BOOK REVIEW

Cortical maps and modern phrenology

ATLAS OF
CYTOARCHITECTONICS
OF THE ADULT HUMAN
CEREBRAL CORTEX BY
CONSTANTIN VON
ECONOMO AND
GEORGE N. KOSKINAS
TRANSLATED REVISED
AND EDITED WITH AN
INTRODUCTION AND
ADDITIONAL APPENDIX
MATERIAL
By *Lazaros C. Triarhou*
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Cortical cytoarchitectonics has had a chequered history. Beginning with Meynert's discovery of the systematic layering of neurons in the cerebral cortex and with Betz's discovery of the giant cells that bear his name, and initially influenced by phrenological ideas, over the years it has gone in and out of favour as conceptual fashions and methods of investigation have changed. Currently, it seems to be enjoying resurgent popularity as modern phrenologists, equipped with the powerful tools of functional MRI, seek to relate tiny pseudo-coloured patches of slightly enhanced cortical activity associated with some limited cognitive function to an underlying structural correlate. The reappearance, therefore, of what was once a classical atlas of human cortical architectonics can be seen as a landmark, especially when accompanied by an insightful survey of the history of the field and its relevance to efforts at localizing function in the human cortex using modern imaging techniques.

Die Cytoarchitektonik der Hirnrinde des erwachsenen Menschen. Atlas mit 112 mikrophotografischen Tafeln in besonderer Mappe, with an accompanying 810 page text volume, which itself contained 162 figures, was written by von Economo and Koskinas, and published in 100 sets by Julius Springer in Vienna in 1925. The atlas was a remarkable piece of work. Every volume consisted of 112 original photographs made as contact prints from large, 40 cm × 40 cm glass negatives taken at a magnification of 100 times from histological sections of the human cortex stained by the Nissl method (Fig. 1). The photographs were unbound and housed in a boxlike case that opened as a book, with an enclosed slip that warned one not to crack them by lifting with one hand and to keep one's sticky fingers off the surface of the plate. In the present volume, the plates have been reproduced at exactly the same dimensions as the original Atlas, with ineluctable clarity and there is a brief accompanying description of each in English.

The text volume that accompanied the original Atlas has not been translated. It was a work of encyclopedic scholarship, which surveyed the whole field of cortical anatomy and physiology from its beginnings, with reproductions of figures from Cajal, Kölliker, Brodmann and many others, and devoted more than 500 pages to descriptions of the 107 cortical areas that the authors felt their cytoarchitectonic investigations had revealed. It would be a daunting task to attempt to translate, and the present editor/translator, Dr Triarhou, a neuroscientist working in Thessalonika, has wisely confined himself to the atlas alone, with a few figures reproduced from the text volume to place the cytoarchitectonic delineations in perspective. The huge amount of quantitative data that von Economo and Koskinas provided in their text about variations in cortical thickness and volume, cell packing densities, the dimensions and shapes of neurons, the ratios of large to small neurons and of neurons to neuroglial cells, and which might find appeal among current modelers of cortical structure and function, thus does not appear in its full majesty. The amount of effort put into collecting and meticulously assembling these data must have been enormous. A couple of tables reproduced by Triarhou from the text volume might persuade interested parties to explore the original German text. This has never been translated into any other language, although in 1927 von Economo published a much abbreviated version in which he included reduced copies of some of the plates of the atlas, and this was translated into English by Parker (von Economo, 1929), as well as into French and Italian.

Trairhou's account of the authors, of the setting in which their atlas was produced, and his discussion of modern efforts to parcellate the human cortex anew, is readable and insightful. Although brief—no more than 40 pages in length—it provides numerous leads for the reader interested in pursuing details of the careers of two remarkable scientists and the history of attempts at defining cortical localization of function in terms of histological structure.

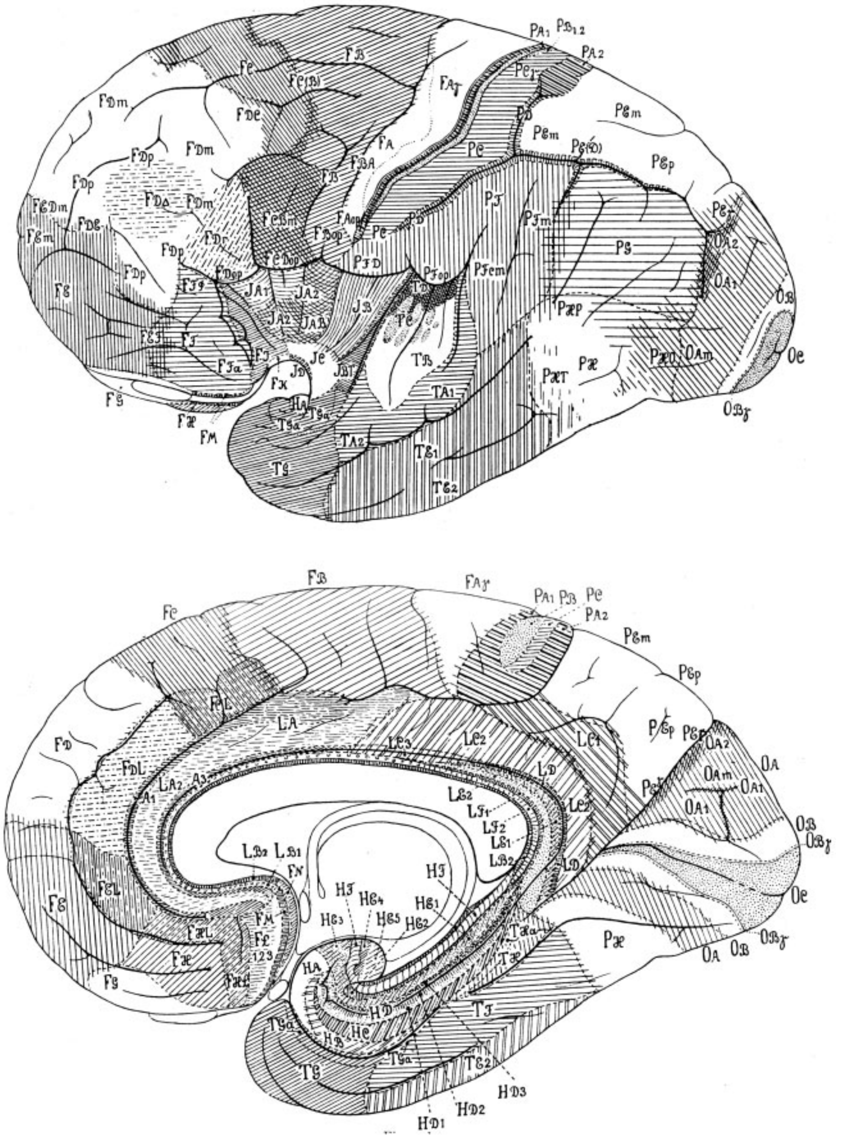

Fig. 1 Lateral (above) and medial (below) views of the cytoarchitectonic fields delineated in the human cerebral cortex by von Economo and Koskinas. From the book under review.

von Economo was from a patrician Greek family with large estates in Northern Greece and Romania. He was independently wealthy and after graduation from the Vienna Medical School in 1901 travelled extensively and was able to work for lengthy periods with some of the major French and German neuroanatomists and neurologists of the time, including Nothnagel in Austria, Pierre Marie in Paris, Bethe in Strassburg, and Kraepelin and Alzheimer in Munich. Returning to Vienna in 1906, he became Assistant in the psychiatric clinic of Julius Wagner von Jauregg at Vienna University and remained in that position, declining offers of professorships throughout the German speaking world as his reputation grew. He refused to be considered as Wagner von Jauregg's successor and only became director of a new research institute associated with the psychiatric clinic in the year of his death (1931). When his family was ennobled in about 1906, he became von Economo and could refer to himself as *Freiherr* or Baron. He should have given up his title, as required by Austrian law after 1919, but it seems that he never did. Some say that at heart he remained a monarchist despite the new order imposed upon Austria as the result of its loss of empire after World War I. As a man of independent means, von Economo was not only able to finance his travels but also the publication costs of his great atlas (about 60 000 marks), and to engage in aeronautical pursuits such as ballooning and flying. He was one of the first licensed Austrian aeroplane pilots, owned his own aeroplanes and served in the infant Austrian air force during the Great War (Fig. 2).

von Economo had grown up in Austrian Trieste and received a broad education in both the physical sciences and

Fig. 2 Constantin von Economo (1876–1931). Photographed in 1910. From von Economo and Wagner-Jauregg (1937).

the humanities. He was an accomplished linguist. His wife, who outlived him by 55 years, recalled him speaking Greek with his father, German with his mother, French with two of his siblings and Italian with a third. He was equally fluent in English and able to give a course of lectures in New York at the opening of the New York Psychiatric Clinic and Hospital in December 1929 (von Economo, 1930). On that occasion, he carried with him a model brain on which the 107 areas that he and Koskinas had delineated in the cerebral cortex were represented by colours. One wonders if the shade of Spurzheim who had in a previous century toured the United States with a phrenologically labelled model head was looking on.

von Economo was a highly regarded neurologist and neuropathologist long before his publication of the great Atlas. In his thesis work, he had demonstrated for the first time the origin and course of the ipsi- and contralateral components of the trigeminal lemniscus by applying Marchi staining to sections from the brains of patients who had succumbed to pontine tumours. But his chief claim to fame lay in his identification and description of the pathology of the disease that he named *encephalitis lethargica*, a peculiar form of stupor associated with pandemic influenza and marked by disseminated inflammatory foci throughout the upper part of the midbrain. By inoculating a monkey with brain tissue from a fatal case, he was able to demonstrate the infectious nature of the disease. He continued to work on this disease throughout his life and it led him into many theoretical considerations about the brainstem regulation of sleep and wakefulness, and the likelihood of the existence of centers for the induction of sleep and arousal.

The idea for the cytoarchitectonic atlas of the human brain grew out of von Economo's lifelong commitment to understanding not only cortical localization of function and its evolution, but also the variability among brains of different individuals, especially those with unique artistic, cultural or scientific endowments—so called elite brains. He was not alone in this. Many of the neuroanatomists of that time, for example Cécile and Oscar Vogt, the teachers of Brodmann and advisers in the preparation of the Atlas, were dedicated to the same mission. Preparation of the Atlas is said to have commenced in 1912 but was curtailed by the outbreak of war and only resumed in 1919 when Koskinas joined von Economo in Wagner von Jauregg's Institute. Koskinas had come to Vienna from Greece in 1916, in order to further his neurological training and he remained there until 1927 when he returned to Greece. He died, aged 90, in Athens in 1975. He seems to have been one of those classically unrecognized and unrewarded figures of science. Before joining von Economo, he had carried out the neuropathological studies that provided the basis for the success of Wagner von Jauregg's use of malarial induced fever in arresting the progress of general paresis of the insane, the then common manifestation of tertiary syphilis. On receiving the Nobel Prize for this treatment and recognizing the contributions of Koskinas, Wagner von Jauregg immediately made over part of the prize money to Koskinas. On his return to Greece, Koskinas was never successful at gaining a professorship at the University or in being elected to the Academy. After one disappointment he was told by one of the Professors that he was too good and that if they had appointed him they would have all had to pick up their top hats and go home. It seems to me that his contribution to the preparation of the Atlas may have been greater than that of von Economo. It was undoubtedly he who supervised the preparation of the blocks of tissue from the brains and their sectioning and staining, as well as the photography and the labelling of the plates. It is perhaps significant that on the backs of the plates there are two stamps: 'geprüft! Dr Koskinas' (proofed by Dr Koskinas) and 'gesehen Prof von Economo' (seen by Professor von Economo). At least that is how the first 20 or so plates of the copies I have seen are labelled. For the remainder, the stamps become a perfunctory 'geprüft'.

An enormous amount of work must have gone into the production of the Atlas; but both it and the accompanying text volume are remarkably short on details. We know that the work was carried out in Wagner von Juaregg's laboratory at the Psychiatric Clinic in Vienna University and that, in addition to the Vogts, they were advised by Otto Marburg, director of the Neurological Clinic and a distinguished neuroanatomist. Three brains provided the basis of the atlas and the photographs came from two of them. The brains were divided into as many as 350, 4 mm thick blocks, cut in such a way that after embedding in paraffin wax, they could be sectioned in a plane that was always perpendicular to the axis of a gyrus or sulcus, thus avoiding tangential views of the cellular lamination which can confuse interpretation. But who did the work and how they went about their duties is not revealed. A 'Fraulein Strasky' who receives cursory mention in the preface may have been the histological technician and a 'Direktor E. Brinkmann of Charlottenburg' seems to have helped with the photography. But details are sparse. They took most of the photomacrographs with a 20 mm focal length Zeiss planar lens, probably using a horizontal optical bench, of the type that was superseded only in the 1960s by the vertical Leitz Aristophot and later by the Nikon Multiphot, both now also consigned to oblivion. The Zeiss optical bench, as copied by Bausch and Lomb in the United States, could still be found in the 1960s and 70s and, even as late as 1981, Alvin Berman and I were able to make use of one at the University of Wisconsin for our atlas of the cat brain. We had the benefit of Kodak filters to enhance contrast of the Nissl-stained sections; von Economo and Koskinas had to make use of a solution of copper sulphate and potassium dichromate placed in a glass container between the light source and the specimen. The depth of field achieved, the clarity and detail with which individual neurons can be visualized in von Economo and Koskinas' photographs is remarkable and nothing has been lost in their reproduction for the new edition. They probably still represent the most comprehensive set of high resolution images of cortical histology that has ever been assembled.

An unkind critic once said that the cytoarchitectonic map of the human cerebral cortex derived by von Economo and Koskinas was but an unsystematic elaboration of that of Brodmann (Lorente de Nó, 1949). Their work was certainly an elaboration in the sense that it delineated 107 areas, whereas Brodmann had identified only 44. But it developed Brodmann's method of study in a manner that, had he lived and possessed the resources, he undoubtedly would have done himself; and unsystematic it definitely was not. Brodmann had merely sampled the human cortex, taking blocks at intervals and leaving large regions unexplored. Probably, today few are aware that his well-known numbers for the cortical areas represent no more than the order in which he had originally sampled the different gyri of the monkey brain. One of the figures reproduced from the text volume of von Economo and Koskinas gives an excellent indication of how systematic and thorough they were in dividing up the hemisphere into blocks for analysis. The cingulate and hippocampal gyri, for example, were divided into 39 blocks numbered in order from the subgenual region to the uncus, every one of which was sectioned, stained and examined microscopically. There was nothing unsystematic about this. Their naming of the areas was also highly systematic, each area being designated by the lobe in which it lay, the part of the lobe it occupied, and its cellular characteristics—with an abbreviation appropriate to each. Thus, in the frontal lobe there are 14 areas labelled from posterior to anterior, F*A* to F*N*; the precentral motor cortex or *Area precentralis* is designated area F*A*γ, the F locating it in the frontal lobe, the *A* in the posterior part of that lobe and the γ its gigantocellular architecture. Similarly, in the occipital lobe, the *Area peristriata* is O*A*, the *Area parastriata* is O*B* and the *Area striata* O*C*. Although adopted by Bonin and Bailey in their atlases of the monkey, chimpanzee and human published between 1947 and 1951, it never really caught on and if used at all nowadays it is only for one or a few isolated areas and often in a hybrid nomenclature with the more popular Brodmann numbers.

Although obviously interested in the areal division of the cerebral cortex as a potential or actual guide to the localization of function, as a basis for defining the characteristics of elite and idiot brains, and for the possibility of locating area-specific pathology in organic brain disease, as exhibited, for example, by atrophy of the motor cortex in amyotrophic lateral sclerosis, von Economo and Koskinas, with their organizational skills, laid the groundwork for much of the way in which we describe and think about cortical structure to this day. It is probable that early modern cortical scientists from whom English speaking neuroscientists of today derive the words and ideas that they use in their research, obtained these from the English translation of von Economo's abbreviated text. Brodmann was not translated into English until 1994 and the Vogts' work has never been translated. von Economo and Koskinas collated much of the work that had been done by Brodmann, the Vogt school; and the British scientists, Bevan Lewis, Bolton and Campbell, and made some important additions of their own. They codified the six-layered organization of the cortical neurons, a scheme adopted by the Vogts and Brodmann from Bevan Lewis and now universally utilized, frequently re-dividing the layers into sublayers as we do today on the basis of differences in neuronal size, shape and packing density; they similarly codified the Vogts' terms *allocortex* for the cortex of the limbic lobe and *isocortex* for the remainder or *neocortex*; they gave us the names that we still use for the principal cell types as seen in Nissl-stained preparations: *pyramidal*, *fusiform* and *granular*, with some special forms found in certain areas, such as the curious, large spindle or corkscrew cells that bear von Economo's name and which he identified as peculiar to the cingulate cortex of the human; they popularized Brodmann's names for the cortical layers based upon the predominant cell forms found in them; they affirmed Brodmann's terms for cortex of different layering characteristics—the granular and agranular *heterotypic cortex* of the sensory and motor areas, respectively, and the *homotypic cortex* characteristic of those wide swathes of association cortex in which the layers are more systematically arrayed; for the granular cortex, they coined the term *koniocortex*, a typically Greek appellation, meaning a cortex strewn with grains of sand; and within the homotypic cortex, they distinguished three types exhibiting different degrees of granularity. Taking these characteristics into account, they identified 54 ‘Grundareas’ or fundamental structural areas, with variants and modifications of these areas bringing the total number to 107.

Who can say whether the map of the human cerebral cortex by von Economo and Koskinas with its 107 areas is any more ‘correct’ than that of Campbell with 14, of Brodmann with 44, of the Vogts with more than 200 or of more recent efforts from the Vogt Brain Research Institute in Düsseldorf whose numbers have not yet been finalized but which seem well on the way to approximating those of the Vogts. The proliferation of cortical areas at the hands of the Vogts and their followers led Le Gros Clark (1952), in a review of Bailey and Bonin’s (1951) *The Isocortex of Man*, to refer to it as the ‘crazy pavement’ school of cortical research. Similar feelings on the part of others undoubtedly led to a decline in the popularity of the search for cortical localization of function in terms of cytoarchitecture. Now, it is back with us in force as researchers armed with magnets of ever increasing field strength and analytical tools of increasing sophistication seek to locate their bright spots of fMRI activity in relation to something that might be a structural subdivision of the cortex. Many seem content with locating a gyrus in a structural image and referring activity located there to what they imagine to be one of Brodmann’s numbered areas from a glance at his schematic map. There are now growing signs of a realization that something more accurate may be desirable. The question remains, however, as to whose judgment we should trust in identifying a cortical area histologically and in outlining its boundaries? Moreover, is it useful to continue dividing the cortex into finer and finer subdivisions merely in the hope that one day these will turn out to represent areas of functional individuality? In making finer and finer subdivisions, we are apt to forget that there are cortical functions that are integrative rather than localized and that cortical areas have an underlying commonality of structure that transcends their parcellation. As Le Gros Clark said in the review mentioned above: ‘The statement of Hughlings Jackson . . . that “difference of structure of necessity implies difference in function” is no doubt broadly true, but the converse is also true.’

The human visual system is a remarkable pattern detector, arguably more sophisticated than any currently available image processing device. It is this capacity that allowed von Economo and Koskinas and others like them to pick out by eye the alterations in laminar thickness and composition and cell packing density that identify the boundaries of cortical fields in histological sections. Some of these are quite distinct and identifiable even by a novice, for example, the boundary between the striate and extrastriate cortex or between the primary motor and somatosensory areas. Others, however, can be remarkably subtle and subject to disagreement even among experienced observers. It is here that an unbiased, objective method is called for and there are signs that this may now be achievable in the algorithm-based mapping procedures introduced by the modern Vogt school, whereby image analysis and multivariate statistical techniques are applied in an observer-independent manner to locate areal borders (Schleicher *et al*., 2005). Even this, however, cannot entirely control for variables introduced by prior processing of the tissue. Nissl-stained sections from paraffin- or celloidin-embedded material always give a much more satisfying picture of brain or spinal cord histology for the reason that, unlike sections cut from frozen specimens, they have as the result of the embedding procedure shrunk by as much as 30%, thus enhancing regions of cell density such as layers of cortex or subcortical nuclei. Then, too, there is the problem of being misled by changes that are purely mechanical as the cortex thins in the floor of a sulcus or is cut obliquely. It was this that von Economo and Koskinas sought to avoid in their meticulously careful orienting of their blocks.

Recognition of the pitfalls inherent in the subjective parcellation of the cortex has not led to much change in the conceptual approach that guided von Economo and Koskinas. The attitude still seems to be: ‘Let’s define enough cortical areas and something functional will turn up’. Or worse: ‘Let’s make a map that all the MRI people will use to match their fMRI images against and then we will have solved the problem’. Cortical architecture can only be given functional meaning when correlated with data of a functional character derived using complementary techniques, preferably from the same brain. This is best seen in microelectrode studies in animals in which the border of a sensory or motor representation, as defined by single- or multi-unit recording or by microstimulation and marked by a microlesion or injection of a dye, is matched to the cytoarchitecture of sections later cut from the same brain. It was this approach, as exemplified in the work of Mountcastle and Powell (1959) on the somatosensory cortex of the monkey and of Hubel and Wiesel (1962) on the visual cortex of the cat, that helped pull the study of cortical cytoarchitectonics out of the doldrums into which it had drifted, and which is now a widely used approach in animals. One cannot always of course record or stimulate extensively in the human brain and, even if one could, opportunities for correlating one’s electrode tracks with the underlying cytoarchitecture of the dead brain would be rare indeed. But a great deal can be achieved by comparing the structure and proximate relationships of cortical areas defined by correlated electrophysiological mapping and cytoarchitectonics in the cortex of experimental monkeys with those delineated in a comparable lobe or region of the human cortex by architectonic analysis, either alone or guided by prior structural or functional MRI. There are also a number of ancillary histological aids that can further this kind of analysis: it is remarkable how the boundaries of many cortical areas defined by cytoarchitecture alone, are perfectly matched by those defined by myelin staining, by histochemical staining for various metabolic enzymes, by receptor binding, or by immunocytochemistry or *in situ* hybridization histochemistry for neuron-specific polypeptides and mRNAs. And in primates, these patterns tend to be maintained across species so that, hopefully, they can be used to help relate areas of known function in monkeys to those of similar function in humans.

Connectivity is also a key element in defining a cortical area. The development of a cortical area, that is to say its emergence as a cytoarchitectural entity, occurs as development proceeds in some as yet incompletely understood manner in close relationship with the thalamic nucleus with which it is to be connected. Removing or redirecting the thalamic afferents or interfering with expression of genes that guide them on their way to the cortex, or help them recognize their target area once there, can change the structural and functional signature of an area of cortex. In the adult brain, the relationship between thalamic nucleus and cortical area can help delineate cortical areas. The lesion studies of Rose and Woolsey (1948), in which they showed how destruction of a cytoarchitectonically defined area in the cortex is accompanied by retrograde degeneration of a specific and predictable thalamic nucleus, also helped bring cortical cytoarchitectonics into the modern era. As with electrophysiological mapping, we cannot place lesions in the human cortex with a view to identifying their thalamic connectivity; and strokes rarely give us small or precisely localized lesions. But a correlation of connection-tracing studies in monkeys with cortical and thalamic parcellation in the human brain can be extremely valuable.

The idea that cortical areas invariably form parts of connectional networks has always been a guiding principle among neuroscientists and there are signs that it is now also coming into vogue in the human brain imaging community. No cortical area is an isolated entity in which a single function is represented. Nor, contrary to many current views, does it merely form one step in a hierarchy of areas proceeding onwards and upwards to some defined or imagined higher function. While there are definite streams of cortico–cortical connections that proceed in identifiable ways from area to area in the cortex, no area is without feedback connections and no area is without re-entrant connections from the thalamus. From what we have been able to gather from experiments in animals, there is a certain predictability about the overall connections of each cortical area, a predictability that is undoubtedly governed, like thalamocortical connections, by mechanisms operating during brain development. By comparing patterns of connectivity in monkeys with cortical cytoarchitecture in humans, we can often arrive at a more reliable parcellation of the human cortex than by cytoarchitectonics alone. Exemplary in this regard are the studies of Price and his colleagues (Öngür *et al*., 2003) on the frontal cortex of monkeys and humans.

Identifying connectivity in the human cortex is not an easy task. New analytical tools in MRI have given us some remarkable images of multiple areas, such as those in the visual system, that are obviously interconnected and display correlated activity in the resting brain (Fox *et al*., 2005). The methods of diffusion tensor imaging (DTI) and diffusion spectrum imaging (DSI) offer the promise of identifying at a high degree of resolution of the bundles of fibres in the white matter that proceed to and from cortical areas. But they do not have the capacity to resolve the fibres as they arise or terminate within the grey matter of a cortical area. It is in the grey matter that connectivity occurs and cortical areas are located in grey matter. Tracking fibre bundles in the white matter without regard to where they begin and end is like studying railway lines without realizing that they begin and end in stations. The gap that exists between our ability to image fibres and our inability to see exactly where they begin and end is one of the limits to our ability to define human cortical areas by their connections. At the present time, we can only hope to do this by correlating connection tracing in monkeys with DTI and DSI in humans. There are signs that this approach is already yielding results of significance (Schmahmann *et al*., 2007).

George Koskinas lived long enough to see the founding of the modern discipline of neuroscience and no doubt would have appreciated all the new techniques that have been brought to bear on the question of how to find functional meaning in cortical architecture. Constantin von Economo did not live to see these developments. Had he done so, von Economo would have found that the conceptual approach to cortical cytoarchitectonics and localization of function had changed but little from his day. The enormous wealth of structural, functional and developmental data that have accrued from modern studies of the cortex would doubtless have fascinated him and might have led to a further encyclopedic volume akin to the text volume that accompanied his Atlas and which still awaits translation. For the moment, we must be content with republication in accessible form of the great Atlas alone. The new publisher, Karger, has done a splendid job of production. The volume is enclosed in a handsome Plexiglas case which after lifting off the lid permits the pages of the book to be opened without removal from the base. It is just the thing for a medical coffee table. Indeed, just add legs and it would become a coffee table in its own right!

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