Supplementary information for

Multilevel atlas comparisons reveal divergent evolution of
the primate brain

Clément M. Garin\textsuperscript{1,*}, Marie Garin\textsuperscript{2}, Leonardo Silenzi\textsuperscript{3}, Rye Jaffe\textsuperscript{1,3}, Christos Constantinidis\textsuperscript{1,4,5}.

\textsuperscript{1} Department of Biomedical Engineering, Vanderbilt University, Nashville, TN 37235
\textsuperscript{2} Département de mathématiques, Université Paris-Saclay, ENS Paris-Saclay, CNRS, Centre Borelli, F-91190 Gif-sur-Yvette, France
\textsuperscript{3} Department of Neurobiology and Anatomy, Wake Forest School of Medicine, Winston Salem, NC 27157
\textsuperscript{4} Program in Neuroscience, Vanderbilt University, Nashville, TN 37235
\textsuperscript{5} Department of Ophthalmology and Visual Sciences, Vanderbilt University Medical Center, Nashville, TN 37232
**Supplementary Table 1:** List of the atlases used in this study

| Species                        | Publication |
|-------------------------------|-------------|
| Homo sapiens                  | (1)         |
| Homo sapiens                  | (2)         |
| Homo sapiens                  | (3)         |
| Pan troglodytes               | (4)         |
| Macaca mulatta                | (5)         |
| Chlorocebus aethiops          | (6)         |
| Callithrix jacchus            | (7)         |
| Saimiri sciureus              | (8)         |
| Microcebus murinus            | (9)         |
| Mus musculus                  | (10) (DSURQE) |
| Rattus norvegicus             | (11)        |
| Oryctolagus cuniculus         | (12)        |
| Pteronotus parnellii          | (13)        |
| Sus scrofa                    | (14)        |
| Ovis aries                    | (15)        |
| Equus caballus                | (16)        |
| Mustela putorius              | (17)        |
| Canis lupus                   | (18)        |
| Felis catus                   | (19)        |
| Monodelphis domestica         | (20)        |
| Level 1 regions | Lvl 1 label | Level 2 regions | Lvl 2 label | Level 3 regions | Lvl 3 label | Level 4 regions | Lvl 4 label |
|----------------|------------|----------------|------------|----------------|------------|----------------|------------|
| Neocortex      | 1          | NA             | 0          | NA             | 0          | Olfactory bulb (OB) | 16         |
| Neocortex      | 1          | NA             | 0          | Cingulate cortex | 200        | NA             | 0          |
| Cortical white matter | 2 | NA | 0 | NA | 0 | NA | 0 |
| Cerebellum | 4 | NA | 0 | NA | 0 | NA | 0 |
| Neocortex      | 1          | Frontal lobe   | 1          | oFC (orbital frontal cortex non PFC) | 1          | Gustatory cortex | 14         |
| Neocortex      | 1          | Frontal lobe   | 1          | oFC (orbital frontal cortex non PFC) | 1          | Orbital proisocortex and preiallocortex (oProiso/preialloC) | 15         |
| Neocortex      | 1          | Frontal lobe   | 1          | Motor and premotor | 2          | BA 6 (supplementary (pre-motor area) | 19         |
| Neocortex      | 1          | Frontal lobe   | 1          | Motor and premotor | 2          | BA 4 (primary motor cortex) | 20         |
| Neocortex      | 1          | Frontal lobe   | 1          | Medial prefrontal cortex (mPFC cing) | 11         | BA 32 | 8          |
| Neocortex      | 1          | Frontal lobe   | 1          | Medial prefrontal cortex (mPFC cing) | 11         | BA 14 | 9          |
| Neocortex      | 1          | Frontal lobe   | 1          | Medial prefrontal cortex (mPFC cing) | 11         | BA 24 | 10         |
| Neocortex      | 1          | Frontal lobe   | 1          | Medial prefrontal cortex (mPFC cing) | 11         | BA 25 | 11         |
| Neocortex      | 1          | Frontal lobe   | 1          | Dorsolateral prefrontal cortex (dlPFC) | 22         | IFJ | 0          |
| Neocortex      | 1          | Frontal lobe   | 1          | Dorsolateral prefrontal cortex (dlPFC) | 22         | BA 10 | 1          |
| Neocortex      | 1          | Frontal lobe   | 1          | Dorsolateral prefrontal cortex (dlPFC) | 22         | BA 9 | 2          |
| Neocortex      | 1          | Frontal lobe   | 1          | Dorsolateral prefrontal cortex (dlPFC) | 22         | BA 46 | 3          |
| Neocortex      | 1          | Frontal lobe   | 1          | Dorsolateral prefrontal cortex (dlPFC) | 22         | BA 8 | 4          |
| Neocortex      | 1          | Frontal lobe   | 1          | Dorsolateral prefrontal cortex (dlPFC) | 22         | BA 55 | 70         |
| Neocortex      | 1          | Frontal lobe   | 1          | Dorsolateral prefrontal cortex (dlPFC) | 22         | BA 33 | 88         |
| Neocortex      | 1          | Frontal lobe   | 1          | Dorsolateral prefrontal cortex (dlPFC) | 22         | BA 9/46 | 88        |
| Neocortex      | 1          | Frontal lobe   | 1          | Ventrolateral prefrontal cortex | 23         | BA 47 | 5          |
| Neocortex      | 1          | Frontal lobe   | 1          | Ventrolateral prefrontal cortex | 23         | BA 45 | 6          |
| Neocortex      | 1          | Frontal lobe   | 1          | Ventrolateral prefrontal cortex | 23         | BA 44 | 78         |
| Neocortex      | 1          | Frontal lobe   | 1          | Orbital PFC (oPFC) | 30         | Orbital cortex | 0          |
| Neocortex      | 1          | Frontal lobe   | 1          | Orbital PFC (oPFC) | 30         | BA 11 | 12         |
| Neocortex      | 1          | Frontal lobe   | 1          | Orbital PFC (oPFC) | 30         | BA 13 | 13         |
| Neocortex      | 1          | Frontal lobe   | 1          | Orbital PFC (oPFC) | 30         | BA 12/47 | 76        |
| Neocortex      | 1          | Frontal lobe   | 1          | Prefrontal cortex (PFC) | 100        | NA | 0          |
| Neocortex | Temporal lobe | Auditory cortex | BA | Description |
|-----------|---------------|-----------------|----|-------------|
| Neocortex | Temporal lobe | Auditory cortex | BA 41/42 | (primary auditory, A1) |
| Neocortex | Temporal lobe | Auditory cortex | BA 21 | Belt (secondary auditory, A2) |
| Neocortex | Temporal lobe | Auditory cortex | BA 41/42 | (primary auditory, A1) |
| Neocortex | Temporal lobe | Auditory cortex | BA 21 | Parabellum (tertiary auditory cortex, A3) |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | Polar_rostrotemporal_cortex (RTP) |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | Ectosylvian area, STS, TE, FST |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | Temporal association area |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | BA 21 |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | BA 20 |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | BA 38 |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | BA 35/36 | (Perihinal, ectorhinal cortex) |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | BA 28 | (entorhinal) |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | Parahippocampal complex |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | BA 27 | (Pre-)Piriform/amygdaloid cortex |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | BA 37 | (Fusiform) |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | Temporoparietal transitional area, Retroinsula (Rt) |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | Insular cortex |
| Neocortex | Temporal lobe | Auditory cortex | BA 22 | BA 52 | (Parainsular cortex) |
| Neocortex | Parietal lobe | Somatosensory cortex | BA 1-3 | (primary somatosensory) |
| Neocortex | Parietal lobe | Somatosensory cortex | BA 43 | |
| Neocortex | Parietal lobe | Somatosensory cortex | BA 43 | |
| Neocortex | Parietal lobe | Somatosensory cortex | BA 5 | secondary somatosensory |
| Neocortex | Parietal lobe | Posterior parietal cortex | BA 5 | |
| Neocortex | Parietal lobe | Posterior parietal cortex | BA 7 | |
| Neocortex | Parietal lobe | Posterior parietal cortex | BA 7 | |
| Neocortex | Parietal lobe | Posterior parietal cortex | BA 39 | (angular gyrus) |
| Neocortex | Parietal lobe | Posterior medial cortex (PMC) | BA 23 | Parietal area medial (PGM) |
| Neocortex | Parietal lobe | Posterior medial cortex (PMC) | BA 26/29/30 | (retrosplenial) |
| Neocortex | Parietal lobe | Posterior medial cortex (PMC) | BA 26/29/30 | (retrosplenial) |
| Neocortex | Parietal lobe | Posterior medial cortex (PMC) | BA 31 | |
| Neocortex | Cortical subplate | Amygdala | BA 17 | (V1, cuneus, striate cortex) |
| Neocortex | Cortical subplate | Amygdala | BA 17 | (V1, cuneus, striate cortex) |
| Neocortex | Occipital lobe | NA | BA 17 | (V1, cuneus, striate cortex) |
| Neocortex | Occipital lobe | NA | BA 18 | (V2) |
| Neocortex | Occipital lobe | NA | BA 19 | (V3, V4, V5, MT, V6) |
| Neocortex | Cerebral nuclei | Striatum | BA 10 | Caudate |
Supplementary Table 2: Region equivalencies across species between four levels of segmentation

This table provides a base for the re-segmentation of the utilized atlases. The label corresponds to the new value attributed to each region in all atlases.

In humans, the atlas was based on a variety of segmentation methods including 210 subjects for the Glasser atlas (1), 40 individuals for the Brainnetome (2). All atlases were normalized to the average template MNI152 (comprising 152 subjects) (21).

Human Glasser (Homo sapiens): The label modifications were based on the original Brodmann names and strictly followed Suppl. Table 1. In order to respect the original authors’ classification, any regions that could not directly relate to a BA were not re-attributed in level 4. No subcortical areas were available for this atlas.

Human Brainnetome (Homo sapiens): The label modifications were based on the original Brodmann names and strictly followed Suppl. Table 1. In order to respect the original authors' classification, any regions that could not directly relate to a BA were not re-attributed in level 4.

Human Brodmann (Homo sapiens): This new segmentation followed Suppl. Table 1 when BA were originally identified, and the other (sub-)regions were not used for level 4. No subcortical areas were available for this atlas.
Chimpanzee (*Pan troglodytes*): The original segmentation was based on gyri instead of BA. Since no atlas based on BA was available, homologies were rarely estimated up to the level 4. The estimation of homologies was based on the table provided with the original version of the Brainnetome atlas. For this species, the posterior limit of the frontal cortex was defined by the posterior limits of the posterior superior frontal gyrus and the precentral gyrus. According to the Brainnetome atlas, the middle frontal gyrus is composed of BA 9/46, 46, 8, 6, and 10, while the superior frontal gyrus is composed of BA 8, 9, 6, and 10. The posterior PFC limits were defined by the medial superior frontal, and posterior middle frontal gyri. We were thus able to define PFC boundaries in agreement with Donahue et al. (22).

Macaque (*Macaca mulatta*): The label modifications were based on the original Brodmann names and strictly followed Suppl. Table 1. In order to respect the original authors' classification, any regions that could not directly relate to a BA were not re-attributed in the level 4. The original version of the Charm atlas did not possess any subcortical regions and was concatenated with the subcortical regions of the SARM atlas (23). The Charm atlas level 5 was used as our basis for cortical segmentation.

Vervet (*Chlorocebus aethiops*): The original segmentation was based on gyri rather than BA. Since no atlas based on BA was available, homologies were rarely estimated up to the level 4. We were not able to define the PFC in this species.

Marmoset (*Callithrix jacchus*): The label modifications were based on the original Brodmann names and strictly followed Suppl. Table 1. In order to respect the original authors' classification, regions that could not directly relate to a BA were not re-attributed in the level 4. We use vM version and the subcortical beta of the atlas of Liu et al. (24). The two atlases were concatenated in one atlas.

Squirrel monkey (*Saimiri sciureus*): The atlas did not cover the whole brain. Only certain regions could be attributed to level 2 or 3. Neocortical volumes of level one were measured based on the segmentation performed with ANTs.

Mouse lemur (*Microcebus murinus*): The label modifications were based on the original Brodmann names and strictly followed Suppl. Table 1.

Mouse (*Mus musculus*): Similarly to rats, most of the regions were re-attributed following the Allen brain classification (25). Very few assumptions were made up to level 4, with the exception of subcortical regions and low order regions (motor/somatosensory/auditory). We define the
PFC as orbital frontal regions, secondary motor cortex and area 24 (prelimbic area was not segmentate) (26, 27).

**Rat (Rattus norvegicus):** Most regions were re-attributed following the Allen brain classification (25). Very few assumptions were made up to level 4, with the exception of subcortical regions and low order regions (motor/somatosensory/auditory). We define the PFC as PFC, orbital frontal regions, pre-limbic areas, secondary motor cortex, and area 24 (26, 27).

**Rabbit (Oryctolagus cuniculus):** The atlas was only segmented into lobes. Few cortical regions, such as entorhinal cortex, were re-segmented up to level four.

**Mustached bat (Pteronotus parnellii):** The original atlas provided very limited segmentation of the neocortex. Few cortical regions, such as olfactory bulbs, were segmented up to level four.

**Pig (Sus scrofa):** The original atlas provided a very similar segmentation as level 3. As a result, few regions were attributed up to the level 4. Lobar segmentation was based on the authors’ original segmentation (prefrontal boundaries were already defined in the original version).

**Sheep (Ovis aries):** The atlas of the Sheep brain (28) does not follow BA classifications. Instead, lobar classification was provided by John et al. (29). Since no division of the cingulate was provided in the original segmentation, we used ITK-SNAP to manually separate the anterior and the posterior cingulate area, following the frontal lobe boundaries (30).

**Horse (Equus caballus):** The atlas only covered a few subcortical regions and three neocortical regions. Neocortical volumes of level one were measured based on the segmentation performed with ANTs.

**Ferret (Mustela putorius):** The atlas of the ferret brain does not follow BA and does not allow re-attribution into clear lobar segmentation. This atlas was mostly used for subcortical regions and neocortex segmentation.

**Dog (Canis lupus):** The dog brain was mostly segmented according to the original lobar segmentation. We also proposed a sub-segmentation of several visual areas into BA 17 and 19, as well as area suprasylvian medialis being segmented into BA 21 (31). The PFC area was delimited by area pregenualis, area genualis (anterior cingulate), area prorealis, area subgenualis, area precruciata medialis, and area subprorealis (32, 33).

**Cat (Felis catus):** The modification of the labels was based on the original Brodmann names and strictly followed Suppl. Table 1

**Short-tailed opossum (Monodelphis domestica):** The original atlas provided very limited segmentation of the neocortex. Few cortical regions, such as olfactory bulbs, were segmented up to level 4.
|                         | Empirical Bootstrap Confidence Interval | Observed Slopes Difference |
|-------------------------|----------------------------------------|-----------------------------|
| Parietal vs Occipital   | [-0.602; 0.543]                         | 0.689*                     |
| Frontal vs Occipital    | [-0.496; 0.476]                         | 0.484*                     |
| Temporal vs Occipital   | [-0.400; 0.356]                         | 0.396*                     |
| Occipital vs Parietal   | [-0.398; 0.714]                         | -0.426*                    |
| Temporal vs Parietal    | [-0.172; 0.259]                         | -0.189*                    |
| Frontal vs Parietal     | [-0.257; 0.345]                         | -0.056                     |

**Supplementary Table 3:** Bootstrap analysis comparing catarrhini’s lobar slope to the slope of other non-catarrhini species.

Bootstrap analysis was achieved on the lobar volumes by randomly assigning species into two groups. First, slope differences were calculated between the groups of interest and their associated samples (corresponding to the difference between the slope of the red and black regression line; Fig. 2). Next, we tested if the slope differences between the two groups were larger than what would be predicted by chance. We ultimately found that the slopes differences between catarrhini and other mammals always fell outside (*) the confidence interval for all comparisons except for frontal vs parietal lobes (expected).
Supplementary Figure 1: Phylogenetic tree constructed using the TimeTree method (34)
**Supplementary Figure 2:** PGLS analyses based on the volumes of the four mammalian cerebral lobes

Red regression lines, prediction intervals, and confidence intervals were calculated for catarrhini (vervets, macaques, chimpanzees and humans -red filled symbols). Black regression lines, prediction intervals, and confidence intervals were calculated for non-catarrhini mammals (open symbols). PGLS analyses were scaled by the regions possessing the lowest slope and classified based on the slope value of catarrhini (A), and non-catarrhini mammals (B). Slope values and confidence intervals are indicated on the plot. The human Brainnetome atlas was used for this analysis. No significant difference was observed with the Glasser atlas.
Supplementary Figure 3: PGLS analyses based on the volumes of the four mammalian cerebral lobes

Red regression lines, prediction intervals, and confidence intervals were calculated for catarrhini ( vervets, macaques, chimpanzees and humans -red filled symbols). Black regression lines, prediction intervals, and confidence intervals were calculated for non-catarrhini mammals (open symbols). PGLS analyses were scaled by the regions possessing the lowest slope and classified based on slope value of catarrhini (A), and non-catarrhini mammals (B). Slope values and confidence intervals are indicated on the plot. The human Brodmann atlas was used for this analysis. In comparison to Glasser and Brainnetome segmentation, the slope of the frontal lobe scaled by the occipital lobe appears higher than when the parietal lobe is scaled by the occipital lobe.
Supplementary Figure 4: Prediction interval deviation matrices based on the human atlas of Brodmann (A) and on the vervet (B) atlas

Matrix recapitulating the results of PGLS analyses performed between all pair of regions. A pair of regions was included if there were at least five species for which corresponding volumes were available. Regions that are not included were removed or were represented in gray squares. For each pair, we evaluated if the volume of a human region (rows) fell outside the 95% prediction limits when scaled by the region (columns). Regions falling outside the 95% prediction limits were included in the colormap. Otherwise, their value was set to zero. The matrix was ordered based on the number of values falling outside the prediction interval. In human (A), little variations were found with the classification based on the Glasser and Brainnetome atlases. In vervets (B), frontal and parietal lobes were found to be expanded (PFC and motor areas were not originally segmented in the vervet atlas).
Supplementary Figure 5: Examples of PGLS analyses on the volumes of three key brain structures scaled by occipital and parietal lobes

Human and chimpanzee PFCs only fall within the 95% prediction intervals (dotted lines) when compared to the parietal lobe, but not with the occipital lobe (A). The human retrosplenial cortex always fell beyond the prediction interval (B). The human auditory cortex fell under the prediction interval when compared to parietal lobe (C). The Glasser atlas was used for humans here.
Supplementary Figure 6: Examples of PGLS analyses on the volumes of two keys brain structures scaled by occipital and parietal lobes

Human and chimpanzee PFCs only fall within the 95% prediction intervals (dotted lines) when compared to the parietal lobe, but not with the occipital lobe (A). The retrosplenial cortex was not included in the Brainnetome atlas. The human auditory cortex fell under the prediction interval when compared to parietal lobe (C). The Brainnetome atlas was used for humans here.
Supplementary Figure 7: Examples of PGLS analyses on the volumes of three key brain structures scaled by occipital and parietal lobes

Human and chimpanzee PFCs only fell within the 95% prediction intervals (dotted lines) when compared to the parietal lobe, but not with the occipital lobe (A). The human retrosplenial cortex fell beyond the prediction interval when compared to the occipital cortex (B). The human auditory cortex fell under the prediction interval when compared to parietal lobe (C). The Brodmann atlas was used for humans.
Supplementary Figure 8: Phylogenetic signal estimates (λ values) (top left), intercept (top right) and slope (bottom left) for the PIDM based on the human Glasser atlas (Figure 3A).
Supplementary Figure 9: Phylogenetic signal estimates ($\lambda$ values) (top left), intercept (top right) and slope (bottom left), for the PIDM based on the human Brainnetome atlas (Figure 3B).
Supplementary Figure 10: Phylogenetic signal estimates (\( \lambda \) values) (top left), intercept (top right) and slope (bottom left) for the PIDM based on the Brodmann atlas (Suppl. Figure 4A).
Supplementary Figure 11: Phylogenetic signal estimates (λ values) (top left), intercept (top right) and slope (bottom left) for the PIDM based on the chimpanzee atlas (Figure 4A).
Supplementary Figure 12: Phylogenetic signal estimates (λ values) (top left), intercept (top right) and slope (bottom left) for the PIDM based on the macaque atlas (Figure 4B).
Supplementary Figure 13: Phylogenetic signal estimates ($\lambda$ values) (top left), intercept (top right) and slope (bottom left) for the PIDM based on the vervet atlas (Suppl. Figure 4B).
Supplementary Figure 14: Phylogenetic signal estimates (λ values) (top left), intercept (top right) and slope (bottom left), for the PIDM with k=1 (bottom right), based on the marmoset atlas (Figure 5A).
Supplementary Figure 15: Phylogenetic signal estimates (λ values) (top left), intercept (top right) and slope (bottom left) for the PIDM based on the mouse lemur atlas (Figure 5B).
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