

A Proposed Number System for the 107 Cortical Areas of Economo and Koskinas, and Brodmann Area Correlations

Lazaros C. Triarhou

Economo-Koskinas Wing for Integrative and Evolutionary Neuroscience, University of Macedonia, Thessaloniki, Greece

Key Words

Human cerebral cortex • Cytoarchitectonics • Economo-Koskinas Atlas • Brodmann area correlation

Abstract

In their *Atlas of Cytoarchitectonics of the Adult Human Cerebral Cortex*, Economo and Koskinas defined 54 'ground,' 76 'variant,' and 107 'modification' areas. The 107 modifications are topographically distributed as 35 frontal, 13 superior limbic, 6 insular, 18 parietal, 7 occipital, 14 temporal and 14 inferior limbic (or hippocampal). One way to make the Economo-Koskinas system more practical is to encode the complex symbol notations of the 107 cortical areas with numbers EK 1 through EK 107. The present study does that, and it further correlates Economo-Koskinas areas with Brodmann areas, based on an overview of the classical and modern neurohistological literature.

Copyright © 2007 S. Karger AG, Basel

Introduction

The aim of this paper is to provide a concise overview of the cortical parcellation scheme into 107 areas proposed by Economo and Koskinas in their *Atlas of Cytoarchitectonics of the Adult Human Cerebral Cortex* [1], and to make more practical an otherwise not easily accessible source of information. Despite the general familiarity among neuroscientists with the Brodmann areas (fig. 1a, b), the present study, along with the preceding paper [2], attempts to make the Economo-Koskinas classification (fig. 1c, d) an option for any modern researcher who opts to follow it.

The topographic distribution of the 107 areas of Economo and Koskinas is summarized in table 1. On pages 218–220 of chapter 5 in their text volume [1], Economo and Koskinas number their 107 cortical modifications (table 2). One way to make the Economo-Koskinas (EK) system more practical [3] is to encode the complex symbol designations of the 107 cortical modifications with numbers EK 1 through EK 107 (table 2 and fig. 2, 3). Table 2 provides the original symbol designations and area names, along with corresponding Brodmann areas [4, 5]. Besides the books of Economo and Koskinas [1], Marburg [6], and Bonin [7], several modern papers [8–23] have been especially helpful in compiling the Brodmann area (BA) juxtapositions for table 2.

Presented at the 5th Forum of European Neuroscience, Vienna, Austria, July 8–12, 2006.

KARGER

Fax +41 61 306 12 34
E-Mail karger@karger.ch
www.karger.com

© 2007 S. Karger AG, Basel
1011–6125/07/0855–0204\$23.50/0

Accessible online at:
www.karger.com/sfn

Lazaros C. Triarhou, MD, PhD
University of Macedonia
Egnatia 156, Bldg. Z-312
GR-54006 Thessaloniki (Greece)
Tel. +30 2310 891 387, Fax +30 2310 891 388, E-Mail triarhou@uom.gr

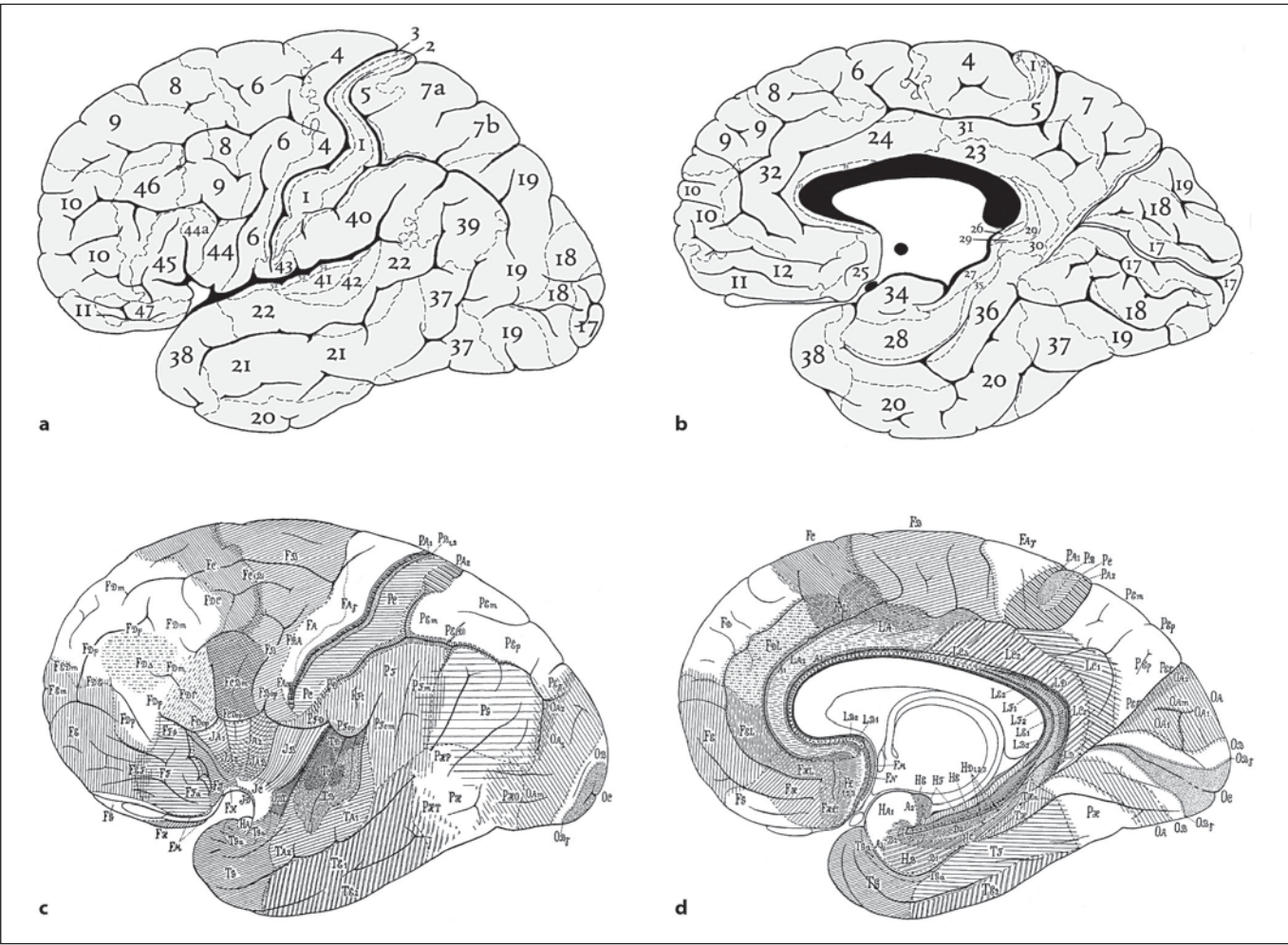


Fig. 1. Cytoarchitectonic cortical area maps of the convexity (a, c) and median facies (b, d) of the human cerebral hemispheres to show the relationship between Brodmann (a, b) and Economo-Koskinas (c, d) area divisions. Brodmann [4] used a numbering system, and Economo and Koskinas [1] a lettering system (cf. table 2 for area correlations in tabular form). Maps a and b newly

redrawn by the author, based on Brodmann figures 85 and 86 [4] included as figures 6 and 7 by Economo and Koskinas in their text volume [1]. Maps c and d correspond to figures 19 and 20 in Economo and Koskinas [1], reproduced with the kind permission of Rights and Permissions Department, Springer-Verlag GesmbH, Vienna.

Table 1. Distribution of the 107 numbered modification areas of Economo and Koskinas [1] in the human cerebral cortex

Lobe	Total number of areas	Numbering codes
Frontal	35	EK 1–EK 35
Superior limbic	13	EK 36–EK 48
Insular	6	EK 49–EK 54
Parietal	18	EK 55–EK 72
Occipital	7	EK 73–EK 79
Temporal	14	EK 80–EK 93
Inferior Limbic or Hippocampal	14	EK 94–EK 107

Frontal Lobe

Frontally, in the region of architectural structure FC (EK 6) – which is larger in size than its homologous BA 8 [18] – one finds on the third frontal gyrus Broca’s area for motor speech, and dorsally on the second and first frontal gyri in area FC the centers for the combined trunk, head and eye movements especially for the so-called ‘spying’ movements of the eyes on the second frontal gyrus [24]. All these movements are presentations of attention. As with speech, such movements involve many mental components and it is remarkable that this fact is expressed in

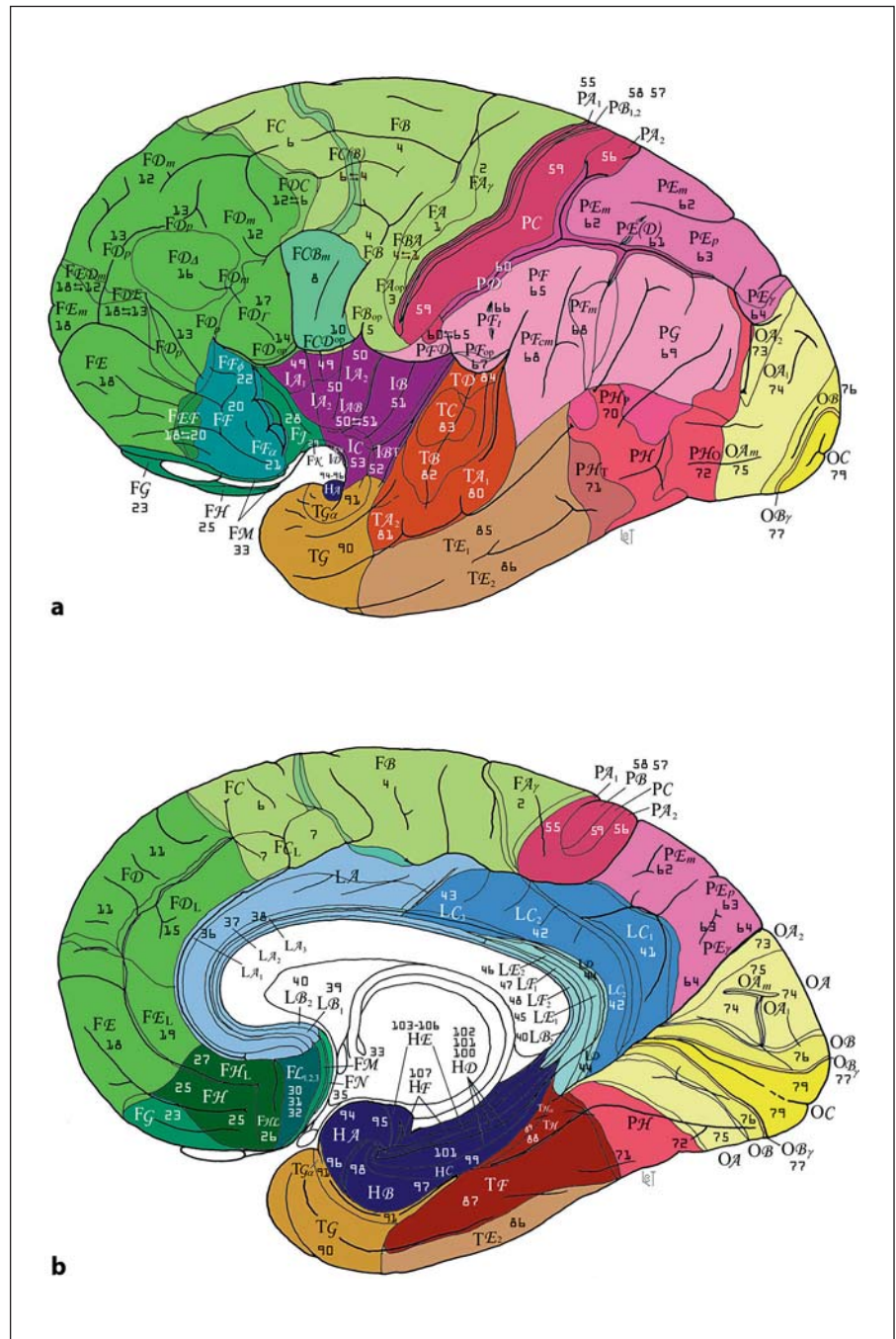


Fig. 2. Convexity (a) and median facies (b) of the human cerebral hemispheres. Economo-Koskinas cortical cytoarchitectonic areas are depicted in both the original lettering system and with EK area modification numbers (provided on pages 218–220 in chapter 5 of their text volume [1] and listed in table 2). Bidirectional arrows (\leftrightarrow) have been used to denote transitional types of cortex. The Sylvian fissure is laid open in the lateral view, and the hippocampal and callosal sulci are laid open in the median view to expose deeper-lying structures. The color-coded representation of the seven lobes and their subregions is based on figures 96 and 97 of Economo and Koskinas [1] (cf. fig. 1c and d in the companion article [2]), with shade variations to indicate different regions, as well as variant, overlapping or transition areas. A model of the human brain, with the various fields of the cortical surface indicated in colors by Economo, was commercially available in the 1920s from Fabrikation Chirurgischer Instrumente Carl Reiner (Mariannengasse 17, Wien IX). Economo used models and demonstration in his December 3, 1929, lecture at the Section on Neurology of the New York Acad-

emy of Medicine; one such model is exhibited at the Institut für Geschichte der Medizin (Institute for the History of Medicine) of Vienna University, alongside Economo's death mask. Area initials and lobe coloring: F, frontal (green); L, superior limbic (blue); I, insular (violet); P, parietal (red); O, occipital (yellow); T, temporal (brown); H, hippocampal (deep blue). Cytoarchitectonically defined lobe boundaries do not coincide exactly with the usual gross anatomical boundaries, especially in the parietal and occipital regions. The drawings of the cytoarchitectonic area maps are based on figures 92 and 93 of Economo and Koskinas [1]; color designations are principally based on their figures 96 and 97 [1].

Table 2. General overview of the 107 cytoarchitectonic modification areas of Economo and Koskinas [1] in the human cerebral cortex, with EK area number designations and Brodmann area correlations

EK area No.	EK area symbol ¹	Area name in English	Area name in Latin	Corresponding Brodmann area ²
<i>Frontal lobe (F)</i>				
Prerolandic region				
1	F \mathcal{A}	Precentral area ³	Area praecentralis	4
2	F \mathcal{A}_γ	Giant pyramidal precentral area	Area praecentralis gigantopyramidalis	4
3	F \mathcal{A}_{op}	Precentral area in operculum	Area praecentralis in operculo	4
4	F \mathcal{B}	Agranular frontal area ⁴	Area frontalis agranularis	6, 8, 9
5	F \mathcal{B}_{op}	Agranular frontal area in operculum	Area frontalis agranularis in operculo	6
6	F \mathcal{C}	Intermediate frontal area	Area frontalis intermedia	6, 8, 32
7	F \mathcal{CL}	Intermedio-limbic frontal area	Area frontalis intermedio-limbica	32
8	F \mathcal{CB}_m	Broca area (magnocellular agranular intermediate frontal area)	Area (frontalis intermedia agranularis magnocellularis in) Broca	44
9	F \mathcal{CI}	Intermediate frontal area at the beginning of the insula	Area frontalis intermedia in limine insulae	8
10	F \mathcal{C}_{op}	Opercular intermediate frontal area	Area frontalis intermedia opercularis	8
Frontal region				
11	F \mathcal{D}	Granular frontal area	Area frontalis granularis	9, 32, 46
12	F \mathcal{D}_m	Magnocellular granular frontal area	Area frontalis granularis magnocellularis	9
13	F \mathcal{D}_p	Parvicellular granular frontal area	Area frontalis granularis parvocellularis	9, 10, 11, 12
14	F \mathcal{D}_{op}	Granular frontal area in operculum	Area frontalis granularis in operculo	9, 10, 11, 12
15	F \mathcal{DL}	Limbic granular frontal area	Area frontalis granularis limbica	32
16	F $\mathcal{D}\Delta$	Middle granular frontal area	Area frontalis granularis media	8, 9, 46
17	F $\mathcal{D}\Gamma$	Triangular granular frontal area	Area frontalis granularis triangularis	45
18	F \mathcal{E}	Frontopolar area	Area frontopolaris	10, 32
19	F \mathcal{EL}	Limbic frontopolar area	Area frontopolaris limbica	32
Orbital (orbitomedial) region				
20	F \mathcal{F}	Granular orbital area ⁵	Area orbitalis granularis	13, 47
21	F \mathcal{F}_α	Agranular orbital area ⁶	Area orbitalis agranularis	47
22	F \mathcal{F}_ϕ	Pretriangular orbital area	Area orbitalis praetriangularis	47
23	F \mathcal{G}	Area of straight gyrus (area recta)	Area recta (area gyri recti)	11
24	F \mathcal{G}_i	Internal straight area	Area recta interna	
25	F \mathcal{H}	Prefrontal area	Area praefrontalis	11–14, 25, 32
26	F \mathcal{HL}	Parolfactory prefrontal area	Area praefrontalis parolfactoria	11–14, 25, 32
27	F \mathcal{HL}	Limbic prefrontal area	Area praefrontalis limbica	32
28	F \mathcal{I}	Frontoinsular area ⁷	Area frontoinsularis	16
29	F \mathcal{K}	Frontal piriform area	Area piriformis frontalis	16
30	F \mathcal{L}_1	Primary parolfactory area ⁸	Area parolfactoria prima	14, 25
31	F \mathcal{L}_2	Secondary parolfactory area	Area parolfactoria secunda	14, 25
32	F \mathcal{L}_3	Tertiary parolfactory area	Area parolfactoria tertia	14, 25
33	F \mathcal{M}	Geniculate area	Area geniculata	25
34	F \mathcal{M}_i	Geniculate area of olfactory triangle	Area geniculata trigoni olfactorii	25
35	F \mathcal{N}	Precommissural area	Area praecommissuralis	
<i>Superior limbic lobe (L)</i>				
Anterior superior limbic region				
36	L \mathcal{A}_1	Precingulate agranular anterior limbic area ⁹	Area limbica anterior agranularis praecingularis	24
37	L \mathcal{A}_2	Anterior cingulate agranular anterior limbic area	Area limbica anterior agranularis cingularis anterior	24
38	L \mathcal{A}_3	Cingulate agranular anterior limbic area limitans	Area limbica anterior agranularis cingularis limitans	24
39	L \mathcal{B}_1	Anterior ultracingulate area	Area ultracingularis anterior	24, 33
40	L \mathcal{B}_2	Area of the induseum ¹⁰	Area indusei	24, 33
Posterior superior limbic region				
41	L \mathcal{C}_1	Dorsal posterior cingulate area ¹¹	Area cingularis posterior dorsalis	31
42	L \mathcal{C}_2	Ventral posterior cingulate area	Area cingularis posterior ventralis	23
43	L \mathcal{C}_3	Posterior cingulate area limitans	Area cingularis limitans posterior	33
Retrosplenial subregion				
44	L \mathcal{D}	Agranular retrosplenial area	Area retrosplenialis agranularis	30
45	L \mathcal{E}_1	Superior retrosplenial area granulosa	Area retrosplenialis granulosa superior	29
46	L \mathcal{E}_2	Inferior retrosplenial area granulosa	Area retrosplenialis granulosa inferior	26, 29
47	L \mathcal{F}_1	Posterior ultracingulate area	Area ultracingularis posterior	26
48	L \mathcal{F}_2	Ultracingulate area oblecta	Area (ultracingularis) oblecta	26

Table 2 (continued)

EK area No.	EK area symbol ¹	Area name in English	Area name in Latin	Corresponding Brodmann area ²
<i>Insular lobe (I)</i>				
49	IA ₁	Dorsal precentral insular area ¹²	Area insulae praecentralis dorsalis	14
50	IA ₂	Ventral precentral insular area	Area insulae praecentralis ventralis	14
51	IB	Postcentral insular area ¹³	Area insulae postcentralis	13
52	IBT	Postcentral insular area at temporal entrance	Area insulae postcentralis in limine temporali	13
53	IC	Orbitoinsular area	Area orbito-insularis	15
54	ID	Piriform insular area	Area insularis piriformis	16
<i>Parietal lobe (P)</i>				
Postcentral region (anterior parietal)				
55	PA ₁	Giant pyramidal postcentral area	Area postcentralis gigantopyramidalis	3a
56	PA ₂	Giant pyramidal postparacentral area	Area postparacentralis gigantopyramidalis	3a, 5
57	PB ₂	Oral postcentral area simplex	Area postcentralis oralis simplex	3, 3b
58	PB ₁	Oral postcentral area granulosa	Area postcentralis oralis granulosa	3, 3b
59	PC	Intermediate postcentral area	Area postcentralis intermedia	1, 2
60	PD	Caudal postcentral area	Area postcentralis caudalis	2, 5a
Superior parietal region				
61	P(D)E	Superior parietal area (transition parietal postcentral area)	Area parietalis superior (area transitoris postcentralis parietalis)	40, 2
62	PE _m	Magnocellular superior parietal area	Area parietalis superior magnocellularis	7, 7a, 5
63	PE _p	Parvicellular superior parietal area	Area parietalis superior parvocellularis	7, 7b, 5b
64	PE _y	Giant pyramidal posterior superior parietal area	Area parietalis superior posterior gigantopyramidalis	7, 7b, 5b
Inferior parietal region				
65	PF	Supramarginal area ¹⁴	Area supramarginalis	40, 7b, 22
66	PF _t	Tenuicortical supramarginal area	Area supramarginalis tenuicorticalis	40, 7b, 22
67	PF _{op}	Opercular supramarginal area ¹⁵	Area supramarginalis opercularis	opercular
68	PF _{cm}	Posterior (magnocellular) supramarginal area	Area supramarginalis columnata magnocellularis (posterior)	40
69	PG	Angular area	Area angularis	39, 7a
Basal parietal region				
70	PHP	Basal (temporooccipital) parietal area at parietal entrance	Area parietalis (temporooccipitalis) basalis in limine parietali	37
71	PHT	Basal (temporooccipital) parietal area at temporal entrance	Area parietalis (temporooccipitalis) basalis in limine temporali	37
72	PHO	Basal (temporooccipital) parietal area at occipital entrance	Area parietalis (temporooccipitalis) basalis in limine occipitali	37
<i>Occipital lobe (O)</i>				
73	OA ₂	Anterior peristriate area ¹⁶	Area peristriata anterior	19
74	OA ₁	Posterior peristriate area	Area peristriata posterior	19
75	OA _m	Magnocellular peristriate area	Area peristriata magnocellularis	19
76	OB	Parastriate area ¹⁷	Area parastriata	18
77	OB _y	Giant pyramidal parastriate boundary	Limes parastriatus gigantopyramidalis	17/18 border
78	OB _Ω	Maculae granulosae of parastriate area	Maculae granulosae areae parastriatae	18
79	OC	Striate area (granulosa) ¹⁸	Area striata (granulosa)	17
<i>Temporal lobe (T)</i>				
Supratemporal region				
80	TA ₁	Posterior superior temporal area	Area temporalis superior posterior	22
81	TA ₂	Anterior superior temporal area	Area temporalis superior anterior	22
82	TB	Magnocellular supratemporal area simplex	Area supratemporalis magnocellularis simplex	42, 22
83	TC	Supratemporal area granulosa ¹⁹	Area supratemporalis granulosa	41
84	TD	Intercalated supratemporal area	Area supratemporalis intercalata	42, 22
Temporal region proper				
85	TE ₁	Middle temporal area proper	Area temporalis propria media	21, 37
86	TE ₂	Inferior temporal area proper	Area temporalis propria inferior	20, 21
Fusiform region				
87	TF	Fusiform area	Area fusiformis	36
88	TH	Hippocampotemporal area ²⁰	Area hippocampotemporalis	35, 36
89	TH _α	Agranular hippocampotemporal area	Area hippocampotemporalis agranularis	35

Table 2 (continued)

EK area No.	EK area symbol ¹	Area name in English	Area name in Latin	Corresponding Brodmann area ²
<i>Temporopolar region</i>				
90	T \mathcal{G}	Temporopolar area ²¹	Area temporopolaris	38, 35, 36, 52
91	T \mathcal{G}_α	Agranular temporopolar area ²²	Area temporopolaris agranularis	38, 35, 36, 52
92	T \mathcal{J}	Temporal piriform area ²³	Area piriformis temporalis	16
93	T \mathcal{K}	Posterior area of substantia perforata	Area substantiae perforatae posterior	
<i>Hippocampal (inferior limbic) lobe (H)</i>				
94	H \mathcal{A}_1	Primary uncinata area	Area uncinata prima	34
95	H \mathcal{A}_2	Secondary uncinata area	Area uncinata secunda	34
96	H \mathcal{A}_3	Tertiary uncinata area	Area uncinata tertia	34
97	H \mathcal{B}_1	Primary parauncinate area	Area parauncinata prima	28
98	H \mathcal{B}_2	Secondary parauncinate area ²⁴	Area parauncinata secunda	28
99	H \mathcal{C}	Rhinal area limitans ²⁵	Area rhinalis limitans	28
100	H \mathcal{D}_1	Presubicular area granulosa limitans	Area praesubicularis granulosa limitans	27
101	H \mathcal{D}_2	Middle presubicular area granulosa	Area praesubicularis granulosa media	27
102	H \mathcal{D}_3	Glomerular presubicular area granulosa	Area praesubicularis granulosa glomerulosa	27
103	H $\mathcal{E}_{1\alpha}$	Glomerular subicular pyramidal area	Area pyramidalis subiculi glomerulosa	
104	H $\mathcal{E}_{1\beta}$	Subicular pyramidal area simplex	Area pyramidalis subiculi simplex	
105	H \mathcal{E}_2	Pyramidal area of Ammon's horn ²⁶	Area pyramidalis cornu Ammonis	
106	H \mathcal{E}_3	Pyramidal area of digitate gyrus of uncus ²⁷	Area pyramidalis gyri digitati unci	
107	H \mathcal{F}	Area of fascia dentata ²⁸	Area fasciae dentatae	

¹ An additional 13 ('transition') areas were marked by Economo and Koskinas [1] on their maps, but not explicitly listed among the 107 'modifications': F $\mathcal{B}\mathcal{A}$, F $\mathcal{C}(\mathcal{B})$, F $\mathcal{C}\mathcal{D}_{op}$, F $\mathcal{D}\mathcal{C}$, F $\mathcal{D}\mathcal{E}$, F $\mathcal{E}\mathcal{D}_m$, F $\mathcal{E}\mathcal{F}$, F \mathcal{E}_m , P \mathcal{C}_γ , P $\mathcal{E}(\mathcal{D})$, P $\mathcal{F}\mathcal{D}$, P \mathcal{F}_m and I $\mathcal{A}\mathcal{B}$.

² On the basis of Economo and Koskinas [1], as well as references [6–23].

³ Primary motor cortex.

⁴ Economo and Koskinas [1] mark in their map a transition area F $\mathcal{B}\mathcal{A}$ which corresponds to Brodmann area 6Va.

⁵ Area F \mathcal{F} partly corresponds to the orbitofrontal proisocortex of the monkey that lies between Brodmann areas 13 and 12 rostrally and the orbitofrontal peripaleocortex caudally [14].

⁶ Not recognized by Brodmann in the human brain. Corresponds probably to granular isocortex in the anterior part of Brodmann area 11 in the macaque, which lies between Brodmann areas 10 rostrally and 13 caudally.

⁷ Peripaleocortex in gyrus transversus insulae (pars inferior) and orbitofrontal peripaleocortex in the monkey [14].

⁸ Areas F \mathcal{L}_1 –F \mathcal{L}_3 in subcallosal gyrus.

⁹ Areas L \mathcal{A}_1 –L \mathcal{A}_3 , anterior cingulate gyrus.

¹⁰ Areas L \mathcal{B}_2 , L \mathcal{F}_1 and L \mathcal{F}_2 belong to the supracommissural hippocampus [18].

¹¹ Areas L \mathcal{C}_1 –L \mathcal{C}_3 , posterior cingulate areas.

¹² Areas I \mathcal{A}_1 and I \mathcal{A}_2 , anterior insula.

¹³ Areas I \mathcal{B} and I $\mathcal{B}\mathcal{T}$, posterior insula.

¹⁴ Rostral inferior parietal lobule.

¹⁵ Economo and Koskinas mark in their map a transition area P $\mathcal{F}\mathcal{D}$ which corresponds to Brodmann area 43 [1, 7].

¹⁶ Anterior preoccipital zone.

¹⁷ Posterior parastriate zone or extrastriate area.

¹⁸ Primary visual cortex.

¹⁹ Primary auditory cortex or supratemporal koniocortex.

²⁰ Posterior part of parahippocampal gyrus [13].

²¹ Temporal pole.

²² According to Economo and Koskinas [1], area T \mathcal{G}_α corresponds to Brodmann area 35.

²³ Temporopolar peripaleocortex in the macaque [14].

²⁴ In Plate CII of their Atlas, Economo and Koskinas [1] describe a tertiary parauncinate area H \mathcal{B}_3 .

²⁵ Economo and Koskinas [1] mention a 'transition' area H $\mathcal{C}(\mathcal{D})$ from H \mathcal{C} to H \mathcal{D} , perhaps corresponding to Brodmann area 48.

²⁶ Hippocampus proper.

²⁷ In his later studies, Economo [24] added areas H \mathcal{E}_4 and H \mathcal{E}_5 .

²⁸ Dentate gyrus.

the anatomical picture of the corresponding area FC by a gradual increase in the number of granule cells in cortical layers II and IV.

Broca's area (BA 44 or Economo-Koskinas area F $\mathcal{C}\mathcal{B}_m$) was considered by Brodmann [4] and Economo and Koskinas [1] as a particular human characteristic. Kreft [25] recognized it in the chimpanzee and Orang-Utan

brain, and Bonin and Bailey [11] and Peden and Bonin [26] in the brain of the macaque.

Tomaiuolo et al. [27] produced a probability map of the pars opercularis of the inferior frontal gyrus using MRI by averaging location and extent in 108 individual normalized brains. The surface area of the pars opercularis is characterized by a distinct type of cortex, which is

cortex and his delineation of BA 4 has been challenged; area $F\mathcal{A}_\gamma$ (EK 2) resembles the frontal core area more closely, with the consequence that a large part of area $F\mathcal{A}$ (EK 1) belongs to nonprimary motor cortex.

Area $F\mathcal{F}$ (EK 20) partly corresponds to the orbitofrontal proisocortex of the monkey that lies intercalated between the caudal orbitofrontal isocortex (BA 13 and 12) rostrally, and the orbitofrontal peripaleocortex caudally. Area $F\mathcal{F}_\alpha$ (EK 21) in the human brain probably corresponds to the granular isocortex in the anterior part of the orbital surface of the frontal lobe (BA 11) in the macaque monkey, which lies intercalated between the frontopolar BA 10 rostrally and BA 13 caudally. Areas $F\mathcal{H}$ (EK 25) and $F\mathcal{H}\mathcal{L}$ (EK 26) in the human brain correspond to the paralimbic dysgranular isocortex (BA 14) on the ventromedial surface of the prefrontal cortex in the macaque monkey, which lies intercalated between the frontopolar granular isocortex (BA 10) rostrally and the orbitomesial archicortical proisocortex of the straight gyrus (BA 25) caudally. Area $F\mathcal{J}$ (EK 28) appears to correspond to the peripaleocortex in the inferior part of the transverse gyrus of the insula, and to the orbitofrontal peripaleocortex in the monkey [14].

Area $F\mathcal{F}$ (EK 20 or BA 47) lies rostrally and ventrally to area $F\mathcal{D}\mathcal{I}$ (EK 17 or BA 45). Petrides and Pandya [28] designate the specific part of the zone previously labeled BA 47 as ventrolateral BA 47/12, which in the monkey receives input from the rostral inferotemporal visual association cortex and temporal limbic areas (i.e. perirhinal and parahippocampal cortices). On the other hand, the dorsally adjacent BA 45 receives input from the superior temporal gyrus (auditory association cortex) and the multimodal cortex in the upper bank of the superior temporal sulcus [28]. Petrides and Pandya [29] also define a BA 9/46, in addition to BA 46 (area $F\mathcal{D}\Delta$ or EK 16); together, BA 9/46 and BA 46 constitute the lower-half of the mid-dorsolateral frontal cortex, and are easily discernible from BA 9 in the upper mid-dorsolateral frontal cortex. BA 9 has basic connections similar to BA 46 and BA 9/46, with the difference that it does not receive input from the lateral parietal cortex; moreover, BA 9 does not exhibit a well-formed layer IV.

In the anterior cingulate cortex [18], areas $F\mathcal{C}\mathcal{L}$ (EK 7), $F\mathcal{D}\mathcal{L}$ (EK 15), $F\mathcal{E}\mathcal{L}$ (EK 19) and $F\mathcal{H}\mathcal{L}$ (EK 27) compare to BA 32; areas $F\mathcal{L}$ (EK 30–32) and $F\mathcal{M}$ (EK 33–34) correspond to BA 25.

Economo and Koskinas [1] mark some transitional types of cortex in their maps, but they do not list them in the 107 modifications (table 2). These include areas $F\mathcal{B}\mathcal{A}$, $F\mathcal{C}(\mathcal{B})$, $F\mathcal{C}\mathcal{D}_{\text{op}}$, $F\mathcal{D}\mathcal{C}$, $F\mathcal{D}\mathcal{E}$, $F\mathcal{E}\mathcal{D}_m$, $F\mathcal{E}\mathcal{F}$ and $F\mathcal{E}_m$. Following

the logic of their nomenclature, areas $F\mathcal{B}\mathcal{A}$, $F\mathcal{D}\mathcal{C}$, $F\mathcal{D}\mathcal{E}$ and $F\mathcal{E}\mathcal{F}$ denote transition forms from one component area to the other (e.g. $F\mathcal{B}\mathcal{A}$ marks the transition of area $F\mathcal{B}$ into $F\mathcal{A}$, $F\mathcal{D}\mathcal{C}$ the transition of $F\mathcal{D}$ into $F\mathcal{C}$, and so on). Moreover, the designation $F\mathcal{C}(\mathcal{B})$ implies a part of area $F\mathcal{C}$ with an admixture of the type of neighboring area $F\mathcal{B}$, while the suffix subscript m in areas $F\mathcal{E}\mathcal{D}_m$ and $F\mathcal{E}_m$ signifies cellular variations, namely, with magnocellular characteristics. Finally, area $F\mathcal{C}\mathcal{D}_{\text{op}}$ denotes a transitional opercular variant between areas $F\mathcal{C}_{\text{op}}$ and $F\mathcal{D}_{\text{op}}$.

Superior Limbic Lobe

In the anterior cingulate cortex [18], area $L\mathcal{A}_3$ (EK 38) corresponds to BA 24, and area $L\mathcal{C}_3$ (EK 43) to BA 33; area $L\mathcal{A}_1$ (EK 36) overlaps with both BA 24 and BA 33. Concerning the retrosplenial archicortex [35], areas $L\mathcal{D}$ (EK 44), $L\mathcal{E}_1$ (EK 45) and $L\mathcal{E}_2$ (EK 46) are comparable to BA 30, BA 29 and BA 26. On the other hand, areas $L\mathcal{B}_2$ (EK 40), $L\mathcal{F}_1$ (EK 47) and $L\mathcal{F}_2$ (EK 48) belong to the supracommissural hippocampus [18].

One concern in the localization of cortical functions in the human brain is the boundary between the retrosplenial/cingulate and parahippocampal cortices. Brodmann [4, 5] depicted the retrosplenial cortex as fully surrounding the posterior and ventral edge of the splenium of the corpus callosum. Economo [24] provided the first subregional map of the posterior cingulate gyrus and showed a termination of the retrosplenial areas $L\mathcal{E}$ (EK 45–46) and $L\mathcal{D}$ (EK 44) at a plane caudal but not ventral to the splenium. Flat maps presented by Vogt et al. [10] show that the border between retrosplenial/posterior cingulate and parahippocampal cortices is caudal but not ventral to the splenium, being in close agreement with the view of Economo [24].

Every section through the retrosplenial cortex includes a segment of allocortical hippocampus and ectosplenial area $L\mathcal{F}$ (EK 47–48 or BA 26). In reviewing Brodmann's map of the posterior cingulate and retrosplenial cortices on the convoluted surface of the human brain, in the light of the findings of Economo and Koskinas [1] and their own immunohistochemical observations, Vogt et al. [10] underline the need for the following modifications: firstly, BA 29 and BA 30 extend further rostral; secondly, BA 30 does not significantly extend onto the caudomedial lobule, and when BA 29m does, it is to a minor extent; thirdly, the retrosplenial cortex does not extend as far ventral around the splenium.

At allocortical-isocortical transition points in the primate telencephalon, anatomists today recognize the concept of a 'dysgranular' cytoarchitecture (i.e. a weakly defined layer IV); such points are found in the orbitofrontal, insular, and anterior and posterior cingulate cortices [10]. Ngowyang [30] had described a 'dysgranular region' (regio dysgranularis) in the frontal lobe, associated with BA 8 and Economo-Koskinas areas FC (EK 6) and FCL (EK 7). Going forward into BA 6, the granular layer appears sporadically, making this area 'hypogranular' or 'dysgranular'; forward of BA 6, the prefrontal cortex, and continuing through BA 10 of the frontal pole, the cortex is 'eugranular' [31].

Area LD (EK 44 or BA 30) is dysgranular rather than agranular, as it was originally thought [10]; its layer IV has a variable thickness, interrupted by large SMI-32 immunopositive neurons (nonphosphorylated neurofilaments) in layers IIIC and Va. Brodmann [4] referred to BA 30 as agranular. Economo [24] was quite explicit that area LD (EK 44) is not merely agranular, but that the 'granulous' layer of area LE (EK 45–46 or BA 29) is not continuous with the isocortical layer of area LC₂ (BA 23 or EK 42). Economo [24] vacillated on the presence of a layer IV in area LD and showed a layer III(IV) below layer III therein. A dysgranular layer IV has a variable thickness and may even disappear as neurons of layer IIIC and Va intermingle. The dysgranular concept for a cortical architecture was obviously not defined during the early years of cortical cytoarchitectonics in terms of chemical signatures of neurons, as histochemical techniques were not available then. In a series of studies spanning over 30 years, Vogt et al. [10] described the dysgranular nature of area LD (BA 30) in the primate brain, using Nissl, Golgi and immunocytochemical methods, and its profound differences with the cytoarchitecture of granular BA 23a.

Insular Lobe

The insular lobe includes the dorsal precentral insular area IA₁ (EK 49), ventral precentral insular area IA₂ (EK 50), postcentral insular area IB (EK 51), orbitoinsular area IC (EK 53) and piriform insular area ID (EK 54). Areas IA, IB and IC correspond to BA 14, BA 13 and BA 15, respectively. The gradual transition of area IA backwards over the central sulcus of the insula to area IB is denoted by Economo and Koskinas [1] as area IAB (marked on their maps but not registered among the 107 modifications), which is characterized by a condensation of the granular layers and a reduction of pyramidal cell size.

Parietal Lobe

Zilles and Palomero-Gallagher [21] provide a comparison of the cytoarchitectonic areas of the parietal lobe as defined by Brodmann [4] and Economo and Koskinas [1]; in their discussion, they include myeloarchitectonic, histochemical and functional considerations from later studies. Briefly, Brodmann [4] defines four areas (BA 1–3 and BA 43) in the postcentral region, whereas Economo and Koskinas [1] six (PA₁, PA₂, PB₁, PB₂, PC and PD, EK 55–60). In the parietal region, Brodmann [4] defines four areas (BA 5, BA 7, BA 39–40), and Economo and Koskinas [1] nine (PED, PE_m, PE_p, PE_γ, PF, PF_t, PF_{op}, PF_{cm} and PG, EK 61–69). According to the same authors [21], the basal parietal region PH (EK 72) most likely belongs to the visual cortex and includes the functionally defined areas V4 and V5.

The proposed subdivisions of the anterior parietal cortex made by Economo and Koskinas [1] are in wide use today, as are those suggested by Brodmann [16]. Area PA (EK 55–56), located in the depths of the central sulcus, is equivalent to BA 3a. Area PB (EK 57–58) is the 'sensory koniocortex', located on the caudal bank of the central sulcus and equivalent to BA 3b. Area PC (EK 59) includes both BA 2 and BA 1; BA 1 appears to be narrower than area PC. Area PD (EK 60) corresponds to part of BA 2.

Concerning the primary somatosensory cortical areas and the subdivision of the posterior parietal lobe into a superior and an inferior lobule, the most accepted terminology today is that of Economo and Koskinas [1], which has also formed the basis for further contemporary cytoarchitectonic analyses and for experimentation in primates [18]. In the posterior parietal cortex, areas PD (EK 60) and PE (EK 62–64) roughly correspond to parts 5a and 5b of BA 5; areas PF (EK 65) and PG (EK 69) to parts 7b and 7a of BA 7 [16]. Brodmann [4] did not delineate any transition zones in the posterior parietal lobe [18]; in contrast, Economo and Koskinas [1] had marked such transition zones between the areas PE, PF, PG, PH and OA in their cortical maps, which are in agreement with the observations of Eidelberg and Galaburda [12].

In the parietal lobe behind the central sulcus of Rolando, between the three sensory spheres which are most important for human understanding, those of touch, sight and hearing located in the postcentral gyrus and in Heschl's supratemporal gyrus and the walls of the calcarine sulcus, there is a wide cortical field on the convexity of the hemisphere occupied by parietal cortical type (type 3).

Next to these areas comes a series of centers, lesions of which produce cognitive deficits (for instance, cortical deafness and lack of understanding of words). Lesions of the most central, caudal, and basal portions of the inferior parietal lobe, which comprises the gyrus angularis and basal portions of the inferior parietal lobe, provoke disturbances of a still higher order in mental and intellectual defect of a sensory-receptive nature [24].

Similarly to the case of the frontal lobe, the parietal areas PC_γ , $PE(\mathcal{D})$, $PF\mathcal{D}$ and PF_m are marked by Economo and Koskinas [1] on their maps, but not included among the 107 modifications (table 2). BA 43 in particular, which Brodmann [4] includes in the operculum, is not considered as an independent area by Economo and Koskinas [1], but as a transitional formation or mixing of areas $P\mathcal{D}$ (EK 60) and PF (EK 65), designated $PF\mathcal{D}$ (indicated as EK 60↔65 in fig. 2a and 3b) [7]. Areas PC_γ and PF_m denote cellular variations containing, respectively, giant pyramidal and magnocellular neurons. Area $PE(\mathcal{D})$ is a variant of area PE with an admixture of the neighboring cortical type $P\mathcal{D}$. In comparing grasp versus pointing tasks, Frey et al. [23] identify two significant foci of activation in the hemisphere contralateral to the performing right hand. The first area is located in the left parietal cortex at the junction of the intraparietal sulcus and the postcentral gyrus. This site is likely within the most superior, rostral aspect of BA 40, corresponding to area PF or PDE .

The functionally defined secondary somatosensory cortex (SII) is located in the parietal operculum, hidden within the Sylvian fissure. BA 40 and BA 43 extend into the parietal operculum and are candidates for SII on topographic grounds; they partially correspond to the opercular modification PF_{op} (EK 67) and to subcentral area $PF\mathcal{D}$, respectively. Based on measurements of the 'gray level index' (an indicator of the volume fraction of neuron somata), Eickhoff et al. [32] identify four heterogeneous cytoarchitectonic regions as anatomical correlates of the human SII, which they term areas OP 1 through 4. Area OP 4 is similar in location to BA 43 and to Economo-Koskinas area $PF\mathcal{D}$, as it contains large pyramidal cells in layers IIIc and Va.

In the supramarginal gyrus of the rostral inferior parietal cortex, Economo and Koskinas [1] subdivide BA 40 into five areas, PF (EK 65), PF_{cm} (EK 68), PF_m , PF_{op} (EK 67) and PF_i (EK 66) which have been confirmed in general lines by Caspers et al. [33] with observer-independent quantitative methods; in the caudal inferior parietal cortex, Caspers et al. [33] distinguish a caudal region termed $P\mathcal{G}_p$ and a rostral region termed $P\mathcal{G}_a$, this latter fitting to area $P\mathcal{G}$ (EK 69) in the angular gyrus (roughly BA 39).

Occipital Lobe

The primary visual area or striate cortex is area OC (EK 79 or BA 17), the parastriate cortex is area OB (EK 76–78 or BA 18), and the peristriate cortex is area OA (EK 73–75 or BA 19) [15]. A border zone located at the boundaries of BA 17 and BA 18 and containing giant pyramidal cells in the lower part of layer III is the Economo-Koskinas area OB_γ (EK 77, limes parastriatus gigantopyramidalis).

The total surface of the koniocortex in the visual sensory sphere (area OC) in both hemispheres was estimated at about 50 cm². The total number of cells about 1.4×10^9 , i.e. 10% of the total number of nerve cells of the entire cortex. The area striata is thus more than four times richer in cells than any other region [24].

Temporal Lobe

Based on pathological and physiological considerations, Economo [24] localized the understanding of the word *speech* in cortical area TA_1 (EK 80) of the left hemisphere, the understanding of the word *sense* in the caudal transitional region of TA_1 towards PF (EK 65), and the understanding of *music* in TA_2 (EK 81) and the temporal pole; appreciation of higher tones in parts in the bottom of the Sylvian fissure, while that of lower tones more towards outer portions. Area TC (EK 83) is koniocortex, i.e. sensory cortex representing the *primary acoustic sphere*, into which run acoustic fibers from the medial geniculate body.

Economo and Horn [34] further investigated the cytoarchitectonics of the auditory cortex in seven adult and two juvenile brains. They found the superior temporal surface and the length of the Sylvian fissure larger on the left side. According to Meyer [35], the initial attempts at investigating the cytoarchitectonics of the auditory cortex were those by Campbell [36], Rosenberg [37], and by Brodmann [4], who had identified it with BA 41, but who largely missed the most characteristic feature that this area shares with all other 'sensory' cortices, i.e. the 'granulation', first described by Economo and Koskinas [1]. Economo and Horn [34] attribute the striking variations in size among individuals and between the two hemispheres possibly to handedness or differences in musicality.

The koniocortex in the human temporal lobe encompasses areas TC (EK 83) and $T\mathcal{D}$ (EK 84) or BA 41 and part of BA 42 and is located on Heschl's gyrus (transverse temporal gyrus); area TA (EK 80–81) contains Wernicke's

speech area, while the cerebral 'belt' areas in all likelihood are BA 22 and part of BA 42, which correspond to areas T \mathcal{A} (EK 80–81) and T \mathcal{B} (EK 82) [17, 38].

Using cytoarchitectonic, myeloarchitectonic, and histochemical criteria, as well as three-dimensional reconstruction based on serial sections, Hackett et al. [39] identified a homologous cortical auditory region in the macaque, chimpanzee, and human brain. It has been known from the classical cytoarchitectonic studies that the human auditory cortex comprises a central 'core' region, characterized by a koniocortical cytoarchitecture and dense myelination, and the surrounding nonprimary 'belt' fields, characterized by para- or pro-koniocortical cytoarchitecture. Within area T \mathcal{C} (EK 83), which closely corresponds to BA 41 and the 'core' region of Hackett et al. [39], Economo and Horn [34] describe 11 distinct types of granular cortex. The 'belt' field of the human auditory cortex [39], on the other hand, seems to correspond to the medial portion of the koniocortical T \mathcal{D} (EK 84) sector of Economo and Koskinas [1] and Economo and Horn [34].

In sections cut perpendicularly to the radial orientation of layer III apical dendrites, the small pyramidal cells are arranged in short radial columns that partially extend into layers II and IV [39]; such a feature seems to correspond to what Economo and Koskinas [1] call 'rain shower formation' (*Regenschauerformation*). With regard to the columnar organization of the belt region, layer III pyramidal cells are arranged in organized vertical columns [39, 40], which Economo and Koskinas [1] call 'organ pipe formation' (*Orgelpfeifenformation*).

Economo and Koskinas [1] and Economo and Horn [34] were among the first to notice individual differences in the auditory fields and marked asymmetries between the two hemispheres: Heschl's gyrus is generally single and longer on the left side and double and shorter on the right side; the planum temporale (located caudally to Heschl's gyrus, in Economo-Koskinas area T \mathcal{B} or EK 82) is larger on the left side [17, 41]. Such asymmetries may underlie the modern idea of a functional differentiation of the two cerebral hemispheres and the predilection of the left hemisphere (right ear) for verbal tests, and that of the right hemisphere (left ear) for music recognition [41].

Suzuki and Amaral [9] make the point that, in contrast to Brodmann [4], Economo and Koskinas [1] divide the medial temporal lobe into a rostral area T \mathcal{G} and two caudal areas, T \mathcal{H} (EK 88) and T \mathcal{F} (EK 87), with area T \mathcal{G} further subdivided into a medial area T \mathcal{G}_α (EK 91) and a larger lateral area T \mathcal{G} (EK 90). Like Elliot Smith [42], Economo and Koskinas [1] also illustrate the temporal

polar cortex as being continuous with the anteroventral portion of the medial temporal lobe. Areas T \mathcal{G} (EK 90) and T \mathcal{G}_α (EK 91) encompass BA 38, anterior BA 35 and anterior BA 36. The nomenclature and cortical demarcations of Brodmann [4] concerning the description of the medial temporal lobe in primates is vague and inconsistent across species [9]. In contrast, the cytoarchitectonic descriptions of the medial temporal lobe by Economo and Koskinas [1], Economo [24], and Bonin and Bailey [11] provide a much more detailed cytoarchitectonic analysis, as determined by Suzuki and Amaral [9] in a re-evaluation of the cytoarchitectonic and chemoarchitectonic connections of the medial temporal lobe in the macaque monkey. Areas T \mathcal{F} (EK 87) and T \mathcal{H} (EK 88) belong to the posterior part of the parahippocampal gyrus, whereas the anterior part of the parahippocampal gyrus comprises mainly the entorhinal cortex and the associated perirhinal cortex [13].

Area T \mathcal{J} (EK 92) seems to be homologous to the hyperchromic, coarse-celled temporopolar peripaleocortex in the macaque monkey [14]. Besides area T \mathcal{J} , the peripaleocortical agranular claustral region (BA 16 in *Cercopithecus*) is also homologous to a certain extent to human area I \mathcal{D} (EK 54) [18].

Hippocampal (Inferior Limbic) Lobe

The inferior limbic lobe contains the hippocampal gyrus, which lies from the isthmus until near the temporal pole and contains the entire uncinate gyrus, the subiculum, the dentate gyrus, and Ammon's horn. Above the splenium, the hippocampal rudiment, induseum griseum, or areas L \mathcal{B}_2 (EK 40) and H \mathcal{F} (EK 107), there is a single layer of densely packed ganglion cells, SMI-32 immunopositive (nonphosphorylated neurofilament protein immunoreactivity). Adjacent to the induseum griseum is the subicular rudiment or area H \mathcal{E} (EK 103–106), which has many fewer and more dispersed neurons. These two areas together form the fasciolate gyrus on the dorsal surface of the corpus callosum [10].

Acknowledgement

The courtesy of the staff of the National Library of Greece, Staatsbibliothek zu Berlin, Librairie Harteveld in Fribourg, Switzerland, Special Collections Department at the Lilly Medical Library of Indiana University, Library of Congress and the National Library of Medicine of the United States is gratefully acknowledged.

References

- 1 Economo C von, Koskinas GN: Die Cytoarchitektonik der Hirnrinde des erwachsenen Menschen. Textband und Atlas. Wien, Springer, 1925.
- 2 Triarhou LC: The Economo-Koskinas Atlas revisited: cytoarchitectonics and functional context. *Stereotact Funct Neurosurg* 2007; 85:195–203.
- 3 Triarhou LC: A proposed number system for the 107 cortical areas of Economo and Koskinas. *Fed Eur Neurosci Soc Abstr* 2006;3: A232.24.
- 4 Brodmann K: Vergleichende Lokalisationslehre der Großhirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues. Leipzig, JA Barth, 1909.
- 5 Garey LJ (ed): Brodmann's Localisation in the Cerebral Cortex. New York, Springer Science, 2006.
- 6 Marburg O: Mikroskopisch-Topographischer Atlas des menschlichen Zentralnervensystems mit begleitendem Texte, Aufl 3. Leipzig, Franz Deuticke, 1927, pp 175–192.
- 7 Bonin G von: Essay on the Cerebral Cortex. Springfield, Charles C Thomas, 1950.
- 8 Rivier F, Clarke S: Cytochrome oxidase, acetylcholinesterase, and NADPH-diaphorase staining in human supratemporal and insular cortex: evidence from multiple auditory areas. *Neuroimage* 1997;6:288–304.
- 9 Suzuki WA, Amaral DG: Where are the perirhinal and parahippocampal cortices? A historical overview of the nomenclature and boundaries applied to the primate medial temporal lobe. *Neuroscience* 2003;120:893–906.
- 10 Vogt BA, Vogt LJ, Perl DP, Hof PR: Cytology of human caudomedial cingulate, retrosplenial, and caudal parahippocampal cortices. *J Comp Neurol* 2001;438:353–376.
- 11 Bonin G von, Bailey P: The Neocortex of *Macaca mulatta*. Urbana, University of Illinois Press, 1947.
- 12 Eidelsberg D, Galaburda AM: Inferior parietal lobule: divergent architectonic asymmetries in the human brain. *Arch Neurol* 1984; 41:843–852.
- 13 Amaral DG, Insausti R: Hippocampal formation; in Paxinos G (ed): The Human Nervous System. San Diego, Academic Press, 1990, pp 711–755.
- 14 de Olmos J: Amygdaloid nuclear gray complex; in Paxinos G (ed): The Human Nervous System. San Diego, Academic Press, 1990, pp 583–710.
- 15 Garey LJ: Visual system; in Paxinos G (ed): The Human Nervous System. San Diego, Academic Press, 1990, pp 945–977.
- 16 Kaas JH: Somatosensory system; in Paxinos G (ed): The Human Nervous System. San Diego, Academic Press, 1990, pp 813–844.
- 17 Webster WR, Garey LJ: Auditory system; in Paxinos G (ed): The Human Nervous System. San Diego, Academic Press, 1990, pp 889–944.
- 18 Zilles K: Cortex; in Paxinos G (ed): The Human Nervous System. San Diego, Academic Press, 1990, pp 757–802.
- 19 Amunts K, Schleicher A, Bürgel U, Mohlberg H, Uylings HBM, Zilles K: Broca's region revisited: cytoarchitecture and intersubject variability. *J Comp Neurol* 1999;412:319–441.
- 20 Shankle WR, Rafii MS, Landing BH, Fallon JH: Approximate doubling of numbers of neurons in postnatal human cerebral cortex and in 35 specific cytoarchitectural areas from birth to 72 months. *Pediatr Dev Pathol* 1999;2:244–259.
- 21 Zilles K, Palomero-Gallagher N: Cyto-, myelo-, and receptor architectonics of the human parietal cortex. *Neuroimage* 2001;14: S8–S20.
- 22 Nielsen FÅ: The Brede database: a small database for functional neuroimaging. *Neuroimage* 2003;19(suppl 1):e1788–e1789.
- 23 Frey SH, Vinton D, Norlund R, Grafton ST: Cortical topography of human anterior intraparietal cortex active during visually guided grasping. *Cogn Brain Res* 2005;23: 397–405.
- 24 Economo C von: Zellaufbau der Grosshirnrinde des Menschen. Berlin, Springer, 1927.
- 25 Kreht H: Zur Architektur der Broca'schen Region beim Schimpansen und Orang-Utang. *Zschr Anat Entwicklungsgesch* 1936; 105:654–677.
- 26 Peden JK, Bonin G von: The neocortex of Hapale. *J Comp Neurol* 1947;86:37–63.
- 27 Tomaiuolo F, MacDonald JD, Caramanos Z, Posner G, Chiavaras M, Evans AC, Petrides M: Morphology, morphometry and probability mapping of the pars opercularis of the inferior frontal gyrus: an in vivo MRI analysis. *Eur J Neurosci* 1999;11:3033–3046.
- 28 Petrides M, Pandya DN: Comparative cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and corticocortical connection patterns in the monkey. *Eur J Neurosci* 2001;16:291–310.
- 29 Petrides M, Pandya DN: Dorsolateral prefrontal cortex: comparative cytoarchitectonic analysis in the human and the macaque brain and corticocortical connection patterns. *Eur J Neurosci* 1999;11:1011–1036.
- 30 Ngowyang G: Die Cytoarchitektonik des menschlichen Stirnhirns. I. Cytoarchitektonische Felderung der Regio granularis und Regio dysgranularis. *Monogr Natl Res Inst Psychol Acad Sin (Shanghai)* 1934;7:1–68.
- 31 DeMyer W: Neuroanatomy. Baltimore, Williams & Wilkins/Harwal, 1988.
- 32 Eickhoff S, Schleicher A, Zilles K, Amunts K: The human parietal operculum. I. Cytoarchitectonic mapping of subdivisions. *Cereb Cortex* 2006;16:254–267.
- 33 Caspers S, Geyer S, Schleicher A, Mohlberg H, Amunts K, Zilles K: The human inferior parietal cortex: cytoarchitectonic parcellation and interindividual variability. *Neuroimage* 2006;33:430–448.
- 34 Economo C von, Horn L: Über Windungsrelief, Maße und Rindenarchitektonik der Supratemporalfläche, ihre individuellen und ihre Seitenunterschiede. *Zschr Ges Neurol Psychiat (Berl)* 1930;130:678–757.
- 35 Meyer A: The search for a morphological substrate in the brains of eminent persons including musicians: a historical review; in Critchley M, Henson RA (eds): Music and the Brain: Studies in the Neurology of Music. London, William Heinemann, 1977, pp 255–281.
- 36 Campbell AW: Histological Studies on the Localization of Cerebral Function. Cambridge, Cambridge University Press, 1905.
- 37 Rosenberg L: Histologische Untersuchung über die Cytoarchitektonik der Heschl'schen Windungen. *Neurol Centralbl (Berl)* 1907; 14:685–686.
- 38 Chirry O, Tardif E, Magistretti PJ, Clarke S: Patterns of calcium-binding proteins support parallel and hierarchical organization of human auditory areas. *Eur J Neurosci* 2003;17:397–410.
- 39 Hackett TA, Preuss TM, Kaas JH: Architectonic identification of the core region in auditory cortex of macaques, chimpanzees, and humans. *J Comp Neurol* 2001;441:197–222.
- 40 Morosan P, Schleicher A, Amunts K, Zilles K: Multimodal architectonic mapping of human superior temporal gyrus. *Anat Embryol (Berl)* 2005;210:401–406.
- 41 Brodal A: Neurological Anatomy in Relation to Clinical Medicine. Oxford, Oxford University Press, 1981.
- 42 Elliot Smith G: A new topographical survey of the human cerebral cortex, being an account of the distribution of the anatomically distinct cortical areas and their relationship to the cerebral sulci. *J Anat Physiol (Lond)* 1907;41:237–254.