ALLEN INSTITUTE for BRAIN SCIENCE
Fueling Discovery

ALLEN **Mouse Brain Atlas**

TECHNICAL WHITE PAPER:
ALLEN REFERENCE ATLAS – VERSION 2 (2011)

OVERVIEW OF UPDATES

The Allen Reference Atlas was created as a resource to support the Allen Mouse Brain Atlas. It was drawn as a classical brain reference atlas comprising a series of flat, 2-dimensional plates: 21 annotated Nissl sections in the sagittal plane and 132 annotated Nissl sections in the coronal plane. To support the online Allen Mouse Brain Atlas, the anatomical information in these reference atlases was extracted to create a 3-D reference space from the atlas to support automated processing and analysis of the *in situ* hybridization (ISH) data generated for the ~20,000 genes covered in the Allen Mouse Brain Atlas. This enabled registration/alignment of ISH data with the reference atlas, calculation and presentation of metrics summarizing the level of gene expression per anatomical region, and searches for genes expressed in a given anatomic structure. The atlas was also released for 3-D navigation in the Brain Explorer® 3-D viewer.

As visible on the 2-D atlas plates, the reference atlas as originally drawn contains far more content than was initially extracted for the original 3-D version of the atlas. In order to take complete advantage of the neuroanatomical reference set, the atlas has now been reprocessed to provide the following benefits:

- Additional brain regions in 3-D and corrections to previous inconsistencies
- Interactive user interface for the 2-D reference atlas plates
- Future integration with the Allen Developing Mouse Brain Atlas reference atlas into a single user interface

The updates to the reference atlas fall into the following categories, which are documented in this white paper:

- Higher-resolution raw images of Nissl sections
- Updates to the ontology to support the addition of neuroanatomical structures
- Increased parcellation of brain regions
- Correction of inconsistencies between atlas plates
- Systematic conversion of traditional atlas drawings to digital annotation database, enabling new interactive graphical atlas viewing

NISSL SECTIONS

The original presentation of the atlas Nissl sections included two pre-processing steps: 1) down-sampling of the image resolution to accommodate the file size limitations in the graphic software, and 2) ad-hoc contrast adjustments. We have improved this dataset by re-imaging the Nissl sections to provide the following benefits:

- High-quality images provided at the same image resolution as our typical ISH data
- Unadulterated Nissl section images as available pre-processing
- Display of both hemispheres of the coronal Nissl atlas

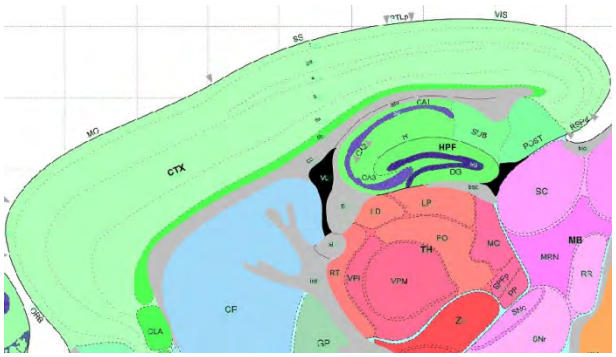
NEW DELINEATIONS OF BRAIN REGIONS

The delineations of 209 reference atlas structures were originally used in several aspects of the Allen Mouse Brain Atlas. The downloadable Brain Explorer 3-D viewer uses these structures for navigation of the reference atlas in 3-D and to serve as a framework for viewing gene expression throughout the brain. Each of the "voxels" representing gene expression from an ISH experiment is annotated such that they belong to one of these 209 reference atlas structures. The summed up quantification of gene expression per each of these 209 structures can be accessed through the API.

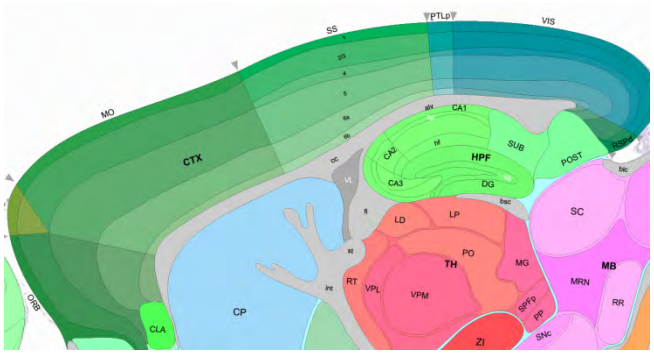
Users have frequently requested access to the full set of structures annotated in the reference atlas. In reprocessing the reference atlas, we were able to extract 738 structures in the coronal plane to increase the utility of the atlas features. The largest proportion of these structures comes from the cerebral cortex, hippocampus, and cerebellum. In the original annotated atlas, the delineations between cortical areas, hippocampal fields, and cerebellar lobes were indicated only by arrows without clear boundaries, and therefore not recognized as distinct anatomical regions from the standpoint of a digital atlas. Thus, a large part of the reprocessing effort involved the conversion of these "virtual" boundaries into actual boundaries. Also, a fraction of the additional structures were not previously extracted due to inconsistent or missing annotation between atlas plates, and these have been corrected as well. Examples are shown figure 1.

A. Cerebral Cortex

Version 1

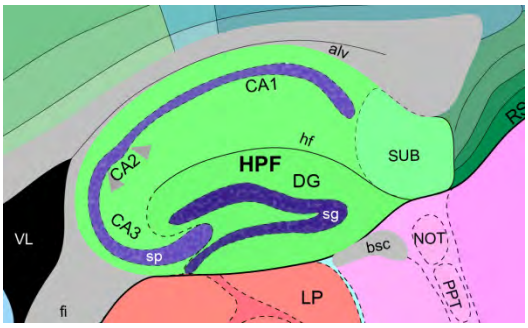


Version 2

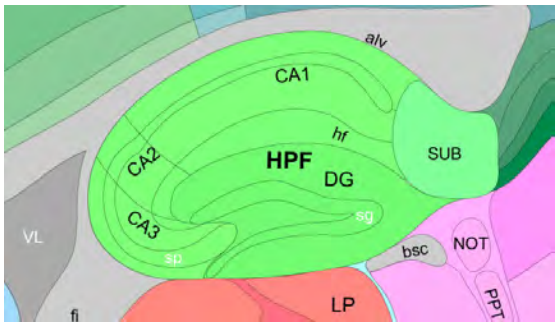


B. Hippocampus

Version 1

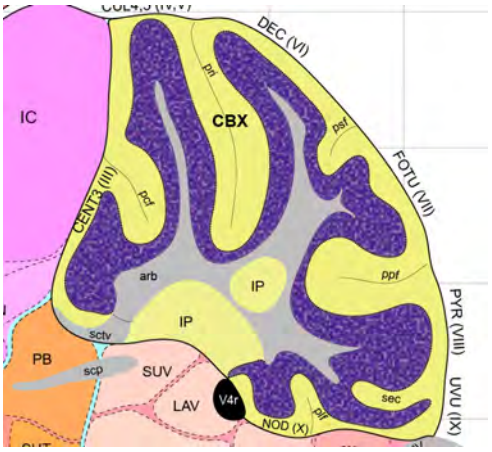


Version 2



C. Cerebellum

Version 1



Version 2

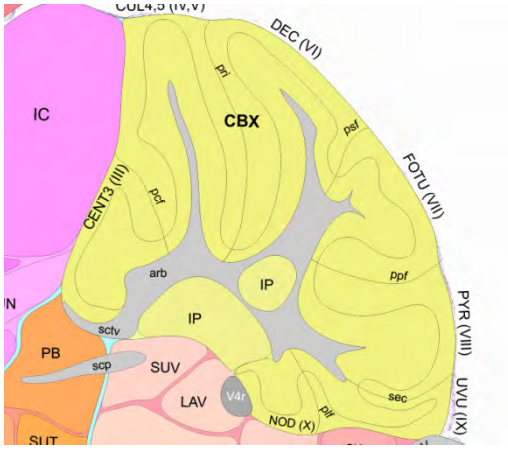


Figure 1. Comparison of structure delineations in the Allen Reference Atlas version 1 vs. version 2.
Examples illustrating the types of annotation updates to the Allen Reference Atlas are shown.

ONTOLOGY AND COLOR SCHEME

In the process of extracting new brain regions from the atlas, it became apparent that many of these regions were not included in the ontology. Changes to the ontology included additions of structures only; no brain structures were deleted. The full list of changes to the ontology are listed in **Appendix 1**.

For example, for each cerebellar lobe, a granular layer, Purkinje layer, and molecular layer have been added. In the dentate gyrus, the subgranular zone, molecular layer, and polymorph layer were also added as children structures of dentate gyrus (granule cell layer was already included in the ontology). A few structure names and acronyms were also corrected for consistent spelling and capitalization.

Alterations have also been made to the color scheme of the ontology and in the final presentation. RGB values assigned to each brain structure according to the logic of the anatomic ontology enable easy discrimination between brain regions by color-coding. In the original reference atlas, one exception was provided for dense cell layers such as the granule cell layer of the cerebellum and dentate gyrus and the pyramidal cell layer of the hippocampus, which were given a textured blue/purple appearance characteristic of the dark staining of these regions by Nissl. Another exception was applied to the olfactory bulb, in which the distinctive look of the glomerular cell layer was mimicked using a special blue/purple texture. These textured regions, while aesthetically pleasing, were at odds with the color assignment in the ontology which enables color-coding of expression analyses and atlas structures within the Brain Explorer 3-D viewer. In the reprocessing, the newest additions to the ontology have also been assigned RGB values, and texturing was eliminated. Instead, in order to differentiate the granule cell layer from the molecular layer, the granule cell layer has been assigned a darker shade of the original parent color. This is also true for the hippocampal granule and pyramidal cell layers.

CORRECTION OF INCONSISTENCIES

Many minor inconsistencies between atlas plates prevented the extraction of coordinates for atlas structures or created inconsistency with the ontology. A few examples are listed below. The full list can be found in **Appendix 2,** and examples of these changes can be found in **Appendix 3**.

- ***Example 1:* Standardization of annotation level across plates.** The anterior olfactory nucleus (AON) has a dorsal, external, lateral, medial, and posteroventral part. In the ontology, none of these regions is divided into layers 1 and 2, although among the atlas plates, these layers are indicated for only some of the sections. Therefore, these layers have been merged within the drawings to be consistent with the ontology and provide consistency across atlas plates.

- ***Example 2:* Correction of hippocampal annotation.** In sagittal atlas plate 7, CA1 and subiculum were not subdivided in the ventral hippocampus. In the reprocessing, the subiculum was separated from the CA, and the ventral region originally annotated as CA1 was subdivided into CA2 and CA3 to be more consistent with sagittal atlas plate 8 and with evidence from molecular markers.

- ***Example 3:* Addition of structures missing from a single atlas plate.** The somatosensory cortex upper limb region was annotated in coronal level 49 but the label was missing in coronal level 50. The upper limb region was added to coronal level 50. See Figure 2.

- ***Example 4: removal of structure inappropriately included on one section.*** The LDT was inappropriately included on coronal level 101, although it was missing from levels 100, 102, and 103. This structure actually should appear beginning in coronal level 104. See figure 3.

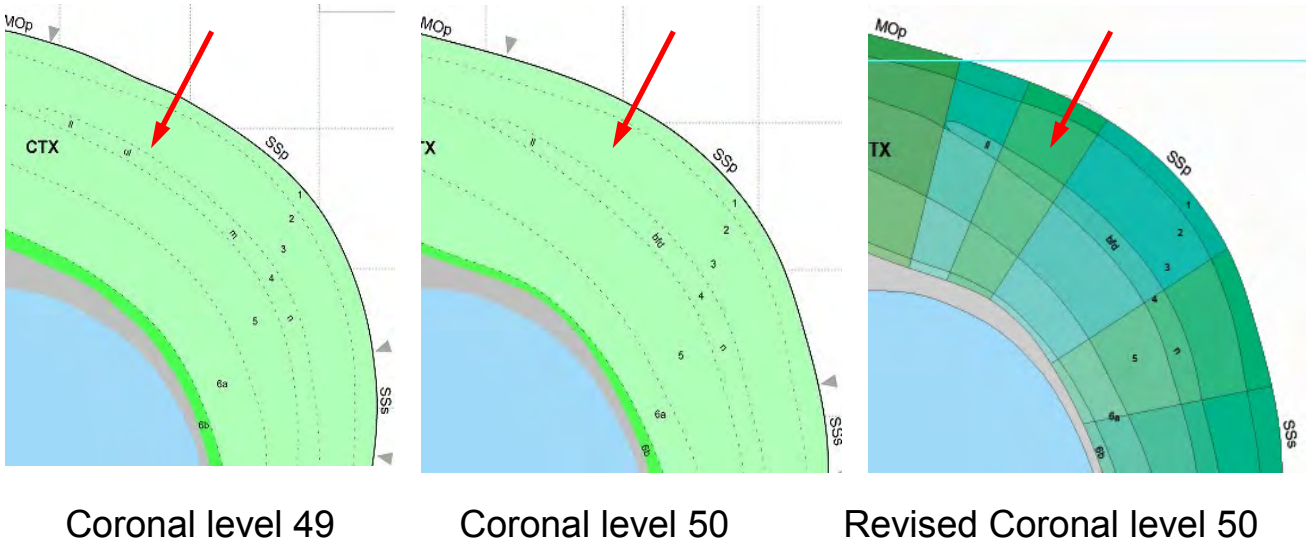


Figure 2. Example of the addition of structures missing from a single atlas plate.
Coronal levels 49 and 50 from the version 1 atlas, showing a missing annotation label in the level 50 plate, and the revised version 2 level 50 plate.

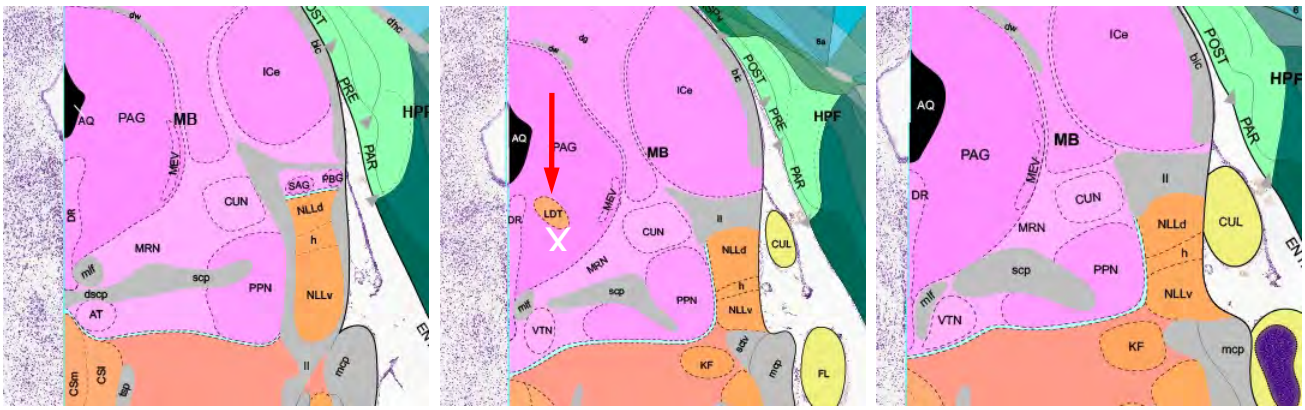


Figure 3. Example of the removal of a structure inappropriately included on one section.
Coronal levels 100-102 from the version 1 atlas, showing the presence an inappropriate structure (LDT) in the level 101 plate (red arrow). This structure was deleted in the version 2 atlas, as noted by the white X.

SYSTEMATIC CONVERSION OF TRADITIONAL DRAWINGS TO DIGITAL ANNOTATION DATABASE

The reprocessing of the reference atlas enables the systematic conversion of the reference atlas from traditional 2-D static plates to a digital annotation database accessed via an interactive user interface. Every region in each atlas drawing is now encapsulated by a closed polygon, assigned to a structure in the ontology and stored in a relational database.

An interactive atlas viewer has been implemented to allow users to explore the atlas at multiple levels of resolution and in context of the underlying Nissl and ontology (Figure 4). The viewer consists of an ontology panel on the left and image panel on the right. Selecting a structure in an image will select and reveal the structure in the ontology tree. Conversely, selecting a structure in the ontology will highlight the structure in the image. If the structure is not in the current image, the viewer will move to the "center" image containing the structure. A user can also select a structure by name/acronym search.

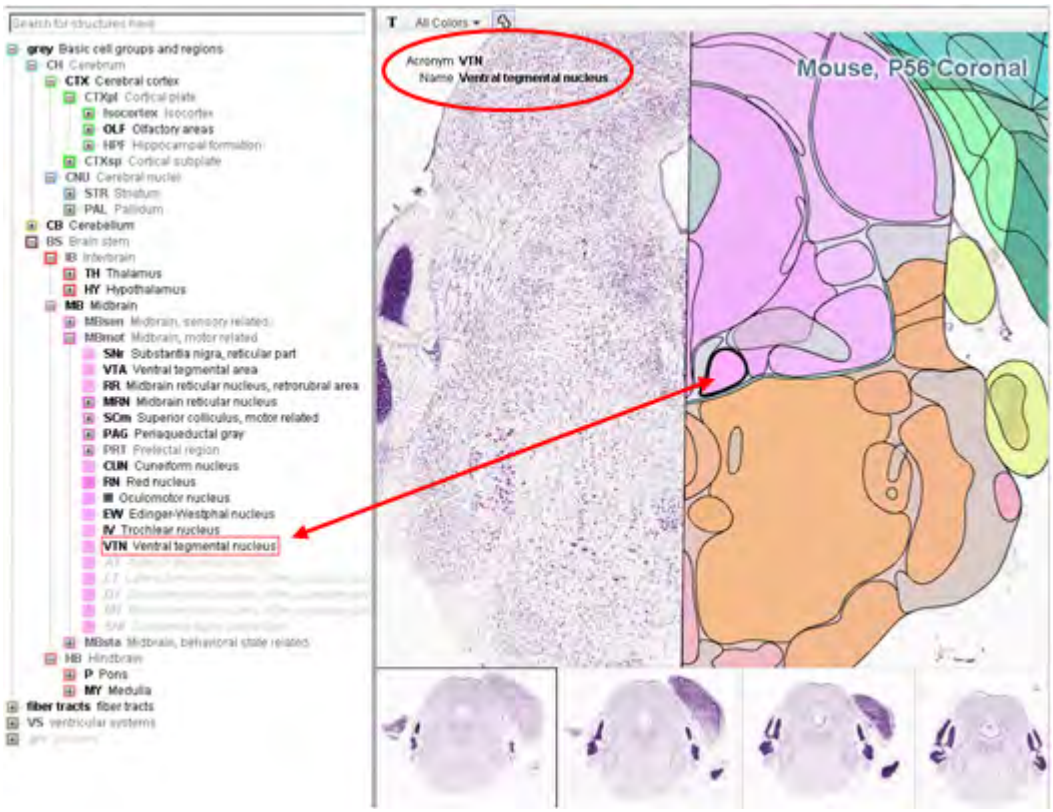


Figure 4. Screen shot of the interactive reference atlas viewer.

The structure name and acronym display (top-left of image panel) is interactively updated as a user moves over structures in the image. Colors and lines may be toggled on and off to see the underling Nissl image. Colors can also be in "Selection" mode where only a selected structure (and all its descendants) is colorized allowing exploration of ontology groupings. (See Figure 5)

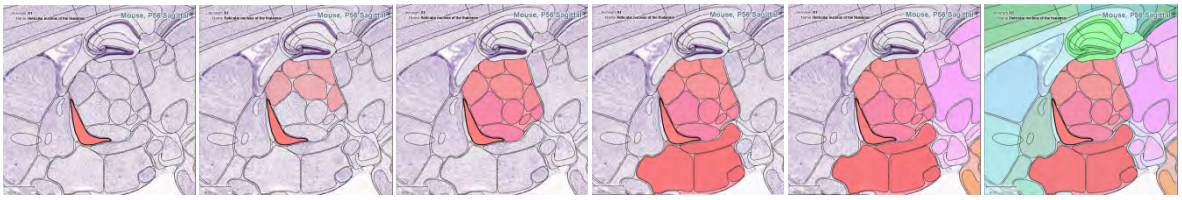


Figure 5. Moving up the ontology from nucleus to brain.
RT (Reticular nucleus of the thalamus), **DORpm** (Thalamus, polymodal association cortex related), **TH** (Thalamus), **IB** (Interbrain), **BS** (Brain stem), **grey** (Basic cell groups and regions).

The interactive atlas viewer can be launched from the "Reference Atlas" tab in the Allen Mouse Brain Atlas.

SUPPORTING 3-D INFORMATICS ANALYSIS AND VISUALIZATION

Changes to the drawings enabled the extraction of a deeper level of annotation, and enables enriched informatics analysis and visualization. The cornerstone of the automated informatics data processing pipeline is a standard 3-D reference space. From the annotation database, over 700 structures were extracted and reconstructed to form 3-D structural annotation for the reference space. The new 3-D reference models have been integrated into the Brain Explorer 2 application allowing for 3-D visualization of the areal parcellation of the isocortex, lobes of the cerebellum, fields of the hippocampus and major subdivisions of the thalamus and hypothalamus. (See Figure 6)

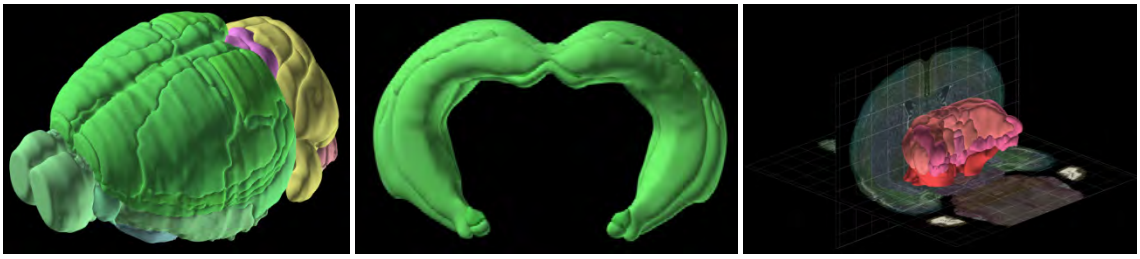


Figure 6. 3-D reference models viewed in the Brain Explorer 2 3-D viewer.
3-D rendering of the entire adult mouse brain (left), hippocampus (center) and internal structures overlaid onto atlas planes (right). Renderings are based on the Allen Reference Atlas version 2 and viewed in the interactive Brain Explorer 2 3-D viewer.

Providing a deeper level of annotation also allows for enriched informatics search tools. For example, the full parcellation of the isocortex into area-layer segments allows for an informatics search for areal and/or laminar enrichment in gene expression (Figure 7). See the Informatics Data Processing whitepaper for more details.

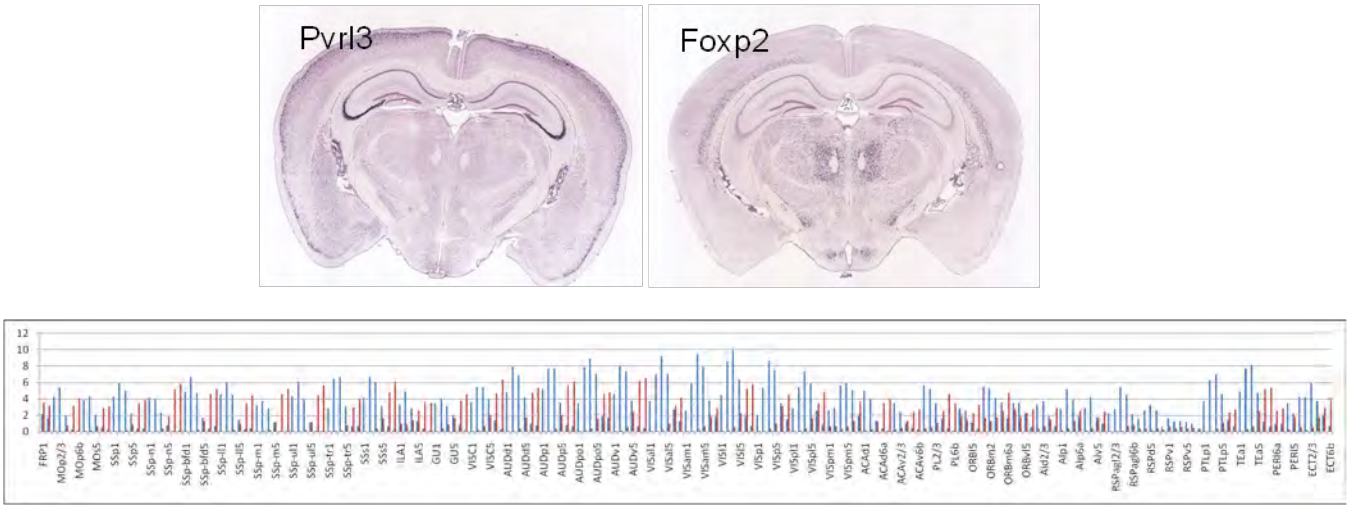


Figure 7. Search for differential expression in cortical layer.
Search for differential expression in cortical layers 2/3 and 6a results in genes poliovirus receptor-related 3 (Pvrl3) and forkhead box P2 (Foxp2). Graphs shows the expression profile of these two genes over the 217 area-layer segments of the isocortex (blue: Pvrl3, red: Foxp2).

APPENDIX 1. CHANGES TO THE ONTOLOGY IN VERSION 2

Structures added to the ontology

acronym[full name]

ANcr1gr [Crus 1, granular layer]

ANcr1pu [Crus 1, Purkinje layer]

ANcr1mo [Crus 1, molecular layer]

ANcr2gr [Crus 2, granular layer]

ANcr2pu [Crus 2, Purkinje layer]

ANcr2mo [Crus 2, molecular layer]

CBXmo [Cerebellar cortex, molecular layer]

COPYgr [Copula pyramidis, granular layer]

COPYpu [Copula pyramidis, Purkinje layer]

COPYmo [Copula pyramidis, molecular layer]

CENT2gr [Lobule II, granular layer]

CENT2pu [Lobule II, Purkinje layer]

CENT2mo [Lobule II, molecular layer]

CENT3gr [Lobule III, granular layer]

CENT3pu [Lobule III, Purkinje layer]

CENT3mo [Lobule III, molecular layer]

CUL4gr [Lobule IV, granular layer]

CUL4pu [Lobule IV, Purkinje layer]

CUL4mo [Lobule IV, molecular layer]

CUL4, 5gr [Lobules IV-V, granular layer]

CUL4, 5pu [Lobules IV-V, Purkinje layer]

CUL4, 5mo [Lobules IV-V, molecular layer]

CUL5gr [Lobule V, granular layer]

CUL5pu [Lobule V, Purkinje layer]

CUL5mo [Lobule V, molecular layer]

DECgr [Declive (VI), granular layer]

DECpu [Declive (VI), Purkinje layer]

DECmo [Declive (VI), molecular layer]

DG-sgz [Dentate gyrus, subgranular zone]

DG-mo [Dentate gyrus, molecular layer]

DG-po [Dentate gyrus, polymorph layer]

FLgr [Flocculus, granular layer]

FLpu [Flocculus, Purkinje layer]

FLmo [Flocculus, molecular layer]

FOTUgr [Folium-tuber vermis (VII), granular layer]

FOTUpu [Folium-tuber vermis (VII), Purkinje layer]

FOTUmo [Folium-tuber vermis (VII), molecular layer]

LINGgr [Lingula (I), granular layer]

LINGpu [Lingula (I), Purkinje layer]

LINGmo [Lingula (I), molecular layer]

ME [Median eminence]

NODgr [Nodulus (X), granular layer]

NODpu [Nodulus (X), Purkinje layer]

NODmo [Nodulus (X), molecular layer]

PAR1 [Parasubiculum, layer 1]

PAR2 [Parasubiculum, layer 2]

PAR3 [Parasubiculum, layer 3]

POST1 [Postsubiculum, layer 1]

POST2 [Postsubiculum, layer 2]

POST3 [Postsubiculum, layer 3]

PFLgr [Paraflocculus, granular layer]

PFLpu [Paraflocculus, Purkinje layer]

PFLmo [Paraflocculus, molecular layer]

PRE1 [Postsubiculum, layer 1]

PRE2 [Postsubiculum, layer 2]

PRE3 [Postsubiculum, layer 3]

PRMgr [Paramedian lobule, granular layer]

PRMpu [Paramedian lobule, Purkinje layer]

PRMmo [Paramedian lobule, molecular layer]

PYRgr [Pyramus (VIII), granular layer]

PYRpu [Pyramus (VIII), Purkinje layer]

PYRmo [Pyramus (VIII), molecular layer]

SIMgr [Simple lobule, granular layer]

SIMpu [Simple lobule, Purkinje layer]

SIMmo [Simple lobule, molecular layer]

SS1 [Somatosensory areas, layer 1]

SS2 [Somatosensory areas, layer 2]

SS3 [Somatosensory areas, layer 3]

SS4 [Somatosensory areas, layer 4]

SS5 [Somatosensory areas, layer 5]

SS6a [Somatosensory areas, layer 6a]

SS6b [Somatosensory areas, layer 6b]

UVUgr [Uvula (IX), granular layer]

UVUpu [Uvula (IX), Purkinje layer]

UVUmo [Uvula (IX), molecular layer]

Modified Structure Acronyms and Names

old acronym[old full name] > new acronym[new full name]

chfl [choroids fissure] > chfl [choroid fissure]

chpl [choroids plexus] > chpl [choroid plexus]

NIS [Nucleus intercalates] > NIS [Nucleus intercalatus]

VisC6b [Visceral area, layer 6b] > VISC6b [Visceral area, layer 6b]

SSp-tr6 [Primary somatosensory area, trunk, layer 6a] > SSp-tr6a [Primary somatosensory area, trunk, layer 6a]

APPENDIX 2. LIST OF CHANGES TO DRAWINGS IN VERSION 2

CORONAL

Addition of polygons

1) Cerebral cortex: Polygons were added based on the existing arrow heads.
2) Hippocampus: Polygons were added based on the existing arrow heads and ISH data.
3) Cerebellum: Polygons were added based on existing labels, and comparison to other published atlases.
4) Subcortical Structures (thalamus, hypothalamus, midbrain, pons, medulla): Polygons were added based on existing labels and comparison to other published atlases.

Resolution of inconsistencies

Coronal levels (from anterior to posterior)

Coronal levels 1-28: Removed texture from MOBgl, and AOBgl in order to create a single polygon for each structure.

Coronal levels 20-21: Merged layers 1 and 2 within AONl and AONe for consistency with ontology.

Coronal level 35: Added polygon for TTv3 for consistency with level 34.

Coronal level 42: Extended layer 6b into ILA based on ISH data (gene, *Ctgf*).

Coronal levels 44-47: Separated MS and NDA into two polygons based on ISH data (gene, *Stmn2*).

Coronal level 50: Extended the NDB and MA to the surface of the brain for consistencies with level 51. Added delineation for SSp-ul (layers 1-6b) for consistency with surrounding levels.

Coronal levels 67-69: Removed structure da within ZI for consistency with ontology.

Coronal level 68: Removed FC based on ISH data (gene, *Pcp4*).

Coronal levels 69-79: Merged two polygons within FC for consistency with ontology.

Coronal levels 78-81: Changed AQ to V3.

Coronal levels 78-80: Added layer CA3slu to ventral CA3 for internal consistency.

Coronal level 79: Removed SUBv, expanding COApm to take its place, and expanded PA downward for consistency with level 80, and ISH data (genes, *Dlk1* and C*hrna7*).

Coronals 79-89: Added layer SUBd-sr between SUBd-sp and SUBd-m for consistency with levels 90-92, and SUBv.

Coronal level 83: Removed PPT based on final print version of Allen Reference Atlas. Renamed IPF to IPN for consistency with ontology.

Coronal levels 83, 84: Removed CA2, replacing it with CA1 based on ISH data.

Coronal levels 84, 86-98: Separated bsc from SCop.

Coronal level 86: Removed upper portion of bsc for consistency between sections.

Coronal level 86, 87: Divided ENTmv into two layers for consistency with surrounding levels.

Coronal levels 88-89: Redrew the border between SUBv-sr and SUBv-m to make them consistent with other levels.

Coronal levels 90-91: Added PRE2 for consistency with level 93.

Coronal level 94, 96, 97: Shifted layer 6b to reach ENTl, for consistency with surrounding levels and ISH data (genes, *Drd1a* and *Ctgf*).

Coronal levels 97-99: Merged two polygons within POST2 and PRE2 in order to be consistent with ontology.

Coronal level 101: Removed LTD within PAG for consistency with other levels.

Coronal level 104: Reduced the size of SCdw.

Coronal level 107: Added CENT3mo.

Coronal level 123: The polygon labeled DEC was named CUL4,5.

Coronal level 123-125: The polygons labeled SIM were named DEC.

Coronal level 126: Removed lateral V4 polygon for consistency with sagittal atlas.

Coronal level 132: Removed LRN polygon based on final print version Allen Reference Atlas.

SAGITTAL

Addition of polygons

1) Cerebral cortex: Polygons were added based on the existing arrow heads. Structure SS was added to ontology (layers 1-6b) to more accurately represent the region called SSp.
2) Hippocampus: Polygons were added based on the existing arrow heads and ISH data.
3) Cerebellum: Polygons were added based on existing labels and comparison to other published atlases.
4) Subcortical Structures (thalamus, hypothalamus, midbrain, pons, medulla): Polygons were added based on existing labels, and comparison to other published atlases.

Resolution of inconsistencies

Sagittal levels (from lateral to medial)

Sagittal level 1: Added FLmo, removed CA3 from this section and replaced it with CA1.

Sagittal level 2: Added FLmo/gr. Renamed DG to CA1-3slm.

Sagittal level 3: Changed PFL to FL, and COPY to PFL.

Sagittal level 4, 5: Changed COPY to PFL.

Sagittal level 5: Extended polygons PRE and ENTm5 to cover undefined area for consistency with other levels.

Sagittal level 6: Changed dorsal half of FL to PFL. Added CA2-so, -sp, -sr, and CA3-so, -sp, -sr to ventral CA1.

Sagittal level 7: Replaced ventral CA1 with CA2-so, -sp, -sr, and CA3.

Sagittal levels 7-8: Merged two SUBv layers to one for consistency with SUBd.

Sagittal level 8-13: GP was divided into GPe and GPi.

Sagittal level 8-16, 18: Added isl for consistency with level 17 and coronal.

Sagittal level 10-12: Renamed ventral CA3-so, -sp, and –sr to DG-mo, -sg, and –po.

Sagittal level 10-21: Divided SC into SCm and SCs based on ISH data (gene, *Dgkh*).

Sagittal level 11: Extended PIR3 into deep AON polygon for consistency with ontology (there is no AON3 in ontology).

Sagittal levels 11-17: Restricted FRP to layers 1 and 2/3 for consistency with coronal drawings.

Sagittal levels 11-18: Created border between PRNr and PRNc.

Sagittal levels 13-16: Created border between LPO and LHA.

Sagittal levels 14-19: Subdivided AON and PIR into two layers for consistency with other levels.

Sagittal level 16, 18: Added islm for consistency with coronal.

Sagttials 17-21: Divided AQ and V4 into two polygons.

Sagittal level 17: Extended NDB to ventral edge of brain for consistency with surrounding levels.

Sagittal levels 17-19: Subdivided TTv into two layers.

Sagittal level 18: Renamed V4r to V4.

Sagittal levels 18-19: Subdivided TTd into two layers.

Sagittal level 19: Added CA2 and FC, and took out CA1.

Sagittal level 19, 21: Subdivided OT into two layers for consistency with other levels.

Sagittal level 20: Added ME, replacing SCH with RCH and ARH. Added TTd1 for consistency with coronal atlas. Divided MS and NDB.

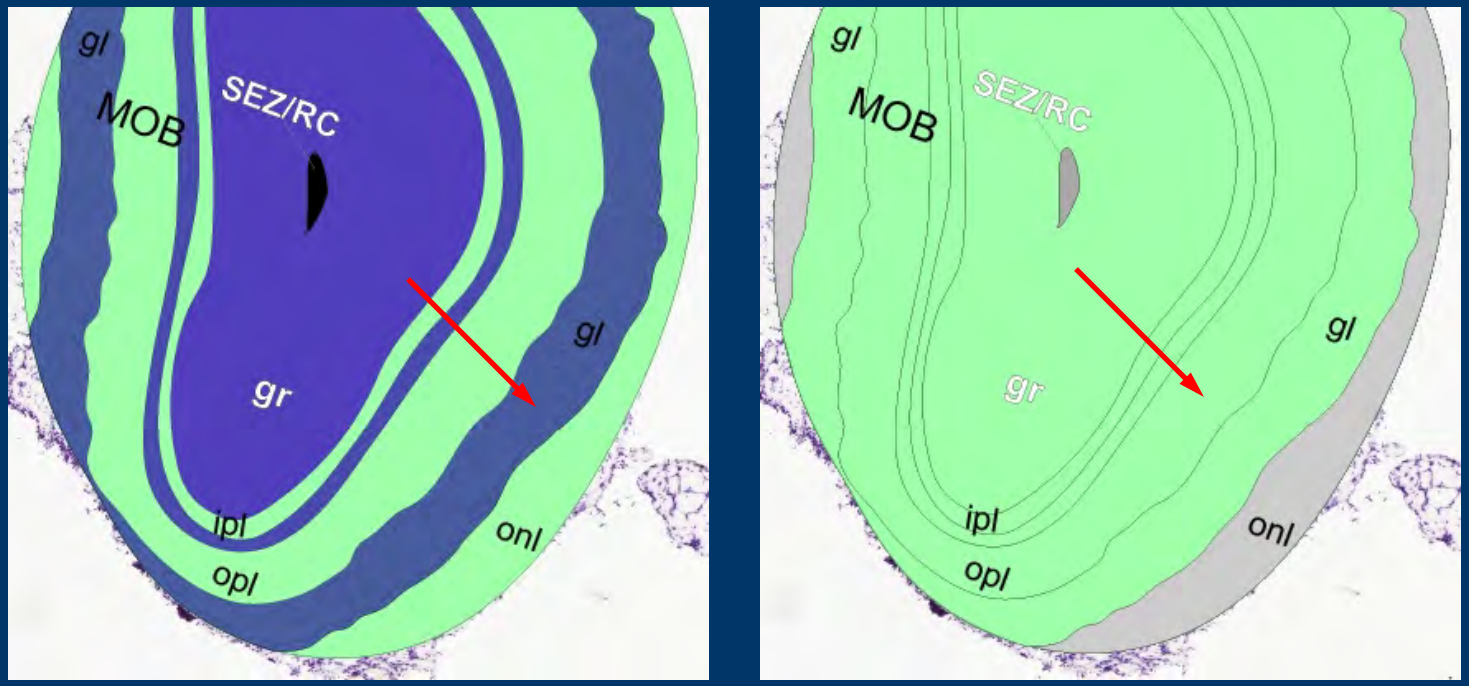
Sagittal level 21: Subdivided TTv and TTd into two layers. Added DG, CA2 and FC.

Appendix 3. Updates to the Allen Reference Atlas for adult mouse brain: correction of inconsistencies.

ALLEN INSTITUTE *for* BRAIN SCIENCE

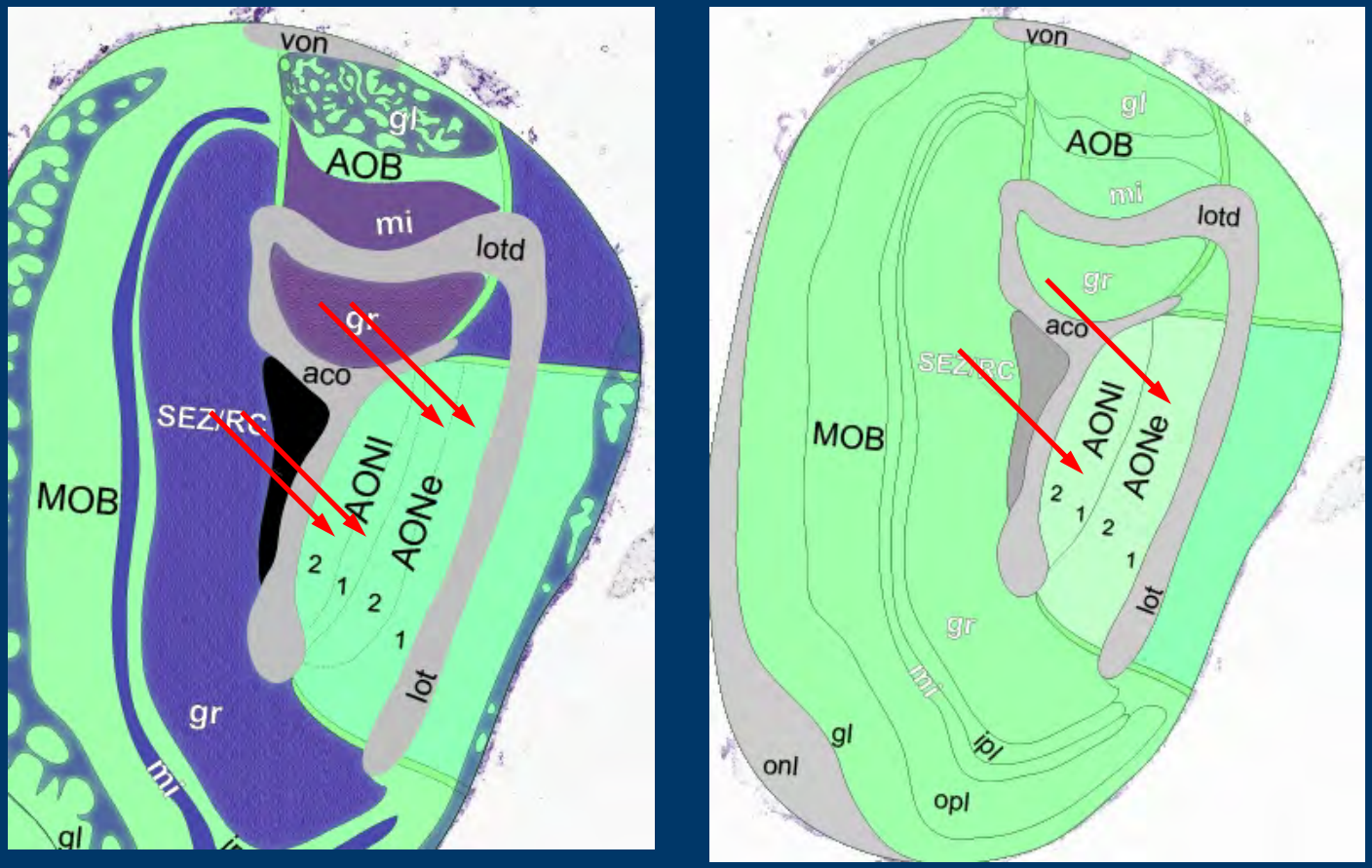
Fueling Discovery

Coronal levels 1-28: Removed texture from MOBgl, and AOBgl in order to create a single polygon for each structure.



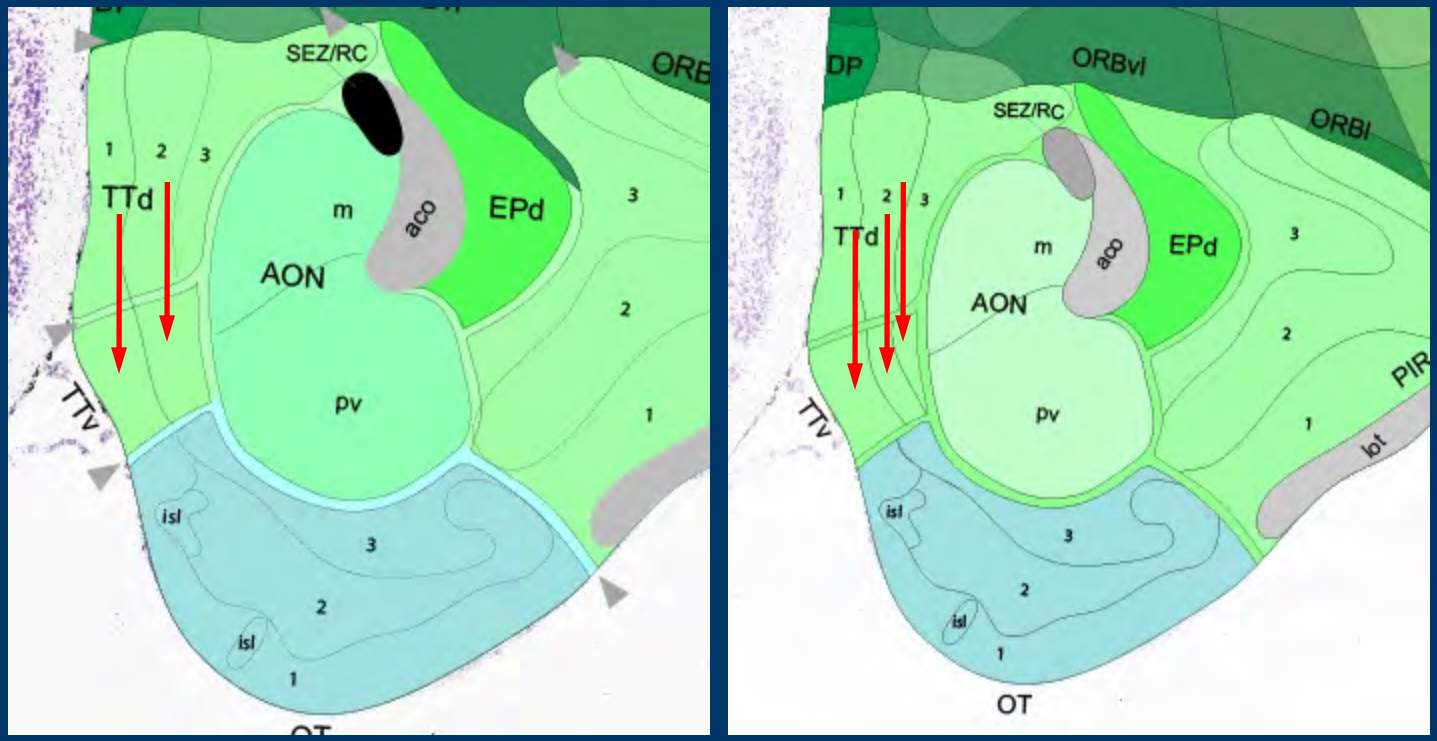
Note: left panel is the original version and right panel is the new version.

Coronal levels 20-21: Merged layers 1 and 2 within AONl and AONe for consistency with ontology.



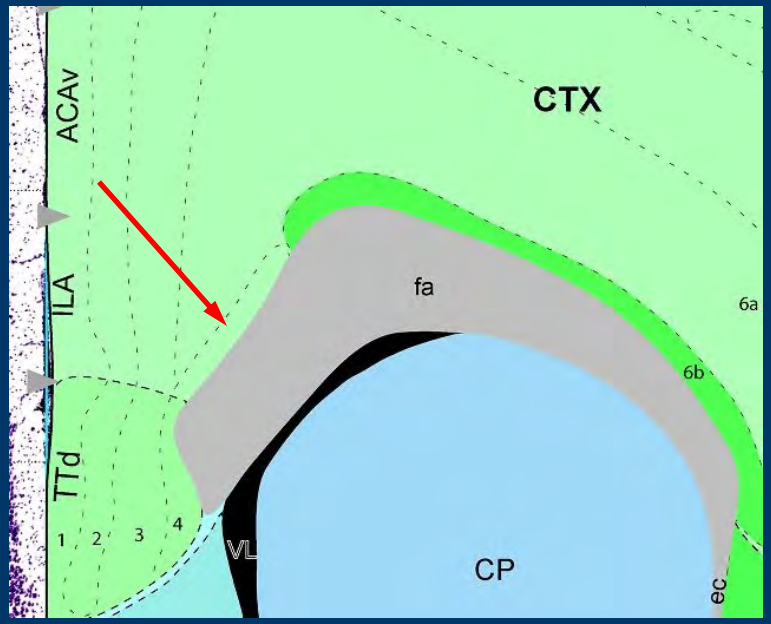
Note: left panel is the original version and right panel is the new version.

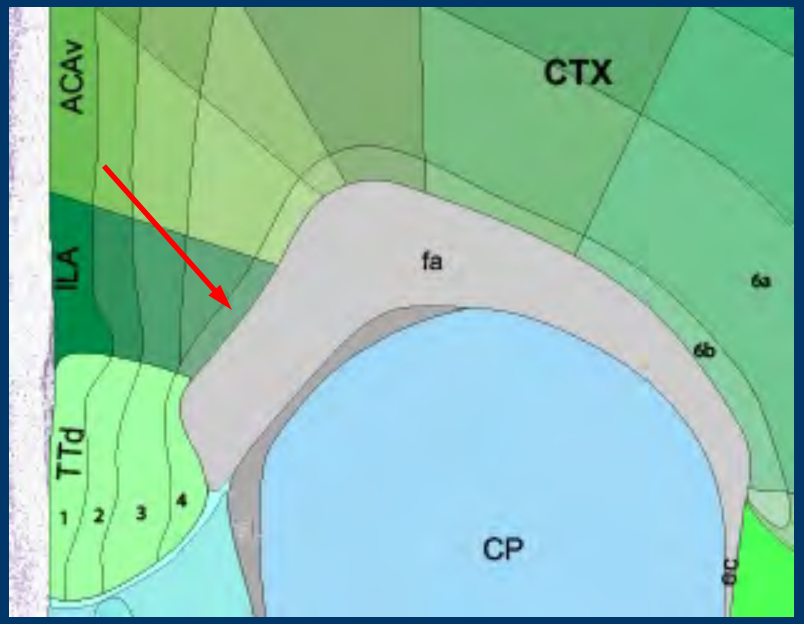
Coronal level 35: Added polygon for TTv3 for consistency with level 34.



Note: left panel is the original version and right panel is the new version.

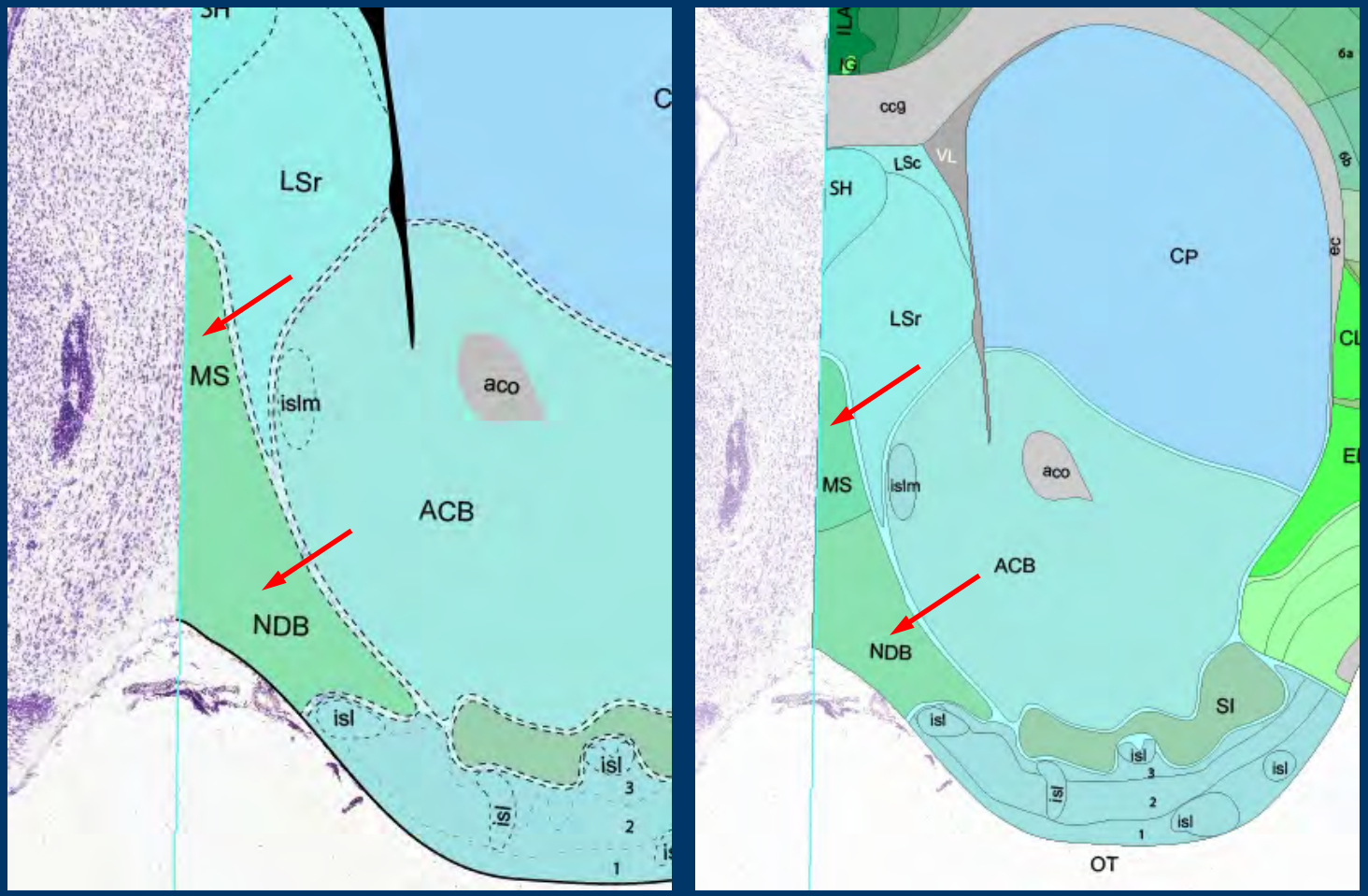
Coronal level 42: Extended layer 6b into ILA based on ISH data (gene, Ctgf).





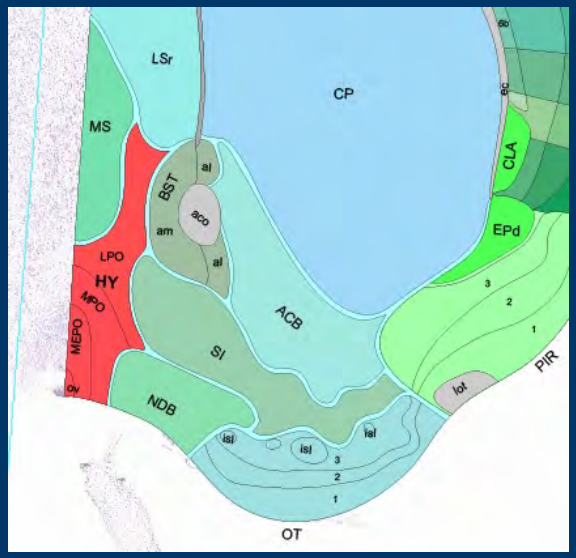
Note: left panel is the original version and right panel is the new version.

Coronal levels 44-47: Separated MS and NDA into two polygons based on ISH data (gene, Stmn2).

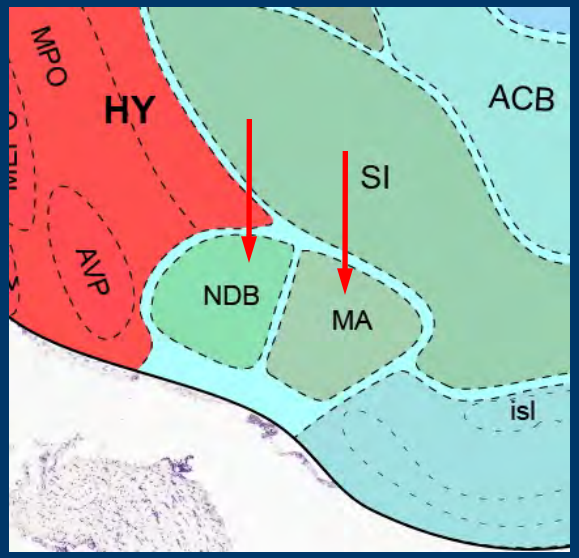


Note: left panel is the original version and right panel is the new version.

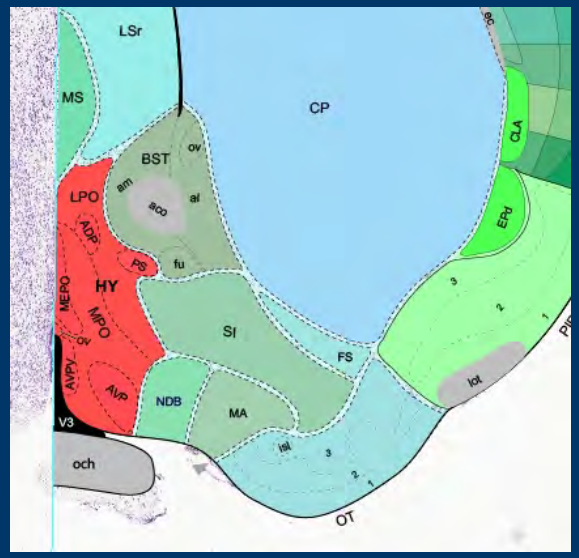
Coronal level 50: Extended the NDB and MA to the surface of the brain for consistencies with level 51.



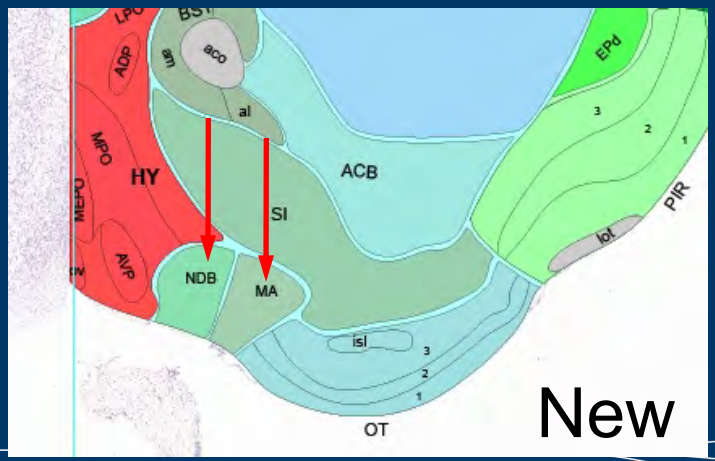
Coronal level 49



Coronal level 50

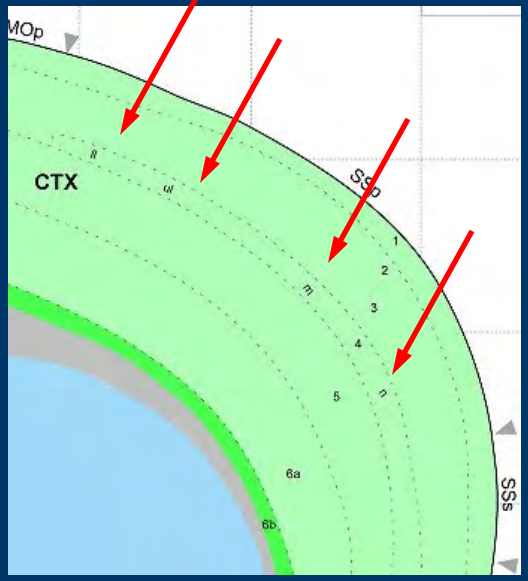


Coronal level 51

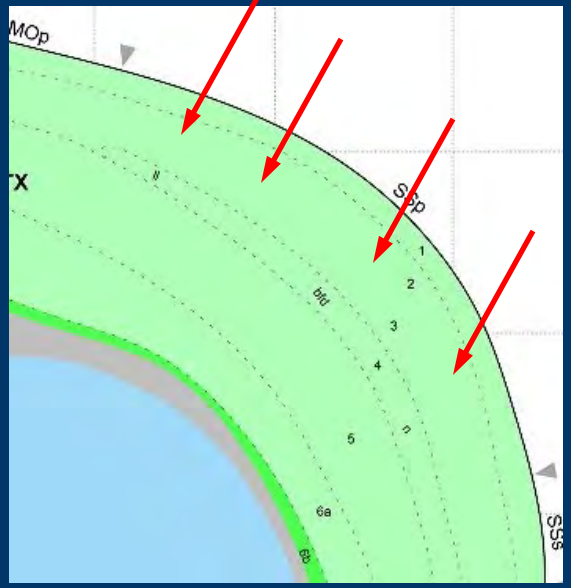


Coronal level 50

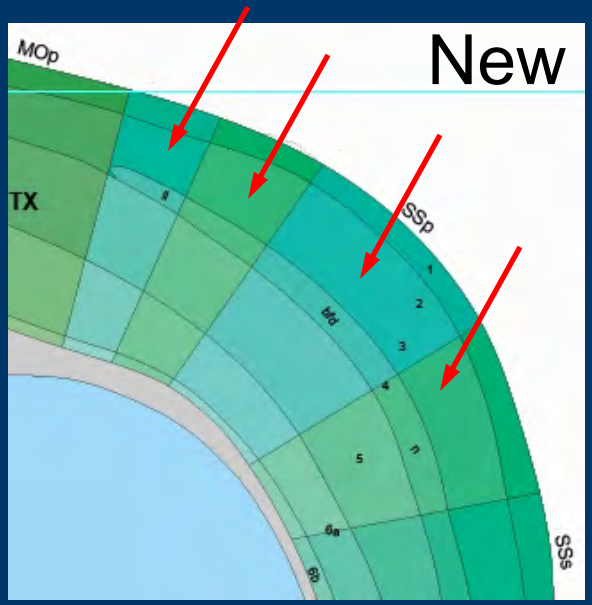
Coronal level 50: Added delineation for SSp-ul (layers 1-6b) for consistency with surrounding levels.



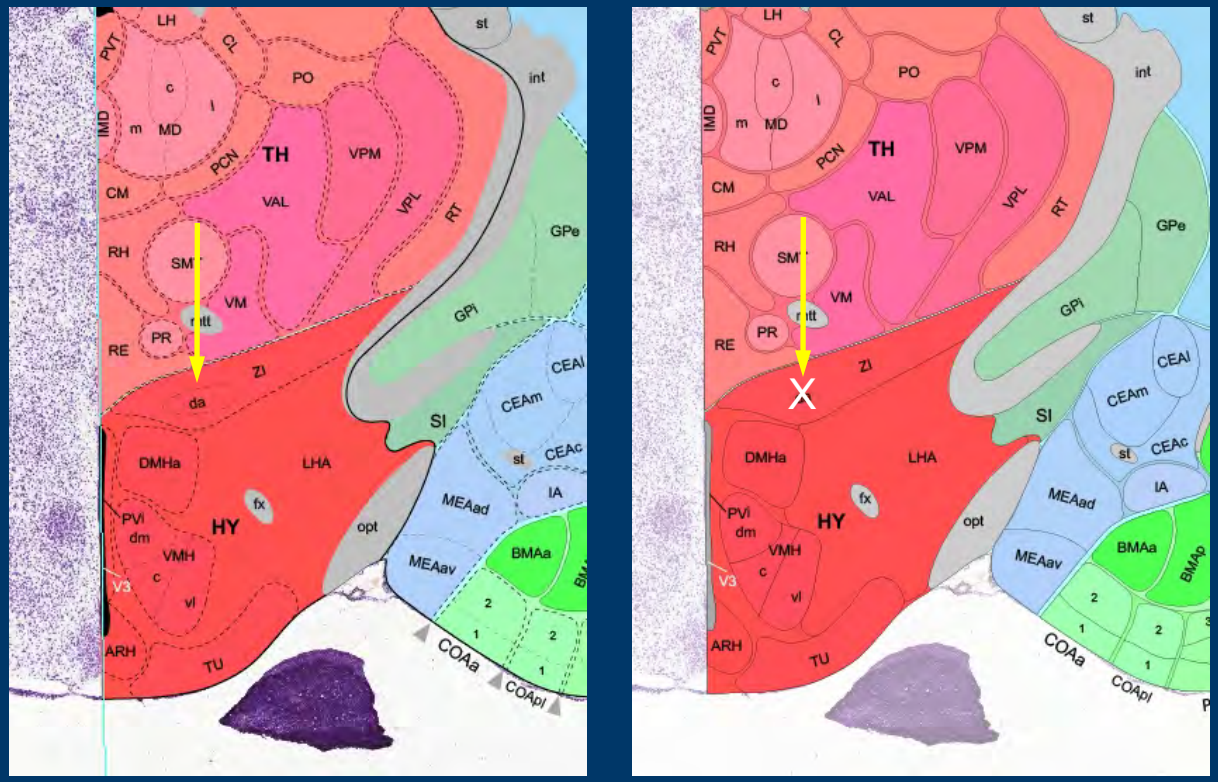
Coronal level 49



Coronal level 50

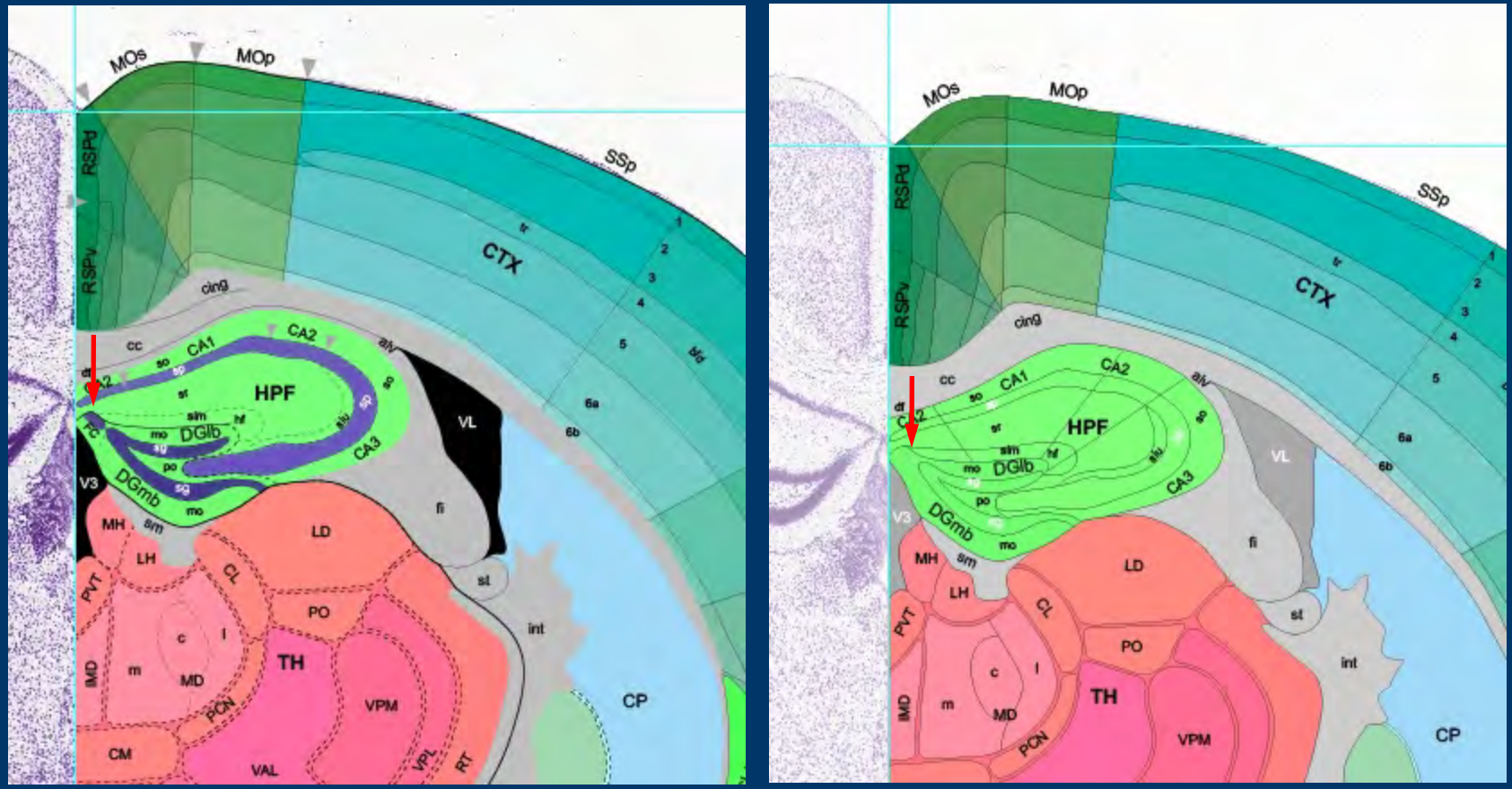


Coronal levels 67-69: Removed structure da within ZI for consistency with ontology.



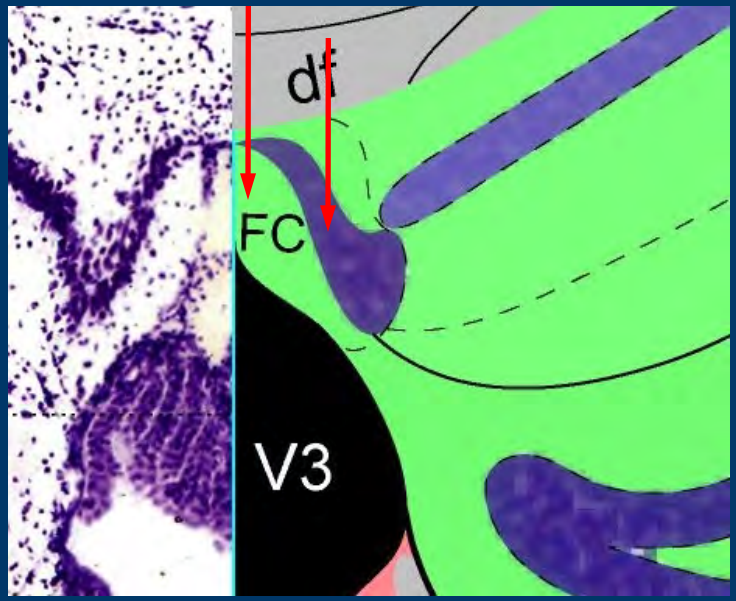
Note: left panel is the original version and right panel is the new version.

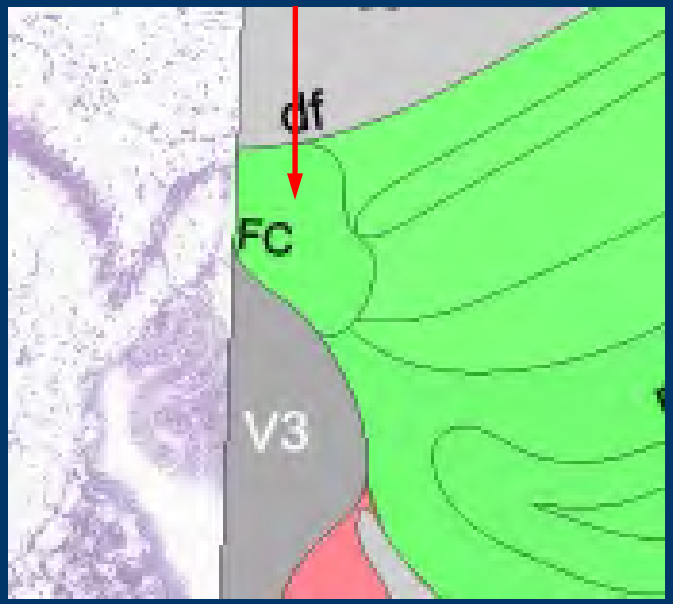
Coronal level 68: Removed FC based on ISH data (gene, Pcp4).



Note: left panel is the original version and right panel is the new version.

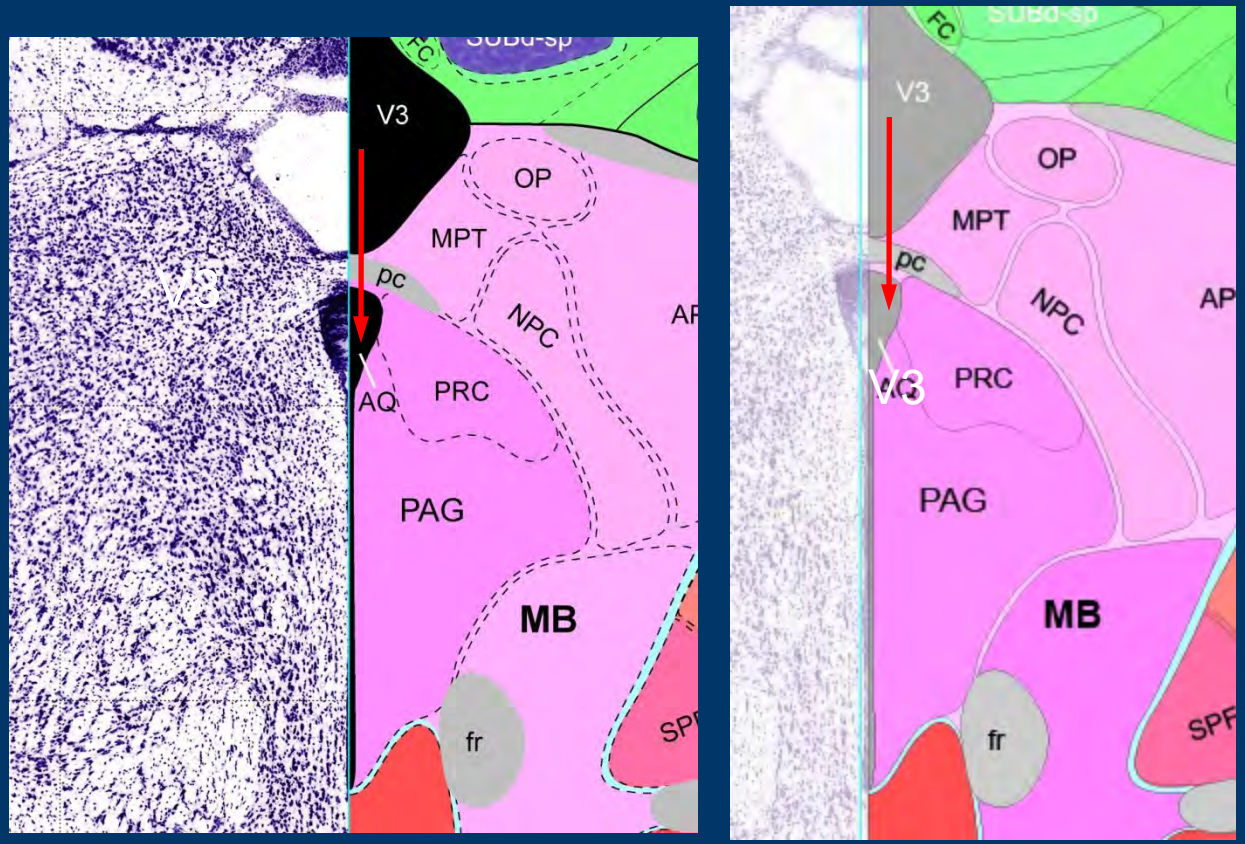
Coronal levels 69-79: Merged two polygons within FC for consistency with ontology.





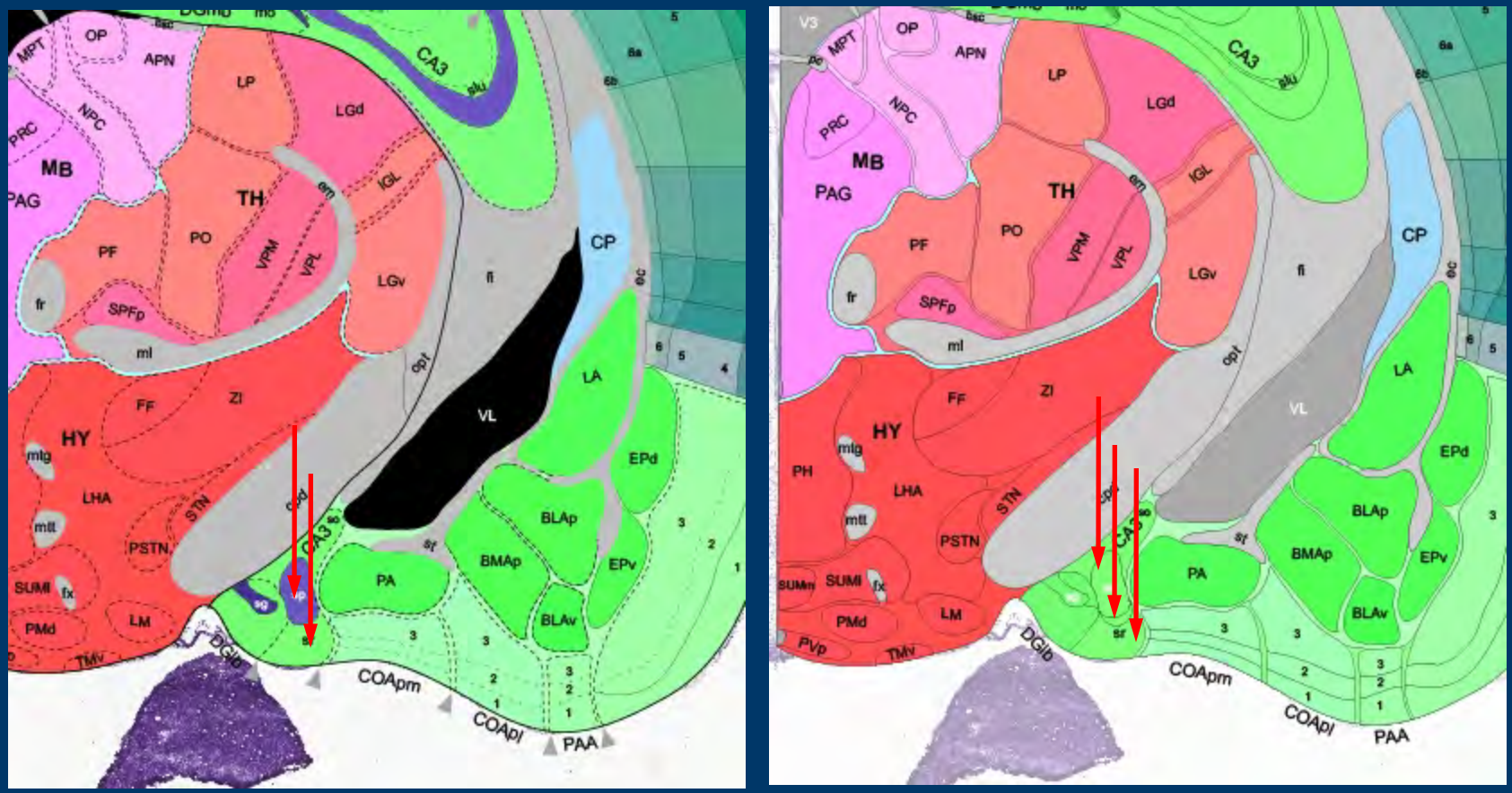
Note: left panel is the original version and right panel is the new version.

Coronal levels 78-81: Changed AQ to V3.



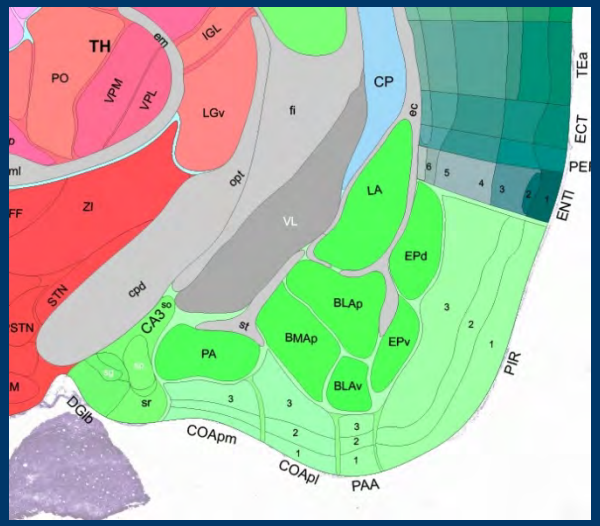
Note: left panel is the original version and right panel is the new version.

Coronal levels 78-80: Added layer CA3slu to ventral CA3 for internal consistency.

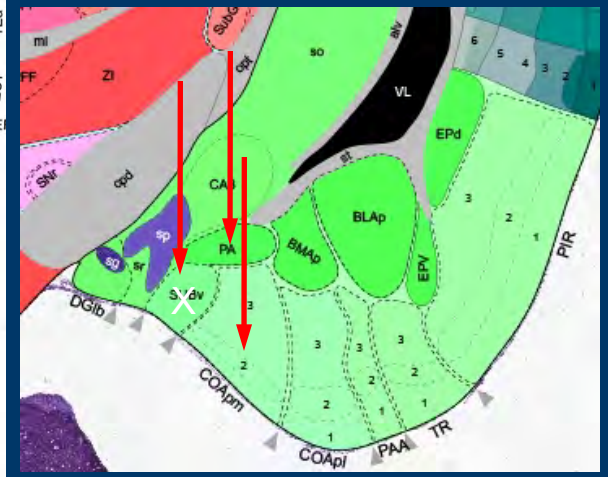


Note: left panel is the original version of CA3 and right panel is the new version.

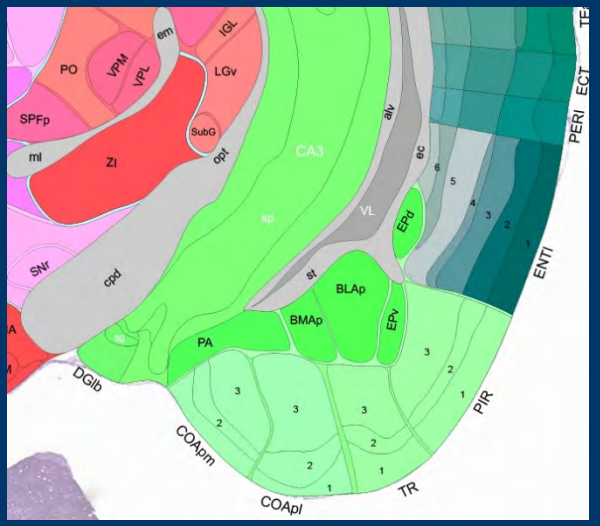
Coronal level 79: Removed SUBv, expanding COApm to take its place, and expanded PA downward for consistency with level 80, and ISH data (genes, Dlk1 and Chrna7).



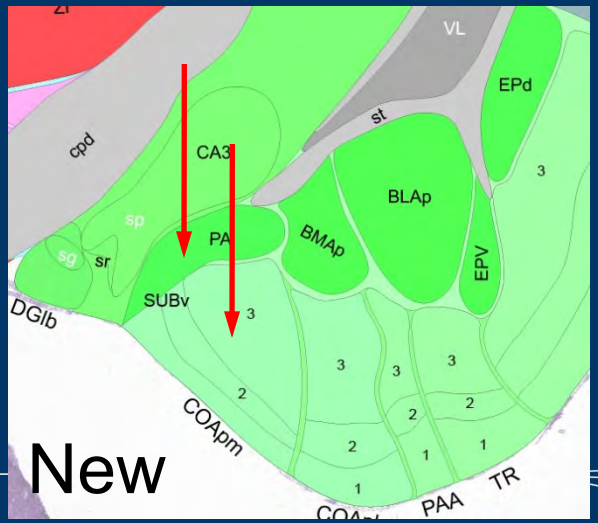
Coronal level 78



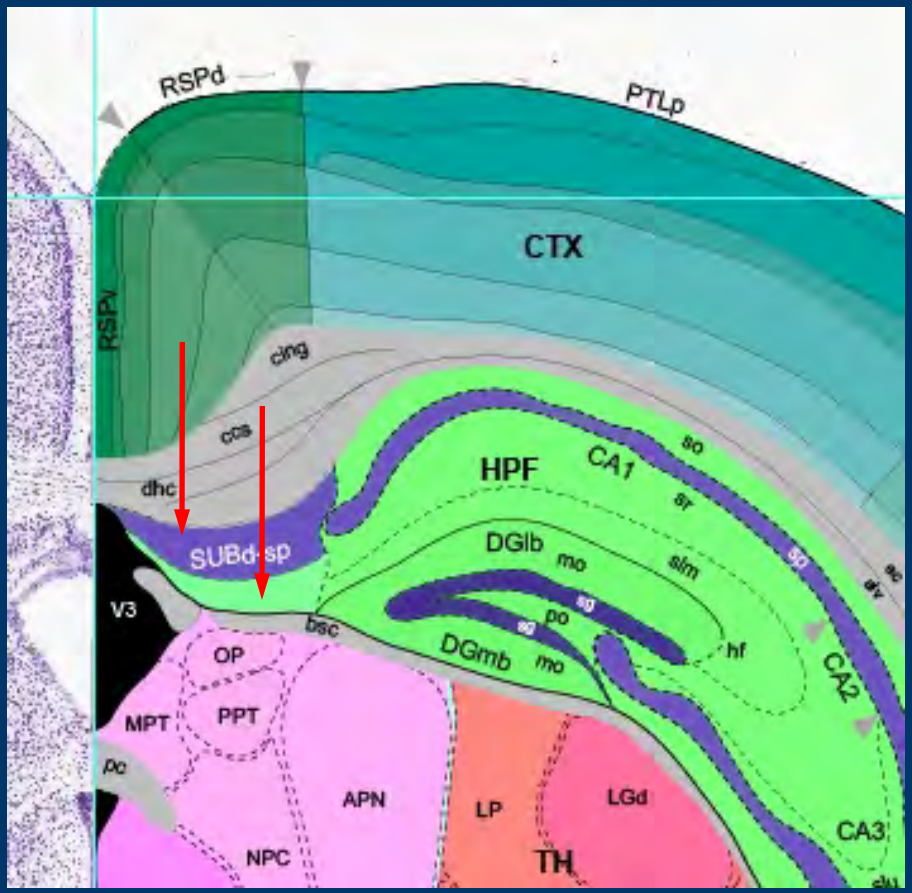
Coronal level 79

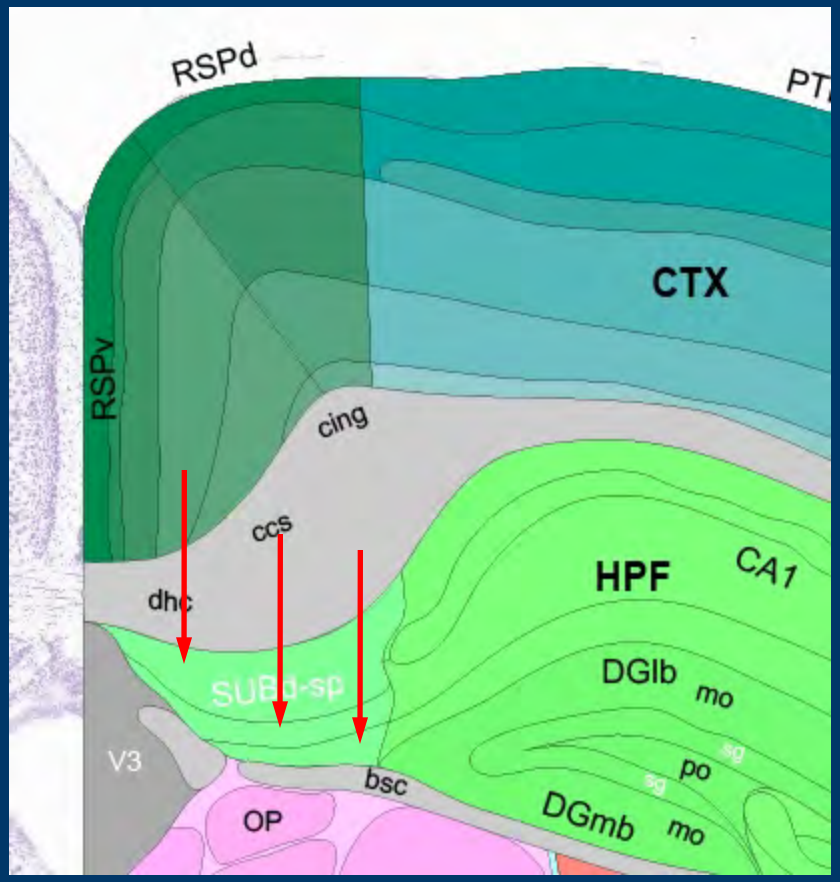


Coronal level 80



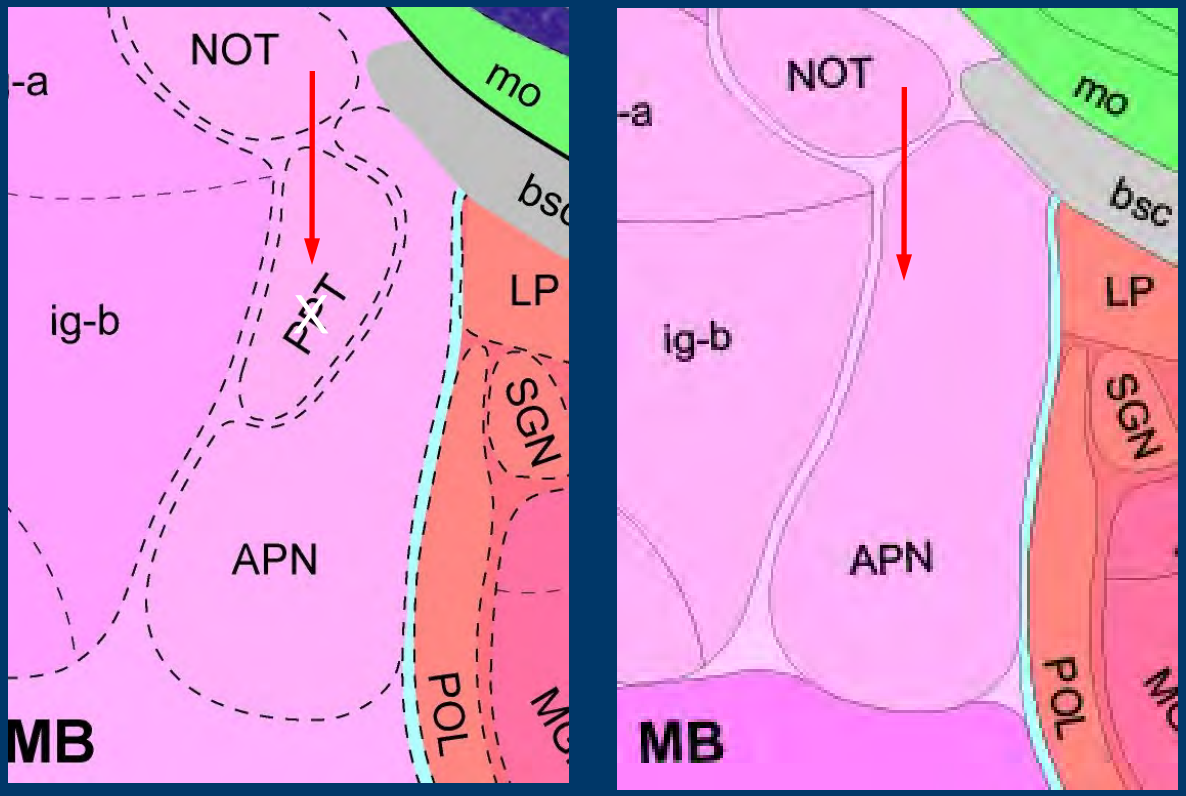
Coronals 79-89: Added layer SUBd-sr between SUBd-sp and SUBd-m for consistency with levels 90-92, and SUBv.





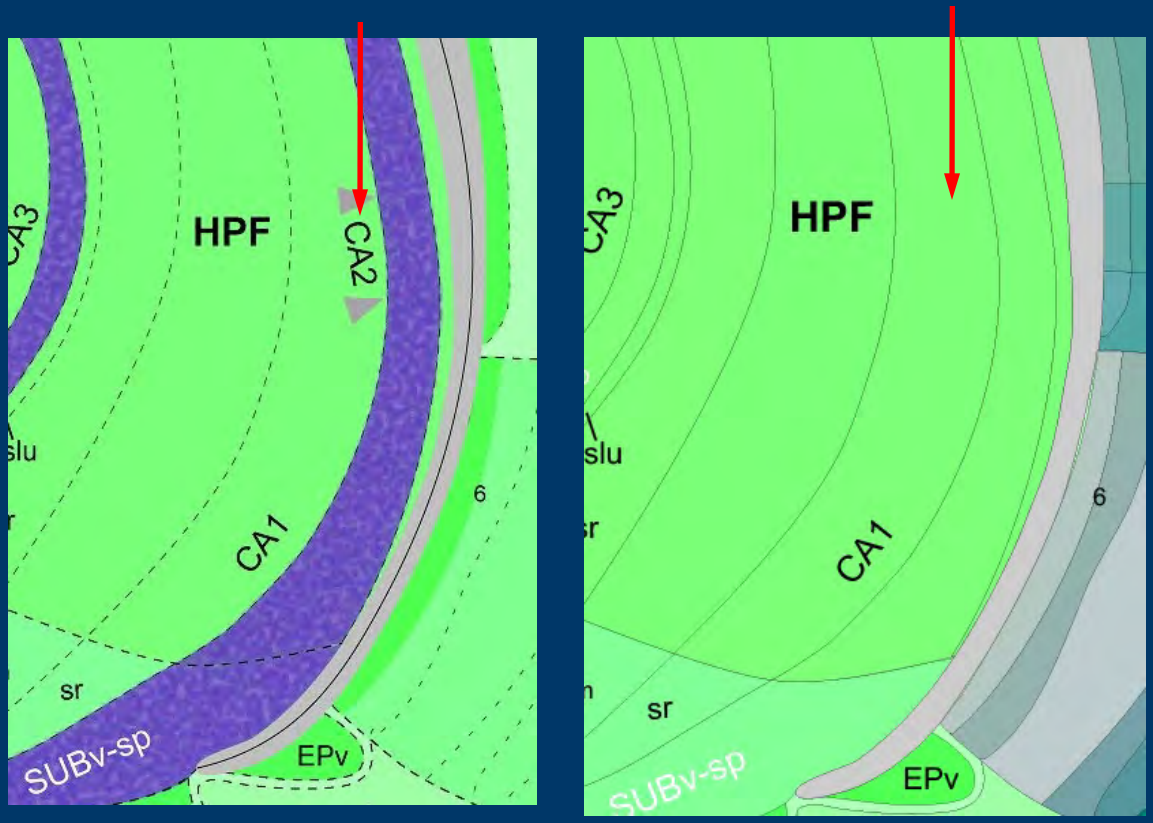
Note: left panel shows the original version of SUB and right panel is the new version.

Coronal level 83: Removed PPT based on final print version of Hong-Wei's atlas. Renamed IPF to IPN for consistency with ontology.



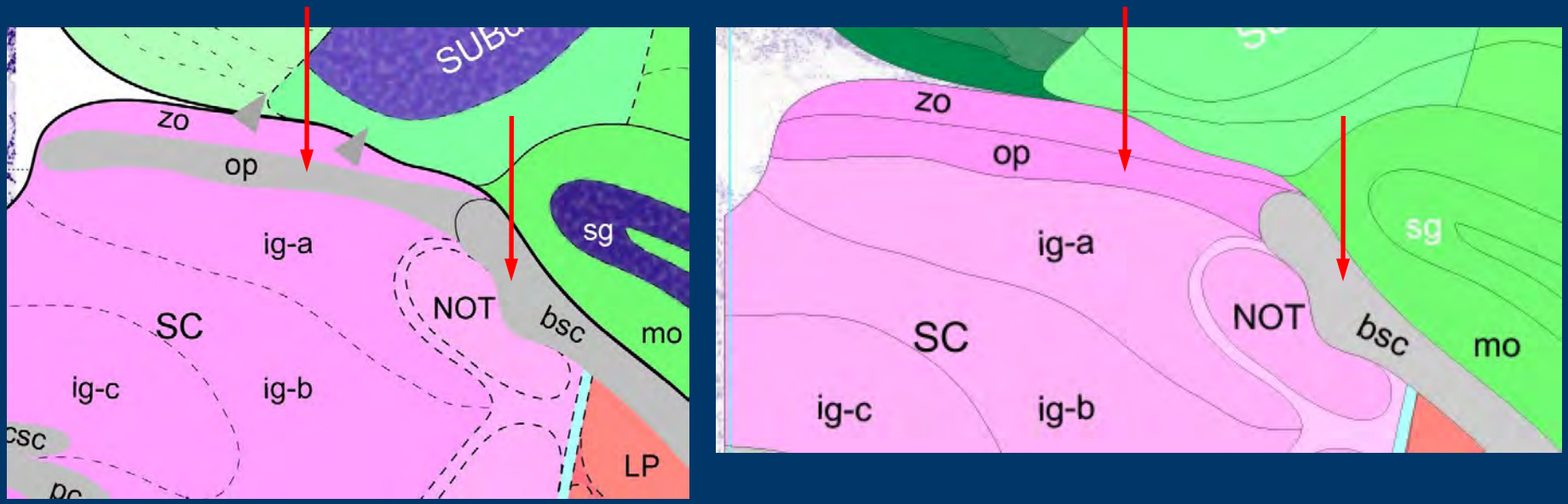
Note: left panel is the original version and right panel is the new version.

Coronal levels 83, 84: Removed CA-2, replacing it with CA1 based on ISH data.



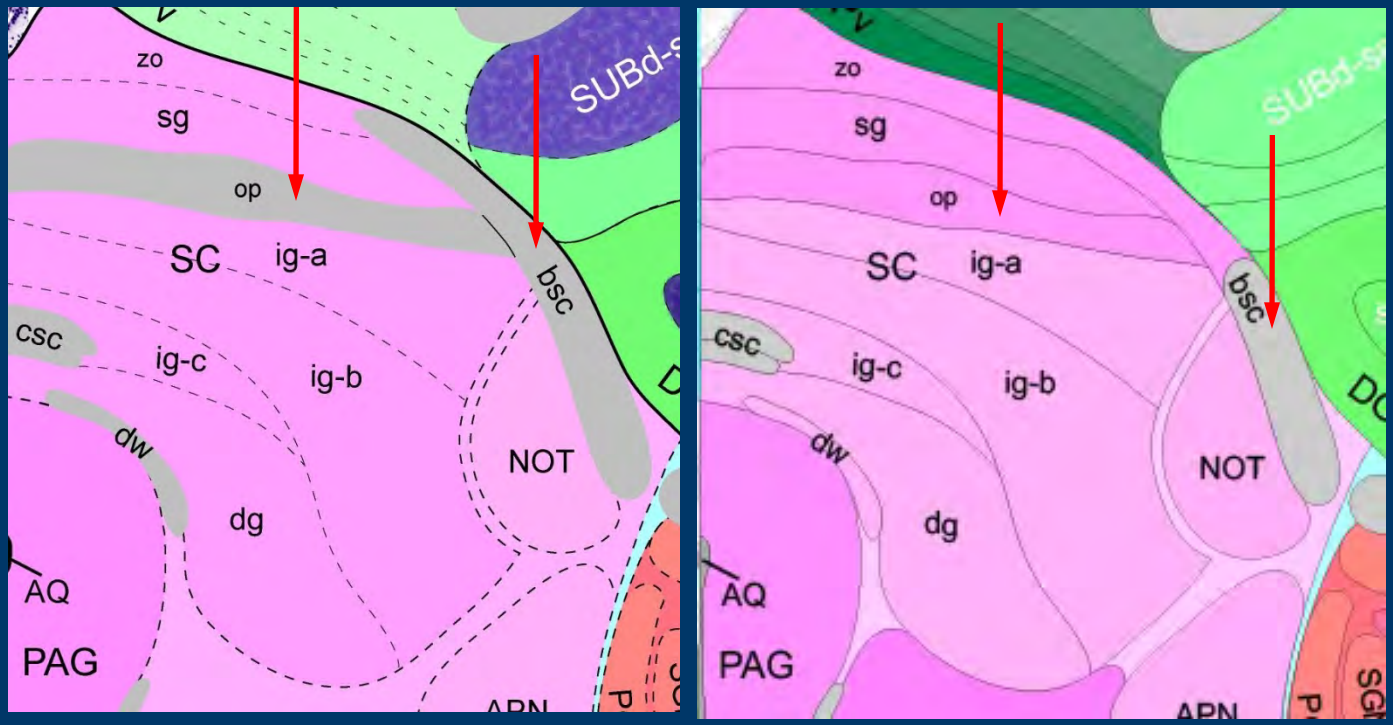
Note: left panel is the original version and right panel is the new version.

Coronal levels 84, 86-98: Separated bsc from SCop.



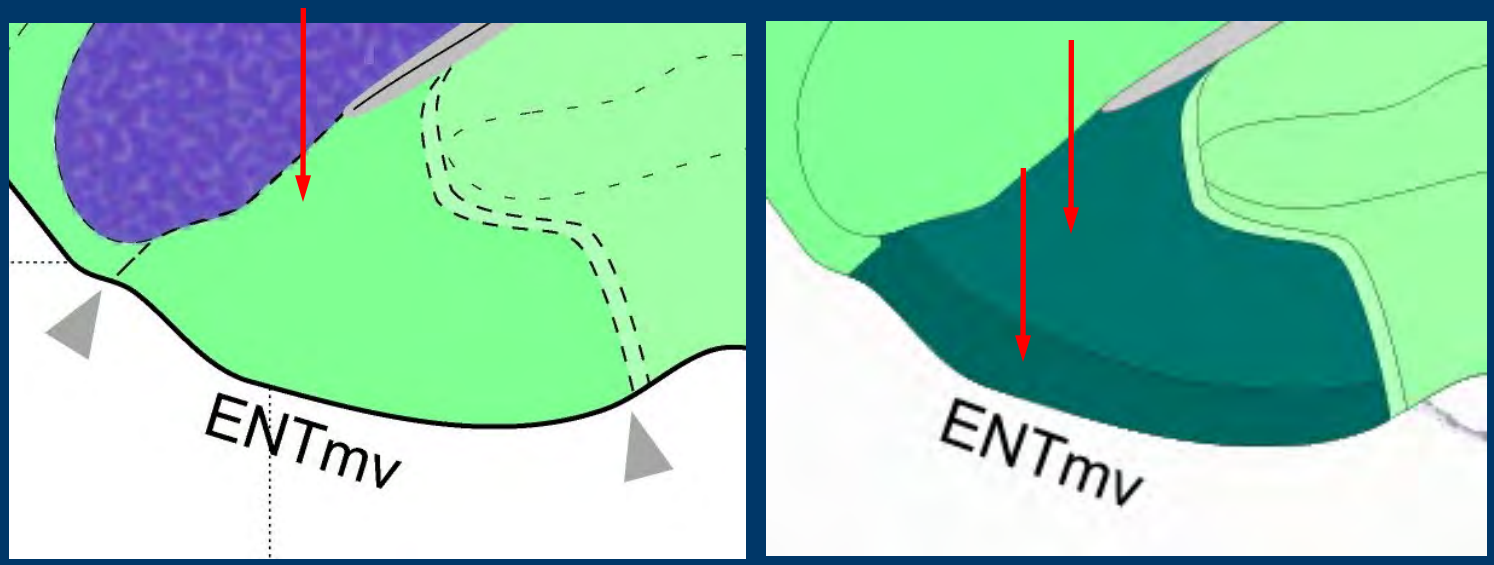
Note: left panel is the original version and right panel is the new version.

Coronal level 86: Removed upper portion of bsc for consistency between sections.



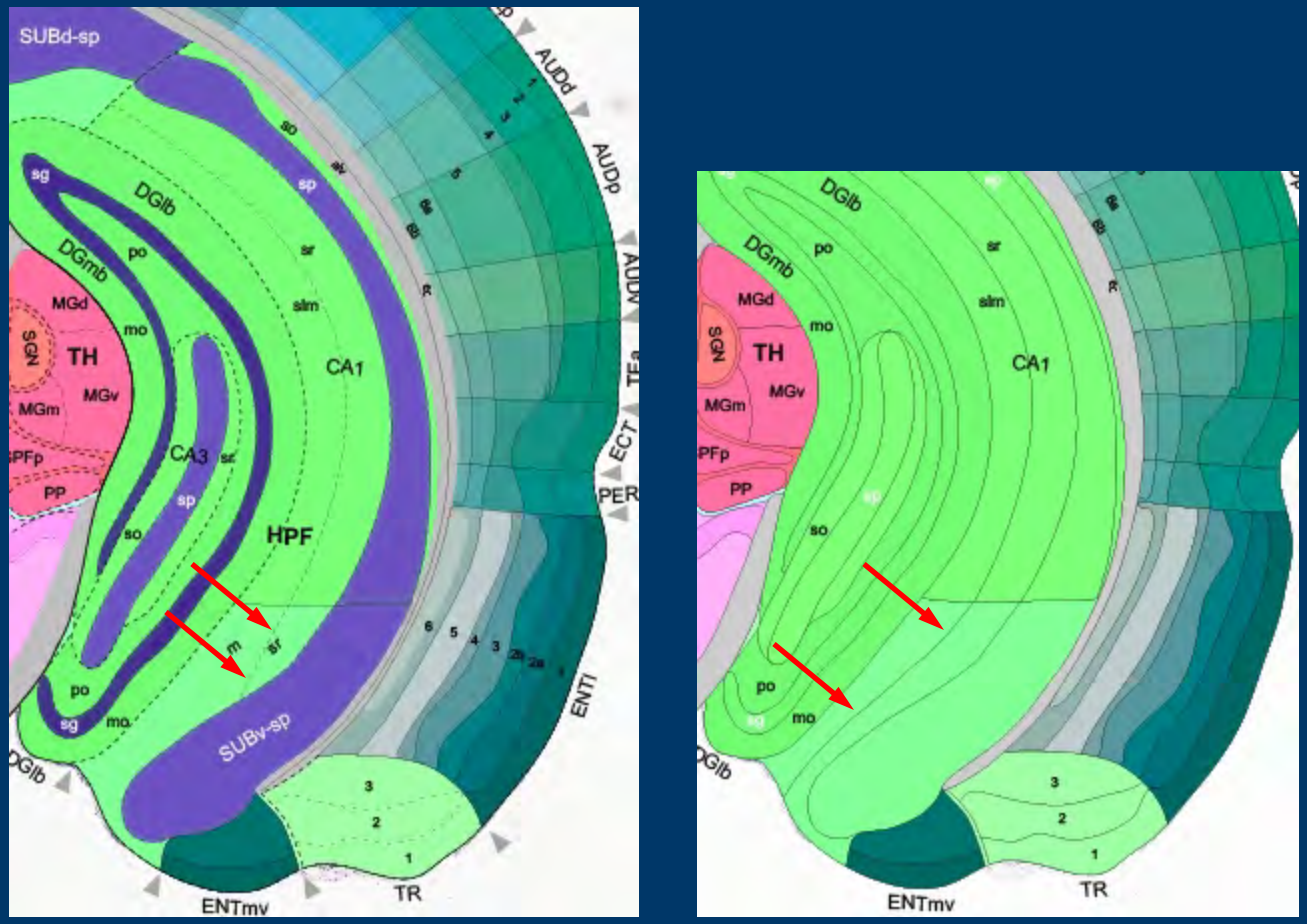
Note: left panel is the original version and right panel is the new version.

Coronal levels 86, 87: Divided ENTmv into two layers for consistency with surrounding levels.



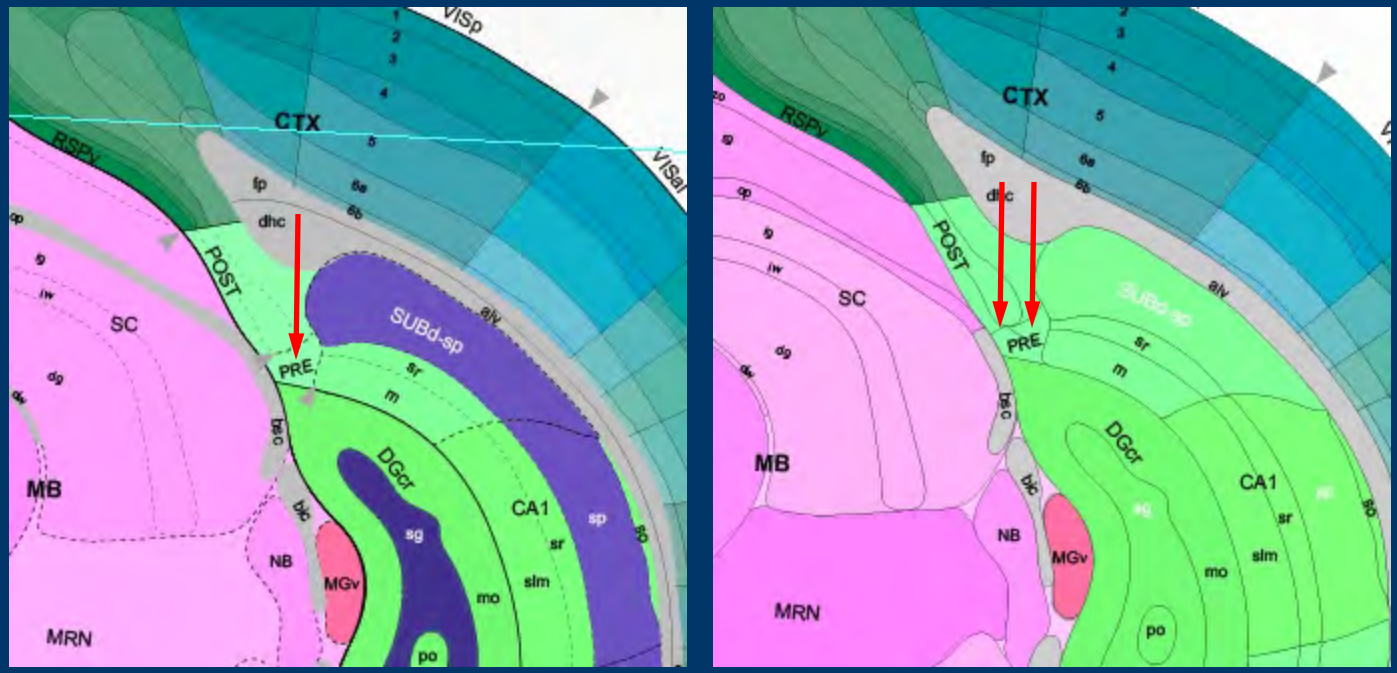
Note: left panel is the original version and right panel is the new version.

Coronal levels 88-89: Redrew the border between SUBv-sr and SUBv-m to make them consistent with other levels.



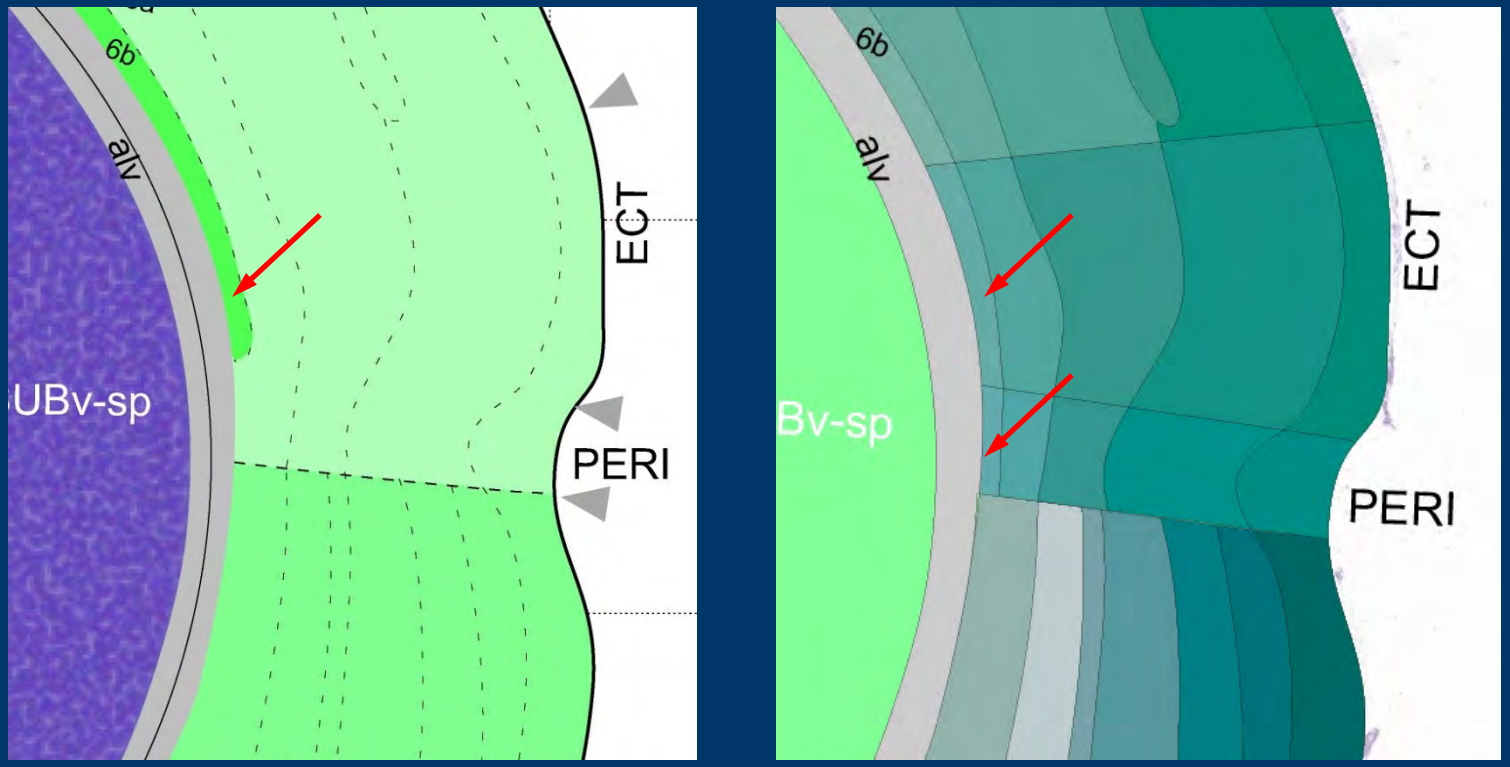
Note: left panel shows the original version of the HPF and right panel is the new version.

Coronal levels 90-91: Added PRE2 for consistency with level 93.



Note: left panel shows the original version of the PRE and right panel is the new version.

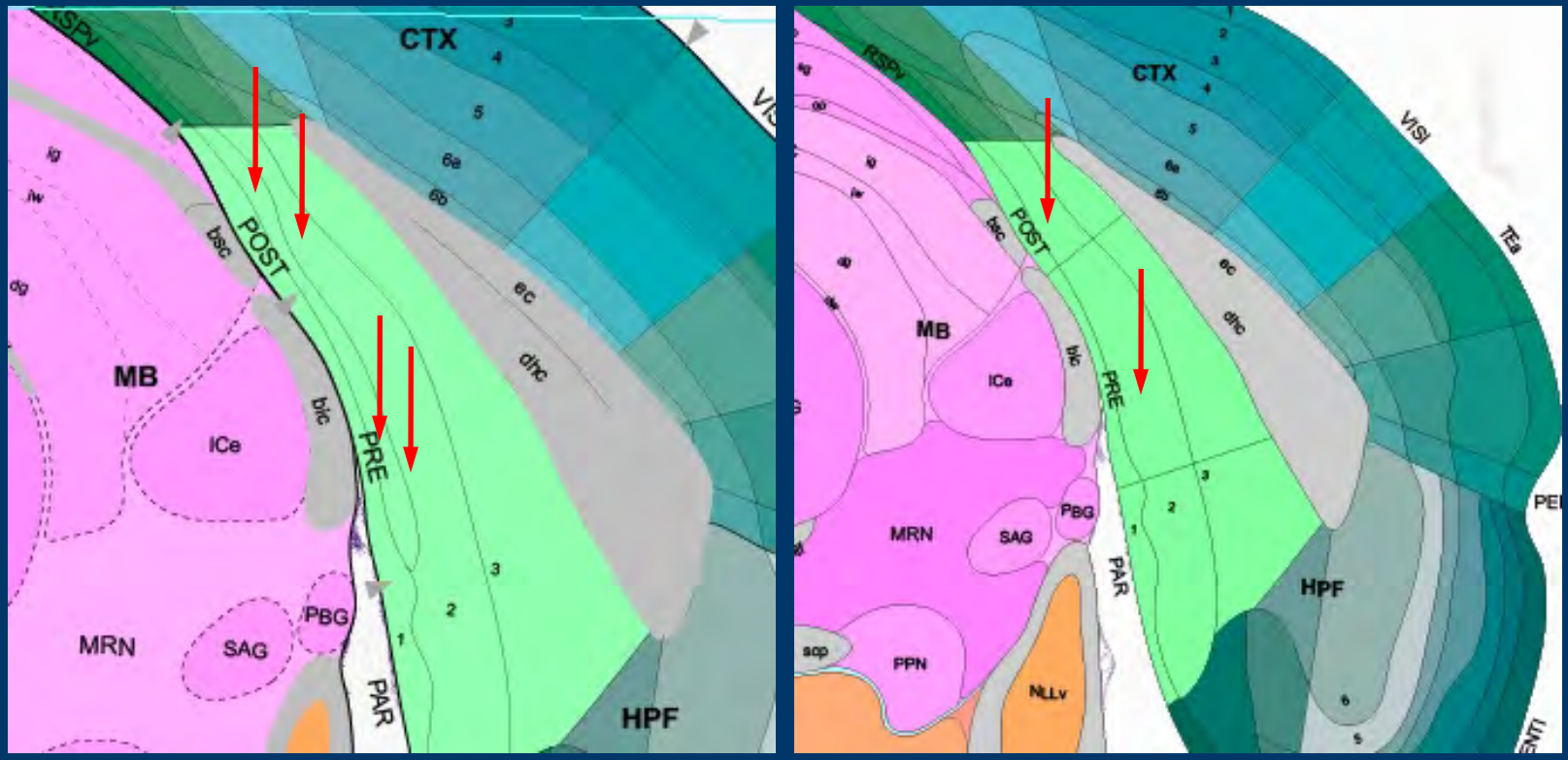
Coronal levels 94, 96, 97: Shifted layer 6b to reach ENTl, for consistency with surrounding levels and ISH data (genes, Drd1a and Ctgf).



FL

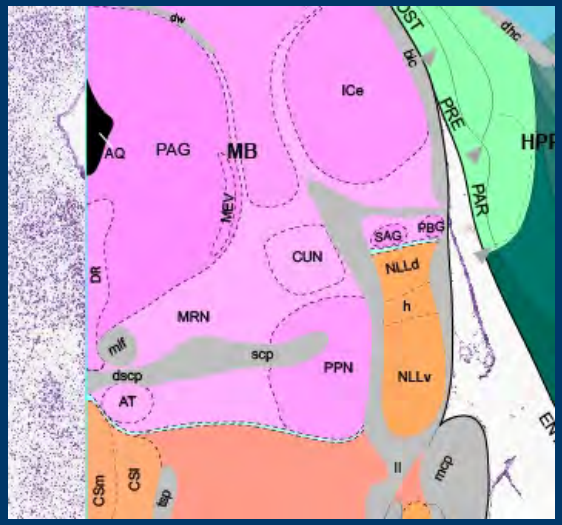
Note: left panel is the original version and right panel is the new version.

Coronal levels 97-99: Merged two polygons within POST2 and PRE2 in order to be consistent with ontology.

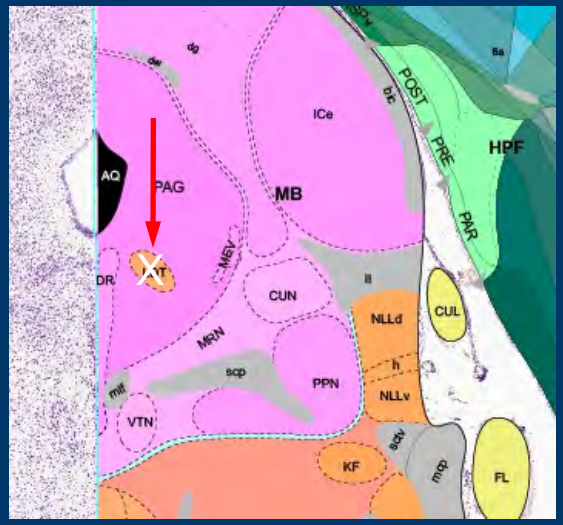


Note: left panel shows the original version of PRE and POST and right panel is the new version.

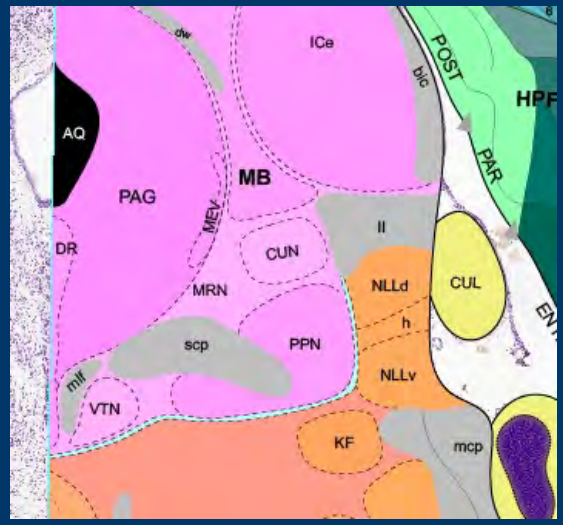
Coronal level 101: Removed LDT within PAG for consistency with other levels.



Coronal level 100

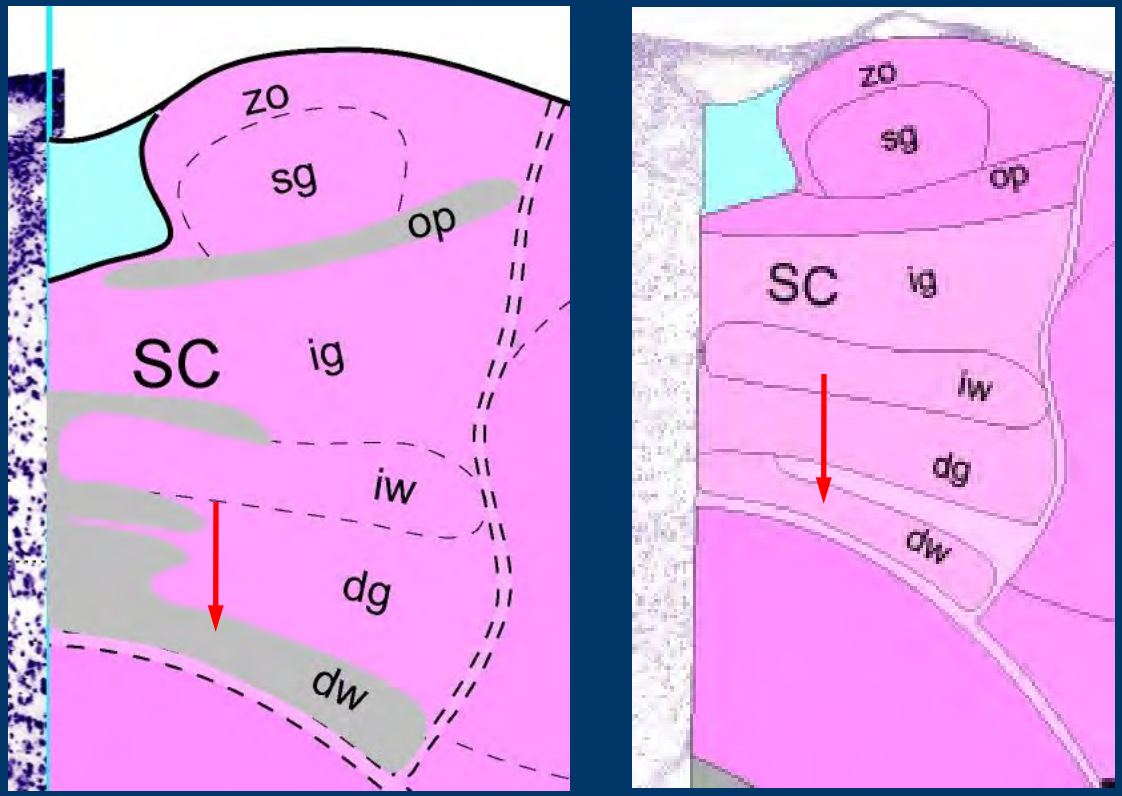


Coronal level 101



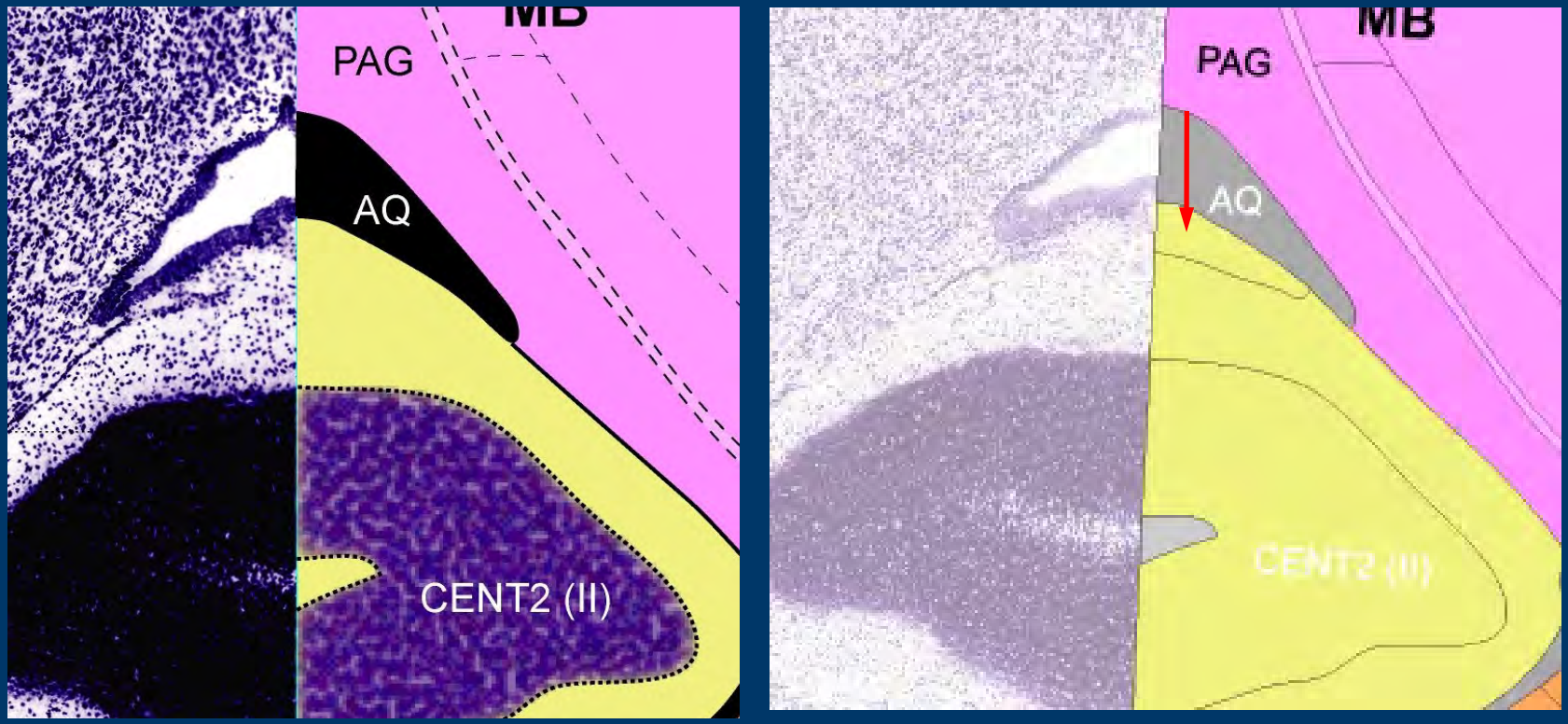
Coronal levels 102

Coronal level 104: Reduced the size of SCdw.



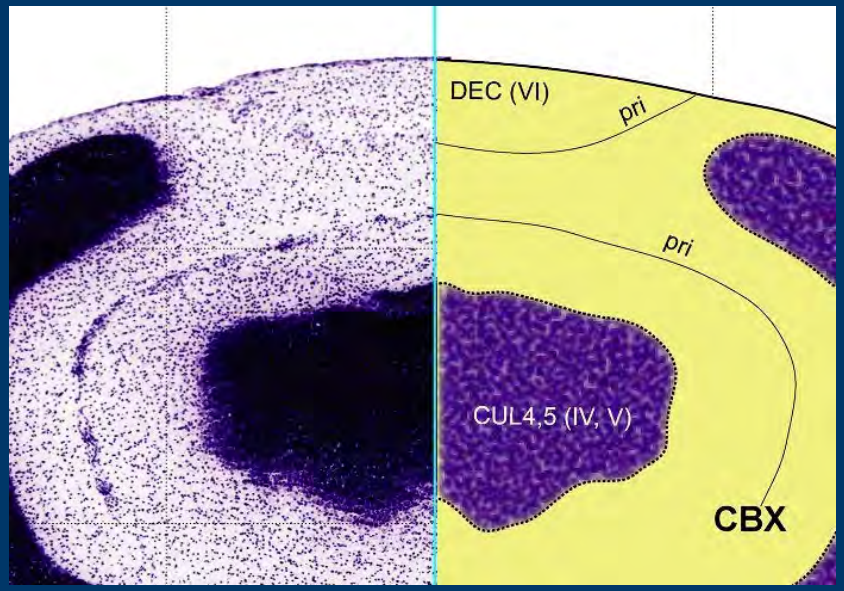
Note: left panel is the original version and right panel is the new version.

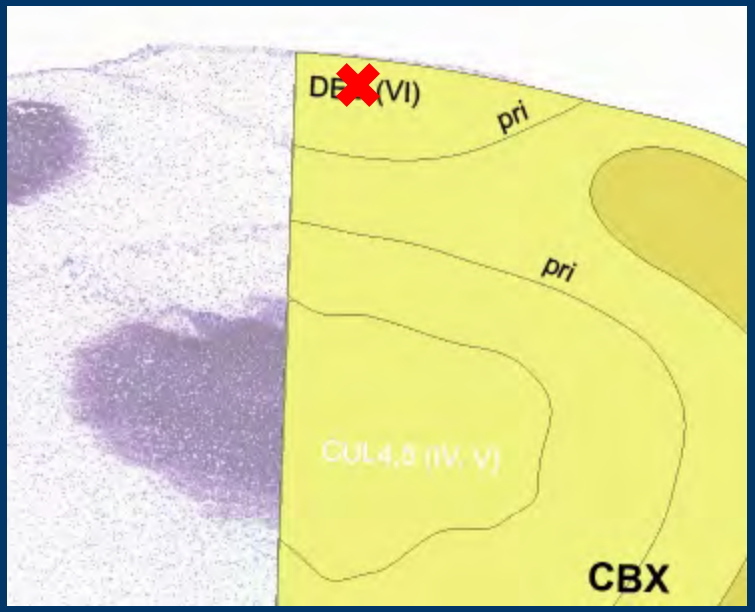
Coronal level 107: Added CENT3mo.



Note: left panel is the original version and right panel is the new version.

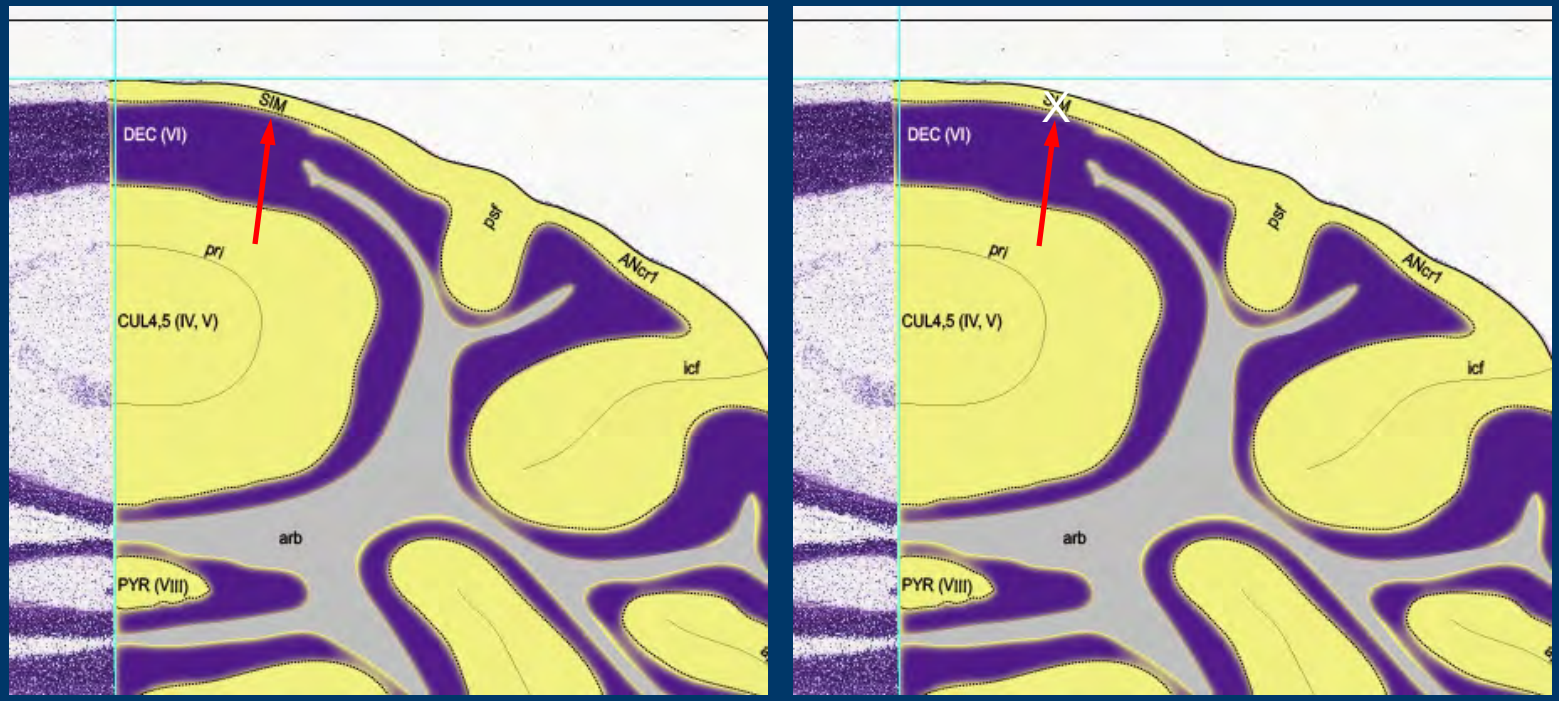
Coronal level 123: The polygon labeled DEC was named CUL4,5.





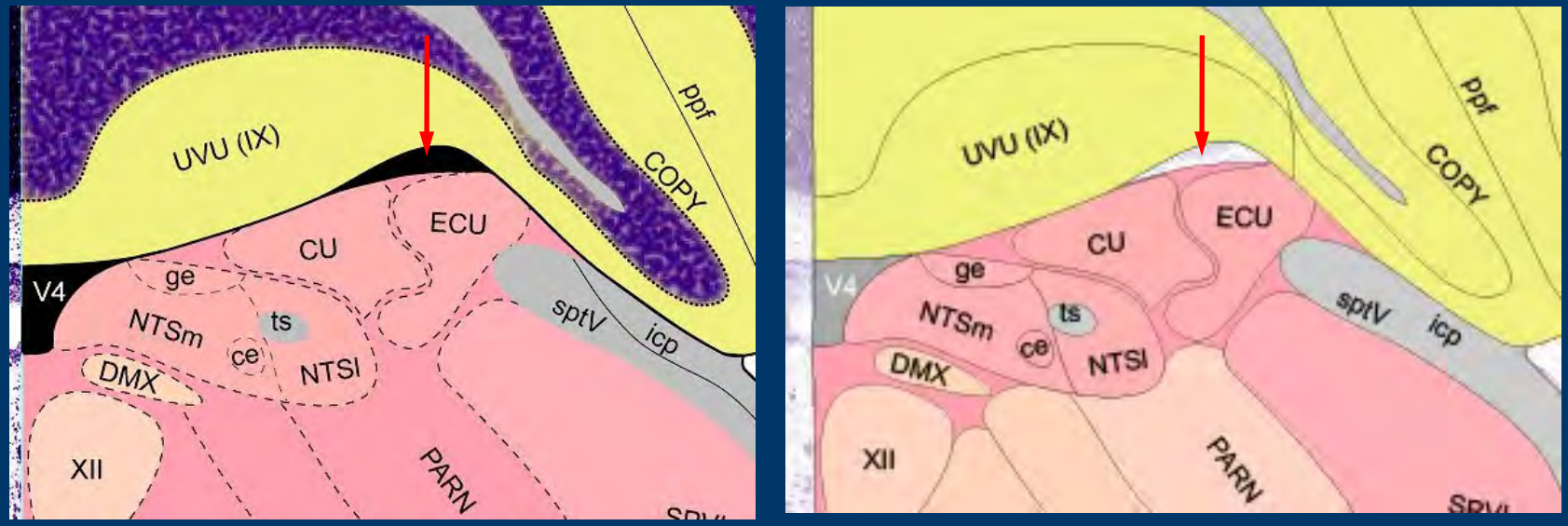
Note: left panel is the original version and right panel is the new version.

Coronal levels 123-125: The polygons labeled SIM were named DEC.



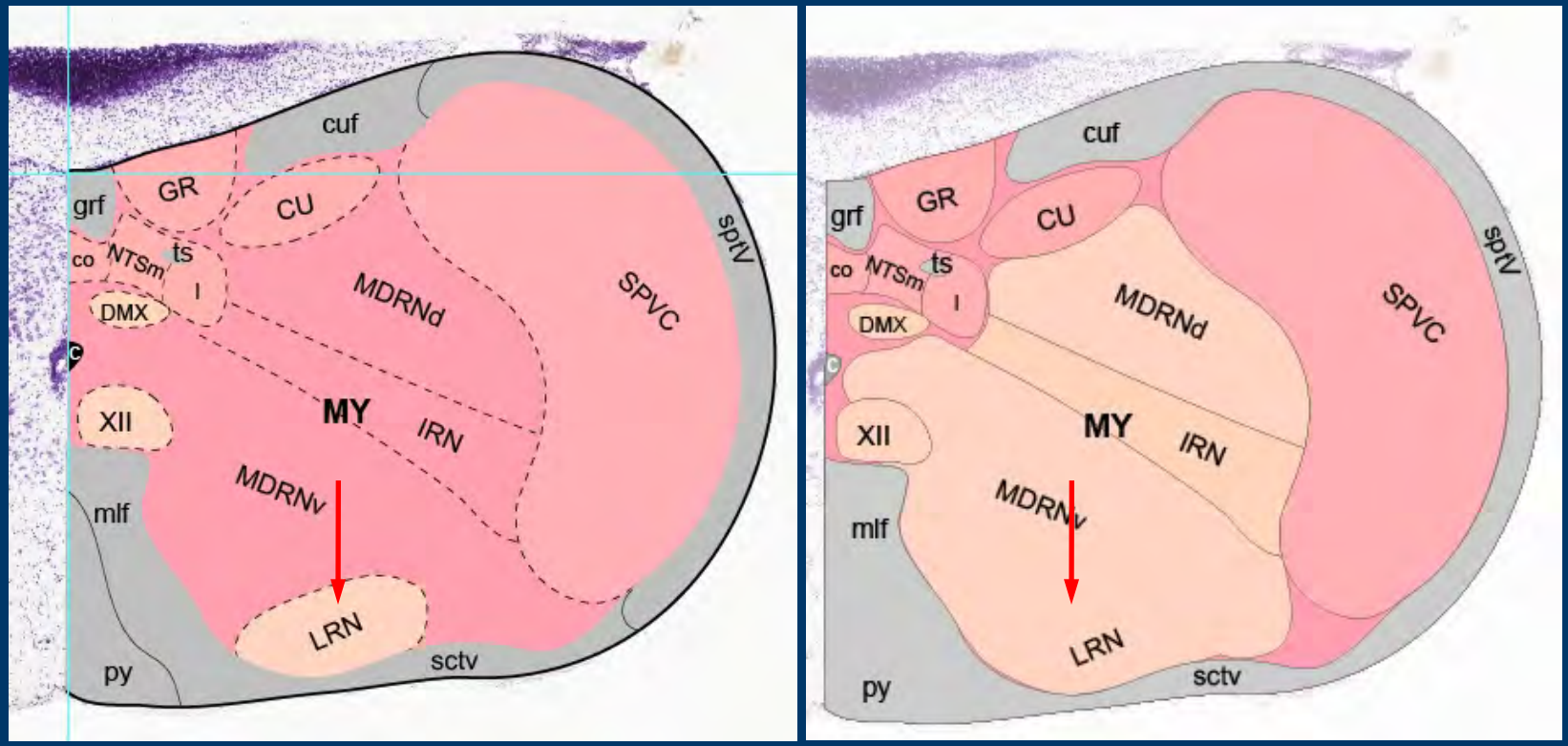
Note: left panel is the original version and right panel is the new version.

Coronal level 126: Removed lateral V4 polygon for consistency with sagittal atlas.



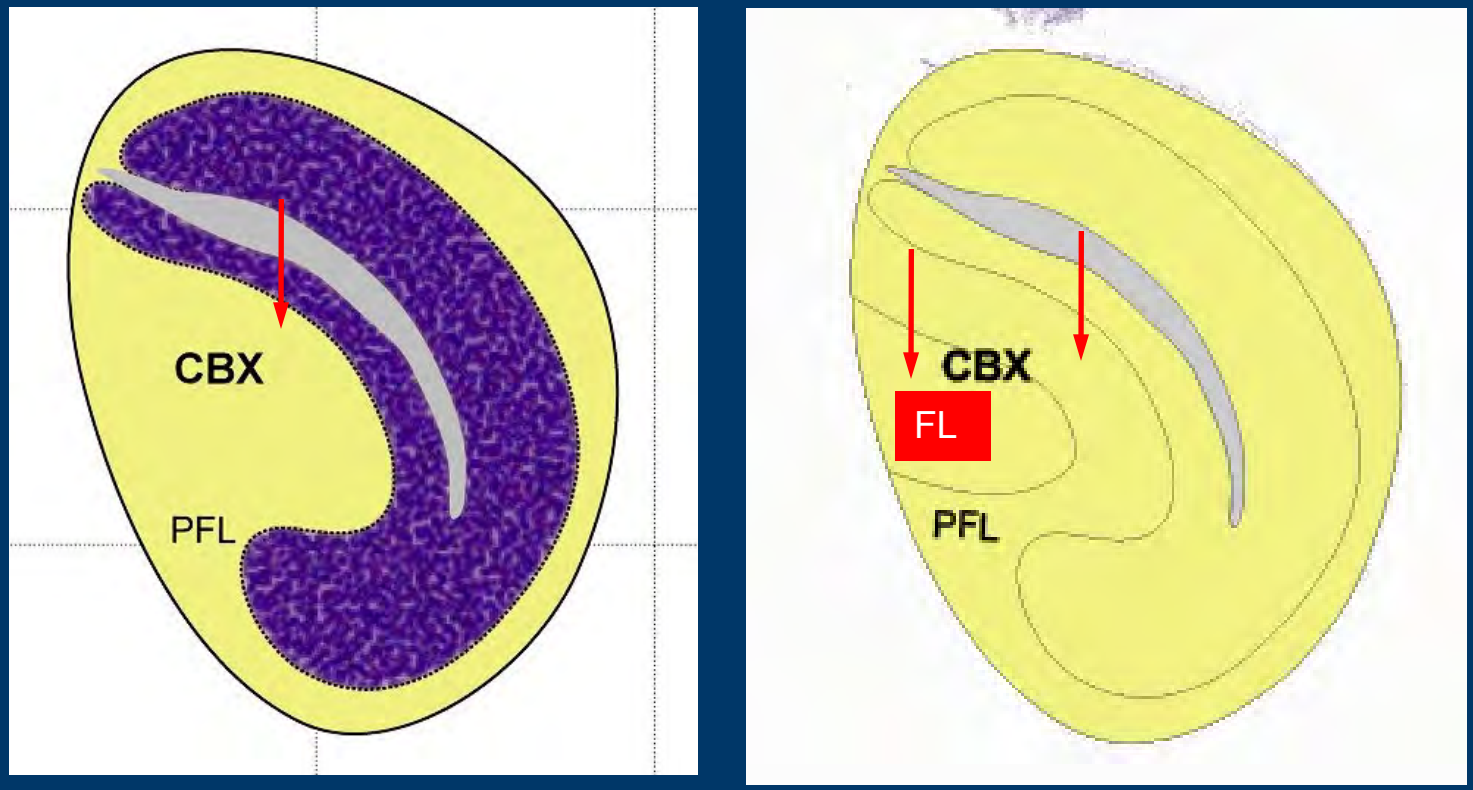
Note: left panel is the original version and right panel is the new version.

Coronal level 132: Removed LRN polygon based on final print version of Allen Reference Atlas.



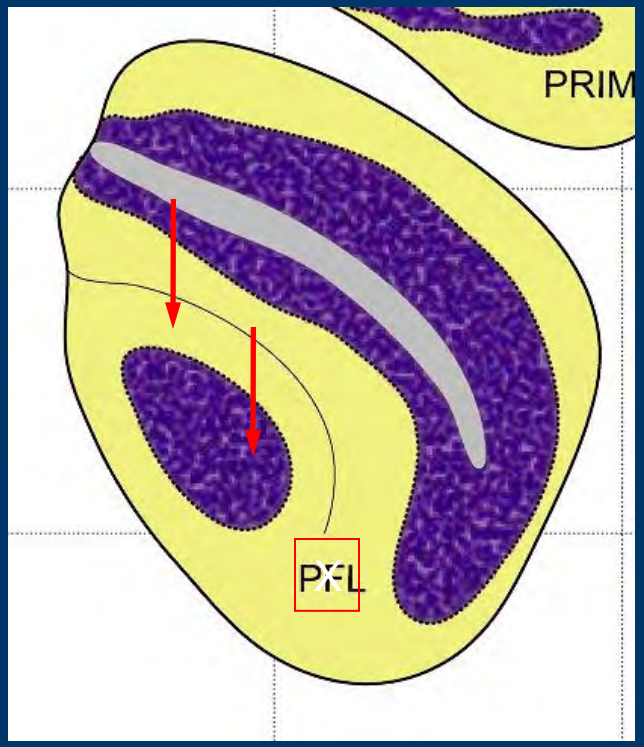
Note: left panel is the original version and right panel is the new version.

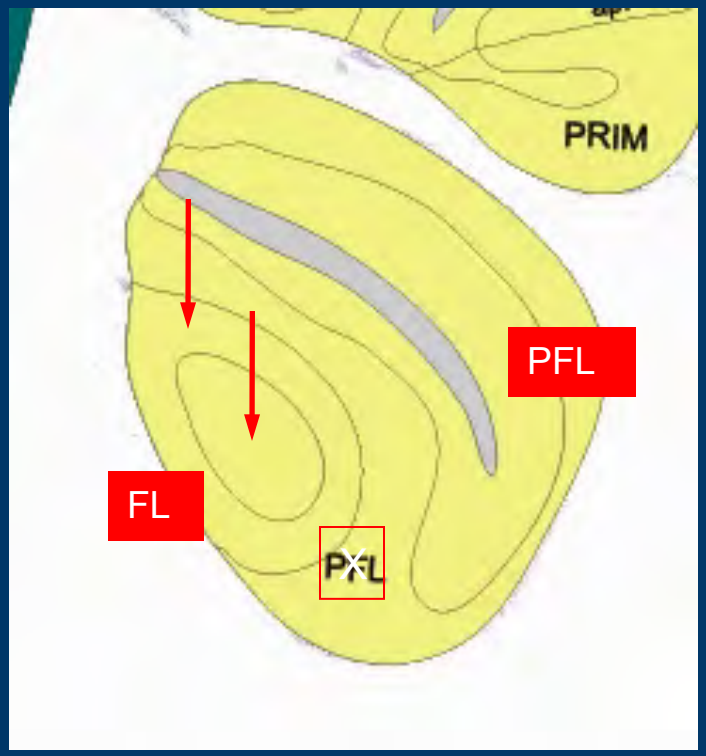
Sagittal level 1: Added FLmo based on Nissl, removed CA3 from this section and replaced it with CA1.



Note: left panel is the original version and right panel is the new version.

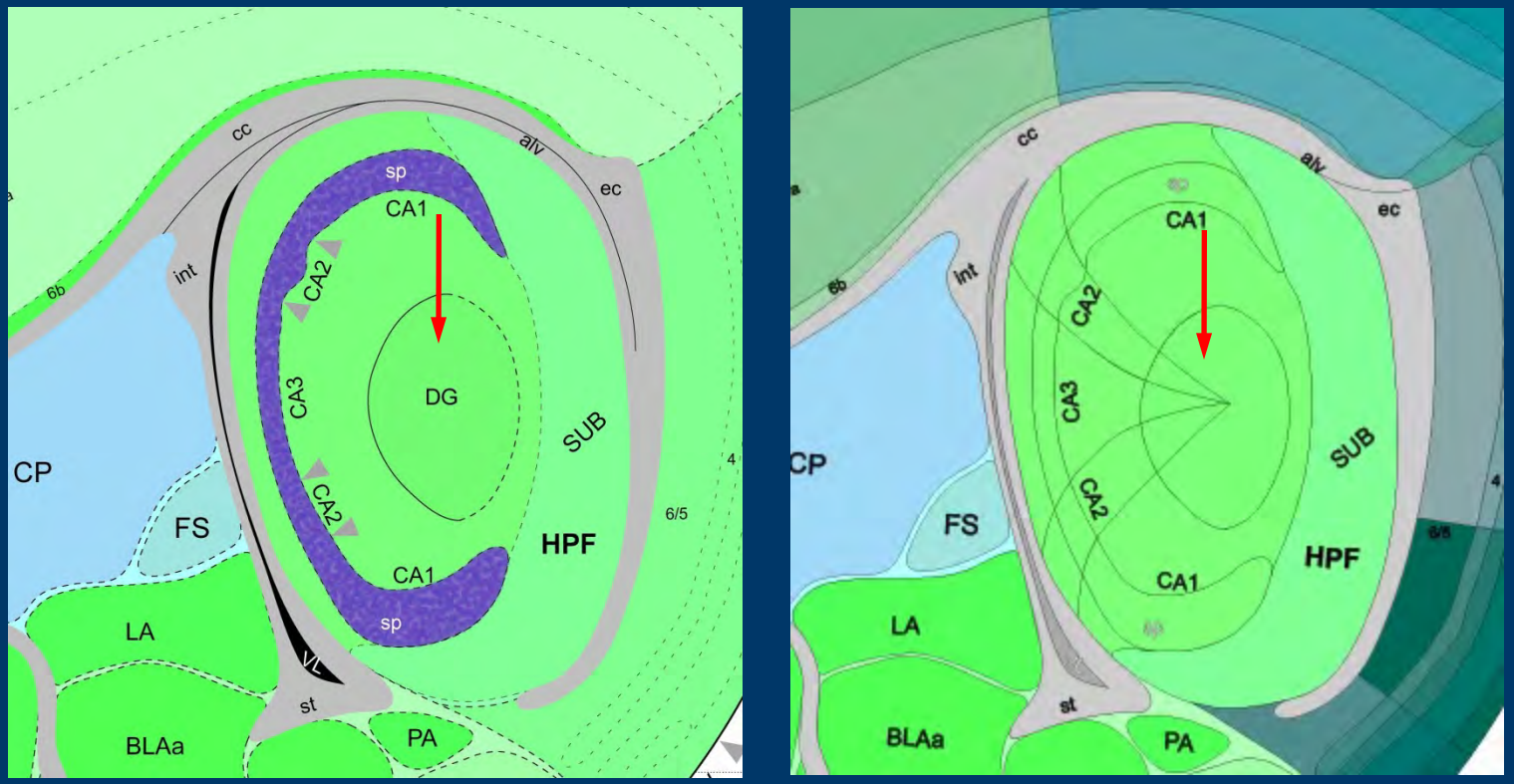
Sagittal level 2: Added FLmo/gr based on Nissl.





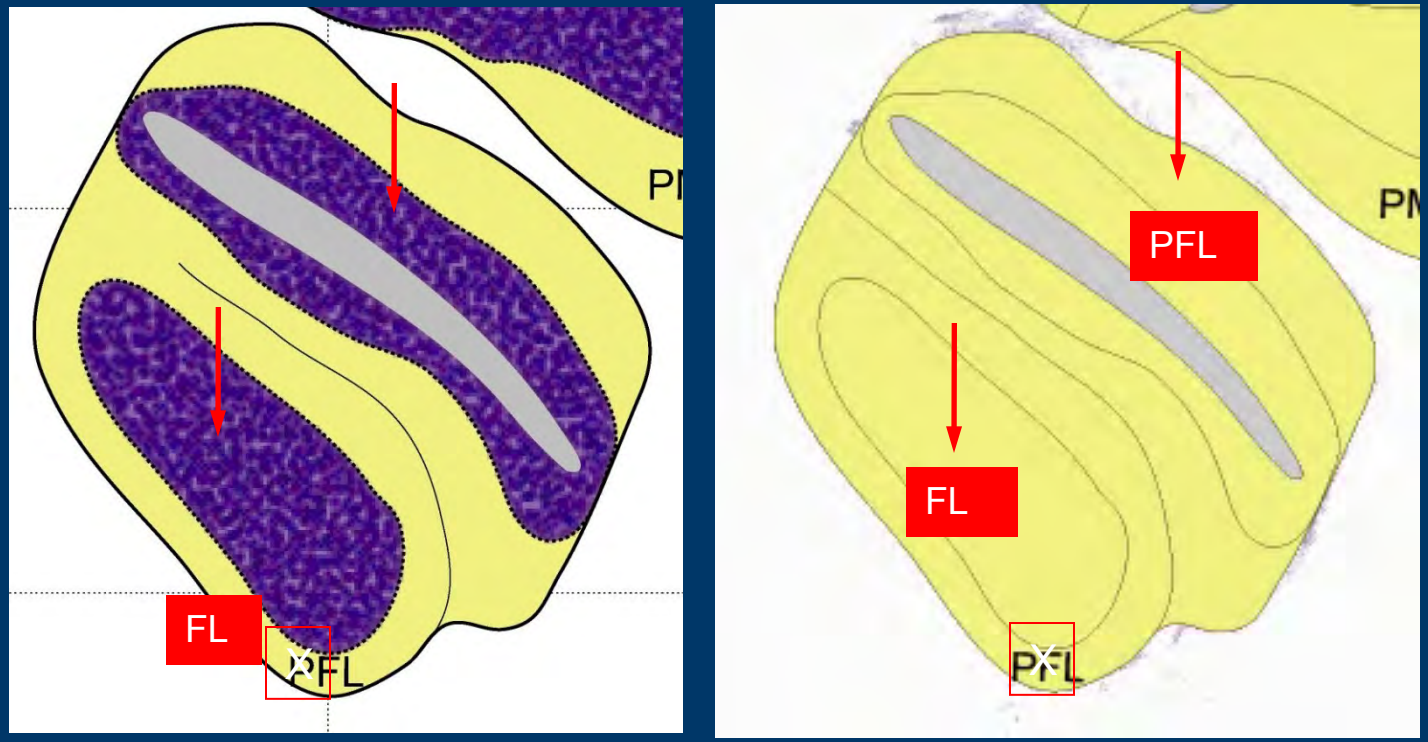
Note: left panel is the original version and right panel is the new version.

Sagittal level 2: Renamed DG to CA1-3slm.



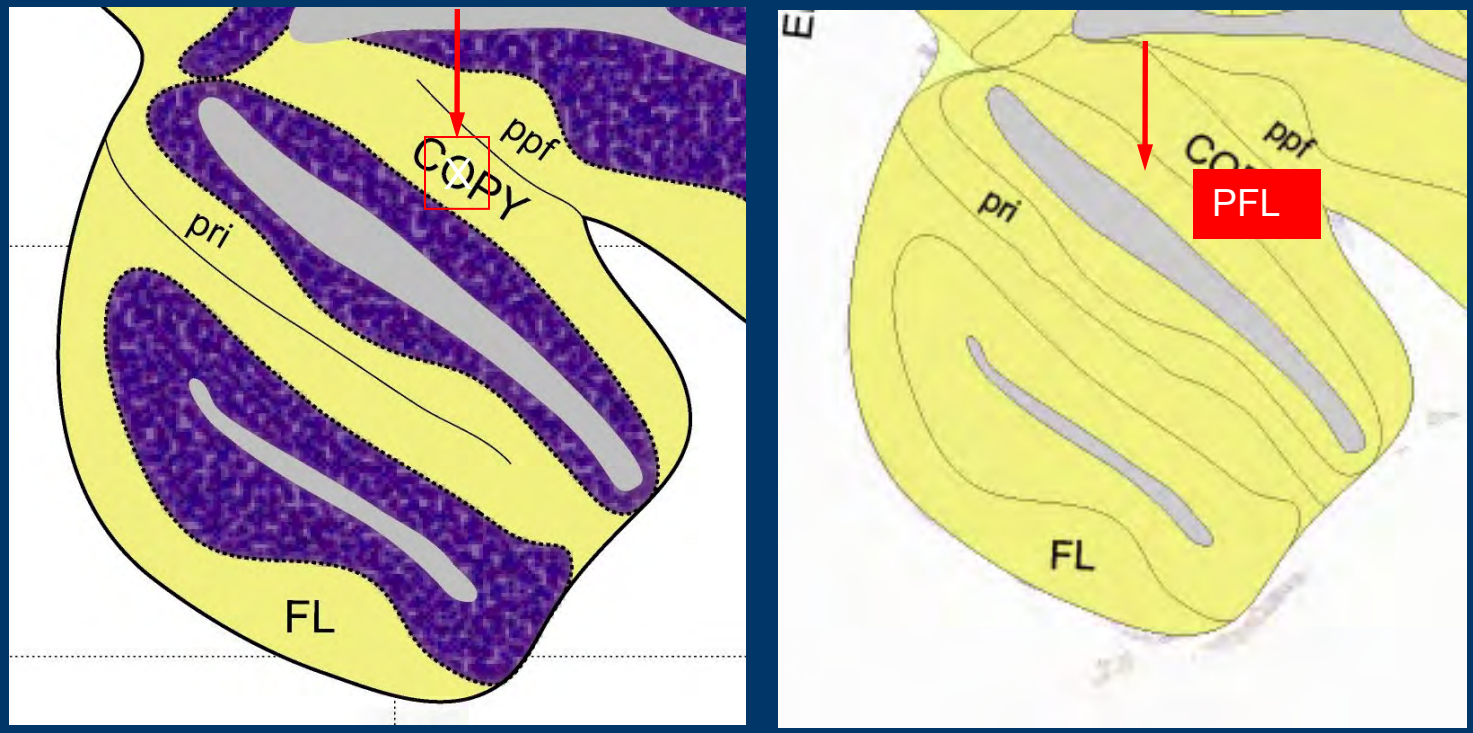
Note: left panel is the original version and right panel is the new version.

Sagittal level 3: Changed PFL to FL, and COPY to PFL.



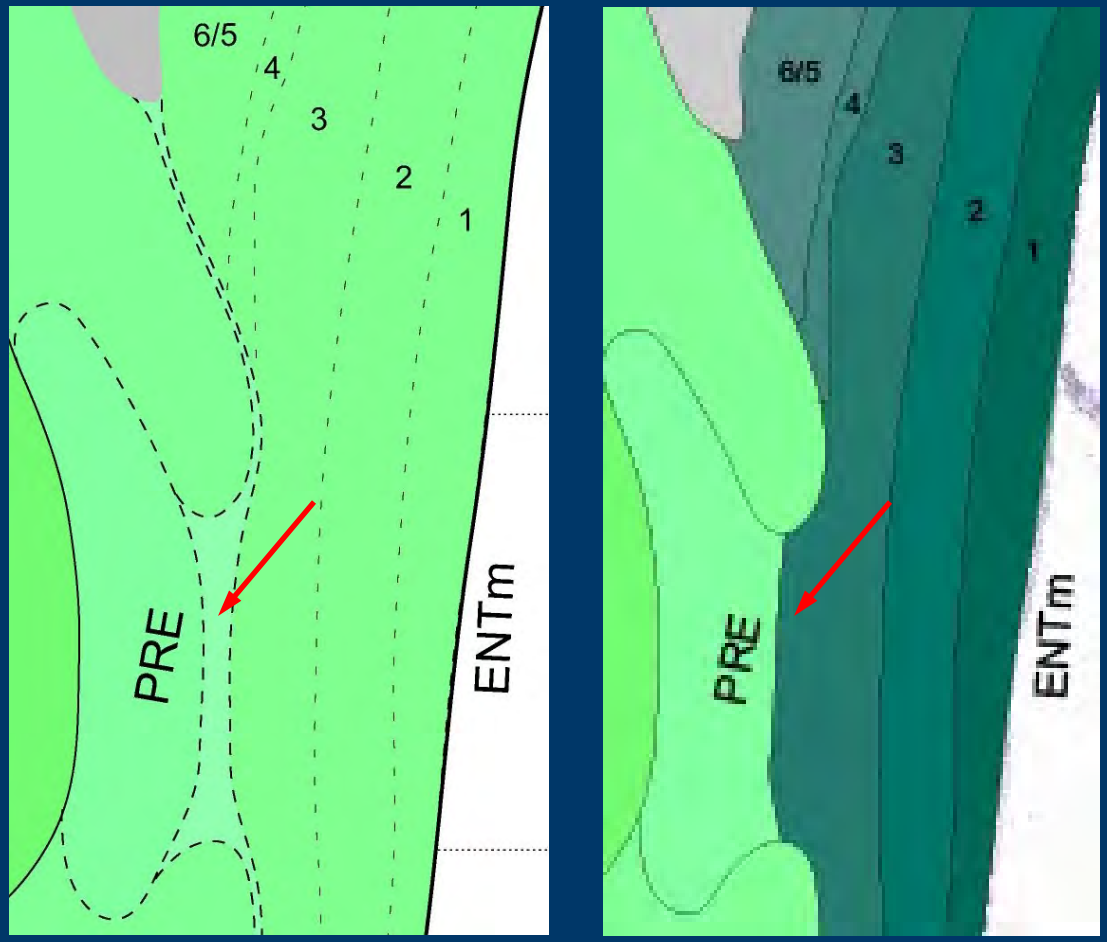
Note: left panel is the original version and right panel is the new version.

Sagittal level 4, 5: Changed COPY to PFL.



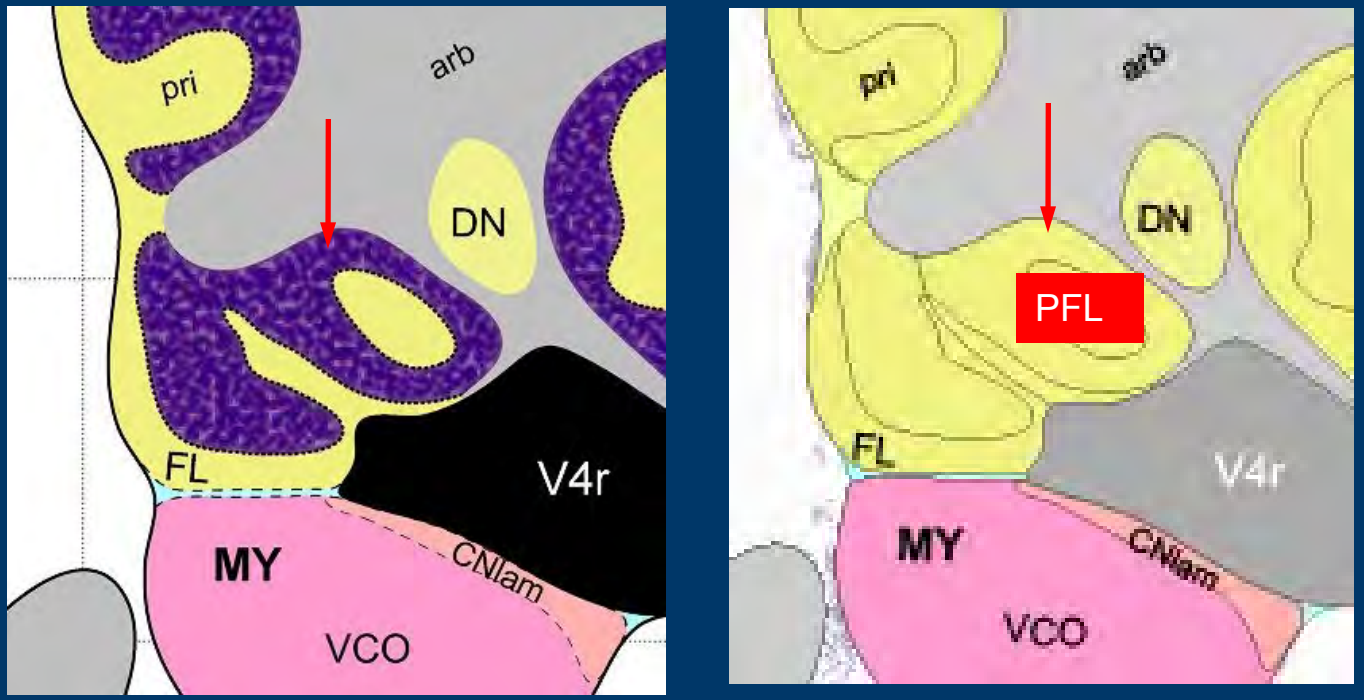
Note: left panel is the original version and right panel is the new version.

Sagittal level 5: Extended polygons PRE and ENTm5 to cover undefined area for consistency with other levels.



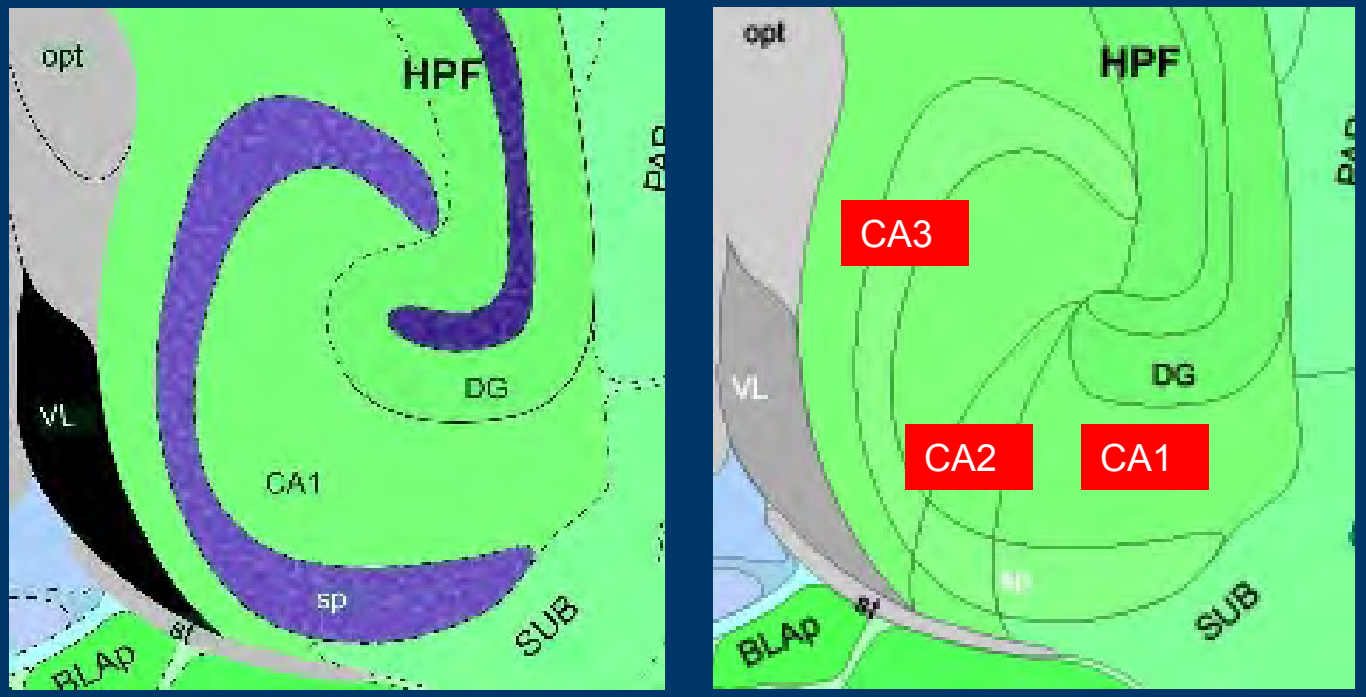
Note: left panel is the original version and right panel is the new version.

Sagittal level 6: Changed dorsal half of FL to PFL.



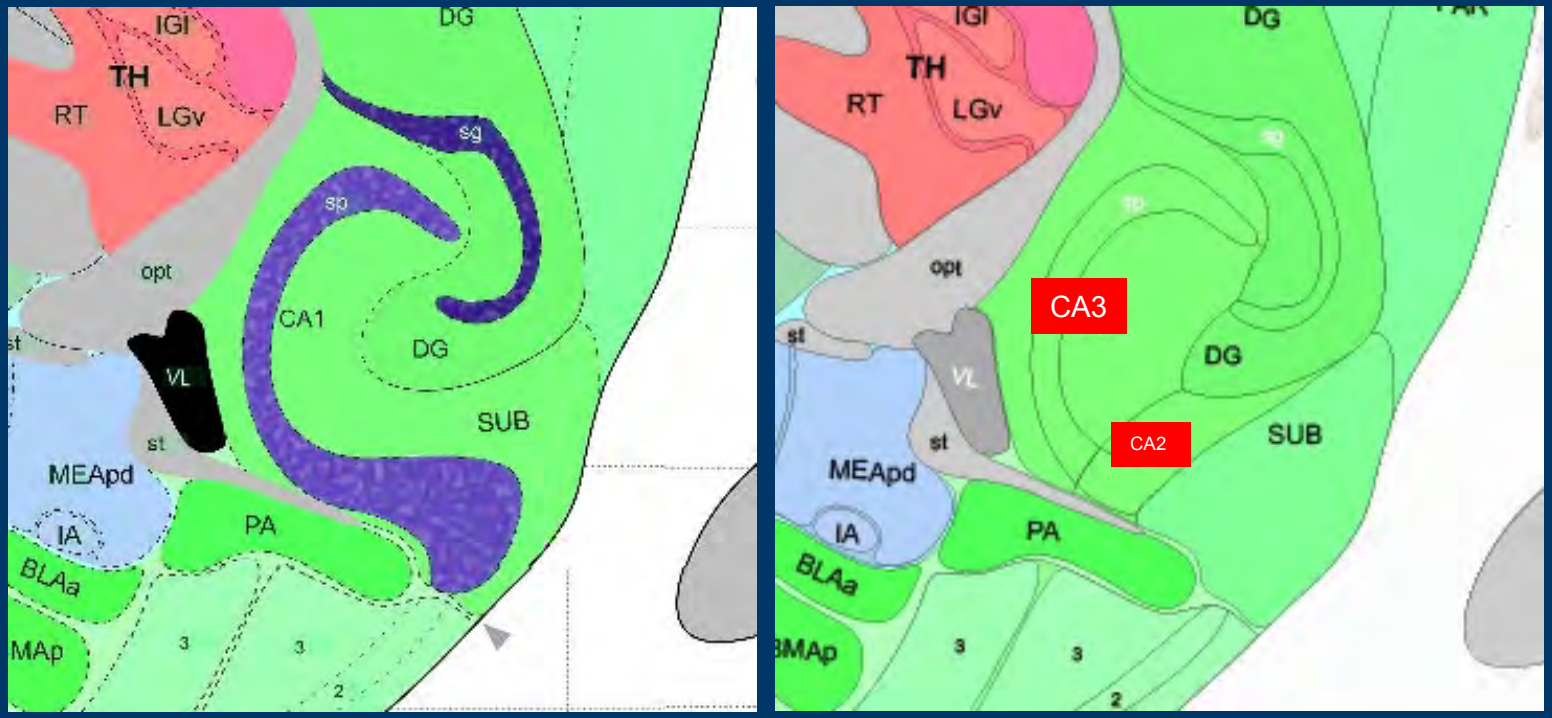
Note: left panel is the original version and right panel is the new version.

Sagittal level 6: Added CA2-so, -sp, -sr, and CA3-so, -sp, -sr to ventral CA1.



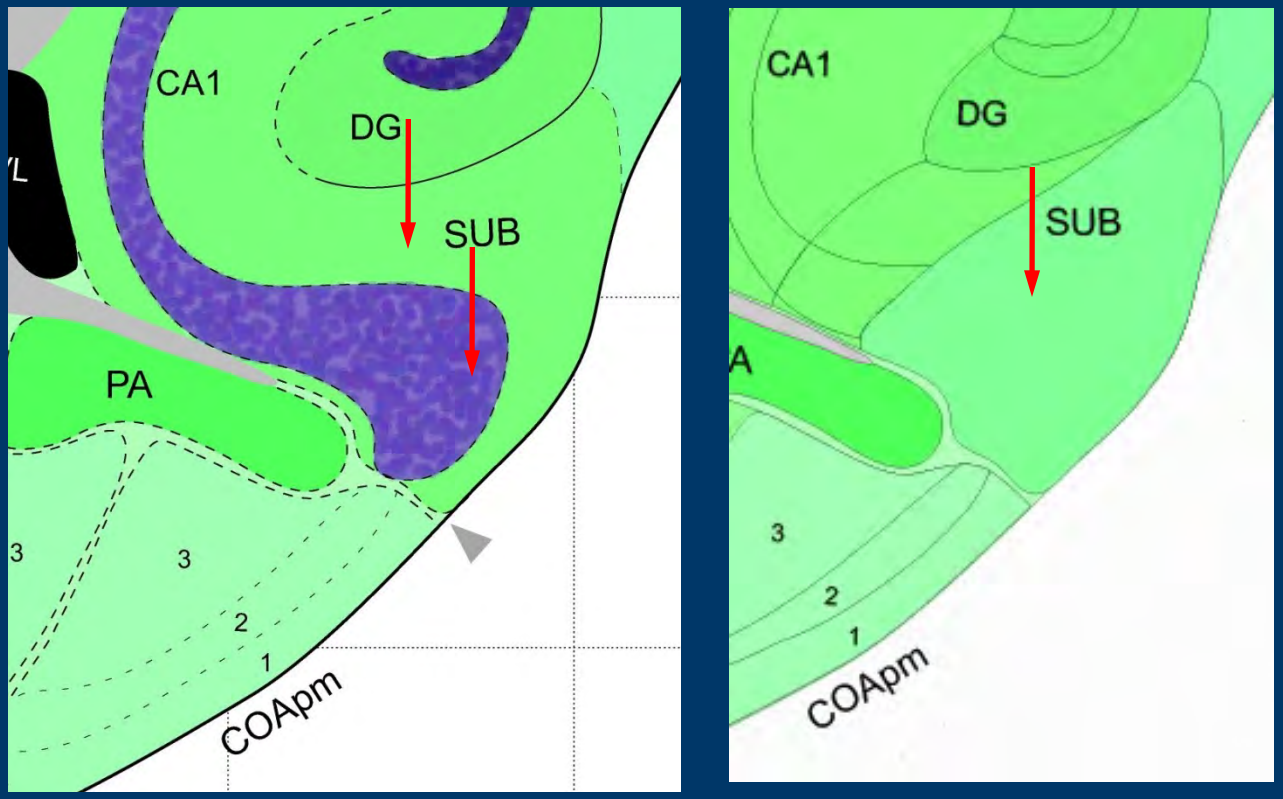
Note: left panel is the original version and right panel is the new version.

Sagittal level 7: Replaced ventral CA1 with CA2-so, -sp, -sr, and CA3.



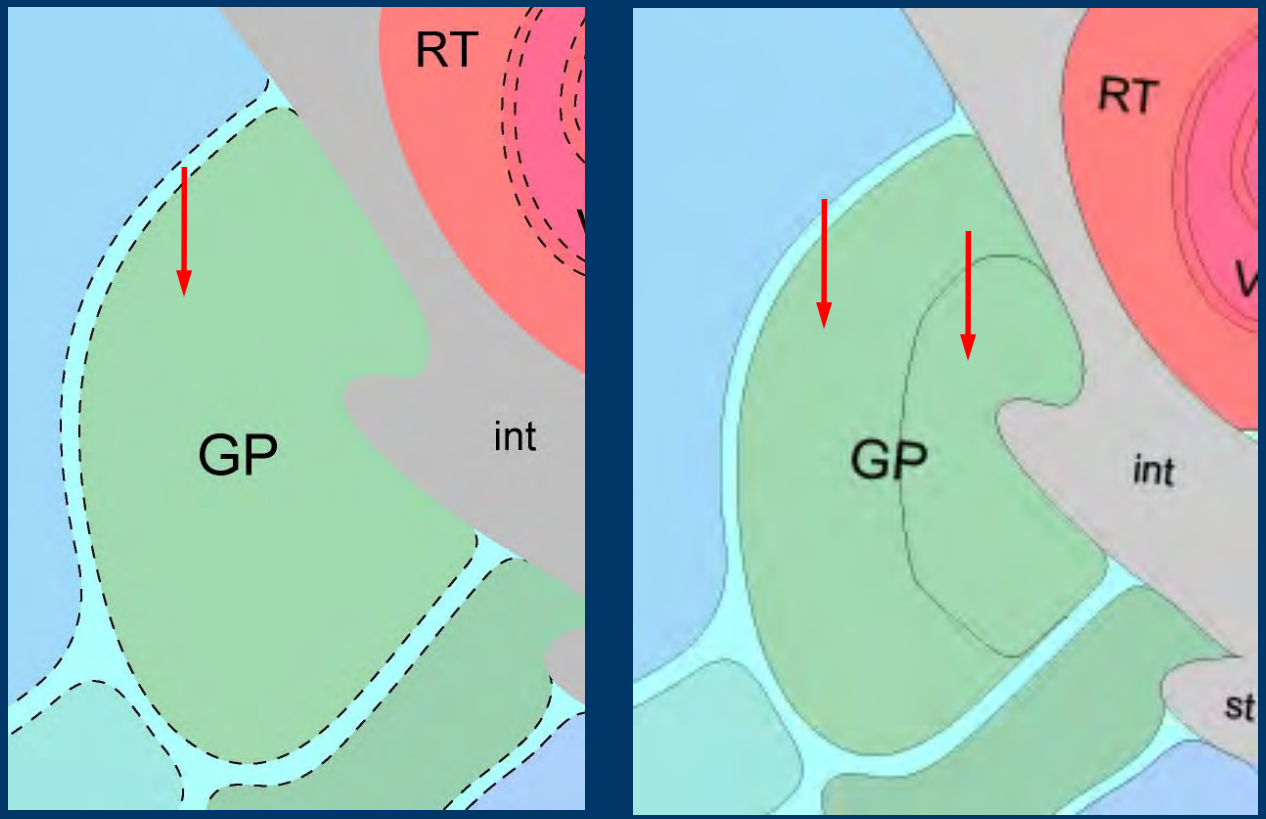
Note: left panel is the original version and right panel is the new version.

Sagittal levels 7-8: Merged two SUBv layers to one for consistency with SUBd.



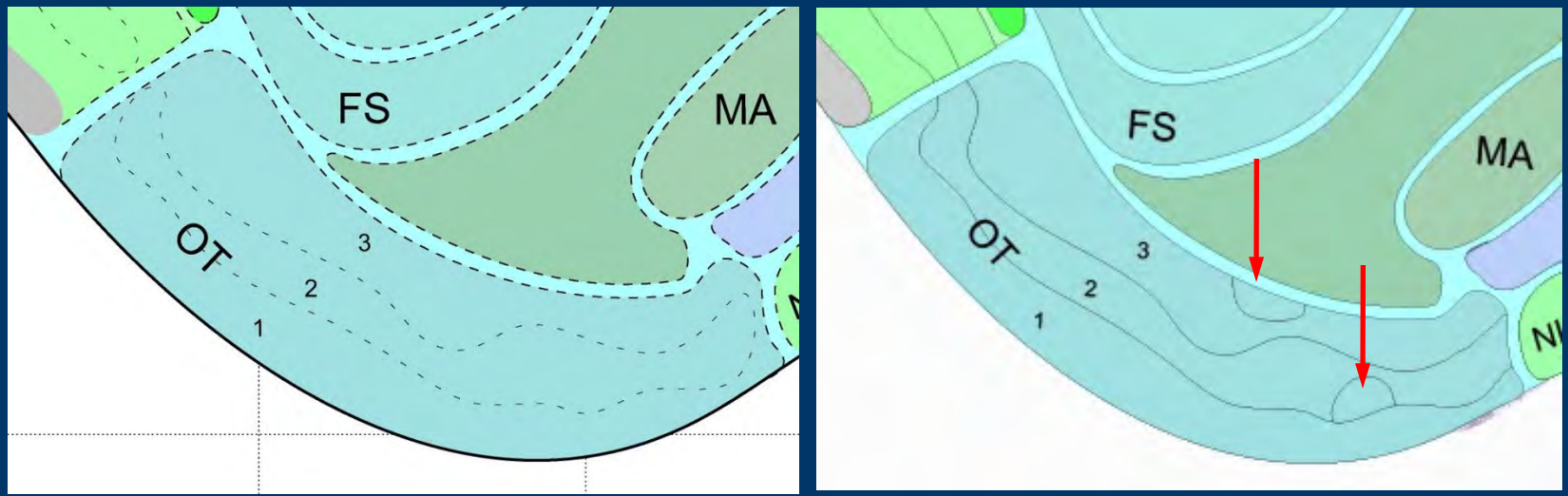
Note: left panel is the original version and right panel is the new version.

Sagittal levels 8-13: GP was divided into GPe and GPi.



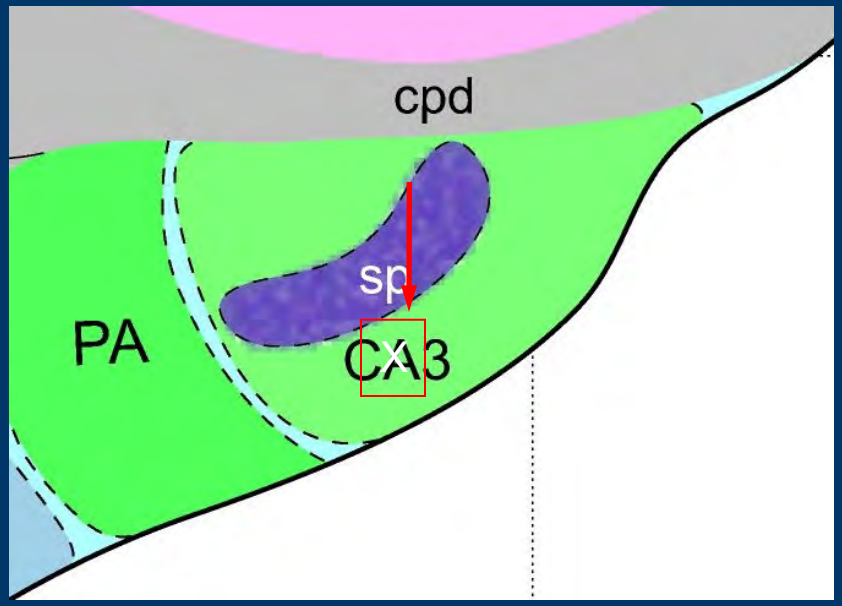
Note: left panel is the original version and right panel is the new version.

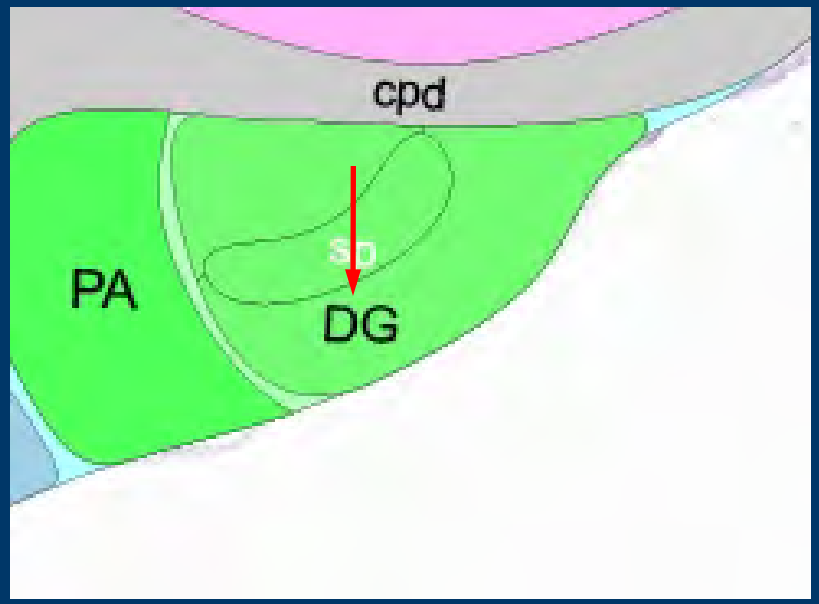
Sagittal levels 8-16, 18: Added isl based on Nissl, for consistency with level 17 and coronal.



Note: left panel is the original version and right panel is the new version.

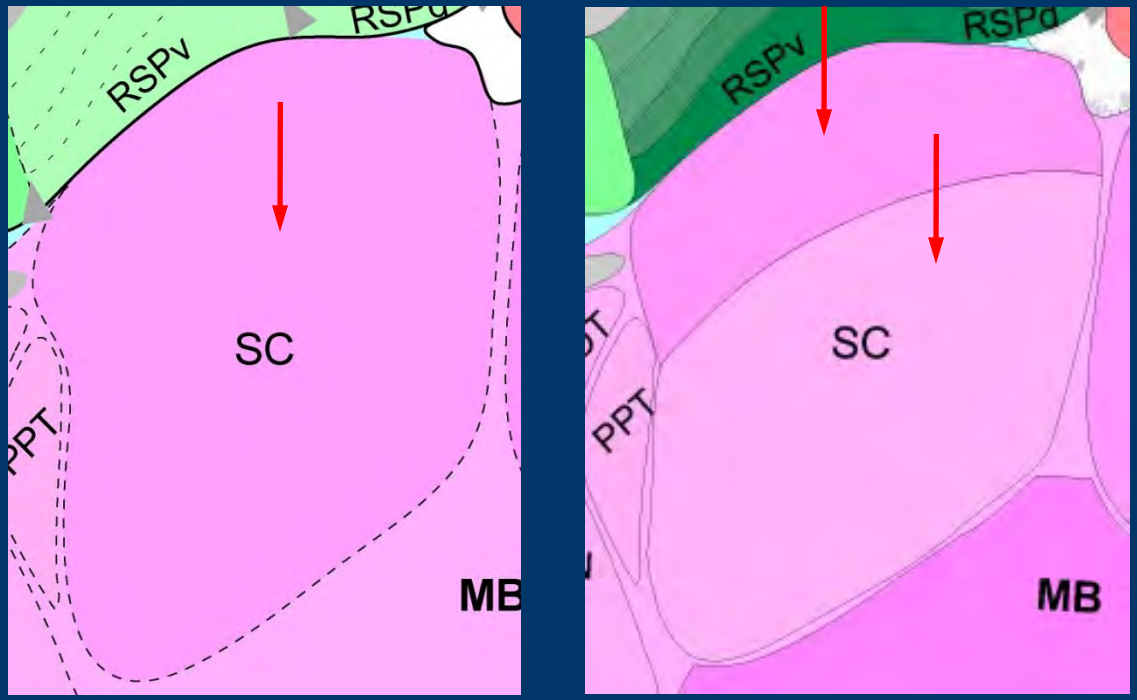
Sagittal levels 10-12: Renamed ventral CA3-so, -sp, and –sr to DG-mo, -sg, and –po.





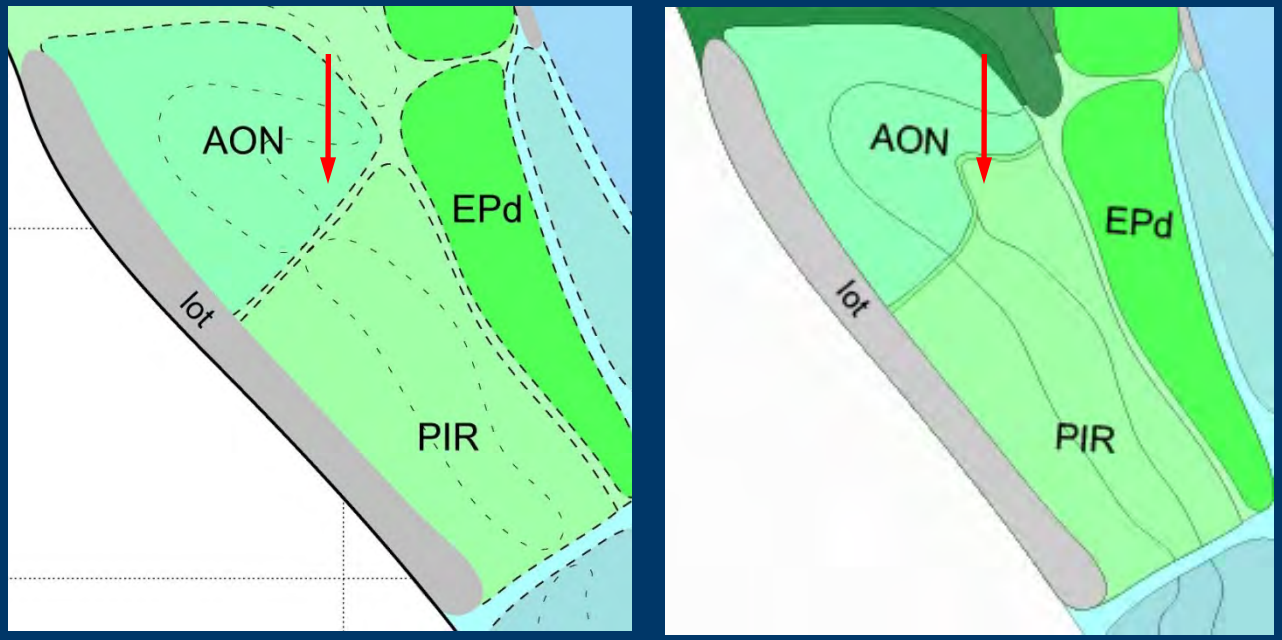
Note: left panel is the original version and right panel is the new version.

Sagittal levels 10-21: Divided SC into SCm and SCs based on ISH data (gene, Dgkh).



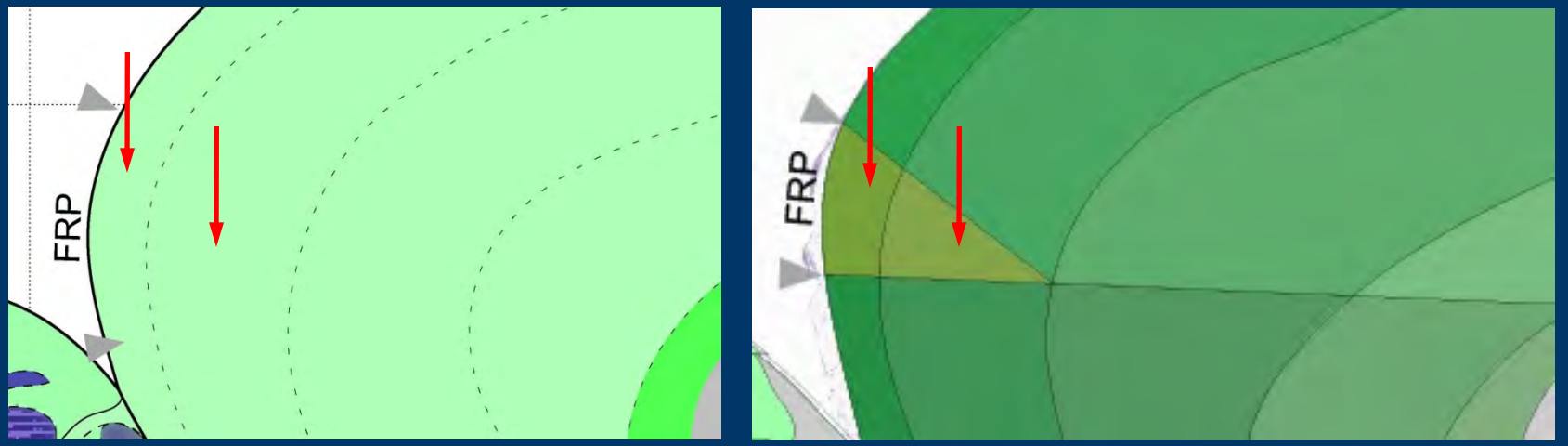
Note: left panel is the original version and right panel is the new version.

Sagittal level 11: Extended PIR3 into deep AON polygon for consistency with ontology (there is no AON3 in ontology).



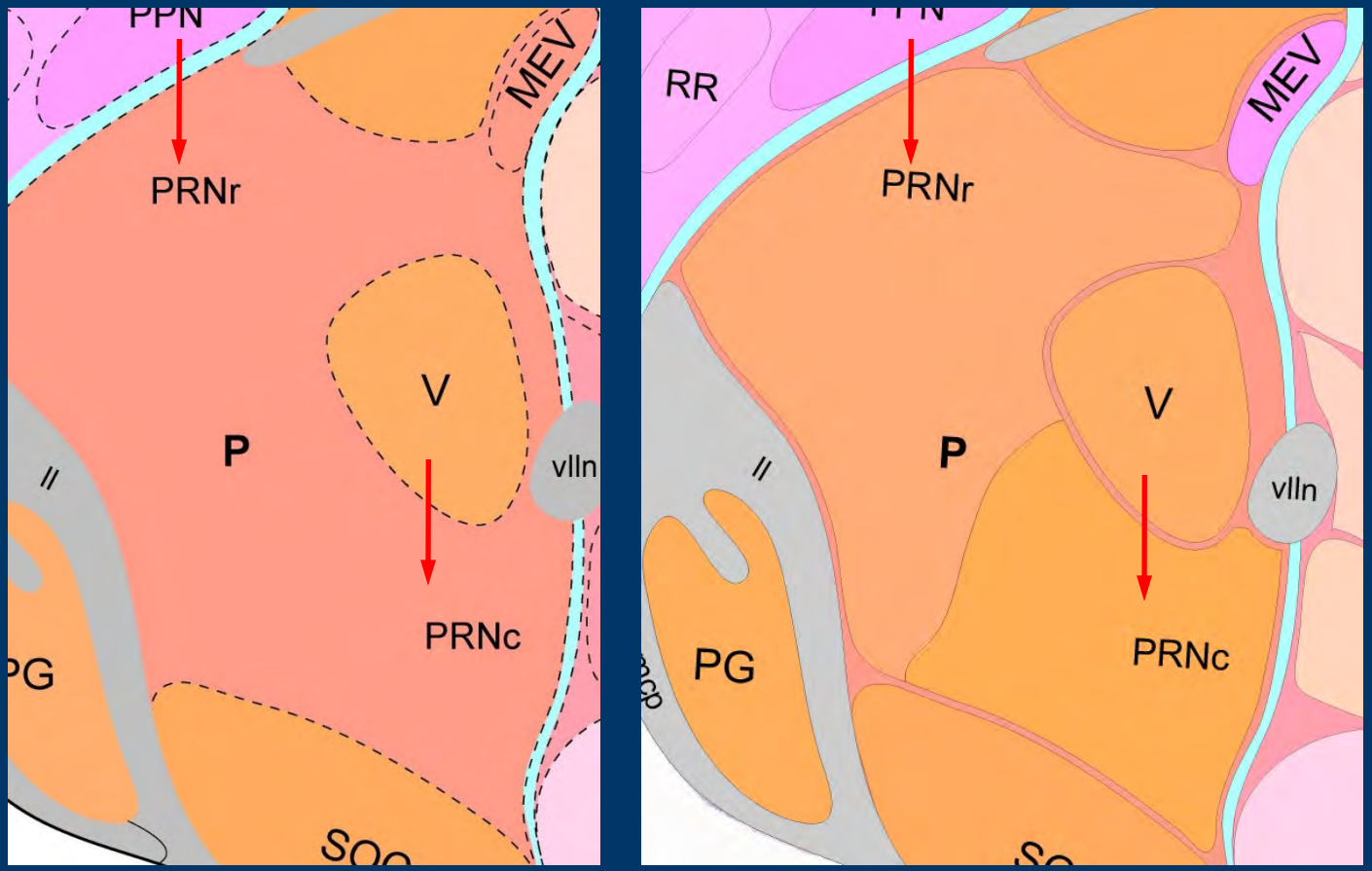
Note: left panel is the original version and right panel is the new version.

Sagittal levels 11-17: Restricted FRP to layers 1 and 2/3 for consistency with coronal drawings.



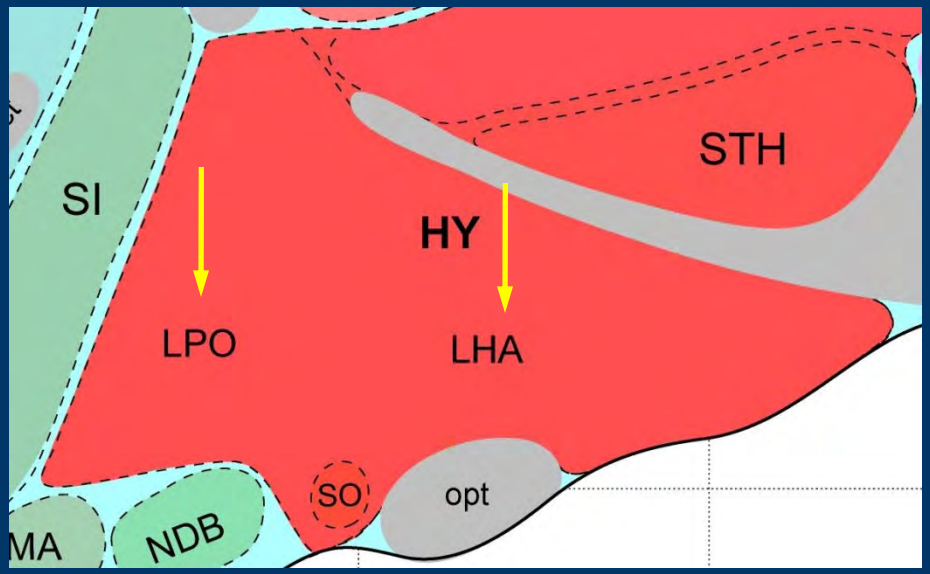
Note: left panel is the original version and right panel is the new version.

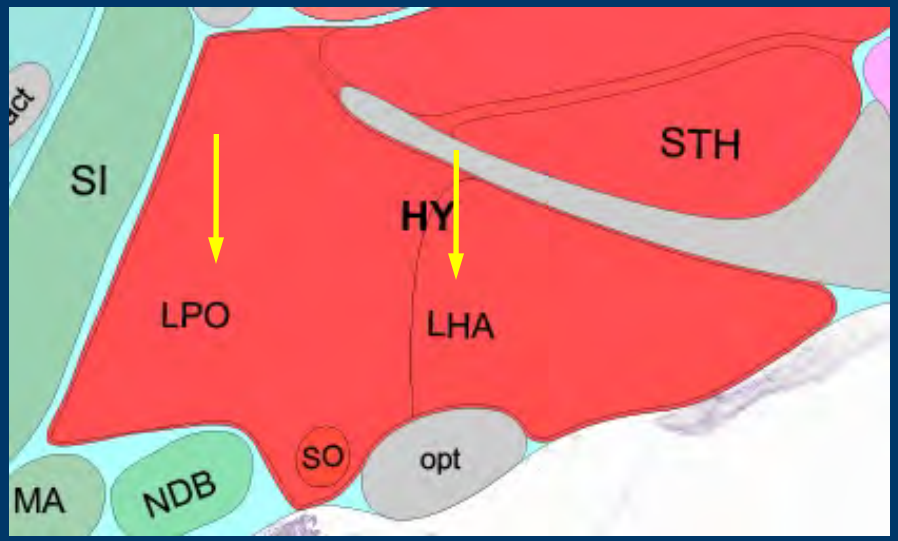
Sagittal levels 11-18: Created border between PRNr and PRNc.



Note: left panel is the original version and right panel is the new version.

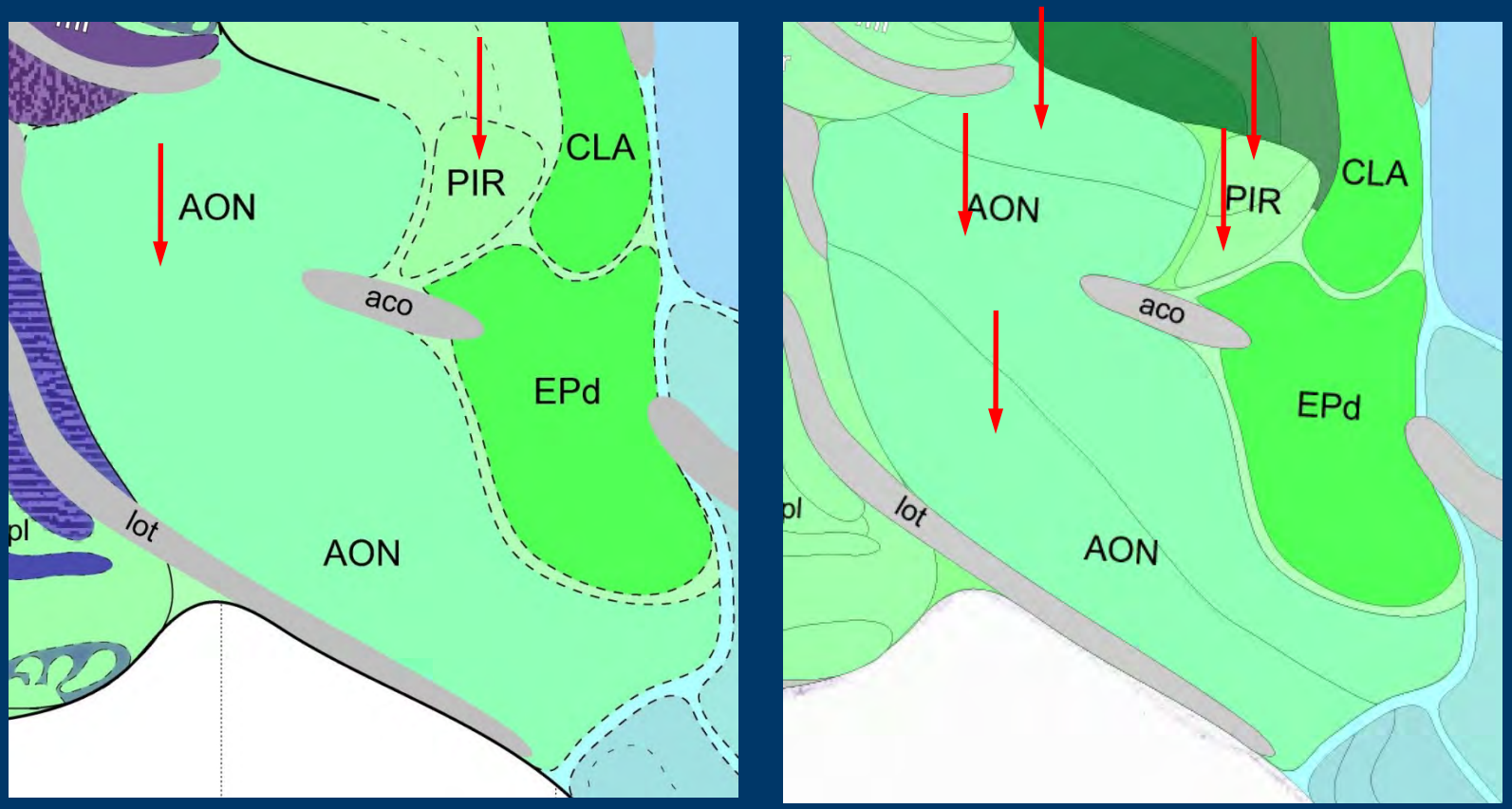
Sagittal levels 13-16: Created border between LPO and LHA.





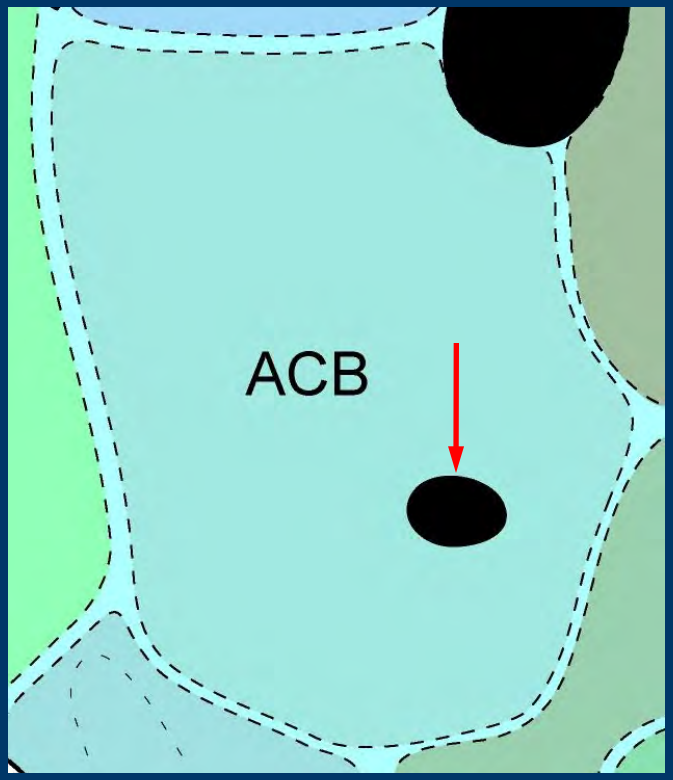
Note: left panel is the original version and right panel is the new version.

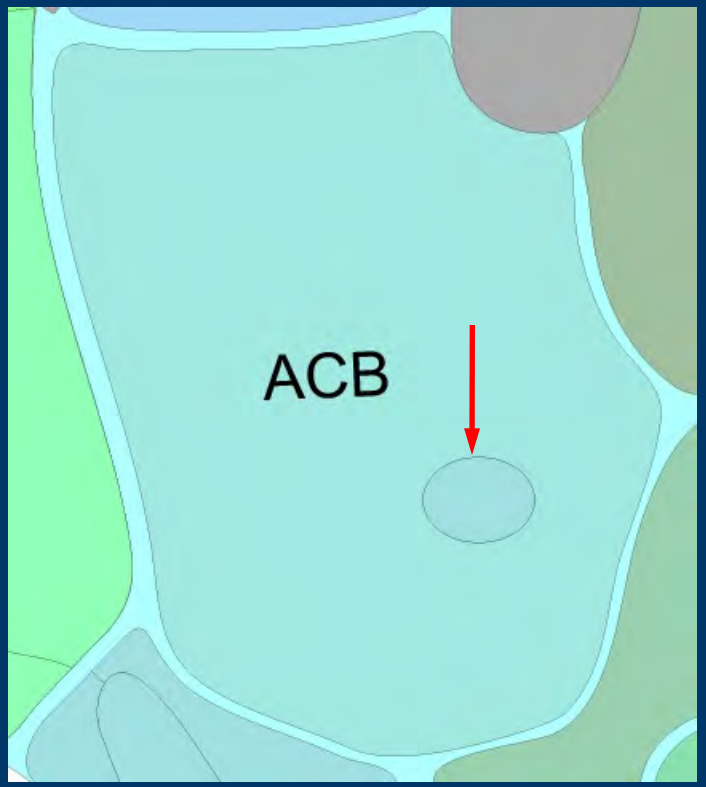
Sagittal levels 14-19: Subdivided AON and PIR into two layers for consistency with other levels and based on Nissl.



Note: left panel is the original version and right panel is the new version.

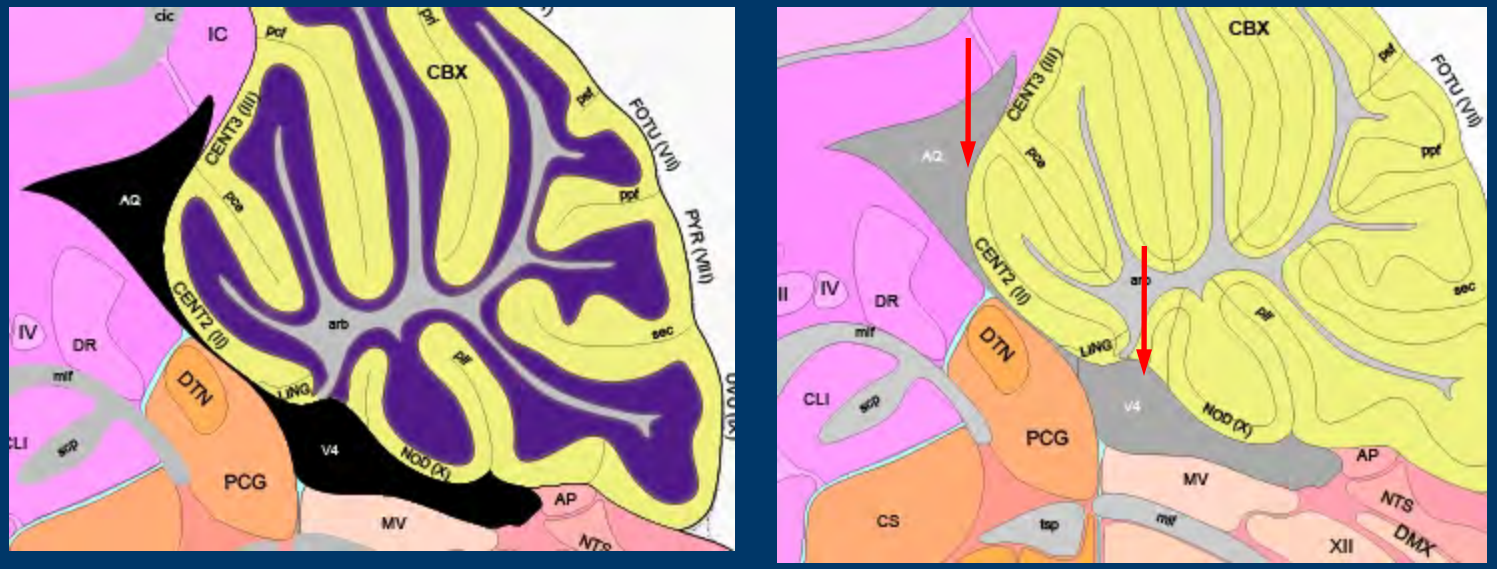
Sagittal levels 16, 18: Added islm for consistency with coronal.





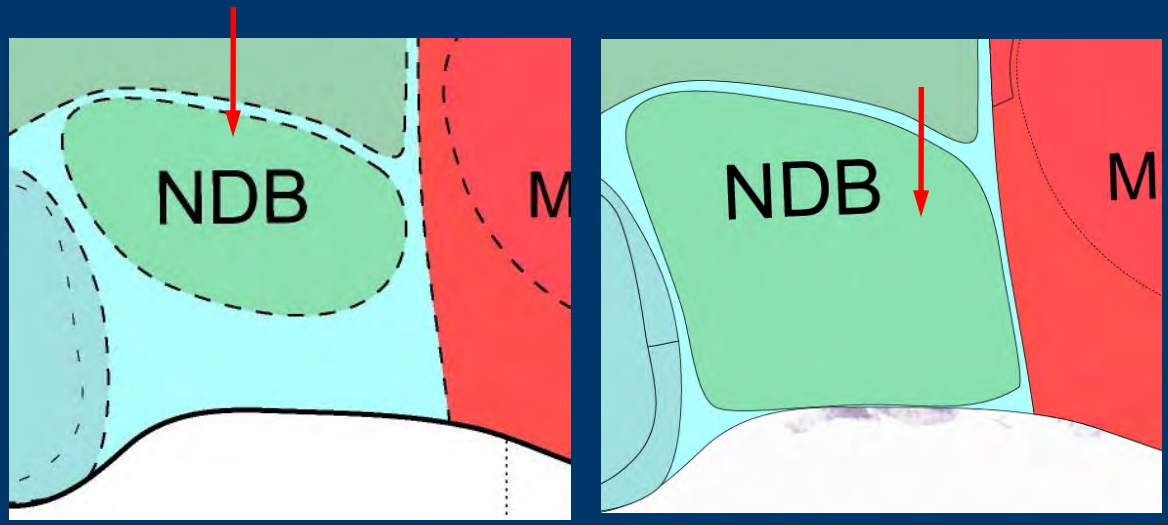
Note: left panel is the original version and right panel is the new version.

Sagittal levels 17-21: Divided AQ and V4 into two polygons.



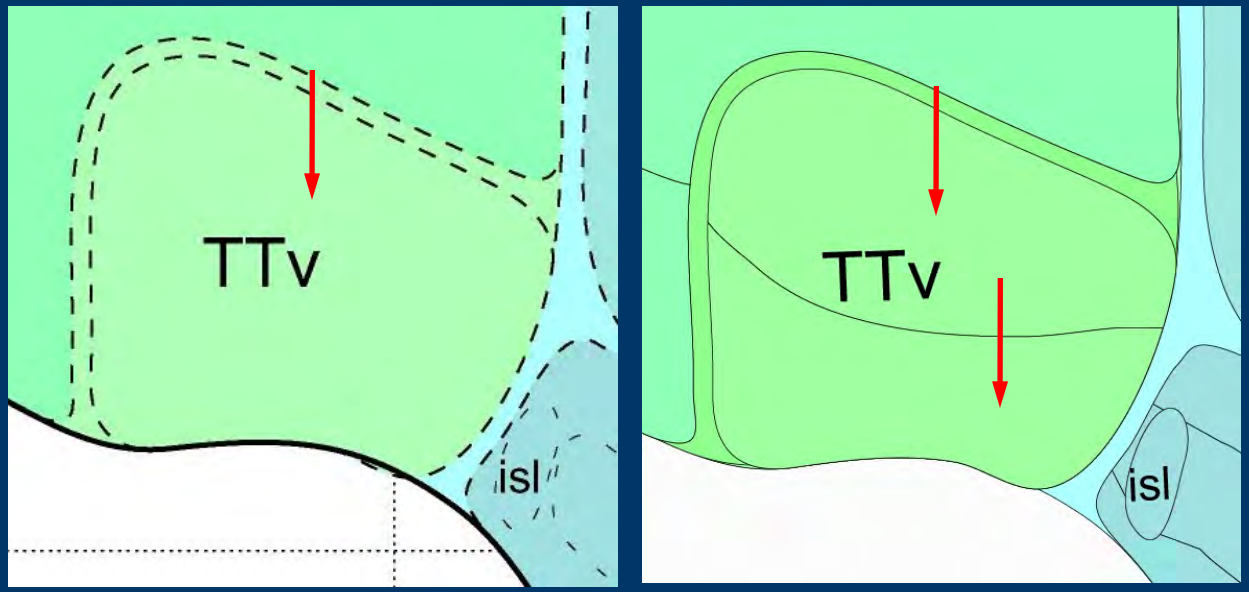
Note: left panel is the original version and right panel is the new version.

Sagittal level 17: Extended NDB to ventral edge of brain for consistency with surrounding levels.



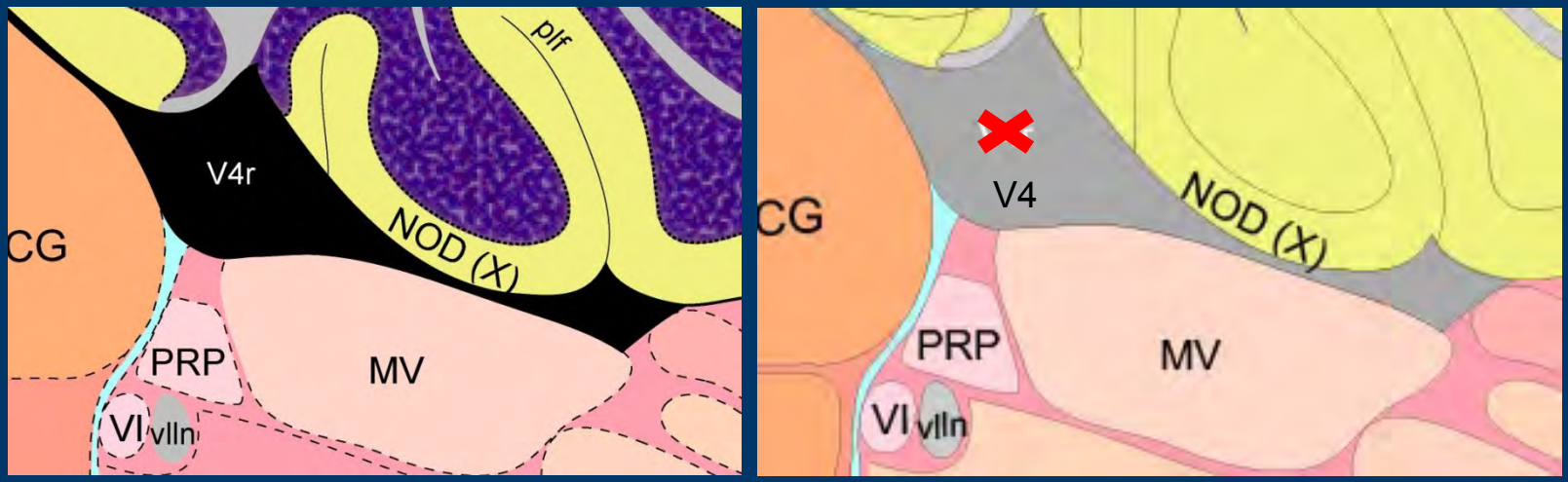
Note: left panel is the original version and right panel is the new version.

Sagittal levels 17-19: Subdivided TTv into two layers based on Nissl.



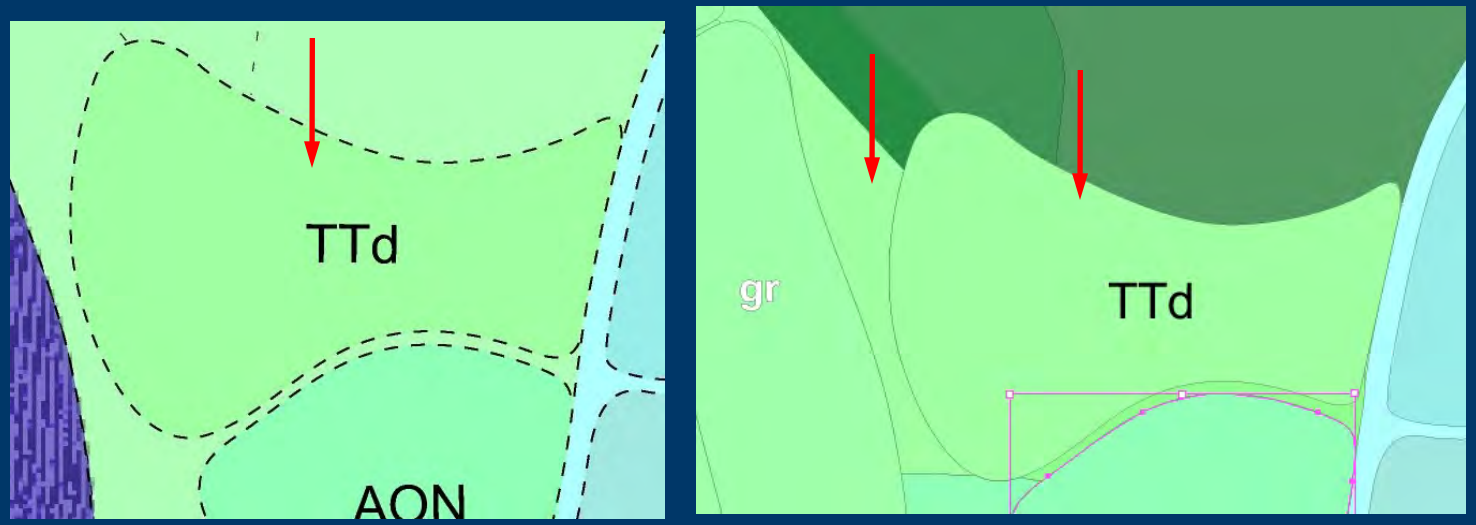
Note: left panel is the original version and right panel is the new version.

Sagittal level 18: Renamed V4r to V4.



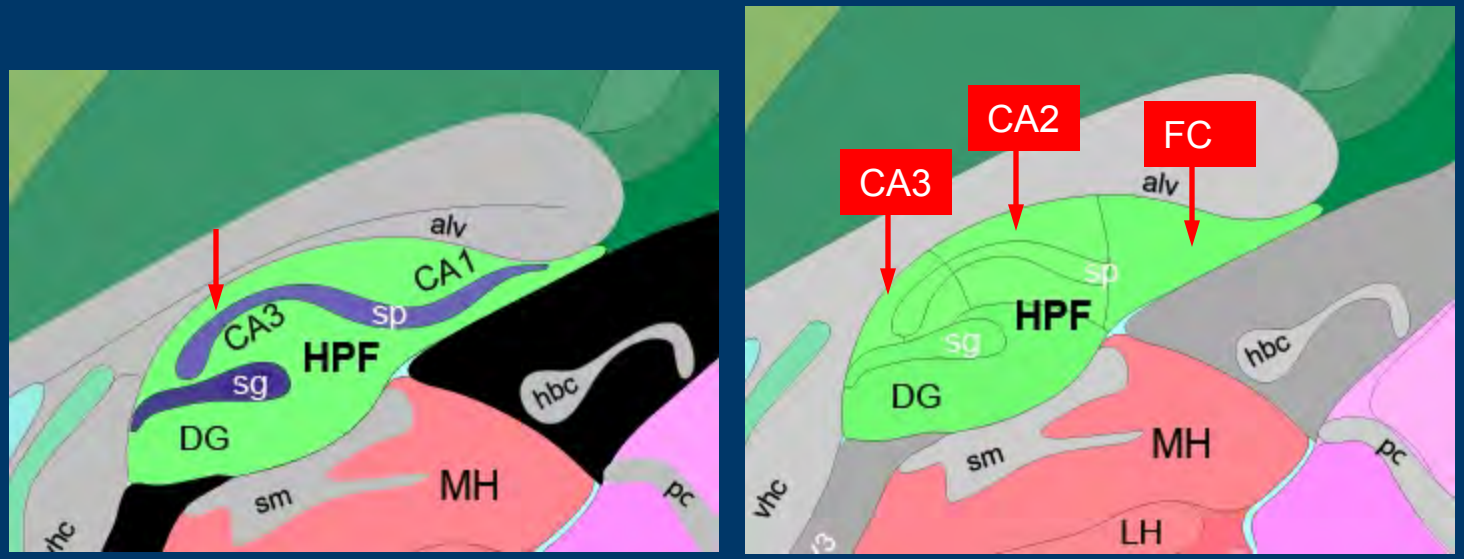
Note: left panel is the original version and right panel is the new version.

Sagittal levels 18-19: Subdivided TTd into two layers based on Nissl.



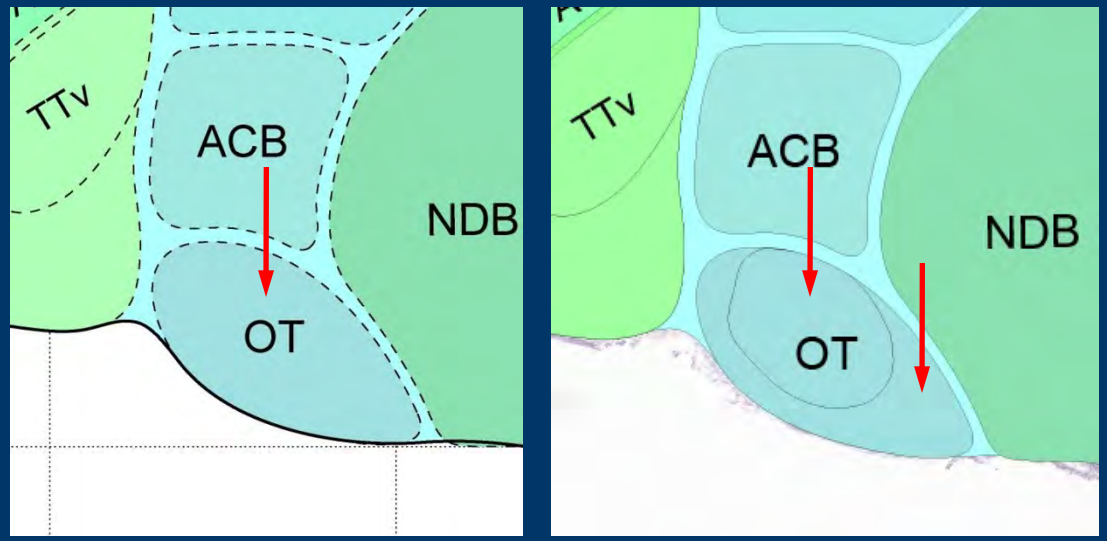
Note: left panel is the original version and right panel is the new version.

Sagittal level 19: added CA2 and FC and took out CA1.



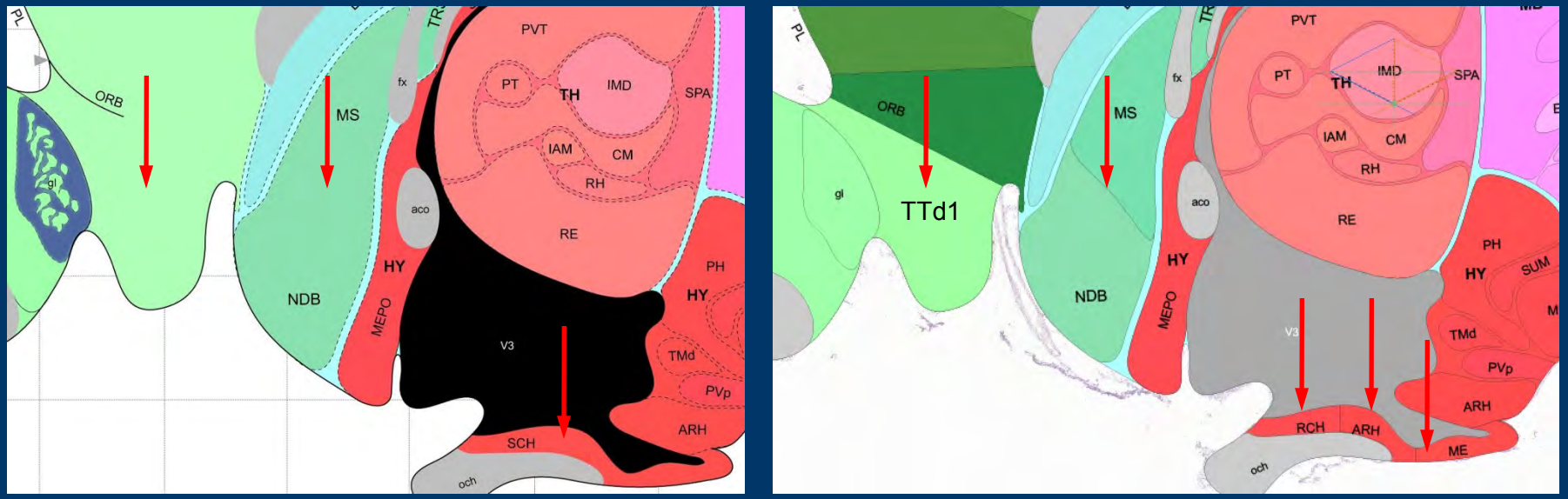
Note: left panel is the original version and right panel is the new version.

Sagittal levels 19, 21: Subdivided OT into two layers for consistency with other levels.



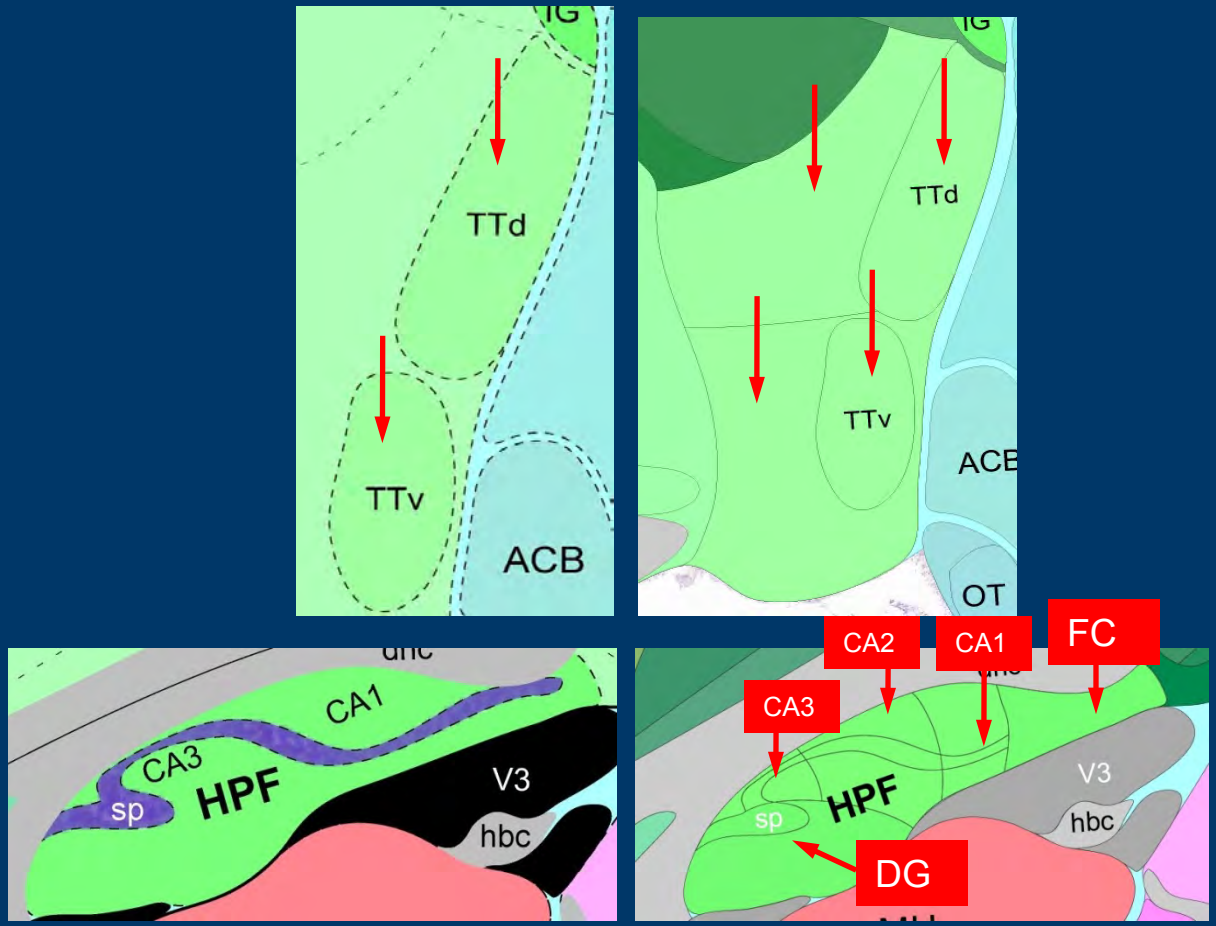
Note: left panel is the original version and right panel is the new version.

Sagittal level 20: Added ME, replacing SCH with RCH and ARH. Added TTd1 for consistency with coronal atlas. Divided MS and NDB.



Note: left panel is the original version and right panel is the new version.

Sagittal level 21: Subdivided TTv and TTd into two layers. Added DG, CA2 and FC.



Note: left panels are the original versions and right panels are the new versions.