

1 **A WHOLE-BRAIN 3D MYELOARCHITECTONIC ATLAS: MAPPING THE**
2 **VOGT-VOGT LEGACY TO THE CORTICAL SURFACE**

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59 The authors declare that there is no conflict of interest related to this manuscript.

60

61 **Abstract**

62 Building precise and detailed parcellations of anatomically and functionally distinct
63 brain areas has been a major focus in Neuroscience. Pioneer anatomists parcellated
64 the cortical manifold based on extensive histological studies of post-mortem brain,
65 harnessing local variations in cortical cyto- and myeloarchitecture to define areal
66 boundaries. Compared to the cytoarchitectonic field, where multiple neuroimaging
67 studies have recently translated this old legacy data into useful analytical resources,
68 myeloarchitectonics, which parcellate the cortex based on the organization of
69 myelinated fibers, has received less attention. Here, we present the neocortical
70 surface-based myeloarchitectonic atlas based on the histology-derived maps of the
71 Vogt-Vogt school and its 2D translation by Nieuwenhuys. In addition to a
72 myeloarchitectonic parcellation, our package includes intracortical laminar profiles of
73 myelin content based on Vogt-Vogt-Hopf original publications. Histology-derived
74 myelin density mapped on our atlas demonstrate close overlap with *in vivo*
75 quantitative MRI markers for myelin and relates to cytoarchitectural features.
76 Complementing the existing battery of approaches for digital cartography, the whole-
77 brain myeloarchitectonic atlas offers an opportunity to validate imaging surrogate
78 markers of myelin in both health and disease.

79 **Highlights (will go as a separate file)**

- 80 • Our myeloarchitectonic atlas builds on extensive meta-analyses-derived and
81 ground-truth histological data.
- 82
- 83 • Our atlas provides qualitative and quantitative 3D information on cortical
84 myelin architecture.
- 85
- 86 • MRI surrogate markers of myelin demonstrate close overlap with histological
87 cortical parcellations, supporting biological validity of non-invasive metrics.
- 88
- 89 • This atlas can be seamlessly integrated into widely used neuroimaging
90 analysis software to inform studies in health and disease.

91 **Introduction**

92 Obtaining precise and detailed parcellations of anatomically and functionally distinct
93 brain areas has been the focus of Neuroscience research for over a century (Zilles et
94 al., 2015; Zilles and Amunts, 2010). Among neuroanatomists of the early 20th century,
95 Brodmann, Vogt and Vogt, and von Economo and Koskinas ardently worked towards
96 generating highly detailed histological maps of the human cortex based on post-
97 mortem data (Triarhou, 2007; Zilles and Amunts, 2010). To parcellate the neocortex,
98 they relied on cytoarchitectonics, characterizing size, shape and distribution of cell
99 bodies across cortical layers (Amunts et al., 2005; Smith, 1927; Triarhou, 2007), and
100 myeloarchitectonics, which studies layering, arrangement, packing and density of
101 myelinated fibers and bundles (Batsch, 1955; Hopf, 1968; Nieuwenhuys, 2013;
102 Strasburger, 1937; Vogt and Vogt, 1919). These histology-derived maps have set the
103 basis for MRI-derived *in vivo* parcellations of cortical boundaries (Huntenburg et al.,
104 2017; Mendes et al., 2019; Nieuwenhuys and Broere, 2020). Nevertheless, knowledge
105 on cytoarchitectonics today remains heavily influenced by the classic work of
106 Brodmann (Brodmann, 1907; Zilles and Amunts, 2010) and many contemporary
107 neuroimaging toolkits contain modified versions of Brodmann's seminal map
108 (Eickhoff et al., 2005; Talairach et al., 1993).

109 Compared to the cytoarchitectonic field, myeloarchitectonics has received less
110 attention. This may be due to the paucity of histology-based myeloarchitectonic data
111 to establish the biological substrates of several MRI markers for myelin
112 characteristics (Lazari and Lipp, 2021; van der Weijden et al., 2020), such as
113 quantitative T1 mapping (Lutti et al., 2014; Marques et al., 2017) and neurite
114 orientation and dispersion density imaging (Zhang et al., 2012). Recently,
115 Nieuwenhuys and co-workers (Nieuwenhuys and Broere, 2017) mapped Vogts

116 myeloarchitectonic atlases to a non-digital, 2D representation of the Montreal
117 Neurological Institute (MNI) Colin27 brain template, by means of manual translations
118 from paper-embedded figures. Harnessing the data generated by Hopf, they further
119 integrated area-specific myelin fiber density estimates into their myeloarchitectonic
120 map (Hopf, 1968, 1957, 1956, 1955; Nieuwenhuys and Broere, 2017).

121 While 2D maps render the knowledge from historical postmortem data more
122 accessible, they cannot be used in quantitative neuroimaging analyses, which usually
123 require 3D stereotaxic volumetric data representation or cortical surface formats. In an
124 effort to address this gap, we built a 3D myeloarchitectonic atlas (MYATLAS) in
125 common space, translating the Nieuwenhuys' boundaries of the Vogt-Vogt atlas to the
126 Colin27 brain template and standard cortical surfaces. Besides providing a *ready-to-*
127 *use* myeloarchitectonic parcellation, we generated intracortical laminar profiles of
128 myelin content from the photometric data gathered from Vogt-Hopf publications. To
129 validate our atlas, we quantified the similarity between the histology-based myelin
130 density and profiles from *in vivo* MRI markers obtained from MP2RAGE-derived
131 qT1 mapping (21, 34, 35). Moreover, we integrated cytoarchitectonic features
132 (Scholtens et al., 2018). Finally, to facilitate integration into existing image
133 processing pipelines, the proposed myeloarchitectonic atlas together with source
134 codes are made publicly available.

135

136 **Materials and Methods**

137 After a short review of prior work, sections below detail the methodology used for the
138 creation of our 3D myeloarchitectonic atlas (MYATLAS) and necessary processing
139 steps to obtain cortical depth profiles from Vogt-Vogt myeloarchitectonic
140 parcellations, as well as cross-modal correlations between myelo- and

141 cytoarchitectural features and *in vivo* qT1 mapping. We further provide instructions
142 for registering the MYATLAS to individual MRI data.

143 Summary of prior work

144 Nieuwenhuys and co-workers recently performed a meta-analysis on potential
145 usability of the historical myeloarchitectural data aggregated from Vogts' papers (see
146 Nieuwenhuys and Broere, 2017 for details). The original cortical division by the
147 Vogts school consisted of a total of 180 myeloarchitectonic cortical fields (64 frontal,
148 30 parietal, 63 temporal, 17 occipital, and 6 insular areas). Their associates Hopf and
149 Vitzthum further refined this work by subdividing the parietal and occipital lobes into
150 multiple sub-areas (Hopf, 1957, 1956, 1955), resulting in 214 regions (64 frontal, 60
151 parietal, 63 temporal, 21 occipital, and 6 insular). Nieuwenhuys et al. applied semi-
152 automatic topological translations and boundary averaging across 17 different views
153 of this analog dataset to project myeloarchitectonic parcellations onto the MNI-
154 Colin27 single subject brain in a non-digital figure format (**Figure 1**).

155 In addition to boundaries, the Vogts investigated intracortical penetration patterns of
156 tangential and radial fiber bundles across cortical laminae (Vogt and Vogt, 1919).
157 They defined major categories of myeloarchitectonic profiles based on two criteria
158 (**Figure 2A**). The first criterion related to the presence of transverse, densely
159 myelinated cortical layers (the bands of Baillarger). Accordingly, cortical specimens
160 can be classified into 4 categories: *bistriate* (two horizontal myelin-rich bands),
161 *unistriate* and *unitostriate* (both indicating only one visible band; for the former, a
162 single cortical layer is covered, whereas for the latter multiple layers are covered by
163 the band), and *astriate* (no striation). Notably, each category has a subtype, depending
164 on the demarcation of a band boundary (*propebistriate*: barely recognizable bands of
165 Baillarger; *propeunistriate*: ill-defined border of inner stripe; *propeastriate*: slight

166 decrease of density in 5a/6a). The second criterion relates to the intrusion depth of the
167 radiate bundles across cortical laminae, further classifying the cortex into *euradiate*
168 (bundles reaching upper border of layer 3b), *infraradiate* (reaching upper border of
169 layer 5b), and *supraradiate* (extending into layers 1-2).

170 Following this work, Hopf (Hopf, 1968, 1957, 1956, 1955) further advanced these
171 myeloarchitectonic parcellation by systematically recording frontal, parietal and
172 temporal lobe myelin contents using analog photodensitometry. Notably, each region
173 has distinct light absorption curves, or cortical depth profiles. This data was recently
174 digitized by Nieuwenhuys (Nieuwenhuys and Broere, 2017), who introduced *mean*
175 *grey levels* (MGL), *i.e.*, digital quantifications of myelin fiber density per cortical
176 area. Ranging from 0 to 255, lower values indicate densely myelinated areas, while
177 high MGL are found in lightly myelinated areas (Edwards et al., 2018; Nieuwenhuys
178 and Broere, 2017). Since MGL are only available for the frontal, parietal and temporal
179 lobes, remaining areas were assigned 255 as a default value. Since Hopf based his
180 work exclusively on the right hemisphere, MGL were available only for the right
181 hemisphere in Nieuwenhuys' work (Nieuwenhuys and Broere, 2017).

182

183 *MRI processing*

184 We created a stereotaxic average of the individual Colin27 brain MRIs, comprising 27
185 T1 weighted scans with 1mm isotropic voxel resolution (Holmes et al., 1998). We
186 then extracted 3D cortical surface models from this template using FreeSurfer (Fischl,
187 2012). Briefly, processing steps included gradient non-uniformity correction (Jovicich
188 et al., 2006), registration to MNI stereotaxic space, intensity normalization, skull
189 stripping, and segmentation into tissue classes (Fischl et al., 2004). Gray-white and
190 gray-CSF interface models were generated through triangular surface tessellation

191 yielding 163,842 vertices (Dale et al., 1999), followed by topology correction,
192 inflation, and spherical registration to fsaverage (Fischl et al., 2001).

193 *2D-to-3D translation of myeloarchitectural parcellations.*

194 As per previous procedures (Pijnenburg et al., 2021; Scholtens et al., 2015), the
195 original Nieuwenhuys' illustration (Nieuwenhuys et al., 2015) was split into eight
196 view planes (lateral, medial, superior, inferior, orbitofrontal, supratemporal, parietal
197 opercular, insular). Carefully cross-referencing different views, a single rater (SY)
198 labeled each parcellation by comparing geometric landmarks between Nieuwenhuys'
199 illustrations and the convexity of the 3D Colin27 brain surface. Labelling was
200 performed with “*tksurfer*” (surfer.nmr.mgh.harvard.edu/fswiki/TkSurfer). Notably,
201 identifiable sulci on the original 2D Colin27 map such as the central and superior
202 temporal sulcus served as systematic landmarks. To optimize anatomical matching of
203 area boundaries, we further relied on the main sulcal patterns surrounding each region
204 to be labeled. A second rater (SJH) evaluated accuracy of each label. For ambiguous
205 areas, *i.e.*, either a mismatch across view planes, or between 2D illustrations and 3D
206 cortical surface, an inter-rater consensus on boundaries was reached to minimize
207 discrepancies by carefully reviewing the original publications and applying manual
208 corrections, if necessary (**Supplementary Table 1**).

209 An inherent limitation of Vogt-Vogt histological data is that all results were reported
210 on the convex pial surface, which does not reveal buried sulci. We thus labelled areas
211 located within these sulci on the white matter surface view on which they are clearly
212 visible and intra-sulcal boundaries can be easily delineated at their bottom. To
213 visualize areas hidden in the depths of the Sylvian fissure (*i.e.*, insula, supratemporal
214 lobe, parietal operculum), invisible even on the white matter surface, we extracted
215 patches of their surfaces, delineated label boundaries and merged them back to the

216 whole-brain data. Notably, some areas appeared multiple times across view planes,
217 preventing their segmentation into a single coherent label. This was addressed by
218 dividing areas into sub-regions; for example, for area 111 appearing differently in the
219 lateral and medial views, we divided it into 111-l, 111-m, ‘l’ and ‘m’ refer to medial
220 and lateral, respectively (see **Supplementary Table 1**). Finally, resulting labels were
221 numbered in accordance to Vogt’s numeric convention and merged with color tables
222 to create a single Freesurfer annotation file (.annot), which contains a total of 214
223 parcellations (**Figure 1C**).

224

225 Quantitative cortical myelin content and intracortical depth profiling

226 MRI allows for *in vivo* quantification of myelin content of the cortical manifold
227 (Stüber et al., 2014; Waehnert et al., 2014). However, validation requires access to
228 histology, which has not been available in a digital format. We thus generated
229 histology-derived quantitative myelin data by recording the MGL index (the averaged
230 myelin fiber density) for each cortical field (Nieuwenhuys and Broere, 2017) and
231 created a *ready-to-analyze* look-up table in excel format for the use with the
232 MYATLAS (**Supplementary Material 1**, “Myeloarchitectural_table.xlsx”). As the
233 MGL for the insula and occipital lobes (34 parcels) were unavailable, they were
234 omitted, totaling 187 values (64 frontal, 60 parietal and 63 temporal areas;
235 **Supplementary Material 1**). We then mapped the myelination density (MGL values)
236 onto the MYATLAS (**Figure 1**).

237 To extract myelin laminar depth profiles from histologically-stained
238 microphotographs (Batsch, 1955; Brockhaus, 1940; Hopf, 1957, 1956, 1955;
239 Strasburger, 1937; Vogt and Vogt, 1919), we screen-captured the histology photos
240 with a fixed format and size, and estimated the gray level intensity across cortical

241 laminae as a surrogate of myelin density. The digitized histological figures were
242 normalized to make intensity values across photos comparable. Absolute gray values
243 were then extracted and plotted as a normalized depth profile across all cortical layers
244 (**Figure 2B**). Information on myeloarchitectonic features, such as fiber bundle types
245 and layer-specific density of each cortical stain, were also recorded (**Supplementary**
246 **Material 1, Figure 2C**).

247

248 *Correlation between myeloarchitectonic features and in-vivo myelin proxy data*

249 We cross-validated myeloarchitectonic features through associations with qT1
250 mapping (Edwards et al., 2018; Mancini et al., 2020; Weiskopf et al., 2015).
251 Compared to conventional weighted sequences, MP2RAGE-derived qT1 images are
252 inherently uniform, theoretically free of other imaging properties like proton density
253 or T2*, and are acknowledged as directly relating to cortical myelin content (Marques
254 et al., 2017; Marques and Gruetter, 2013; van der Weijden et al., 2020). For qT1
255 sampling, we selected the 202 individuals from the Leipzig Study for Mind-Body-
256 Emotion Interactions (LEMON) dataset (Babayan et al., 2019). Details of LEMON
257 acquisition protocols and preprocessing steps have been described in detail (Mendes
258 et al., 2019).

259 To correlate the depth of profiles acquired from digitized histological data
260 microphotographs with *in vivo* intracortical qT1, we positioned 10 equivolume
261 surfaces between the inner and outer cortical interface using
262 *equivolumetric_surfaces.py* (https://github.com/kwagstyl/surface_tools.git). These
263 surfaces systematically sampled the axis perpendicular to the cortical ribbon, with
264 interpolation at each vertex (Hong et al., 2017, 2016).

265 *Correlation of myelin content with von Economo-Koskinas cytoarchitectonic data*

266 To verify the neurobiological significance of MYATLAS, we correlated the MGL
267 with von Economo-Koskinas' cytoarchitectonic features of *gyral dome thickness*,
268 *cellular density* and *cell size* (Scholtens et al., 2018, 2015). Since *gyral dome*
269 *thickness* is reported as a range, region-specific averages were calculated. *Cellular*
270 *densities* were averaged across all cortical layers, whereas *cell size* was calculated
271 according to $[H_{\text{mean}} \times W_{\text{mean}}]$; with H_{mean} (Height) = $[H_{(\text{min-max})}/2]$ and W_{mean} (Width) =
272 $[W_{(\text{min-max})}/2]$ per individual cortical layer and then averaged across all layers. To
273 allow for between-atlas correlation, we matched the boundary of parcels using a
274 winner-takes-all approach to assign each parcel of the von Economo-Koskinas' atlas
275 to our parcellation.

276

277 *Use of the MYATLAS and associated features*

278 All parcellations and MGL maps are available in two widely used formats (gifti and
279 nifti [*'dlabel'* for MGL and *'dscalar'* for parcellation]) and two brain spaces (Colin27
280 and Conte69, both with 32k vertices). We further provide the original, manual parcel
281 translation file (*'rh.vogt_vogt.annot'*) for use with FreeSurfer. Finally, to facilitate
282 implementation, we also provide Bash scripts which convert the original labels from
283 the MNI-Colin27 brain to single-subject space using FreeSurfer *'mri_label2label'*
284 (*mapping_colin27_labels_onto_individuals[_batch].sh*). Finally, we generated a
285 flipped version of the left hemisphere atlas based on symmetric hemispheric
286 registration (*'xhemi'* command in FreeSurfer).

287

288 **Results**

289 3D myeloarchitectonic atlas

290 The MGL patterns were similar between the MYATLAS and the Nieuwenhuys map
291 (**Figure 1**). Indeed, the lowest MGL values were found in highly myelinated primary
292 sensory areas (somatosensory areas 67, 69–71II of the postcentral gyrus; auditory
293 cortex, areas 145–157) and primary motor cortices (areas 39, 42, 43). Notably, similar
294 to Vogt’s observation of continuous changes of architectural features, our 3D map
295 displayed gradually decreasing myelin content in areas distant from primary cortices.
296 Reflecting this pattern, higher-order areas (including areas 49-51 of the frontal pole)
297 and precuneus (areas 81-85) revealed higher MGL (*i.e.*, less myelination), compared
298 to the rest of the brain. There were some noteworthy exceptions to this pattern of
299 hierarchy-dependent myelin profiles, previously recognized by Vogt, with densely
300 myelinated clusters, comprising the orbitofrontal (60 and 61), intraparietal (86, 87),
301 and posterolateral (169-172) and basal (173-177, 179-180) temporal areas. These
302 clusters have also been consistently identified both *ex vivo* and on structural MRI
303 (Glasser and Van Essen, 2011; Nieuwenhuys and Broere, 2017), all relating to visual
304 processing (Nieuwenhuys and Broere, 2017). Notably, areas 173,174 177,179-80
305 correspond to two newly discovered distinct cytoarchitectonic areas FG3 and FG4 of
306 the fusiform gyrus (Lorenz et al., 2017).

307

308 Intracortical depth profiling based on Vogt-Vogt classifications

309 **Figure 2A-B** illustrate 3D maps of fiber penetration patterns derived from Vogt-Hopf
310 studies stratified with respect to the presence of the bands of Baillarger and bundle
311 intrusion types (see **Method** ‘*prior work*’ for stratification details). Specifically,
312 within available areas, high-order cognitive regions showed either the *unistriate*

313 (temporal and frontal areas) or *bistriate* (parietal) subtype. In contrast, the bundle
314 intrusion types were relatively homogeneous, with majority of the areas containing
315 the *euradiate* subtype. **Figure 2C** shows patterns of myelination density across lobes.

316

317 Correlation between surface-mapped MGL and in vivo myelin metrics

318 We found a positive correlation between our histology-derived MGL and *in vivo* qT1
319 values ($p < 5 \times 10^{-7}$, $r = 0.39$), indicating close correspondence between these surrogate
320 metrics of myelin. **Figure 3A** illustrates the group-averaged qT1 map of 202 subjects
321 selected from the LEMON dataset (Babayán et al., 2019). The lowest qT1 values were
322 found in heavily myelinated primary cortices, with a decrease when moving towards
323 higher order areas. Notably, low qT1 values found in the posterolateral temporal lobe
324 likely indicate the dense myelination of the dark cluster described by Vogt
325 (Nieuwenhuys and Broere, 2017). **Figure 3B** illustrates the correspondence between
326 photodensitometric quantifications of cortical myelin content and *in vivo* qT1 depth
327 profiles.

328

329 Correlation between surface-mapped MGL and cytoarchitectonic features

330 Only cell size was found to correlate with myelin density as represented by MGL ($r =$
331 -0.27 , $p < 0.0001$; **Figure 3C**), where smaller cell sizes were associated with higher
332 myelin density. While *gyral dome thickness* trended towards a similar relationship (r
333 $= -0.12$, $p < 0.09$), *cell density* did not ($r = 0.03$, $p > 0.7$). These findings are in line
334 with previous studies showing that axons of smaller sensory neurons are often
335 unmyelinated (Lee et al., 1986, p. 198). Notably, pyramidal axons of the central motor
336 cortex exhibit complex myelination patterns (Micheva et al., 2016), which differ
337 between cortical layers (Tomassy et al., 2014). Thus, it is conceivable that these

338 complex interactions might not be captured by the limited resolution of a simplified
339 metric such as MGL.

340

341 Code and Data availability

342 The MYATLAS, lookup tables, source codes and the scripts for applying the atlas to
343 Colin27 and Conte69 brain templates as well as to individual brains
344 (“*mapping_colin27_labels_onto_individuals_batch.sh*”) are available from this link
345 (<https://bic.mni.mcgill.ca/~noel/noel-myelin>). A README file together with detailed
346 descriptions of the downloadable files are available from the same web repository. All
347 imaging-derived files are in FreeSurfer MGH and NIFTI formats and can be viewed
348 with standard software (*e.g.*, FreeView, FSLEyes or *wb_view*). The scripts used for
349 data processing are available from the authors upon request.

350

351 **Discussion**

352 Digital reconstructions of histological brain atlases constitute an important resource
353 for contemporary neuroimaging. Such reconstructions expand availability of
354 previously inaccessible, yet highly comprehensive, observations. Building upon the
355 Vogt legacy, we present the MYATLAS, a 3D myeloarchitectonic digital cartography
356 to assist neuroimaging mapping studies. To facilitate broad application, we provide
357 the atlas together with the codes and data files. Moreover, to mitigate inter-individual
358 variability, the parcellations and MGL maps are available both on a single- and a
359 multi-subject group templates in stereotaxic space. Integration of detailed,
360 quantitative data on cortical myelination will allow future neuroimaging research to

361 assess their findings based on both myelin density and microstructure, enhancing
362 biological validity.

363 Variations in myelination relate to various aspects of neocortical structure and
364 function, including connectivity and hierarchical processing (Boshkovski et al., 2021;
365 Huntenburg et al., 2017; Royer et al., 2020). Moreover, disrupted myeloarchitectural
366 properties may reflect the pathological underpinning of neurological disorders (Nord
367 et al., 2019). Thus, classification of cortical myeloarchitectonic areas and patterns
368 through parcellation and MGL mapping has significant translational potential in both
369 health and disease. Future neuroimaging studies may leverage this information to
370 elucidate pathological whole-brain myeloarchitectural patterns, for instance in
371 multiple sclerosis (Rahmanzadeh et al., 2021) and epilepsy (de Curtis et al., 2021;
372 Drenthen et al., 2019).

373 Our atlas aggregates histology-derived myeloarchitectural information, depth-
374 dependent photometric density, as well as corresponding *in vivo* qT1 profiles, together
375 with myeloarchitectural subtypes categorized into laminar and depth intrusion
376 patterns of fiber bundles. Notably, the high congruence between histology-derived
377 quantifications of myelin density through MGL and qT1 lends further biological
378 validity to this *in vivo* microarchitectural surrogate metric easily implementable in
379 clinical settings (Hogan, 2017; Waehnert et al., 2016). Notably, recent developments
380 in advanced imaging sequences, such as myelin water imaging (van der Weijden et
381 al., 2020) or high-field laminar fMRI (Trampel et al., 2019), allow for an increasingly
382 detailed study of cortical myelin contents. In this regard, our histology-validated
383 depth profiles can be harnessed as ground-truth data to validate future *in vivo* imaging
384 studies investigating myeloarchitecture (O’Muircheartaigh et al., 2019; Yuan et al.,
385 2021).

386 A few noteworthy points should be considered when applying MYATLAS to new
387 data. First, as this atlas is based on consensus evidence (*i.e.*, cortical boundaries) from
388 several studies and does not incorporate information on inter-individual variability of
389 myeloarchitectural characteristics. This limitation may however be mitigated by
390 employing our atlas in conjunction with probabilistic cortical mapping approaches,
391 such as *Julich Brain* (Amunts et al., 2020). Additionally, our digital atlas does not
392 contain information on potential left-right asymmetries, since the original sources also
393 do not contain any lateralization information. Nevertheless, a recent quantitative MRI
394 study investigating myeloarchitectural metrics of the language system revealed
395 heterogenous lateralization patterns (Yuan et al., 2021): While inferior frontal areas
396 were left lateralized, the middle and superior temporal gyrus (Heschl's gyrus and
397 planum temporale) was found to be right lateralized. As such, future research should
398 therefore be directed at potential functional implications of myeloarchitectural
399 lateralization patterns in larger cohorts. Additionally, since measures of myelination
400 density (namely MGL and cortical depth profiles) are unavailable for the occipital
401 lobe and the insula, a whole-brain neuroimaging correlation remains somewhat
402 partial. However, due to their high congruence, this limitation could be resolved by
403 extrapolating MGL from qT1 *in vivo* data, preferably acquired at ultra-high magnetic
404 field strengths (Sengupta et al., 2018).

405 Future applications of our architectonic mapping framework may include correlations
406 between myeloarchitectonic density and myelin-related genes (Donkels et al., 2020;
407 Glasser et al., 2016). For instance, building on our procedures from MGL-qT1 cross-
408 correlation, it is now possible to relate myelin-related gene expression to
409 myeloarchitectonic features within individual cortical parcellations. Such efforts may

410 provide further insights on the role of specific genes in health and disease

411 (Rahmanzadeh et al., 2021; Sprooten et al., 2019).

412

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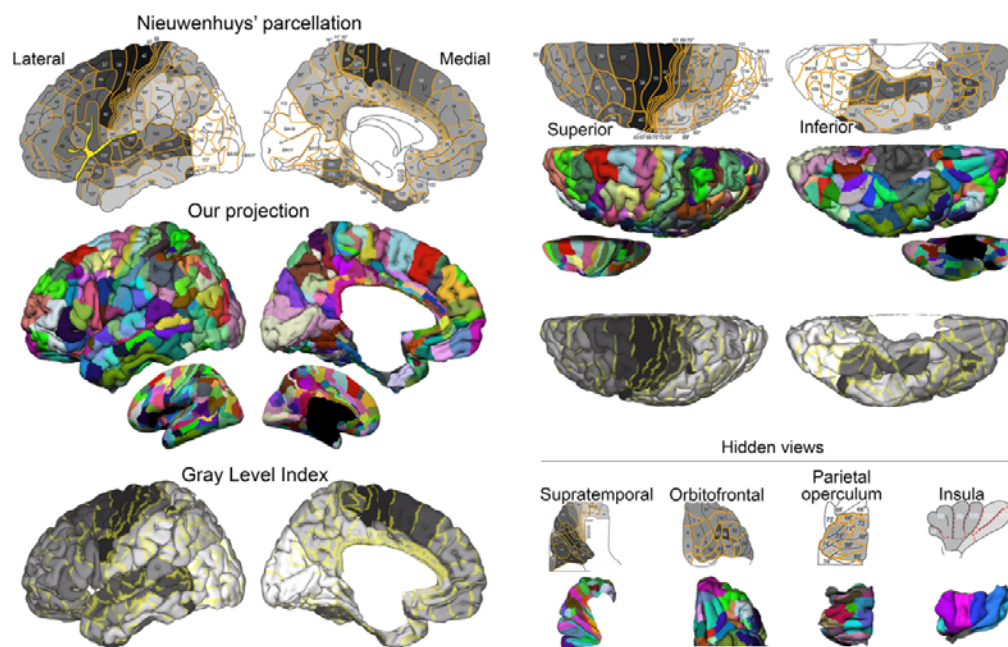
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- 656

657 **Figures**

658

659 Figures 1

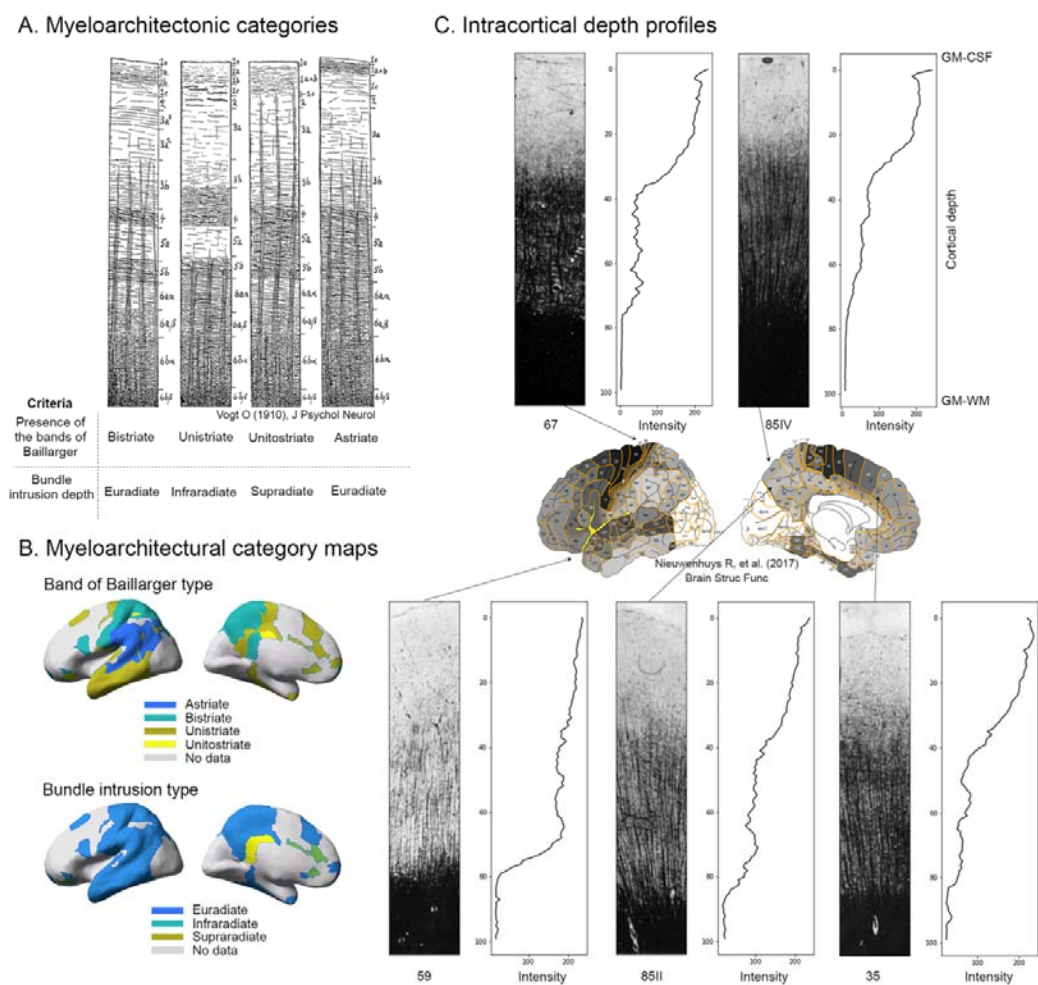


660

661 **FIGURE 1. Construction of the 3D myeloarchitectonic MNI atlas (MYATLAS).** Manual
662 cortical parcellations (based on the topological transformation of Vogt-Vogt parcellation) across
663 view planes (lateral, medial, superior, inferior; on pial and inflated surfaces), with the 3D
664 projection and mean gray level index measuring the degrees of myelination. Hidden areas within
665 the orbitofrontal region, the supratemporal lobe, and the parietal operculum were labeled by
666 extracting view planes similar to the original publication; they were then merged back with the
667 whole-brain surface once segmentations were finished (panel on the right bottom).

668

669 **Figure 2**



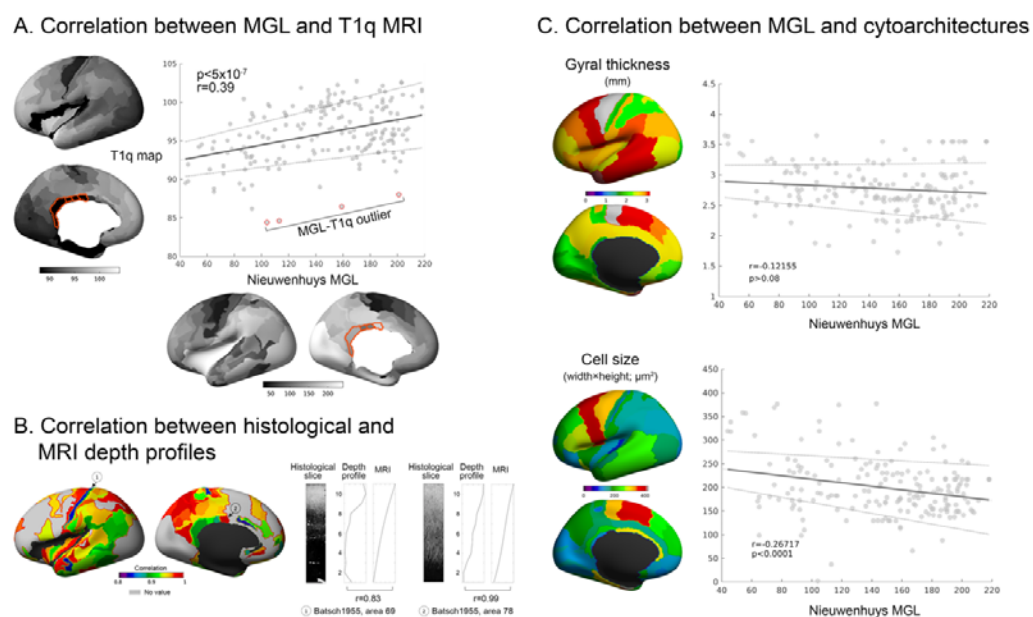
670

671 **Figure 2. Intracortical depth profiling based on Vogt-Hopf histological data.** A) Categories of
 672 myeloarchitectonic features based on laminar and bundle intrusion patterns; B) Mapping of feature
 673 information onto the cortical surface; *no data* indicate subtype information unavailable from the
 674 original literature. C) Examples of myelin-stained cortical areas across full cortical depth with their
 675 corresponding depth profiles (maps shown in **Supplementary Material 1**).

676

677

678 **Figure 3**



679

680 **Figure 3. Correlation of *in vivo* MRI markers and cytoarchitectural features.** **A)** Whole-brain
 681 spatial correlation between *in vivo* quantitative T1w MRI (T1q) and mean gray level (MGL) index.
 682 Outliers ($>\pm 2SD$ qT1) in the posterior cingulate are in red). **B)** Whole-brain depth profile correlation
 683 between qT1 and photodensitometry-derived cortical myelin content; only areas with available depth
 684 profiles are presented. Two areas with the highest and lowest correlation between histology and qT1
 685 MRI are given as examples. **C)** Whole-brain spatial correlation between MGL and cytoarchitectural
 686 features derived from von Economo-Koskinas literature (*i.e.*, gyral dome thickness and cell size).
 687

688

689 **Supplementary Table 1 – Label indices for discordant views across brain areas**

Area index	Discordant views (See Figure 1C)	View followed
109	Lateral, inferior	inferior
111	Lateral, medial	Split into two segments
112	Lateral, medial	Split into two segments
120	Lateral, medial	medial
127	Lateral, inferior	lateral
128	Lateral, inferior	Lateral
175	Medial, inferior	inferior
176	Medial, inferior	inferior
178	Medial, inferior	inferior

690

691 **Supplementary Table 2 –FreeSurfer command line code**

```
#!/bin/bash

CASE=${1}
SRCDIR=${2} # ex) /[downloaded file path]/COLIN27_FS/label/Vogt_Areas_final
TRGDIR=${3} # ex) [your directory for individual freesurfer processing]
FILEDIR=${4} # ex) [downloaded file path]
print=""

label_name=( 1 2 3 4 5 6 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 30
31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59
60 61 62 63 64 65 66 67 67.III 67.IV 68.I 68.II 68.III 69 70.m 70.I 70.II 71.m 71.I 71.II 72
73.I 73.II 73.III 74.I 74.II 75.m 75.s 75.i 76.s 76.I 77 78 79 80 81 82 83.I 83.II 83.III 83.IV
84 85.I 85.II 85.III 85.IV 86 87 88.a 88.p 89.a 89.m 89.p 89.ip 89.t 90.a 90.m 90.p 90.ip
90.t 90.o 91 92 93 94 95 96 97 98 99 100 101 102 103 104 105 106 107 108 109 110 111.I
111.m 112.I 112.m 113 114 115 116 117 118 119 BA18 BA17 120 121 122 123 124 125
126 127 128 129 130 131 132 133 134 135 136 137 138 139 140 141 142 143 144 145 146
147 148 149 150 151 152 153 154 155 156 157 158 159 160 161 162 163 164 165 166 167
168 169 170 171 172 173 174 175 176 177 178 179 180 181 182 )

if [ ! -e ${TRGDIR}/${CASE}/label/rh.vogt_vogt.annot ]; then

    ${print} mkdir ${TRGDIR}/${CASE}/label/Vogt_Areas_final
    for label in "${label_name[@]}"
    do

        ${print} mri_label2label --srclabel ${SRCDIR}/rh.${label}.label --
        srcsubject colin27 --trglabel
        ${TRGDIR}/${CASE}/label/Vogt_Areas_final/rh.${label}.label --
        trgsurface ${CASE} --regmethod surface --hemi rh

    done

    mris_label2annot --s ${CASE} --h rh --ctab ${FILEDIR}/vogt.ctab --a vogt_vogt
    --ldir ${TRGDIR}/${CASE}/label/Vogt_Areas_final/ --nhits
    overlapped_vertex.mgh --no-unknown

fi
```

692