

# 1 HIPPOMAPS: MULTISCALE CARTOGRAPHY OF HUMAN

## 2 HIPPOCAMPAL ORGANIZATION

3  
4 Jordan DeKraker<sup>1</sup>, Donna Gift Cabalo<sup>1</sup>, Jessica Royer<sup>1</sup>, Ali R. Khan<sup>2</sup>, Bradley Karat<sup>2</sup>, Oualid Benkarim<sup>1</sup>,  
5 Raul Rodriguez-Cruces<sup>1</sup>, Birgit Frauscher<sup>3</sup>, Raluca Pana<sup>1</sup>, Justine Y. Hansen<sup>1</sup>, Bratislav Mistic<sup>1</sup>, Sofie L.  
6 Valk<sup>4,5,6</sup>, Jonathan C. Lau<sup>2</sup>, Matthias Kirschner<sup>7</sup>, Andrea Bernasconi<sup>1</sup>, Neda Bernasconi<sup>1</sup>, Sascha  
7 Muenzing<sup>5</sup>, Markus Axer<sup>5</sup>, Katrin Amunts<sup>5,6</sup>, Alan C. Evans<sup>1\*</sup>, Boris C. Bernhardt<sup>1\*</sup>

8  
9 <sup>1</sup> McConnell Brain Imaging Centre, Montreal Neurological Institute and Hospital, McGill University, Canada

10 <sup>2</sup> Robarts Research Institute, University of Western Ontario, Canada

11 <sup>3</sup> Department of Neurology, Duke University Medical Center, Durham, NC, United States

12 <sup>4</sup> Otto Hahn Group Cognitive Neurogenetics, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

13 <sup>5</sup> Institute of Neuroscience and Medicine INM-1, Research Centre Jülich, Germany

14 <sup>6</sup> C. & O. Vogt Institute for Brain Research, University Hospital Düsseldorf, Heinrich-Heine-University, Germany

15 <sup>7</sup> Division of Adult Psychiatry, Department of Psychiatry, University Hospitals of Geneva, 2, Chemin du Petit-Bel-Air, CH-1226,  
16 Thonex, Switzerland

17 \*co-senior authors

## 18 ABSTRACT

19 The hippocampus has a unique microarchitecture, is situated at the nexus of multiple macroscale  
20 functional networks, contributes to numerous cognitive as well as affective processes, and is highly  
21 susceptible to brain pathology across common disorders. These features make the hippocampus a model  
22 to understand how brain structure covaries with function, in both health and disease. Here, we introduce  
23 HippoMaps, an open access toolbox and online data warehouse for the mapping and contextualization of  
24 hippocampal data in the human brain (<http://hippomaps.readthedocs.io>). HippoMaps capitalizes on a  
25 novel hippocampal unfolding approach as well as shape intrinsic registration capabilities to allow for  
26 cross-subject and cross-modal data aggregation. We initialize this repository with data spanning 3D *post-*  
27 *mortem* histology, *ex-vivo* 9.4 Tesla MRI, as well as *in-vivo* structural MRI and resting-state functional  
28 MRI (rsfMRI) obtained at 3 and 7 Tesla, together with intracranial encephalography (iEEG) recordings in  
29 epilepsy patients. HippoMaps also contains validated tools for spatial map association analysis in the  
30 hippocampus that correct for autocorrelation. All code and data are compliant with community standards,  
31 and comprehensive online tutorials facilitate broad adoption. Applications of this work span  
32 methodologies and modalities, spatial scales, as well as clinical and basic research contexts, and we  
33 encourage community feedback and contributions in the spirit of open and iterative scientific resource  
34 development.

## 35 INTRODUCTION

36 The hippocampus has long been regarded as a model to understand how brain structure spatially covaries  
37 with function (Bahr, 1995; Eichenbaum, 2000). On the one hand, hippocampal anatomy has been  
38 recognized to be organized in both anterior-posterior and proximal-distal dimensions (Duvernoy et al.,  
39 2013; Olsen et al., 2019). Anterior-posterior organization is emphasized in foundational descriptions of its

40 anatomical segments (*i.e.*, head, body, and tail) as well as functional gradients along the hippocampal  
41 long axis (Bouffard *et al.*, 2023; Poppenk *et al.*, 2013; Przeździk *et al.*, 2019; Strange *et al.*, 2014; Vogel  
42 *et al.*, 2020; Vos de Wael *et al.*, 2018). Perpendicular to this, there is a preserved arrangement of  
43 hippocampal subfields along the proximal-distal (also referred to as medio-lateral) axis (Genon *et al.*,  
44 2021; Insausti & Amaral, 2004; Olsen *et al.*, 2019; Paquola, Benkarim, *et al.*, 2020; Ramón y Cajal, 1904;  
45 Yushkevich *et al.*, 2015). These macroanatomical and microstructural features have been suggested to  
46 directly relate to hippocampal circuit organization and its embedding within macroscale functional  
47 networks (Knierim & Neunuebel, 2016; S. Leutgeb & Leutgeb, 2007; Rolls, 2016), contributing to  
48 specific hippocampal computations and its role as a nexus connecting paralimbic, sensory, and  
49 heteromodal association systems, notably the default mode network (Andrews-Hanna, Reidler, Sepulcre,  
50 *et al.*, 2010; Buckner *et al.*, 2008; Smallwood *et al.*, 2021; Vos de Wael *et al.*, 2018). Its broad involvement  
51 in multiple macroscale networks is clearly compatible with the key role the hippocampus plays in  
52 numerous cognitive and affective processes, including memory and language function, together with  
53 affective reactivity, stress as well as spatial navigation (Barnett *et al.*, 2024; O’Keefe & Nadel, 1978;  
54 Stachenfeld *et al.*, 2014, 2017; Whittington *et al.*, 2022). Notably, the hippocampus is also recognized as  
55 one of the proximate evolutionary origins of the neocortex (Puelles *et al.*, 2019; Sanides, 1969), making it  
56 a candidate structure to investigate principles of evolutionary conservation and innovation in the primate  
57 lineage (Eichert *et al.*, 2023). Collectively, these insights contribute to the notion that the hippocampus is  
58 a microcosm of the brain, and that an assessment of its sub-regional organization provides key insights  
59 into human neural architectures.

60  
61 The fine-grained subregional organization of the hippocampus contrasts the somewhat coarse assessment  
62 of this structure by most contemporary neuroimaging investigations, which often still treat this complex  
63 archicortical structure as a single entity (Jordan DeKraker *et al.*, 2021), or even erroneously label it as  
64 ‘subcortical’. This is, in part, due to technical limitations: since the hippocampus is thinner and more  
65 tightly convoluted than the neocortex, it is difficult to appreciate its cortical architecture in magnetic  
66 resonance imaging (MRI) or the extent of its 3D convolutions in sparse histology slices. More recently,  
67 relatively few studies have compared its microstructural to mesoscale structural and functional features  
68 directly, with most studies opting instead to apply subfield parcellation as a proxy (Caldairou *et al.*, 2016;  
69 Iglesias *et al.*, 2015; Kulaga-Yoskovitz *et al.*, 2015; Olsen *et al.*, 2019; Romero *et al.*, 2017; Yushkevich  
70 *et al.*, 2010). Here, we introduce HippoMaps, an open access toolbox and online data warehouse for (*i*)  
71 the surface based mapping and analytical unfolding of hippocampal subregional features, (*ii*) the  
72 contextualization of a given hippocampal map (derived from *e.g.*, a typical task-based functional MRI  
73 experiment or structural abnormality map in disease) with respect to normative hippocampal data  
74 obtained from histology and imaging, and for offering (*iii*) a non-parametric statistical framework to  
75 establish the correlation across standardized surface maps, while controlling for spatial autocorrelation.  
76 HippoMaps adopts best practices and methods developed throughout the neocortical mapping community  
77 (Alexander-Bloch *et al.*, 2018; Glasser *et al.*, 2013; Lepage *et al.*, 2017; Markello *et al.*, 2022), and we  
78 provide a set of tools, tutorials, and guidelines for broad adoption and continued development.

79  
80 HippoMaps benefits from multiple recent technical innovations in hippocampal image processing and  
81 analysis. First, it leverages a unified hippocampal segmentation and surface mapping approach using deep  
82 learning-based image processing (Jordan DeKraker *et al.*, 2022), imposing a known prior topology  
83 (Jordan DeKraker *et al.*, 2018) and shape-inherent inter-subject alignment (DeKraker *et al.*, 2023). Similar

84 to neocortical surface extraction and registration procedures (Boucher *et al.*, 2009; Dale *et al.*, 1999;  
85 Fischl, Sereno, & Dale, 1999; Fischl, Sereno, Tootell, *et al.*, 1999; Kim *et al.*, 2005; Lyttelton *et al.*, 2007;  
86 MacDonald *et al.*, 2000), this allows for topology-informed inter-subject registration to a standardized  
87 unfolded space (Jordan DeKraker *et al.*, 2023). This has begun a new wave of high-sensitivity  
88 hippocampally-focused studies in topics including the mapping of histology features (J. DeKraker *et al.*,  
89 2020; Paquola, Benkarim, *et al.*, 2020), blood perfusion (Haast *et al.*, 2023; Ngo *et al.*, 2023),  
90 biophysically-constrained diffusion (Karat *et al.*, 2023), hippocampal sclerosis (Ripart *et al.*, 2023),  
91 neurodevelopmental trajectories (Hanson *et al.*, 2023), functional connectivity (Cabalo *et al.*, 2023;  
92 Lariviere *et al.*, 2023; Xie *et al.*, 2023), visual receptive field mapping (Leferink *et al.*, 2023), and cross-  
93 species comparison (Eichert *et al.*, 2023). With the increasing aggregation of hippocampal features in a  
94 common reference space, it is now possible to devise repositories that allow for a broad contextualization  
95 of hippocampal findings. Such work may aid in the interpretation of findings from new studies and  
96 experiments, for example by allowing for the cross-referencing of these results against established  
97 features of hippocampal functional and structural organization.

98  
99 At the level of the neocortex, there has been an increasing repertoire of comprehensive open tools for  
100 contextualization of findings, including BALSAs (David C. Van Essen *et al.*, 2017), NeuroVault  
101 (Gorgolewski *et al.*, 2015), and NeuroMaps (Markello *et al.*, 2022), as well as other contextualization  
102 methods incorporated in statistical software such as BrainStat (Lariviere *et al.* 2022) and the ENIGMA  
103 toolbox (Lariviere *et al.* 2022). With HippoMaps, we expand anatomy-driven neuroinformatics to the  
104 hippocampus, and provide a high-quality and broad multimodal online repository of normative maps,  
105 using a common folded and unfolded surface representational space. We initialize the HippoMaps  
106 repository with a spectrum of data spanning 3D histology, structural MRI and resting-state functional  
107 MRI (rsfMRI) obtained at field strengths of 3 and 7 Tesla from healthy individuals, as well as intracranial  
108 encephalography (iEEG) collected from epilepsy patients. We provide tools for high-definition  
109 hippocampal visualization and contextualization. Moreover, we incorporate adapted methods to control  
110 for autocorrelation when assessing spatial maps to one another, a key for accurate enrichment analysis in  
111 the hippocampus (Alexander-Bloch *et al.*, 2018; Karat *et al.*, 2023; Vos de Wael *et al.*, 2020). Finally,  
112 provide an example of how future hippocampal mapping studies can use spatial correlation with  
113 HippoMaps to contextualize results, linking structure and function. This is supported by online tutorials to  
114 reproduce all results shown here (<https://github.com/HippAI/hippomaps> or [https://github.com/MICA-](https://github.com/MICA-MNI/hippomaps)  
115 [MNI/hippomaps](https://github.com/MICA-MNI/hippomaps)), with extensibility so future studies may contribute their methods and mapped data  
116 (<https://osf.io/92p34/>).

## 117 **METHODS**

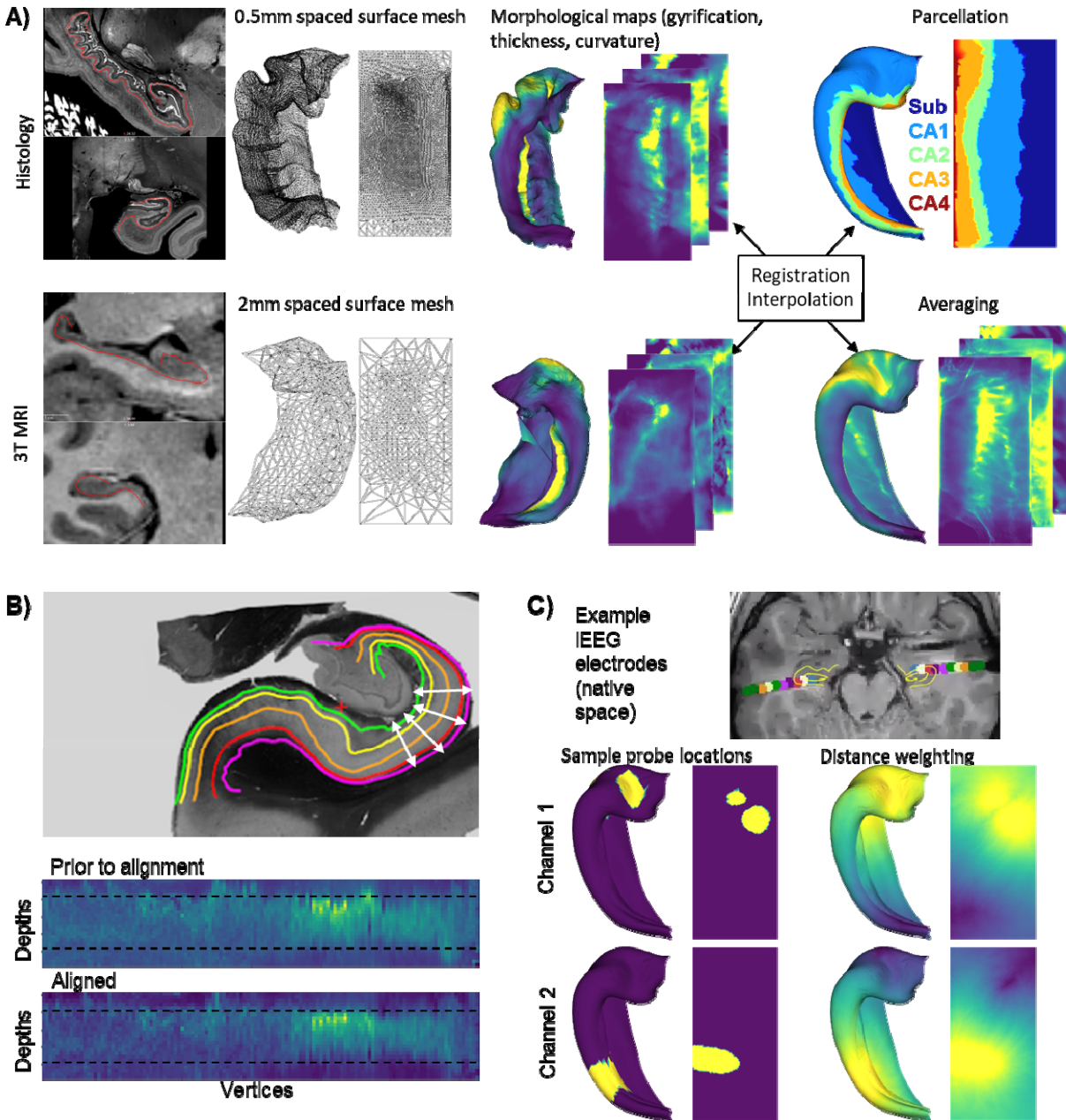
### 118 **Datasets**

119 To provide broad coverage of many areas of hippocampal research, we initialize HippoMaps with 30  
120 novel minimally processed but spatially aligned data spanning 3D *post-mortem* histology, high field *in-*  
121  *vivo* structural as well as resting-state functional MRI (rsfMRI), and intracranial electroencephalography  
122 (iEEG). These data originate from open source resources including BigBrain (Amunts *et al.*, 2013),  
123 AHEAD (Alkemade *et al.*, 2022), MICs (Royer *et al.*, 2022), the MNI open iEEG atlas (Frauscher *et al.*,  
124 2018), and are further supplemented with locally collected data including further healthy structural and

125 functional MRI obtained at 3 Tesla and 7 Tesla, as well as iEEG data obtained in epilepsy patients that  
126 also underwent pre-implantation multimodal MRI. See the **Supplementary Materials** for details of each  
127 dataset and preprocessing.

## 128 **Surface mapping**

129 Data processing details are available in the **Supplementary Methods**. Briefly, minimal preprocessing  
130 was applied to each dataset using *micapipe* v0.2.2 (<https://github.com/MICA-MNI/micapipe>) for  
131 structural and functional MRI (Cruces *et al.*, 2022) and custom code for other data. Though the  
132 processing of each data modality differs, they were each mapped to a standardized folded and unfolded  
133 surface space using *HippUnfold* v1.3.0 (Jordan DeKraker *et al.*, 2022). Briefly, this entails tissue type  
134 segmentation using a deep UNet neural network, fitting of inner, outer, and midthickness surfaces to  
135 hippocampal gray matter, mapping to a standardized unfolded rectangular space, and then registration in  
136 unfolded space to a standard, histology-derived generated atlas (Jordan DeKraker *et al.*, 2023). This  
137 standardized space is, thus, made equivalent across all subjects. Notably, despite surface meshes having  
138 differing tessellations (**Figure 1A**), they can be interpolated in unfolded space to match microscale  
139 features (*e.g.*, 3D reconstructed histological stains) to MRI or *vice versa*, spanning a scale of micrometers  
140 to millimeters.  
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**Figure 1.** Mapping multiscale data to standardized hippocampal surfaces. **A)** Surface folding and density are matched to the sample shape and resolution. Mapping to a standardized unfolded space enables registration and interpolation across scales, which can then be followed by parcellation, averaging, or comparison by spatial correlation. **B)** Depth-wise microstructural profiles are calculated by fitting surfaces at multiple depths (yellow-orange-red), including extrapolated surfaces over surrounding tissues (green and pink). Profiles at a given vertex are then translated vertically to maximize alignment to the average before being cut off at the gray matter boundary. **C)** Sparse data like depth electrodes or tissue punches are mapped to a hippocampal surface, and their data are extrapolated across the hippocampal surface proportionally to geodesic distance.

In addition to inner, midthickness, and outer surfaces, any number of intermediate surfaces can be generated at different depths or linearly extrapolated around the outer bounds of the hippocampus (**Figure 1B**) (Marcus *et al.*, 2011). This is especially useful for sub-millimetric data, where laminar or microstructural profile information can be extracted. In this case, we illustrate a function for refining



155 alignment of such profiles using vertical (that is, in the laminar direction) translations. This data-driven  
156 refinement leverages image intensity to mitigate slight differences in boundary criteria or segmentation  
157 errors between different parts of the hippocampus, without making strong assumptions about how  
158 different laminae are stained (provided they are consistent within the sample).

159  
160 Using a similar approach, even sparsely sampled data can be spatially mapped across the hippocampus  
161 (**Figure 1C**). In this case, we map the centroids of iEEG channels to their nearest corresponding  
162 hippocampal vertices. However, in principle, this could also apply to other sparse (or scattered) data such  
163 as tissue punches, other invasive recording devices, small resections, or other irregularly spaced sampling  
164 methods. We then map iEEG channel data to all vertices within <5mm of the channel centroid, and  
165 average data across all channels from all patients with a weighting proportional to geodesic distance from  
166 those vertices. This extrapolation method is more robust than a linear or nearest-neighbour extrapolation,  
167 which would be strongly driven by only one or a few nearby vertices with data mapped to them, while  
168 also still preserving some spatial preference for data from nearby channels.

## 169 **Significance testing**

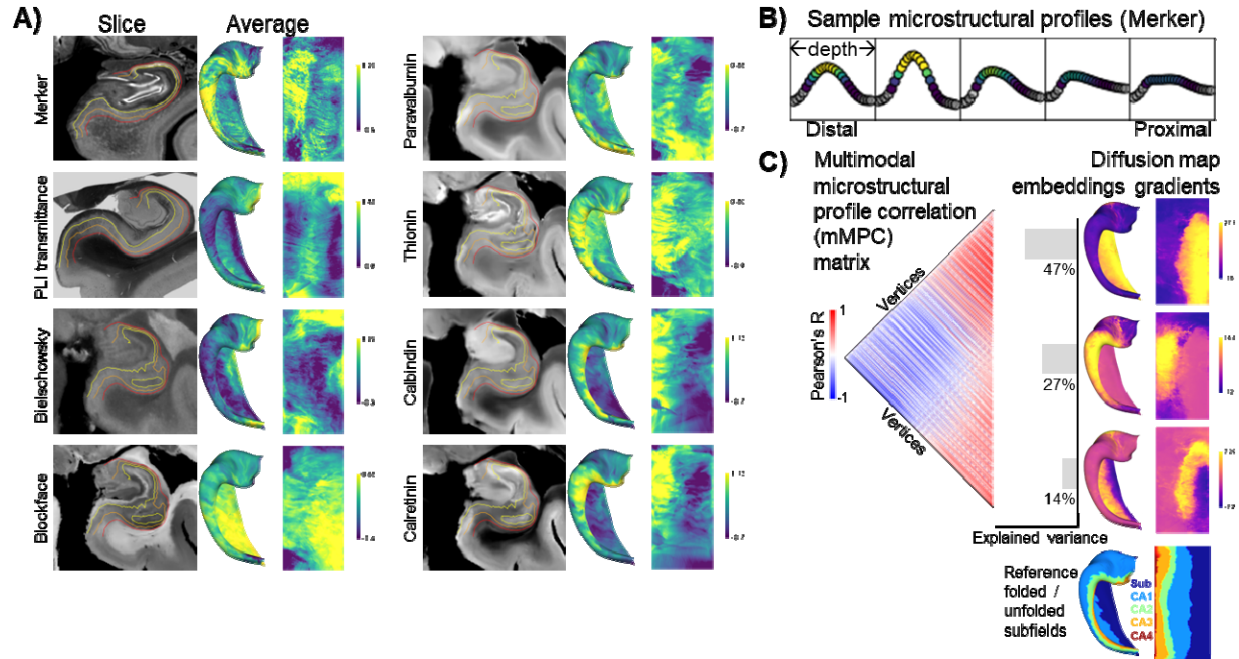
170 Spatial autocorrelation can compromise statistical significance testing when testing correlations between  
171 continuous maps (Alexander-Bloch *et al.*, 2018). HippoMaps provides two types of permutation test to  
172 ensure robustness against this issue: Moran spectral randomization (Wagner & Dray, 2015) and “spin”  
173 test randomization (Alexander-Bloch *et al.*, 2018; Karat *et al.*, 2023; Vos de Wael *et al.*, 2020). To make  
174 it suitable for the hippocampus, spin permutation tests include wrapping of the anterior-posterior and  
175 proximal-distal edges of the hippocampus, making the topology of a torus (see (Karat *et al.*, 2023) for  
176 details).

## 177 **RESULTS**

178 We present novel hippocampal maps in a standardized folded and unfolded space for each of the datasets  
179 outlined above. This includes 30 distinct group-averaged maps which have been attentively preprocessed  
180 and curated. Within each methodology, some interpretation and summarization via dimensionality  
181 reduction is offered, and finally we compare all maps across methodologies in the “Feature combinations”  
182 section.

## 183 **Histology**

184 Histology is considered a neuroanatomical gold standard, and is the basis for most parcellations and  
185 descriptions of brain regions (Amunts *et al.*, 2020; Brodmann, 1909; Eickhoff *et al.*, 2018; Paquola *et al.*,  
186 2019). Here we examined data collected from BigBrain Merker staining for cell bodies (Amunts *et al.*,  
187 2013), 3D polarized light imaging (PLI) of neural processes (M. Axer *et al.*, 2011), and the AHEAD  
188 dataset with different stains serving as markers of neurons, myelin, and subtypes of interneurons  
189 (Alkemade *et al.*, 2022) (**Figure 2A**). Most features showed banding in the proximal-distal direction, in  
190 alignment with the subfield atlas shown in **Figure 1**.



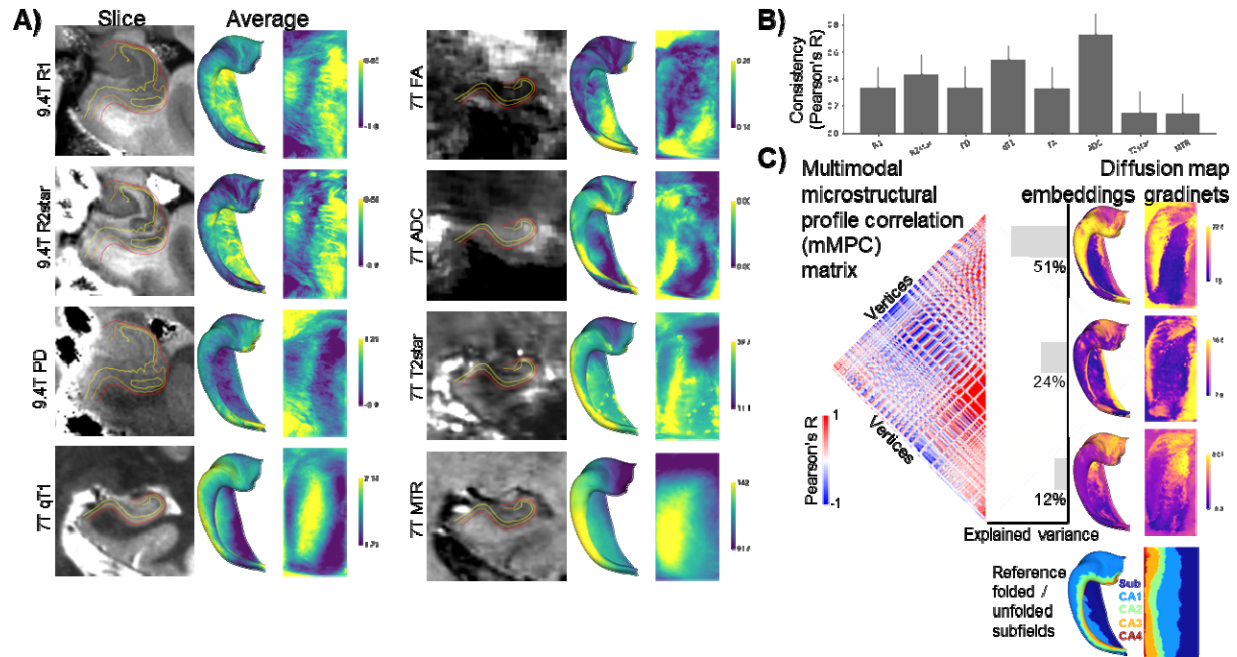
191  
 192 **Figure 2.** Histology mapping, depth-wise microstructural profiles, and dimensionality reduction. **A)** Sample slices and averaged  
 193 3D maps of histological features. Maps are averaged across depths and, where possible, samples. **B)** Example of microstructural  
 194 profile shapes from five evenly spaced bins across the proximal-distal axis of the Merker stain map. Grey indicates points outside  
 195 of the gray matter mask. **C)** Correlation between microstructural profiles, concatenated across modalities, at each vertex (left).  
 196 Dimensionality reduction into primary diffusion embedding gradients 1-3 (right).  
 197

198 Microstructural (or laminar) profiles are shown for five ROIs across the proximal-distal axis of the  
 199 BigBrain Merker stain (**Figure 2B**). They show a tight unimodal distribution in the distal CA fields, and a  
 200 more bimodal distribution in the subiculum as expected based on their known laminar architectures  
 201 (Duvernoy *et al.*, 2013). Profiles for all vertices were concatenated across all stains to make multimodal  
 202 profiles, a common method for characterizing laminar structure (Schleicher *et al.*, 1999). Next,  
 203 multimodal covariance matrices between vertices were calculated (mMPC matrix) (**Figure 2C**). Diffusion  
 204 map embedding, a non-linear dimensionality reduction technique (Coifman *et al.*, 2005; Margulies *et al.*,  
 205 2016; Vos de Wael *et al.*, 2020), decomposed the mMPC matrix into primary components, or gradients,  
 206 that highlighted the differences between vertices with respect to all modalities and depths. In the first  
 207 gradient, a sharp boundary was seen between the subicular complex and proximal CA1 and the rest of the  
 208 hippocampus. The second and third gradients in turn highlighted the CA2-3 regions and CA1 with parts  
 209 of the subiculum, respectively. This is data-driven evidence that subfields across the proximal-distal  
 210 extent of the hippocampus, rather than anterior-posterior or other patterns, account for structural variance  
 211 in the hippocampus with respect to these stains. These data-driven decompositions, thereby, echo classical  
 212 and recent neuroanatomy descriptions of hippocampal microstructure (Ding & Van Hoesen, 2015;  
 213 Duvernoy *et al.*, 2013; Olsen *et al.*, 2019).  
 214

## 215 Structural MRI

216 MRI is a key tool for studying human neuroanatomy and structure-function relations due to its non-  
 217 invasive nature and potential for biomarker discovery. 7 Tesla (7T) and *ex-vivo* 9.4T scanning are

218 especially powerful, achieving greater resolution and contrast than typical 3T or 1.5T clinical scans  
 219 (Duyn, 2012; Opheim *et al.*, 2021). Here, we provide healthy normative maps for such scans (**Figure 3A**)  
 220 including popular acquisitions: quantitative T1 relaxometry (qT1) and its non-quantitative *ex-vivo*  
 221 inverse: R1, T2\* and its inverse R2\*, proton density, diffusion weighted imaging (DWI) estimates of  
 222 fractional anisotropy (FA) and apparent diffusivity coefficient (ADC), and magnetic transfer ratio (MTR).



223 **Figure 3.** Structural MRI mapping, inter-sample consistency, and dimensionality reduction. **A)** Sample slices and averaged 3D  
 224 maps of histological features. Maps are averaged across depths and, where possible, samples. **B)** Consistency, as measured by the  
 225 correlation between all pairs of individual sample maps, **C)** Correlation between microstructural profiles, concatenated across  
 226 modalities, at each vertex (*left*). Dimensionality reduction into primary diffusion embedding gradients 1-3 (*right*).  
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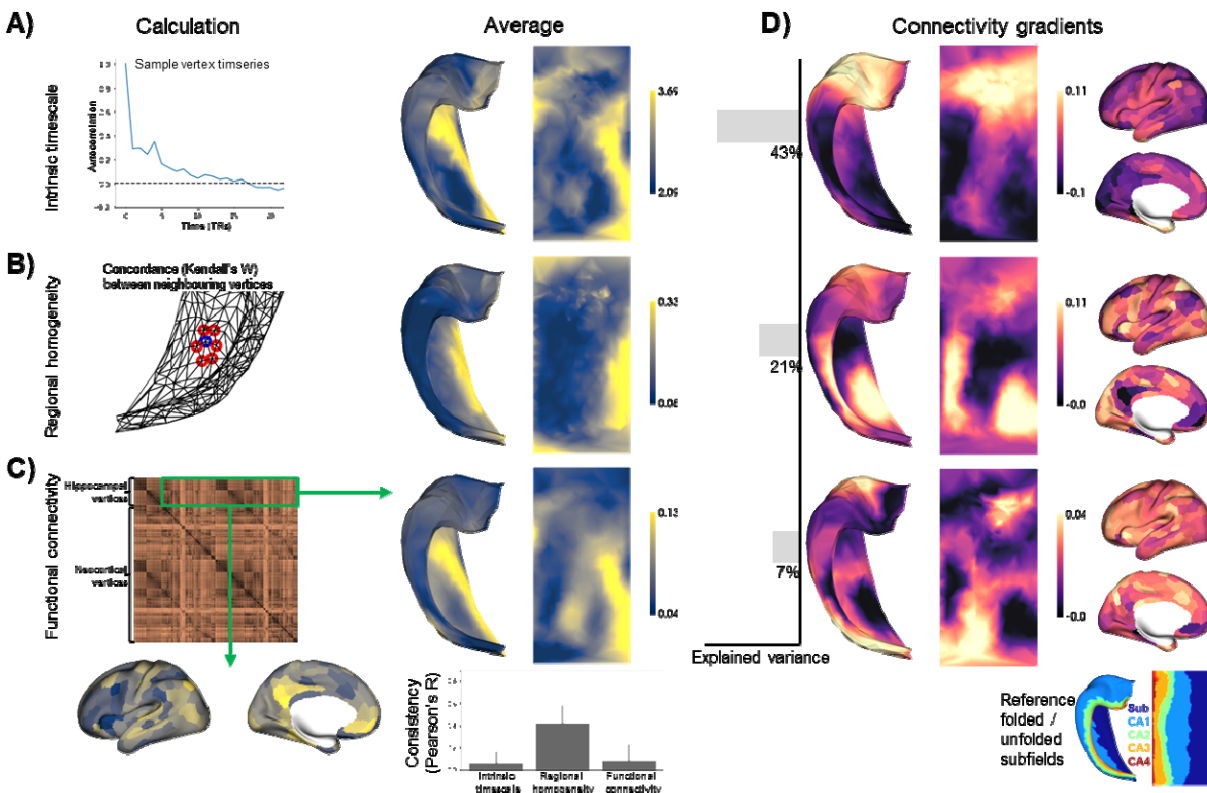
229 Multiple scans were available for averaging (n=4 left+right hippocampi at 9.4T and n=20 left+right  
 230 hippocampi at 7T), enabling a calculation of consistency across samples via Pearson's R (**Figure 3B**).  
 231 DWI and qT1 maps were also calculated in a second validation dataset, consisting of 82 locally scanned  
 232 healthy participants (including the subset from the MICA-MICs dataset) with a 3T scanner, which  
 233 showed similar patterns (**Figure S1**). mMPCs were generated as above and were reduced using diffusion  
 234 map embedding into primary gradients, which again highlighted differences across subfields. Only the  
 235 third gradient showed anterior-posterior differences, largely within the CA1 subfield.

## 236 Functional MRI

237 Functional MRI during the resting state (rsfMRI) allows interrogation of intrinsic brain function via the  
 238 analysis of spontaneous activity and its statistical dependencies, and has become a key technique in the  
 239 mapping of functional-anatomical systems (Biswal *et al.*, 1997; Buckner *et al.*, 2008; Smith *et al.*, 2009).  
 240 Here, we examined several features of rsfMRI in 88 healthy participants scanned at 3T. Intrinsic  
 241 timescale is a measure of the time it takes for the temporal autocorrelation to drop below a threshold  
 242 (Golesorkhi *et al.*, 2021; Wolff *et al.*, 2022) (**Figure 4A**). On a functional level, this is thought to be  
 243 driven in part by recurrent connections that maintain activity patterns on the order of seconds (Fallon *et*  
 244 *al.*, 2020). Regional homogeneity considers the similarity between adjacent vertices' time series, which is



245 thought to indicate the extent of horizontal (*i.e.*, between cortical columns) excitatory connectivity (Zang  
 246 *et al.*, 2004) (**Figure 4B**). Finally, macroscale functional connectivity is by far the most popular rsfMRI  
 247 feature, with many rich properties that have been explored with respect to white matter connections  
 248 (Damoiseaux & Greicius, 2009; Greicius *et al.*, 2009; Honey *et al.*, 2009), network properties  
 249 (Schmittmann *et al.*, 2015; van den Heuvel & Sporns, 2013), organizational gradients (Bernhardt *et al.*,  
 250 2022; Margulies *et al.*, 2016; Paquola *et al.*, 2019; Park *et al.*, 2021), and many other summary metrics.  
 251 For simplicity, we examined connectivity between all hippocampal vertices and neocortical parcels from  
 252 the Schaeffer400 parcellation (Schaefer *et al.*, 2018) (**Figure 4C**). The consistency of maps was examined  
 253 as above, and all measures were significantly greater than zero. Repetition of these analyses in a smaller  
 254 sample of 7T rsfMRI data showed consistent results (**Figure S2**).



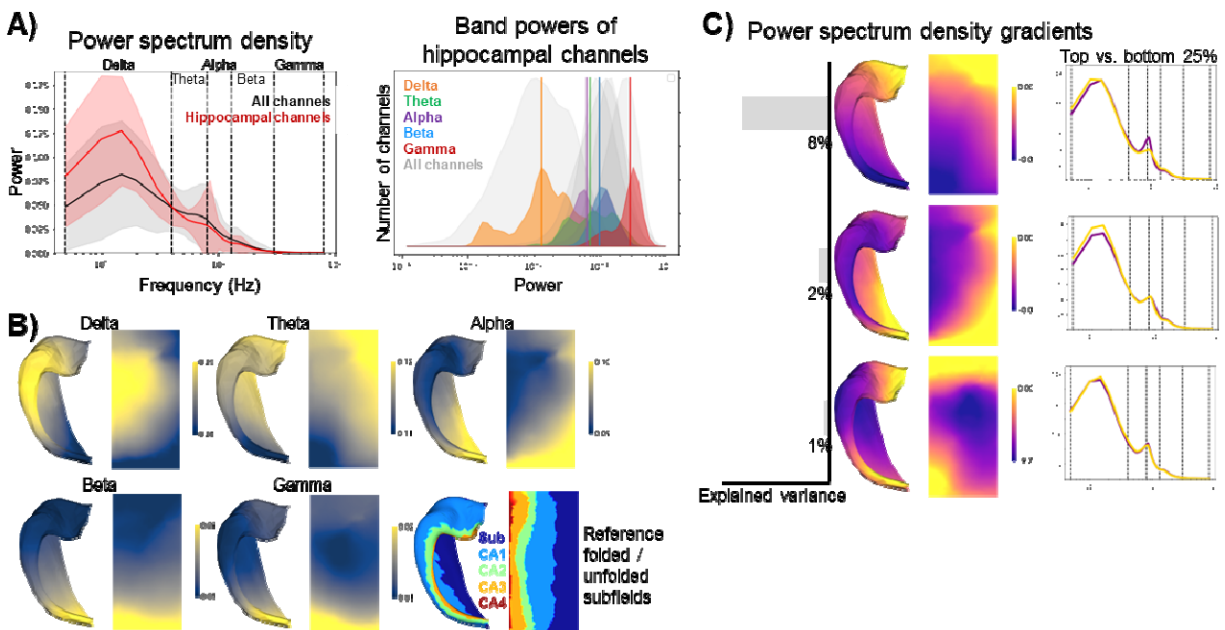
255 **Figure 4.** Functional MRI properties. Resting state (rsfMRI) data were used to calculate **A**) intrinsic timescale (recurrence), **B**)  
 256 regional homogeneity (short range connectivity), and **C**) functional connectivity (long range; to the neocortex). **D**)  
 257 Decomposition of functional connectivity patterns across hippocampal vertices into primary diffusion map embedding gradients.  
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 259

260 As mentioned above, functional connectivity is a rich measure that can be summarized in many ways.  
 261 Here, we identified gradients of intrinsic hippocampal connectivity variations (**Figure 4D**) using the  
 262 aforementioned non-linear decomposition techniques. Consistent with previous work (Genon *et al.*, 2021;  
 263 Poppenk *et al.*, 2013; Przeździk *et al.*, 2019; Strange *et al.*, 2014; Vogel *et al.*, 2020; Vos de Wael *et al.*,  
 264 2018), we found anterior-posterior differentiation in the first hippocampal gradient, together with  
 265 proximal-distal banding with CA1 in particular differing from the other subfields. Neocortical  
 266 counterparts of this gradient show that anterior and CA1 regions shared more connectivity with temporal  
 267 pole, insula, and frontal regions whereas more posterior and non-CA1 subfields shared connectivity with  
 268 more posterior parietal and visual areas, again consistent with previous findings (Vos de Wael *et al.*,  
 269 2018). The second gradient also showed differentiation of CA1 from subiculum and CA2-3 in the more

270 middle and posterior regions, with neocortical correspondences to medial prefrontal and posterior  
271 cingulate regions for CA1 and more visual areas for CA2-3 and posterior subiculum.

## 272 Intracranial EEG

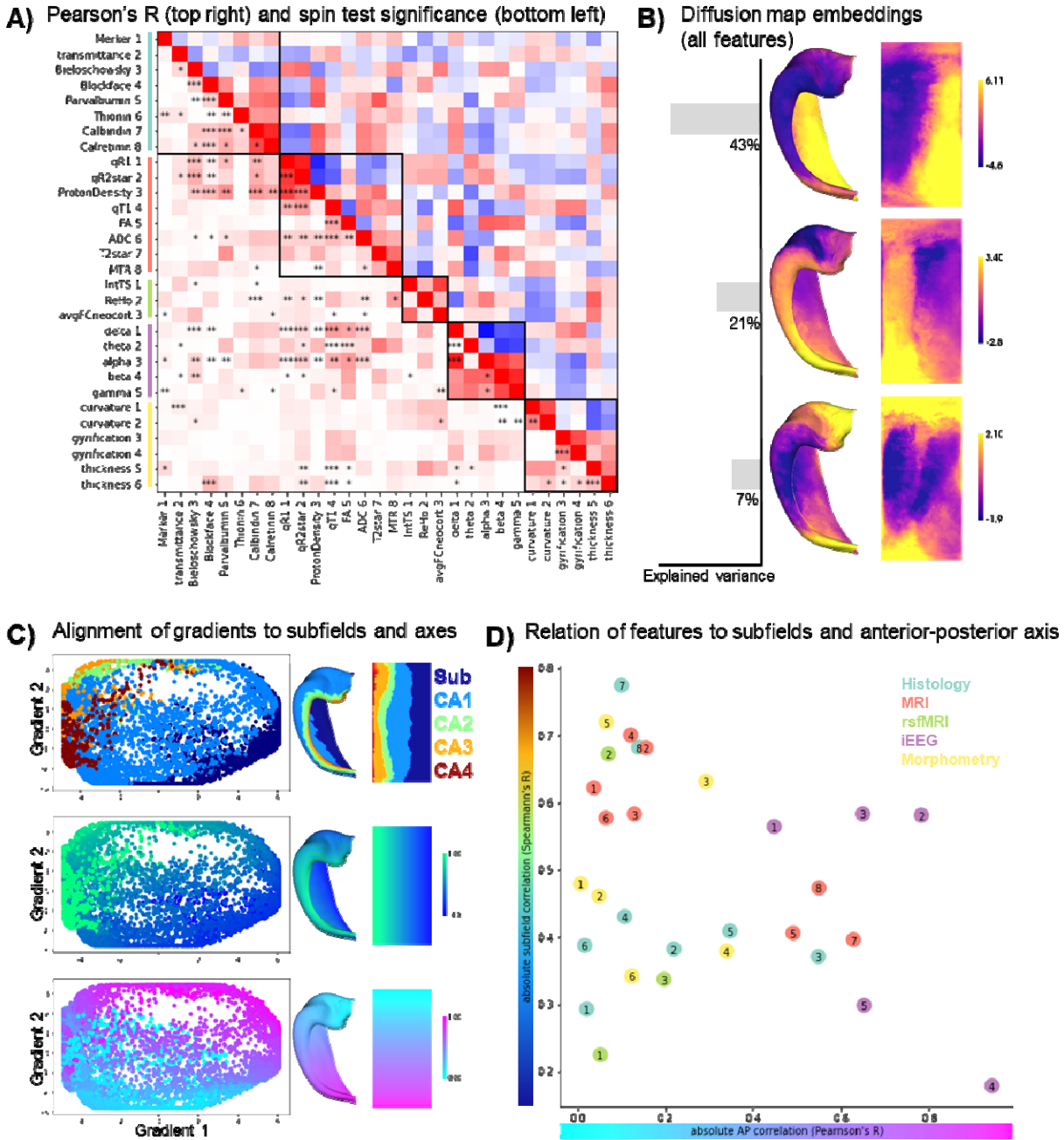
273 Invasive recording methods such as iEEG provide a direct measure of neural activity at high temporal  
274 resolution, but typically have lower spatial coverage and are limited to neurological patient populations.  
275 In that sense, they can be considered as scattered spatial data, which can be interpolated or extrapolated  
276 for hippocampal mapping as described in **Figure 1C**, or following previous approaches (Frauscher *et al.*,  
277 2018). We employ common measures of the periodic component of iEEG data, as shown by power  
278 spectrum density and additionally further simplified to Delta, Theta, Alpha, Beta, and Gamma band  
279 powers from low to high frequencies, respectively. Power spectrum densities and band powers derived  
280 from hippocampal channels resembled those derived from all channels (**Figure 5A**). Extrapolating  
281 channel information across neighbouring vertices from a given hippocampus, a spatial pattern emerged in  
282 which both proximal-distal and anterior-posterior differences were seen (**Figure 5B**). Band power is a  
283 limited measure of the full power spectrum density though, and so in **Figure 5C** we performed gradient  
284 mapping of the full power spectrum density. This showed a primary anterior-posterior gradient driven by  
285 higher Theta and Alpha power in the posterior and higher Delta power in the anterior hippocampus. The  
286 second gradient showed increased Delta power in the anterior and posterior hippocampus, while the third  
287 gradient showed a slight increase in Delta and decrease in Theta in the subiculum. Results were consistent  
288 when using an open iEEG atlas (Frauscher *et al.*, 2018) or locally collected data in patients (Paquola,  
289 Seidlitz, *et al.*, 2020), showing largely conserved patterns in **Figure S3**.



290  
291 **Figure 5.** Intracranial EEG (iEEG) properties from time periods deemed “normal” in implanted patients assessed during resting  
292 state. **A)** (left) power spectrum density plots of all channels (n=4279) and hippocampal channels (<5mm from any hippocampal  
293 midthickness vertex) (n=81), standard deviation shaded. (right) lognormal power within each band for each hippocampal channel,  
294 with vertical lines indicating the median and with corresponding bands from all channels in gray. **B)** Spatial extrapolation  
295 weighted by geodesic distance shows largely anterior-posterior differences in band powers. **C)** Power spectrum densities reduced  
296 into primary diffusion map embedding gradients.

## 297 **Feature combinations**

298 The biggest advantage of a common hippocampal mapping space is that it allows for direct spatial  
299 correlation between features from different scales and methods. In Figure **6A**, we examined relationships  
300 between all maps shown above using Pearson's R with an adapted spin test significance testing to control  
301 for spatial autocorrelation in the data. This revealed many greater-than-chance correlations, both within  
302 methodologies and between. Finally, we additionally compared morphological measures of thickness,  
303 gyrification, and curvature which are generated within the *HippUnfold* workflow (**Figure S4**). Previous  
304 work (J. DeKraker et al., 2020) showed that these features differed between MRI and histology, with the  
305 latter showing greater detail including more gyrification and lower thickness. After group-averaging, each  
306 of these features was significantly spatially correlated between histology and MRI.



307  
 308 **Figure 6.** Relationship between all hippocampal maps. **A)** correlation matrix of all features, after resampling to a common  
 309 0.5mm vertex-spacing surface. **B)** Diffusion map embeddings 1-3 across all features. **C)** Alignment of gradients 1 and 2 to  
 310 hippocampal subfields, proximal-distal, and anterior-posterior axes. **D)** Absolute correlation between each feature map and the  
 311 anterior-posterior axis (Pearson's R) and the maximum permuted subfield labels (Spearman's R).  
 312

313 We performed a dimensionality reduction across all features from all figures using diffusion map gradient  
 314 embeddings. For visualization, we plotted components 1 and 2 with colour coding according to subfield  
 315 and continuous anterior-posterior and proximal-distal gradients (**Figure 6C**). The proximal-distal and  
 316 anterior-posterior axes of the hippocampus are closely aligned to gradients 1 and 2, respectively, with  
 317 gradient 1 explaining approximately twice the variance (**Figure 6B**). This suggests that while these two



318 axes emerge as natural summaries of many hippocampal feature maps, the proximal-distal direction is  
319 stronger.

320

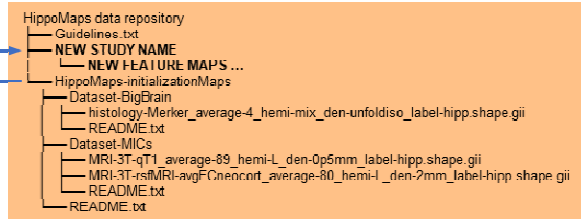
321 **Figure 6D** provides a summary of which measures are most correlated with the anterior-posterior and  
322 subfield axes of the hippocampus. As expected, the strongest subfield relationships were observed in  
323 histological features such as Calbindin and Calretinin staining, or thickness measures at a histological  
324 level of precision. Many structural 9.4T and 7T features also showed strong subfield correlations,  
325 especially qT1 and qR1. This is encouraging given the increasing availability and adoption of quantitative  
326 T1 sequences (Bidhult *et al.*, 2016; Haast *et al.*, 2016; van der Weijden *et al.*, 2021). The employed  
327 rsfMRI and iEEG features were still moderately correlated with subfield division, but iEEG and rsfMRI  
328 gradients in particular showed strong correlations with the anterior-posterior hippocampal axis. Some  
329 caution should be exercised here: iEEG data were sparsely sampled and so after extrapolation each band  
330 power map was very smooth, which could amplify correlation values (but not significance, since spin test  
331 permutations were used to control for spatial autocorrelation). Note also that laminar profiles were not  
332 used in this analysis, and histological measures in particular can benefit from the information added by  
333 such methods due to their high precision.

### 334 Usability experiment and documentation

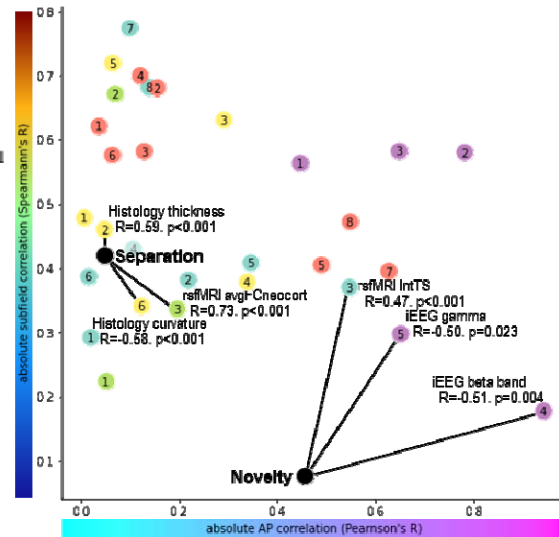
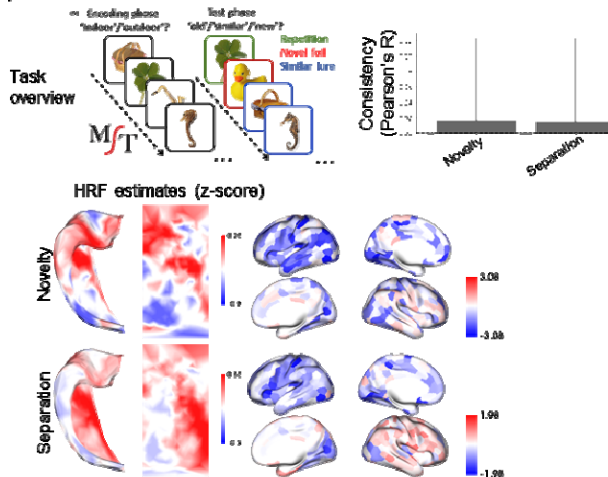
335 HippoMaps as an open toolbox and online data warehouse paves the way for multiple new research  
336 avenues, examples of which are shown in **Figure 7**. We anticipate that as hippocampal mapping studies  
337 are performed in other research areas, authors can use the initial maps provided here as comparisons and  
338 will upload their own maps in the spirit of open and reproducible science, and also to boost the visibility  
339 of their work. To this end, we provide a set of Python tools, well documented example code to reproduce  
340 the maps shown here (labeled as tutorials), and guidelines for how other experimenters should upload  
341 their maps to this repository. We have and will continue to answer questions and create community  
342 resources via GitHub (<https://github.com/HippAI/hippomaps> or [https://github.com/MICA-](https://github.com/MICA-MNI/hippomaps)  
343 [MNI/hippomaps](https://github.com/MICA-MNI/hippomaps)), and all current maps are available on the Open Science Framework  
344 (<https://osf.io/92p34/>).

### A) Example study design employing HippoMaps

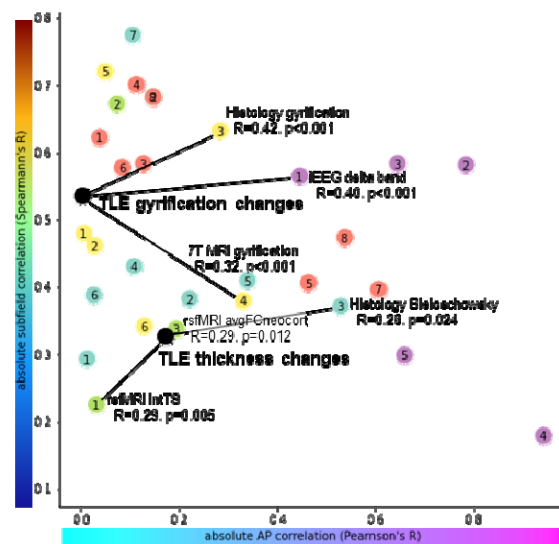
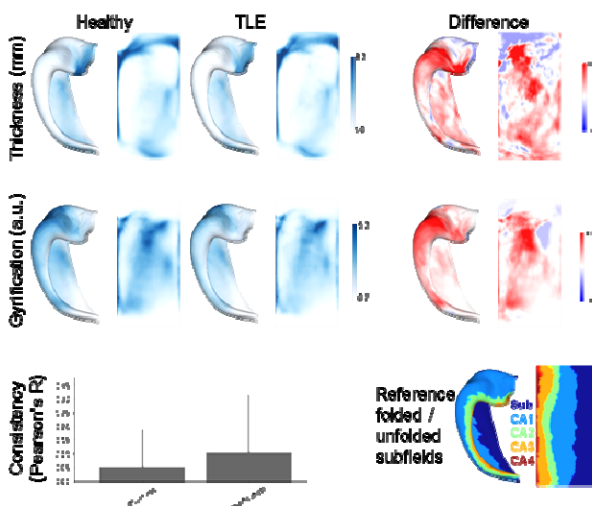
- Dataset collection**
  - feature extraction
  - HippoUnfold surface fitting
- HippoMaps interactions**
  - plotting and vertex-wise analysis
  - fetch relevant comparison maps
  - spin test comparison
- Interpretation and publishing**
  - is the study data correlated to a target measure/map
  - does the study data reveal novel hippocampal structure
  - is the study sample significantly different from the norm
- Contribute to HippoMaps**



### B) Example task-fMRI maps



### C) Case-control differences in TLE



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**Figure 7.** Examples of HippoMaps usage. **A)** New experiments can utilize HippoMaps tools and resources while also contributing new maps to the repository. Only example repository maps are shown, with descriptive naming and additional details to be provided in README files. **B)** task-fMRI during the Mnemonic Similarity Task (MST) to probe the haemodynamic response function (HRF) magnitudes during successful pattern separation and novel trials. These maps are then compared to all others (right), listing the top three strongest correlations (black lines). **C)** Morphological differences between ipsilateral temporal lobe epilepsy (TLE) patients and healthy controls

**Figure 7A** shows a generic use case of HippoMaps wherein a new finding is contextualized by comparison to other maps in HippoMaps, and data is in turn contributed to HippoMaps to extend its utility in future work. **Figure 7B** illustrates an example experiment with task-fMRI using the Mnemonic

356 Similarity Task (MST) designed to probe pattern separation, a task thought to preferentially involve  
357 hippocampal subregions (Pishdadian *et al.*, 2020; Stark *et al.*, 2019). This can be seen most strongly in  
358 subiculum for the successful pattern separation trials, whereas trials with novel stimuli showed anterior-  
359 posterior differentiation. Comparing these maps directly to microcircuit features provides context for the  
360 demands of these two task conditions: pattern separation was strongly correlated to detailed maps of  
361 curvature, thickness, and neocortical connectivity, whereas novelty was moderately correlated to intrinsic  
362 timescale, beta band power, and gamma band power (**Figure 7B**, right). Further task-fMRI results from  
363 an object-pairing memory task, as well as replication data of the MST at 7T, are shown in **Figure S5**.

364  
365 **Figure 7C** illustrates an example experiment comparing 35 temporal lobe epilepsy (TLE) patients to 81  
366 healthy, age- and sex-matched controls scanned at 3T MRI. Reductions in hippocampal thickness and  
367 gyrification are seen, with the greatest changes in CA1 and CA4 subfields, which have previously been  
368 identified as vulnerable areas (Blümcke *et al.*, 2012, 2013; Duvernoy *et al.*, 2013; Steve *et al.*, 2020).  
369 Comparing thickness reduction patterns to other maps shows moderate correlations with rsfMRI  
370 properties of intrinsic timescale, neocortical connectivity, and histological Bieloschowsky staining.  
371 Gyrification loss was strongly correlated with healthy gyrification in histology and 7T MRI, and iEEG  
372 delta band power.

## 373 **DISCUSSION**

374 Despite its critical role in human brain organization in both health and disease, the field lacks a  
375 standardized framework to aggregate, represent, and compare structural and functional features of the  
376 hippocampus. The current work presented HippoMaps as a centralized toolbox and online data warehouse  
377 for hippocampal subregional analysis and contextualization. HippoMaps is based on a standardized  
378 hippocampal reference space for data aggregation, sharing, and analysis, which leverages recent advances  
379 in automated hippocampal segmentation and computational unfolding (Jordan DeKraker *et al.*, 2022), as  
380 well as improvements for cross-modal and cross-subject alignment (DeKraker *et al.*, 2023). This  
381 repository is initialized with 30 novel maps of hippocampal subregional organization, aggregating a broad  
382 array of features from 3D *post-mortem* histology, *ex-vivo* 9.4 Tesla MRI, alongside with *in-vivo* structural  
383 and resting-state functional MRI (rsfMRI) obtained at 3 and 7 Tesla, as well as intracranial  
384 encephalography (iEEG) collected from a large cohort of epilepsy patients. This is further extended by a  
385 host of tools for visualization and contextualization, as well as online tutorials that recreate the maps  
386 shown here and demonstrate how new data can be incorporated and analyzed. HippoMaps will provide  
387 key guidance to: (i) compare hippocampal features derived from different methods, in particular to cross-  
388 reference *in-vivo* imaging measures with *ex-vivo* and *post-mortem* data, (ii) interrogate structure-function  
389 relationships, for example by contextualizing task-based fMRI findings or intracranial neural recording  
390 against spatial patterns obtained from anatomical and microstructural measures, (iii) contextualizing case-  
391 control deviations in clinical populations against established principles of subregional hippocampal  
392 organization, and (iv) refining our understanding of hippocampal circuitry, by mapping its functional  
393 connectivity and microstructure for a better understanding of its computational operations and transfer  
394 functions at the subregional level. HippoMaps is fully open access and designed according to community  
395 standards (<http://hippomaps.readthedocs.io>), to facilitate its dissemination and usability. As such, we  
396 anticipate that HippoMaps will represent a powerful analytical ally for fundamental and clinical  
397 neuroscientists alike. Considering the unique role the hippocampus plays in human neuroanatomy and

398 cognition (Duvernoy *et al.*, 2013; O’Keefe & Nadel, 1978) and its likely important computational  
399 properties (Knierim & Neunuebel, 2016; S. Leutgeb & Leutgeb, 2007), it may furthermore provide key  
400 insights and guidance into the design and validation of emerging bio-inspired AI architectures.

401  
402 We anticipate that surface-based registration will become the standard for hippocampal mapping, as it has  
403 in the neocortex (Fischl, Sereno, Tootell, *et al.*, 1999; Glasser *et al.*, 2013; Ma *et al.*, 2023; Robinson *et al.*,  
404 2014; D. C. Van Essen *et al.*, 1998). HippoMaps is a major step in advancing the usability of this  
405 methodology, generating utilities, scientific context, and an open community for examining the  
406 hippocampus in detail. Moreover, our repository is designed to employ the same data standards that have  
407 already been extensively developed for neocortical brain imaging data including Brain Imaging Data  
408 Standards (BIDS) (Gorgolewski *et al.*, 2016); NIFTI/GIFTI file formatting (Glasser *et al.*, 2013); and  
409 Findability, Accessibility, Interoperability, and Reusability (FAIR) principles (Gorgolewski & Poldrack,  
410 2016; Wilkinson *et al.*, 2016). Despite its demonstrated benefits, surface-based alignment is not yet  
411 universal for the neocortex and certainly still in its infancy for the hippocampus. Thus, while we  
412 encourage the use of surface-based methods, we also provide code and examples of how to map  
413 volumetrically aligned hippocampal data (*e.g.*, in a standard volumetric space such as MNI152 or others)  
414 to hippocampal surfaces for comparison and contribution to HippoMaps. In the field, work progresses at  
415 the level of hippocampal subfield parcellation at the level of histology, for example to derive additional  
416 subregional divisions (González-Arnay *et al.*, 2024; Henriksen *et al.*, 2010; Igarashi *et al.*, 2014).  
417 Moreover, there have been ongoing efforts by the neuroimaging community to harmonize boundary  
418 heuristics (Olsen *et al.*, 2019; Yushkevich *et al.*, 2015). Under the HippoMaps framework, descriptions go  
419 beyond typical unitary descriptions of the hippocampus and beyond its parcellation into subfields to the  
420 level of mapping vertex-wise or columnar structure of hippocampal archicortex. The columnar level  
421 represents an important structural and functional modularization of the brain (Mountcastle, 1997), and has  
422 the potential to unlock new facets of hippocampal computation. As such, different subfield parcellations  
423 can also be converted to surface format and integrated seamlessly within the HippoMaps warehouse.  
424 Thus, we apply considerable futureproofing, and we encourage the broader hippocampal research  
425 community to upload their own maps to this repository under our support, curation, and online guidelines  
426 and tutorials.

427  
428 Multi-feature aggregation as in the HippoMaps repository provides extensive opportunities to assess  
429 relationships between hippocampal structure and function, to cross-validate *in-vivo* measures with *ex-vivo*  
430 and *post-mortem* imaging as well as histological data. Structural and microstructural data derived from  
431 3D histology and MRI currently aggregated support a close alignment of many feature maps with the  
432 classic subfields account of the hippocampal circuitry. Moreover, several measures, particularly those  
433 derived from functional modalities such as rsfMRI or iEEG, lend additional evidence for anterior-  
434 posterior differentiation of the hippocampal formation. Specifically, gradient decomposition of  
435 hippocampal rsfMRI connectivity and iEEG power spectrum densities showed that anterior-posterior  
436 differentiation captured most inter-regional variance, whereas histological and structural MRI measures  
437 showed primarily proximal-distal or subfield-related differentiation. It is notable that some features  
438 showed extreme intensity values at the anterior and posterior edges - these are relatively small in native  
439 space and so have limited constituent data and are prone to misalignment artifacts. Thus, the anterior and  
440 posterior edges of each map should be interpreted with some caution. Nevertheless, the consistently  
441 repeated structural motifs across the anterior-posterior axis of the hippocampus are suggestive of parallel



442 repeated computations being performed on different input and output information across the anterior-  
443 posterior hippocampal axis, in line with prior accounts (Poppenk *et al.*, 2013; Strange *et al.*, 2014). These  
444 two dimensions have also been suggested to topographically represent the functional embedding of the  
445 broader mesiotemporal region in large-scale functional networks, in particular default mode and multiple  
446 demand networks (Andrews-Hanna, Reidler, Sepulcre, *et al.*, 2010; Buckner *et al.*, 2008; Duncan, 2010),  
447 which provides a potential substrate for the parametric mixing of both functional systems in macroscale  
448 brain function (Paquola, Benkarim, *et al.*, 2020). It is, therefore, not surprising that two axes explain the  
449 greatest proportion of the variance across all maps in the current repository as well, consolidating the  
450 notion that a two dimensional organization may serve as a powerful summary descriptor for a broad array  
451 of hippocampal structural and functional features (Genon *et al.*, 2021).

452  
453 We provide adapted methods to control for autocorrelation when comparing spatial maps to one another  
454 in the hippocampus. We specifically adapted Moran's spectral randomization and "spin test" permutation  
455 testing that have previously been introduced to study neocortical data (Alexander-Bloch *et al.*, 2018;  
456 Karat *et al.*, 2023; Vos de Wael *et al.*, 2020; Wagner & Dray, 2015). These methods reveal robust  
457 correlations between many of the maps included here. Many of these relationships support the validity of  
458 the methods being applied, for example between *in-vivo* qT1 and *ex-vivo* R1 which are inverses of one  
459 another. Another example is that functional connectivity of the hippocampus was strong to default mode  
460 neocortical areas, as shown in previous work (Andrews-Hanna, Reidler, Huang, *et al.*, 2010; Norman *et al.*,  
461 2021; Vos de Wael *et al.*, 2018; Ward *et al.*, 2014), with connectivity being strongest in the  
462 subiculum. This recapitulates the role of the subiculum as the primary output structure of the  
463 hippocampus, and contributions of the hippocampus to functions typically ascribed to the default mode  
464 network such as mind-wandering, episodic recall, or future-thinking that are frequent during rest (Bellana  
465 *et al.*, 2017; Buckner, 2010; Christoff *et al.*, 2016; Fox *et al.*, 2015; Ross & Easton, 2022; Schacter *et al.*,  
466 2017; Yang *et al.*, 2020). Some relationships reveal novel information about the methods themselves: PLI  
467 transmittance is thought to reflect many microscopic structures under the broad heading of "neural  
468 processes" or "nerve fibers" (H. Axer *et al.*, 2001; Dammers *et al.*, 2012). Across the extent of the  
469 hippocampus, this feature correlated with Beilsochowsky and Thionin staining, R2\*, average neocortical  
470 functional connectivity, and, most significantly, rsfMRI intrinsic timescale. Intrinsic timescale is  
471 hypothesized to relate to recurrent connections (Chaudhuri *et al.*, 2014), which could indeed be supported  
472 by dense neural processes. Finally, we illustrate contextualization via nonlinear gradient decomposition  
473 across maps. When applied to all maps, we show data-driven separation of subfields, in line with previous  
474 work. We also note that in this latent space, CA4 closely resembles CA1, even though they are not  
475 adjacent topologically. This fits descriptions of CA4 as having a wide pyramidal layer with large and  
476 dispersed neurons, similar to CA1 (Duvernoy *et al.*, 2013), and indeed in some cases these two areas have  
477 similar disease vulnerabilities (Blümcke *et al.*, 2012). Future work may determine more selectively what  
478 features make these two regions similarly vulnerable or examine why in some disease subtypes one is  
479 affected without the other.

480  
481 At the level of the neocortex, several packages already exist to facilitate the contextualization of results  
482 (Larivière *et al.*, 2023, 2021; Markello *et al.*, 2022). With HippoMaps, such an approach is now also  
483 possible for the hippocampal region, and we demonstrate the contextualization of task fMRI maps during  
484 an episodic memory paradigm as well morphological alterations in patients with temporal lobe epilepsy  
485 relative to healthy individuals. Such approaches can help to clarify the hypothetical role of

486 microstructural features in specific hippocampal computations, such as pattern separation (Bakker et al.,  
487 2008; J. K. Leutgeb et al., 2007; Schmidt et al., 2012), pattern completion (Guzman et al., 2016; S.  
488 Leutgeb & Leutgeb, 2007), and novelty detection (Chen *et al.*, 2011; Larkin *et al.*, 2014). These  
489 previously assumed relations of function to microstructure have generally relied on parcellations of the  
490 hippocampus into stereotyped subfields; with HippoMaps, it is instead possible to compare functional and  
491 microstructural maps directly without any predefined subfield labelling. In addition to offering potential  
492 increases in anatomical specificity, this representation may also lend itself more naturally to sensitive  
493 spatial correlation with autocorrelation control through permutation testing. One area for future work will  
494 lie in consolidating mesoscale connectivity with detailed descriptions of the internal hippocampal  
495 circuitry, which will not only help to further understand the computations of specific hippocampal  
496 subregions but which may also clarify the different substrates of computation (Beaujoin et al., 2018;  
497 Bennett & Stark, 2016; Berron et al., 2016; Karat et al., 2023; Lacy et al., 2011; Ly et al., 2020). Indeed,  
498 hippocampal circuitry has inspired the basic ways in which we think about biological computation,  
499 spurring principles such as long-term potentiation (Hebb, 2005), and carrying important inventions like  
500 the Boltzmann machine (Ackley et al., 1985) and Tolman Eichenbaum machine (Whittington *et al.*,  
501 2020). Even recent theories and computational models still center around hippocampal structure as told  
502 through a stereotyped subfield architecture (Gandolfi et al., 2023; Whittington et al., 2020). Formal  
503 mapping, rather than stereotyped descriptions, can extend this work, building up biological plausibility of  
504 such models and scaffolding our understanding of these systems. For this reason, HippoMaps may also  
505 provide precise macro-, meso- and micro-scale hippocampal features in a common same space to further  
506 identify and harness computational properties of its circuitry.

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