, 2007) form an additional cluster. Thus, the cytoarchitectonically based classification coincides with a definition into a dorsal and a ventral stream which relates to connectivity and function (Ungerleider and Mishkin, 1982). We may conclude that cytoarchitecture underlies brain function.

Cytoarchitectonic analysis of the visual cortex, striate, and extrastriate visual areas may serve as an example (Fig. 2). In this study, profiles were sampled from seven areas of the occipital lobe: areas 17 and 18 (Amunts and others, 2000), areas hOc3v and hOc4v of the adjoining ventral occipital cortex (Rottschy et al., 2007), areas hOc3d and hOc3a of the neighboring dorsal extrastriate cortex (Kujovic, personal communication), and area hOc5, the cytoarchitectonic correlate of the motion sensitive complex V5/MT+ (Malikovic et al., 2007). The latter five areas are located in the region roughly corresponding to Brodmann's area 19 (Brodmann, 1909). Approximately 30 profiles were measured for each of the 7 areas in ten different brains. Features were extracted from the profiles, and a cluster analysis using the Euclidean distance as the multivariate distance measure was performed. The algorithm proposed areas 17 and 18 as the two areas which were most distinct from the other 5 areas (Fig. 2). The ventral areas hOc3v and hOc4v form a distinct large cluster; the dorsal areas hOc3d, hOc3a, and hOc5 form an additional one, whereby this cluster can further be subdivided into hOc3d, hOc3a on the one hand, and hOc5 on the other hand. The result of the analysis nicely agrees with the visual inspection of the occipital lobe—areas hOc3v and hOc4v are much more similar to each other than areas 17 and 18, a fact that probably contributed to the oversimplified subdivision of the occipital cortex into three areas by Brodmann (1909), von Economo and Koskinas (1925) and other historical maps (Zilles and Clarke, 1997). More importantly, the clustering of the areas based on their cytoarchitectonic similarities corresponds to the segregation of the visual cortex into a dorsal and a ventral stream, which is related to connectivity and function (Ungerleider and Mishkin, 1982). We may hypothesize that the analyses of cytoarchitecture, in analogy to receptor architecture (Zilles and others, 2002a), are capable to disclose functional relationships of areas in other brain regions as well.

Conclusions

I. Macroanatomical landmarks are problematic for a reliable and sufficiently precise localization of cluster of activation obtained by functional imaging because sulcal and gyral patterns are extremely variable and macroanatomical landmarks do not match (in nearly all cases) architectonically defined borders.
II. Cytoarchitectonic probabilistic maps currently offer the most precise tool for the localization of brain functions as obtained from functional imaging studies. It is expected that such maps will cover the whole cortical surface within the next few years.
III. Cytoarchitecture is more than labeling—it reflects the inner organization of cortical areas, relating to the functional properties of these regions.

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