



ANTERIOR OLFACTORY NUCLEUS (AON)

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Introduction

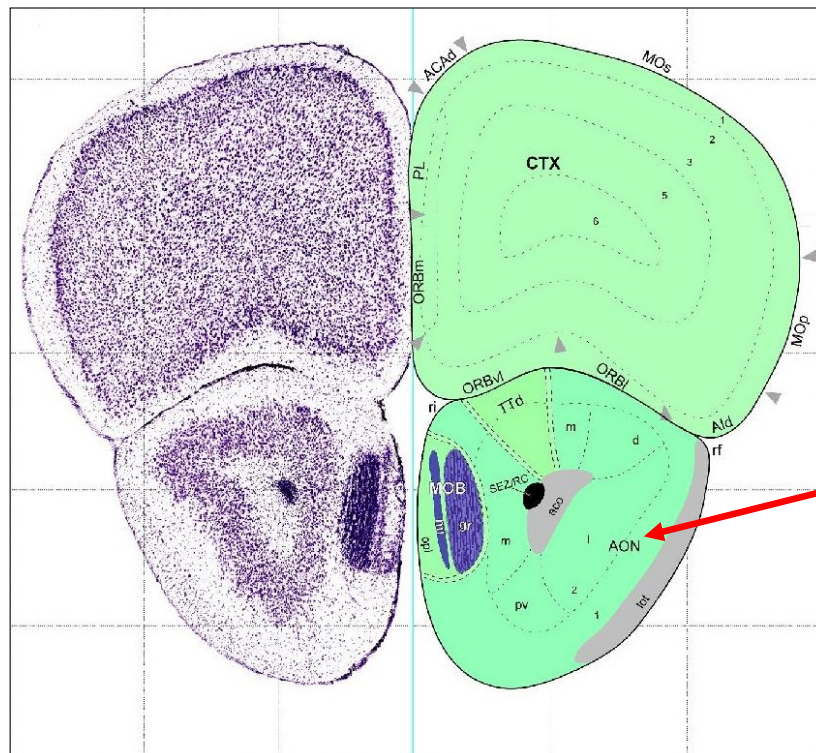
This report contains a gene expression summary of the anterior olfactory nucleus (AON), derived from the [Allen Brain Atlas](#) (ABA) *in situ* hybridization mouse data set. The structure's location and morphological characteristics in the mouse brain are described using the Nissl data found in the [Allen Reference Atlas](#). Using an established algorithm, the expression values of the AON were compared to the values of the macro/parent-structure, in this case the olfactory areas, for the purpose of extracting regionally selective gene expression data. The genes with the highest ranking selectivity ratios were manually curated and verified. 50 genes were then selected and compiled for expression characterization. The experimental data for each gene may be accessed via the links provided; additional data in the sagittal plane may also be accessed using the [ABA](#). Correlations between gene expression in the AON and the rest of the brain, across all genes in the coronal dataset (~4300 genes), were derived computationally. A gene ontology table (derived from DAVID Bioinformatics Resources 2007) is also included, highlighting possible functions of the 50 genes selected for this report.

To read more about how our 50 Select Genes list is derived, please refer to the [Fine Structure Annotation white paper](#).

Allen Reference Atlas Coronal Levels: 19-38

Allen Reference Atlas Sagittal Levels: 11-19

Shown below is a plate from the Allen Reference Atlas, depicting the AON (level [28](#)):



Description of Structure:

LOCATION and STRUCTURAL ANATOMY:

The hierarchical relationship within the brain is depicted below in the structure [legend](#). The Allen Reference Atlas (based on Nissl-stained sections scanned at 10X) was the primary resource for the following descriptions.

For additional information please refer to the [Allen Reference Atlas white paper](#).
[BrainInfo](#) houses a search engine that allows searches for structure name aliases.

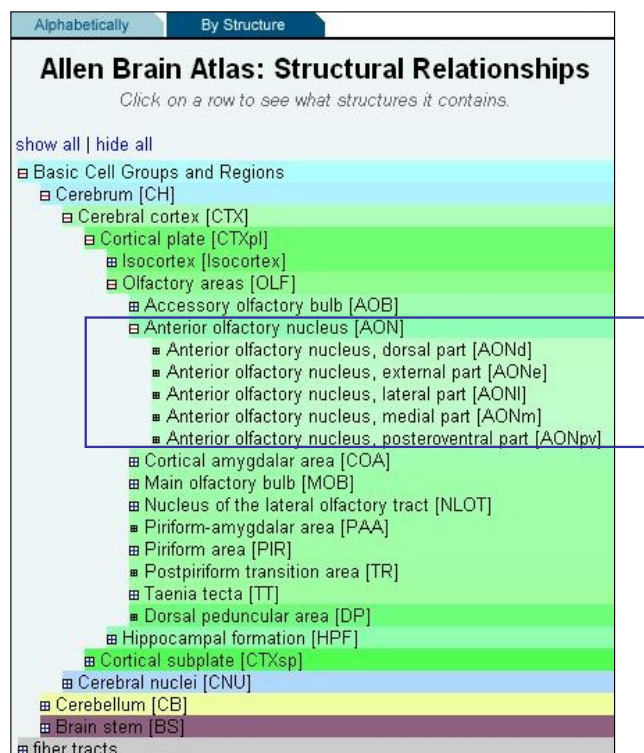
The anterior olfactory nucleus (AON) is a substructure of the olfactory areas, located within the rostral portion of the cerebral cortex. The AON is comprised of dorsal (AONd), external (AONe), lateral (AONI), medial (AONm) and posteroventral (AONpv) subdivisions. Rostrally, the AONe surrounds the remaining subdivisions, and is therefore easily distinguished from them; the borders between the internal nuclei are difficult to distinguish.

In the coronal plane, the AON presents most rostrally within the main olfactory bulb (MOB). It can first be seen at the lateral aspect of the MOB bordering the subependymal zone/rhinocoele (SEZ/RC). Caudally, the AONe disappears and the internal areas spread medially until they fully surround the SEZ/RC. At its most caudal aspect, the AONI is no longer present, and only the AONm and AONpv subdivisions remain. The caudal edge of the AON is consistent with the emergence of the nucleus accumbens.

In sagittal sections, the AON emerges just lateral to the junction of the MOB and the rest of the brain. The AON lies caudal to the MOB and rostro-dorsal to the piriform cortex. Continuing medially, the AON appears on either side of the SEZ/RC and the olfactory limb of the anterior commissure, and extends slightly rostrally into the MOB. At the midline, the AON is supplanted by the taenia tecta (TT).

The cells in the AONe are more densely packed than in the internal areas. The internal nuclei are separated from the AONe by a thin, cell-sparse layer. The size of the cells in the AON make this structure easily distinguished from the anterior commissure and the lateral olfactory tract.

The appearance and location of the AON can be appreciated on the following two pages. Nissl-stained sections and Allen Reference Atlas plates reveal the cytoarchitecture and extent of the AON, and its location in relation to surrounding structures.

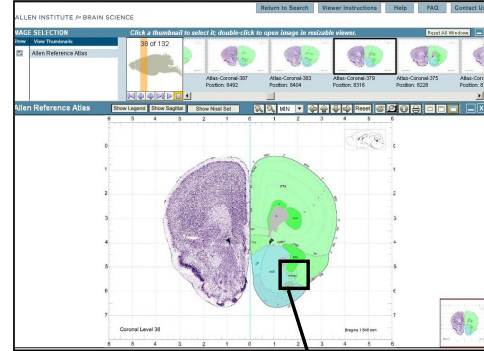
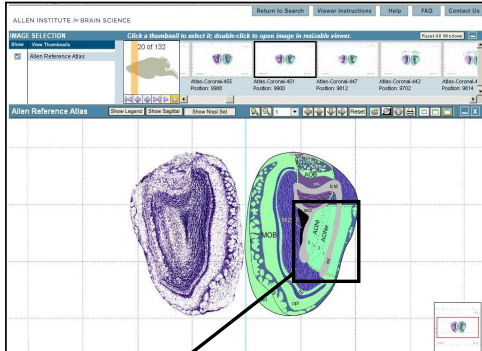


Atlas and Nissl:

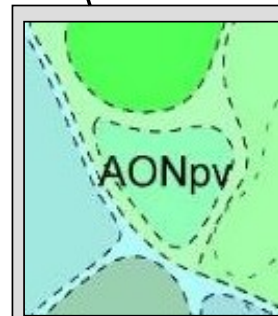
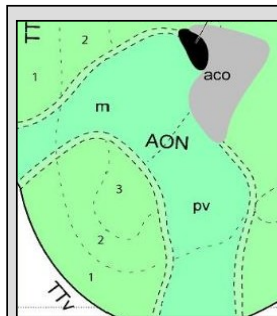
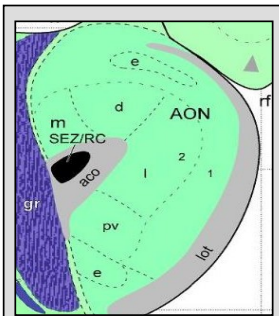
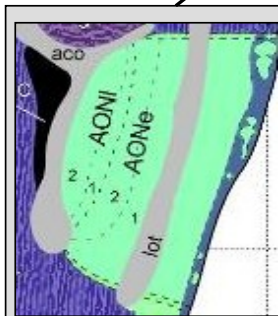
Coronal:

Rostral

Caudal



Reference Atlas

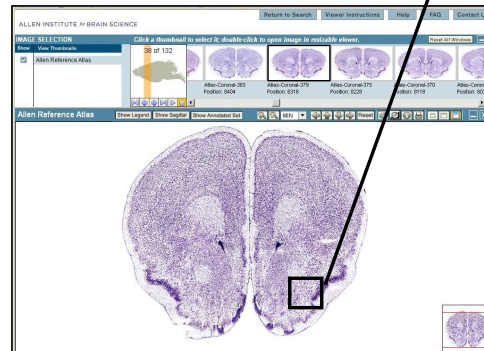
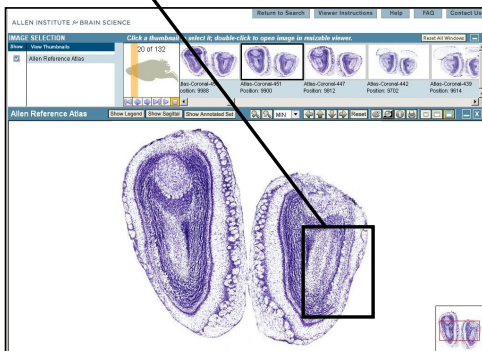
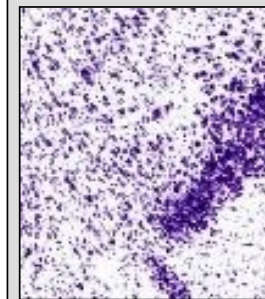
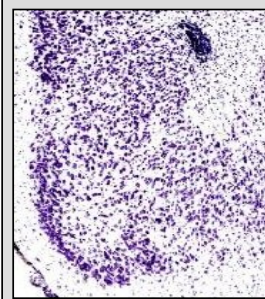
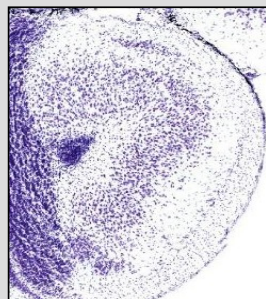
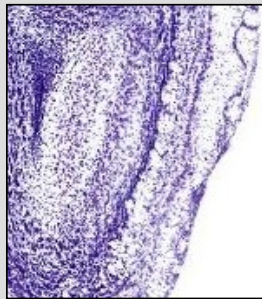


Level 20

Level 26

Level 32

Level 38

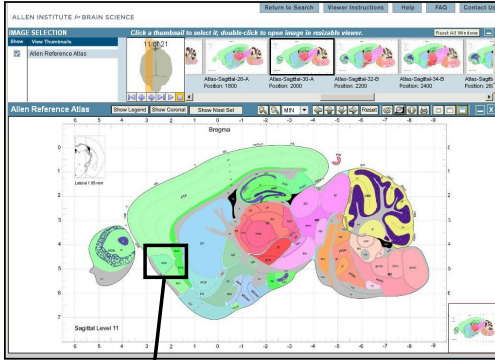


Nissl

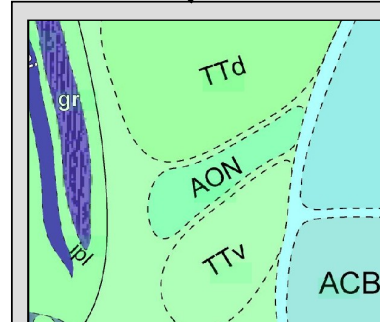
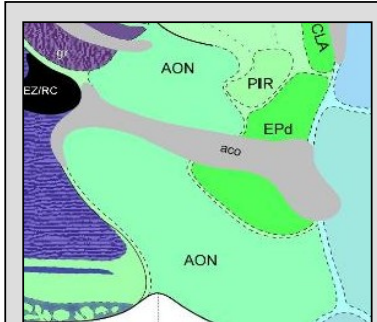
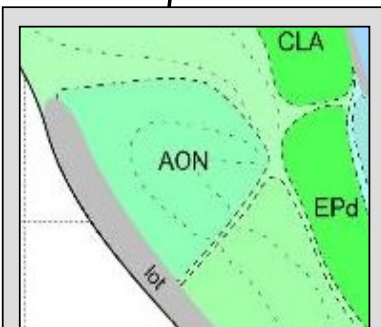
Atlas and Nissl: Sagittal:

Lateral

Medial



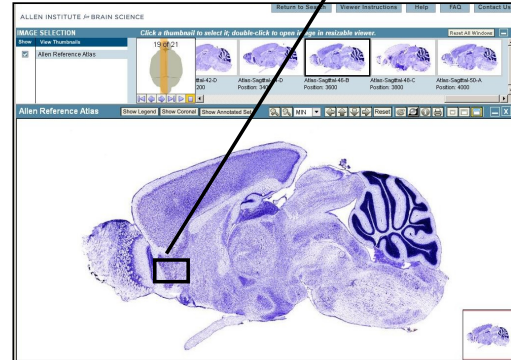
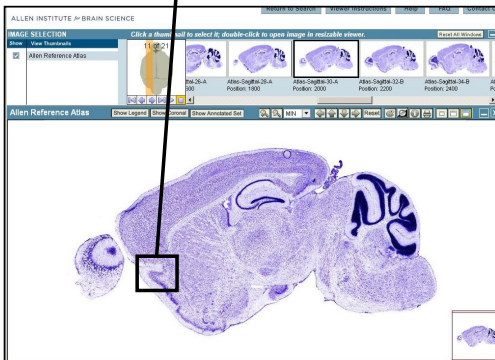
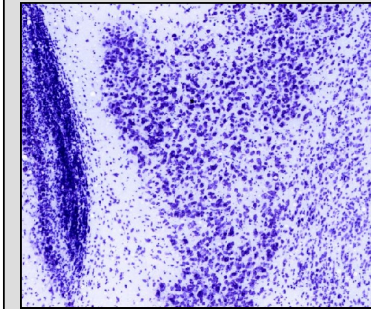
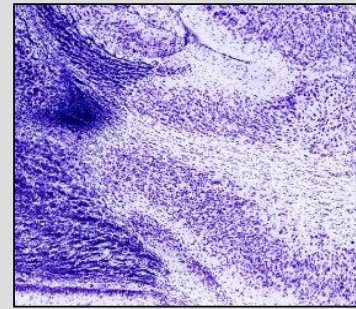
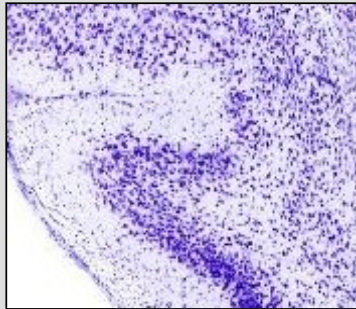
Reference Atlas



Level 11

Level 15

Level 19



Nissl

In Situ Hybridization Expression Patterns of 50 Select Genes:

The *in situ* hybridization (ISH) data below presents the anterior olfactory nucleus' anatomical and cytoarchitectural characteristics in the context of actual gene expression. In addition to presenting molecularly defined borders, ISH gene expression patterns also aid in phenotyping cell populations that otherwise can not be differentiated on purely morphological grounds.

The 50 genes in this section were selected based on a mathematical algorithm to identify gene expression patterns that allow selective identification of the anterior olfactory nucleus. The gene expression patterns were then verified manually. As such, these genes do not represent the only genes found in this structure, genes specific to this structure, or genes expressing at the highest level within this structure.

Please refer to our protocol in the [Data Production Processes white paper](#).

To read about heat map conversion, refer to the [Informatics Data Processing white paper](#).

The expression data subsequently presented can be further explored, in coronal and sagittal planes, at [brain-map.org](#).

Two major portions of the AON can be distinguished based on gene expression: the AONE and the remaining internal areas (AONI, AONm, and AONpv). This set of genes display three expression patterns. Approximately half of the genes presented are expressed throughout the entire AON, with similar expression in the internal and external regions. The remaining genes are either preferentially expressed in the AONE or are preferentially expressed in the internal areas. The AON is easily distinguished from its surrounding structures in these ISH studies, although the individual nuclei of the internal portions remain equally difficult to distinguish.

Cellular density expression key		Cellular intensity expression key	
None	No expression	No color	Very low intensity
Sparse	Very few cells expressing	Blue	Low intensity
Scattered	Less than 10% of cells expressing in scattered pattern	Green	Medium intensity
Medium	10-80% of cells expressing	Yellow	High intensity
High	Greater than 80% of cells expressing	Red	Very high intensity

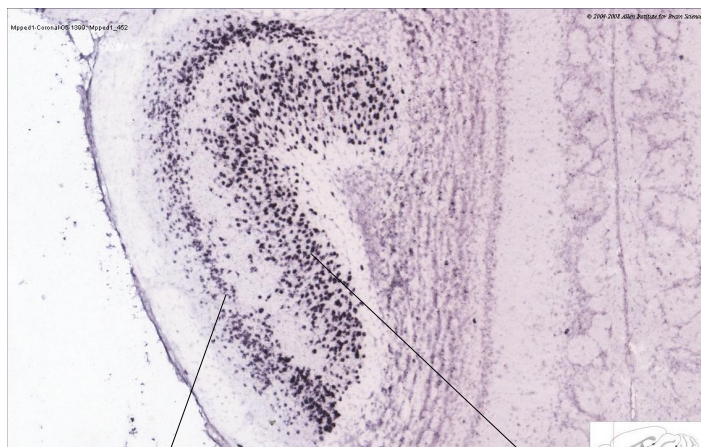
To view heat map at [brain-map.org](#), right click on the ISH image and select "Show Expression Analysis."

ISH DATA The images below were selected to highlight various expression patterns of the AON.

ISH

Mpped1

Coronal: The gene expressed below allows the visualization of the external nucleus and the internal areas of the AON.



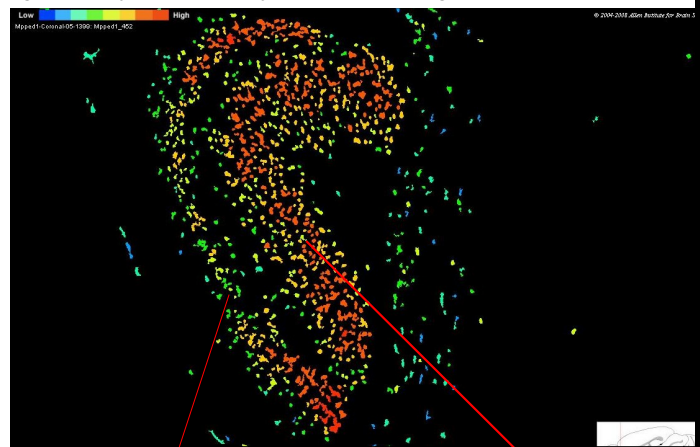
Anterior olfactory nucleus, external part

Anterior olfactory nucleus, internal areas

Heat map

Mpped1

Coronal: Both the external and internal parts of the AON show high density and intensity expression for gene Mpped1.

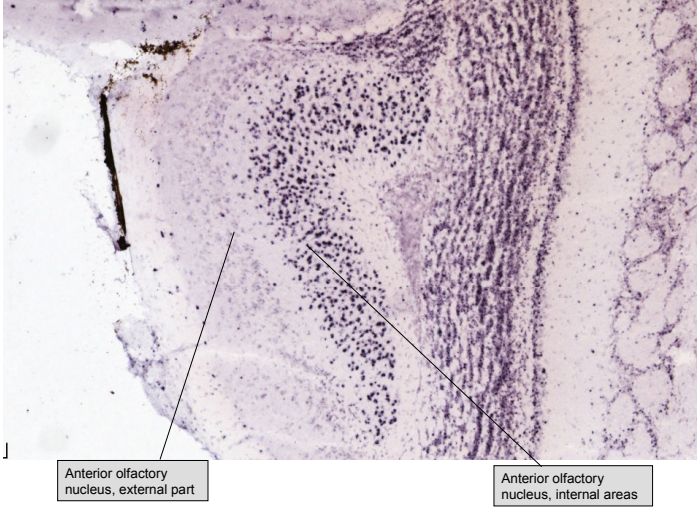


Anterior olfactory nucleus, external part

Anterior olfactory nucleus, internal areas

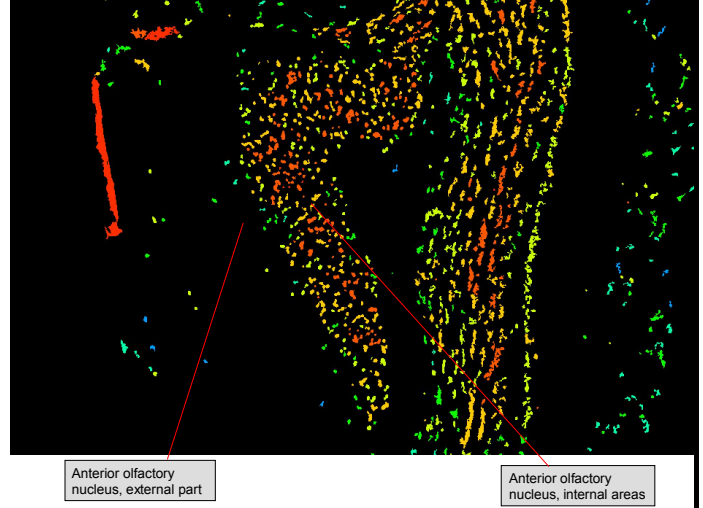
ISH
Grik2

Coronal: Preferential expression in the internal portions of the AON.



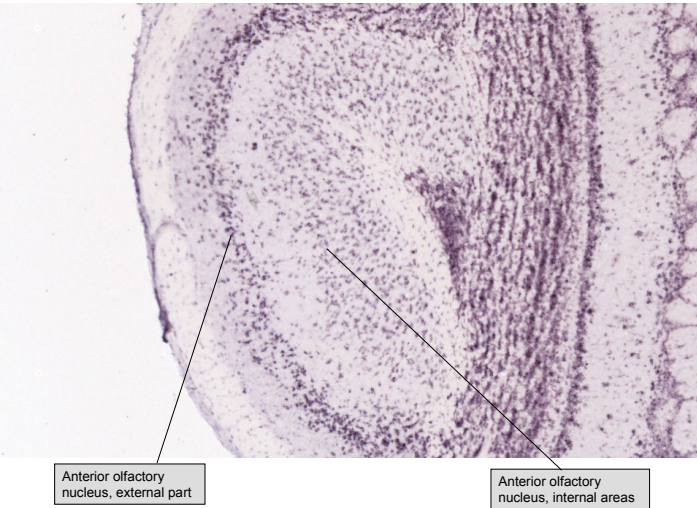
Heat map
Grik2

Coronal: The high density and intensity of Grik2 expression can be seen here, limited to internal nuclei.



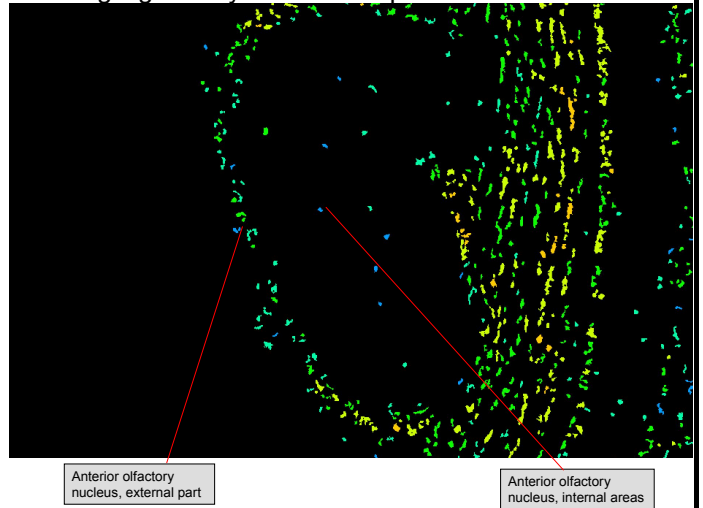
ISH
Shb

Coronal: Expression is limited to the external nucleus of the AON.



Heat map
Shb

Coronal: A distinct lack of expression in the internal nuclei is highlighted by the heat map.



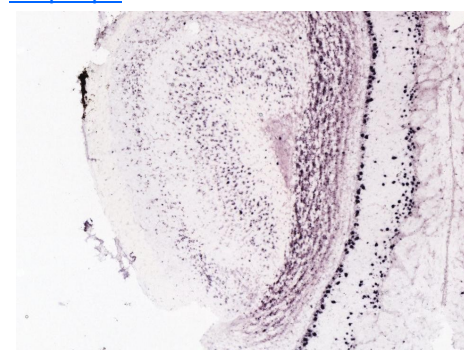
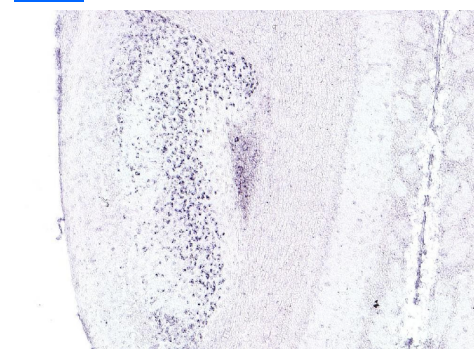
50 SELECT GENES:

This gene list was generated by manual curation of an [algorithmically](#) derived list that compared gene expression values of the AON to those of the olfactory areas. Categories of expression are [subjectively](#) grouped by relative expression characteristics.

Curation of 50 Select Genes List: February 2008

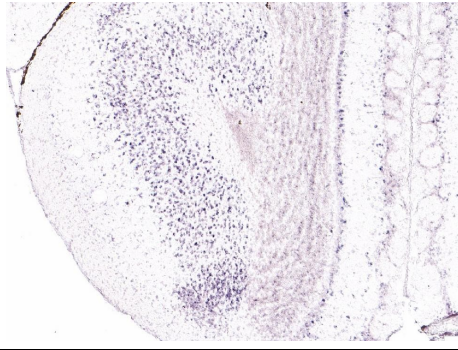
Widespread expression throughout the AON

Number	Gene Symbol	Gene Name	Expression Pattern
1	Ndst4	N-deacetylase/N-sulfotransferase (heparin glucosaminy) 4	Widespread; medium-high density, high intensity
2	Ppfibp1	PTPRF interacting protein, binding protein 1 (liprin beta 1)	Widespread; medium density and intensity with scattered intensity medium-high intensity
3	Nfia	nuclear factor I/A	Widespread; medium-high density and intensity
4	Fjx1	four jointed box 1 (Drosophila)	Widespread; medium density and intensity
5	Htr2c	5-hydroxytryptamine (serotonin) receptor 2C	Widespread; medium-high density and intensity
6	Prss23	protease, serine, 23	Widespread; high density medium intensity with scattered density high intensity
7	Pcsk5	proprotein convertase subtilisin/kexin type 5	Widespread; high density, medium intensity
8	L1cam	L1 cell adhesion molecule	Widespread; high density, low intensity
9	Calb2	calbindin 2	Widespread; scattered density, high intensity
10	Pip5k1a	phosphatidylinositol-4-phosphate 5-kinase, type 1 alpha	Widespread; medium-high density, medium intensity
11	2900093B09Rik	RIKEN cDNA 2900093B09 gene	Widespread; high density and intensity
12	AW125753	expressed sequence AW125753	Widespread; high density and intensity
13	Mpped1	metallophosphoesterase domain containing 1	Widespread; high density and intensity
14	mCG141917	AB mCG141917	Widespread; medium density and intensity
15	Robo2	roundabout homolog 2 (Drosophila)	Widespread; high density and intensity
16	Wnt7b	wingless-related MMTV integration site 7B	Widespread; medium density and intensity
17	Rps15a	ribosomal protein S15a	Widespread; medium density, low intensity
18	Nmbr	neuromedin B receptor	Widespread; medium density and intensity
19	1810041L15Rik	RIKEN cDNA 1810041L15 gene	Widespread; medium density and intensity
20	Id4	inhibitor of DNA binding 4	Widespread; medium density, low intensity
21	Tnip2	TNFAIP3 interacting protein 2	Widespread; medium density, low intensity
22	Grik3	glutamate receptor, ionotropic, kainate 3	Widespread; high density medium intensity with scattered density high intensity
23	Lrp8	low density lipoprotein receptor-related protein 8, apolipoprotein e receptor	Widespread; medium density and intensity
24	Lrrn3	leucine rich repeat protein 3, neuronal	Widespread; high density and intensity
25	Nr2f1	nuclear receptor subfamily 2, group F, member 1	Widespread; medium-high density and intensity
26	Lhfp	lipoma HMGIC fusion partner	Widespread scattered-medium density, medium-high intensity

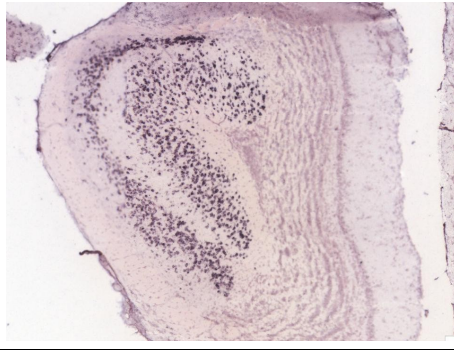
[1.Ndst4](#)[2.Ppfibp1](#)[3.Nfia](#)

Widespread Expression throughout the AON

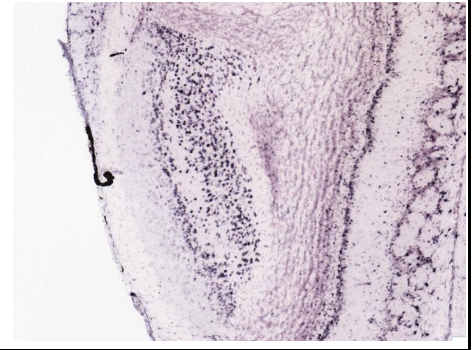
[4.Fjx1](#)



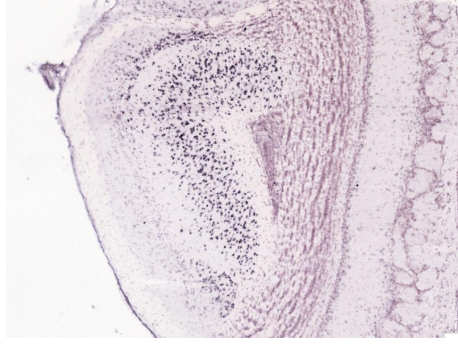
[5.Htr2c](#)



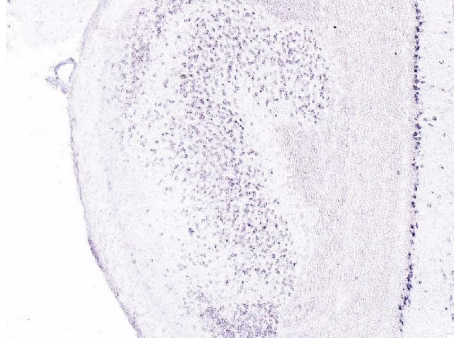
[6.Prss23](#)



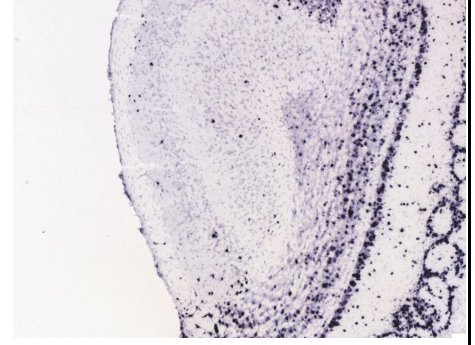
[7.Pcsk5](#)



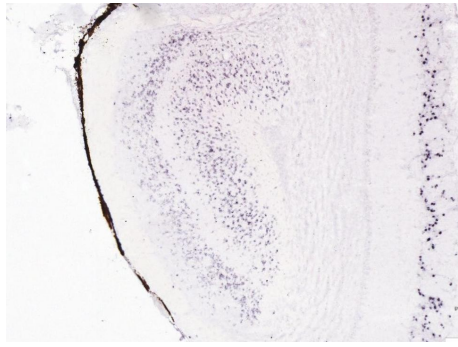
[8.L1cam](#)



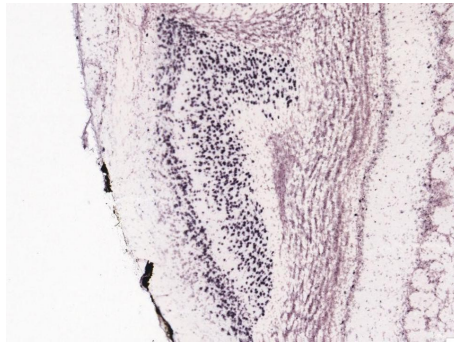
[9.Calb2](#)



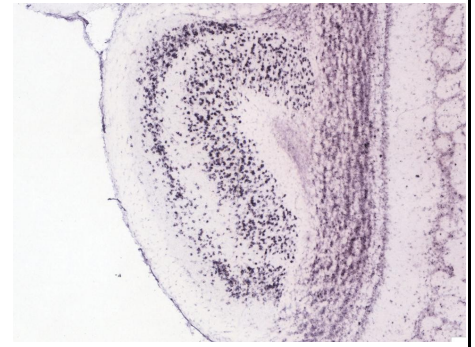
[10.Pip5k1a](#)



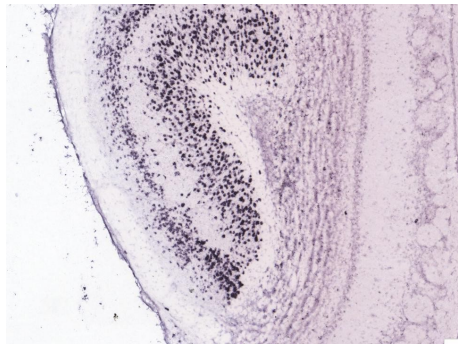
[11.2900093B09Rik](#)



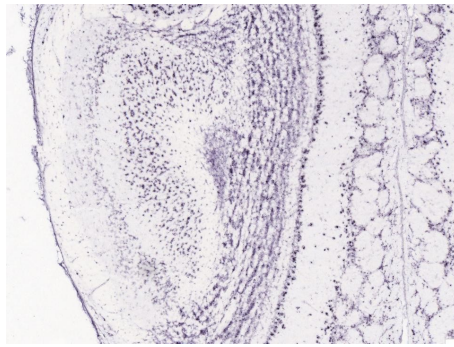
[12.AW125753](#)



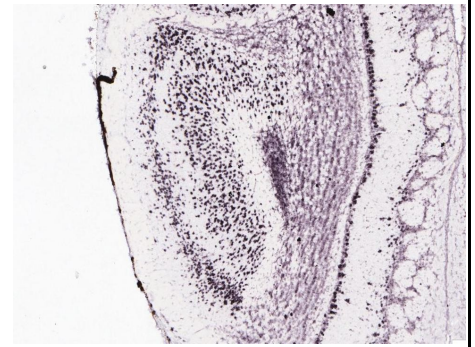
[13.Mpped1](#)



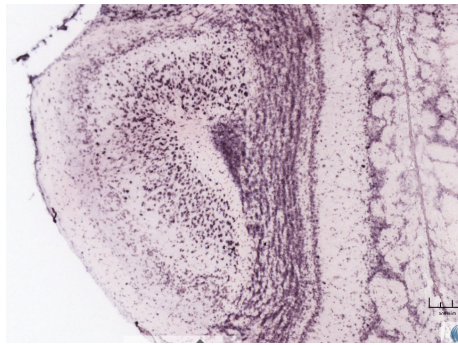
[14.mCG141917](#)



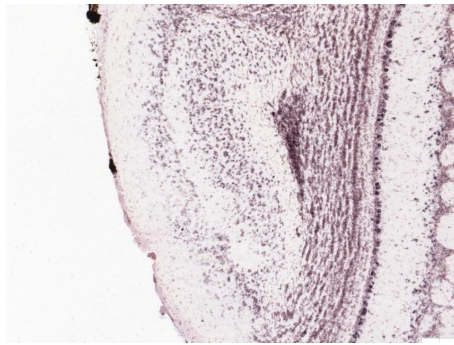
[15.Robo2](#)



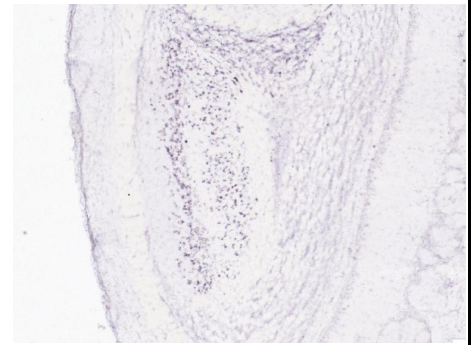
[16.Wnt7b](#)



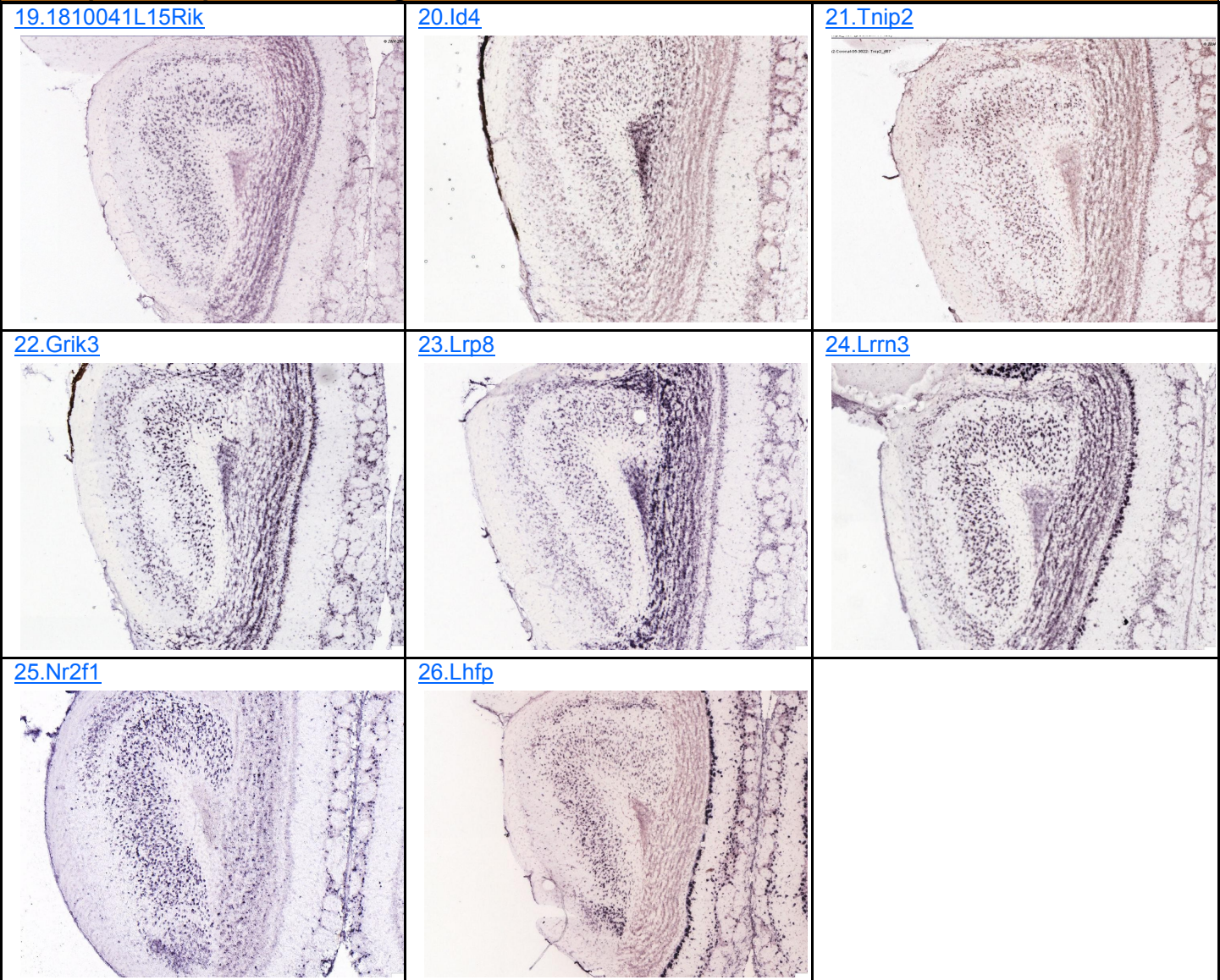
[17.Rps15a](#)



[18.Nmbr](#)



Widespread Expression throughout the AON

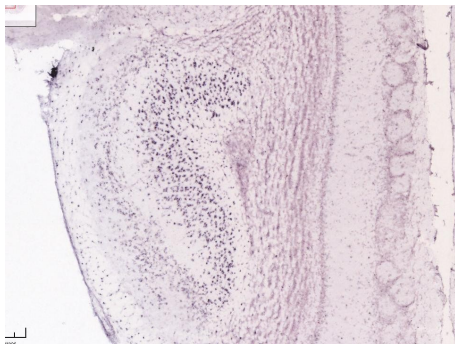


Preferential Expression in Internal Nuclei

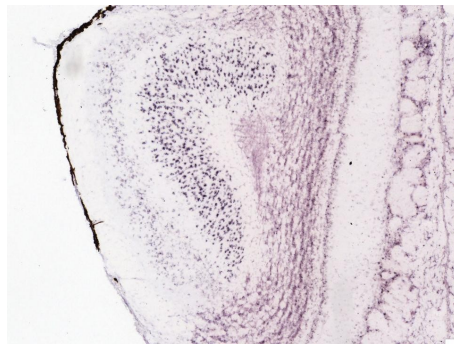
27	2310015N21Rik	RIKEN cDNA 2310015N21 gene	Internal: widespread, medium density and intensity; External: widespread, scattered-medium density low intensity
28	Cpne8	copine VIII	Internal: widespread, medium density and intensity; External: widespread, scattered-medium density low intensity
29	A830018L16Rik	RIKEN cDNA A830018L16 gene	Internal: widespread; medium-high density, medium-low intensity; External: scattered density, low density low intensity
30	Slitrk4	SLIT and NTRK-like family, member 4	Internal: widespread, high density medium intensity with medium density high intensity; External: widespread, high density low expression
31	St3gal1	ST3 beta-galactoside alpha-2,3-sialyltransferase 1	Internal: widespread, medium density and intensity; External: widespread, low density and intensity
32	Nrip1	nuclear receptor interacting protein 1	Internal: widespread, high density medium-high intensity; External: widespread, medium density low intensity
33	Tpbq	trophoblast glycoprotein	Internal: widespread, high density and intensity; External: low density medium intensity

34	Lin7a	lin-7 homolog A (<i>C. elegans</i>)	Internal: widespread, medium density medium intensity; External: widespread, low density and intensity
35	Homer2	homer homolog 2 (<i>Drosophila</i>)	Internal: widespread, medium-high density high intensity; External: widespread, sparse density medium intensity
36	Fzd3	frizzled homolog 3 (<i>Drosophila</i>)	Internal: widespread, high density medium-high intensity; External: deep/internal, medium-high density medium density
37	Pvr1	poliovirus receptor-related 1	Internal: widespread, high density and intensity; External: medium density and intensity
38	Slit1	slit homolog 1 (<i>Drosophila</i>)	Internal: widespread, medium-high density low-medium intensity; External: low density and intensity
39	Syt17	synaptotagmin XVII	Internal: widespread, medium density and intensity; External: widespread, medium density low intensity
40	Trpc4	transient receptor potential cation channel, subfamily C, member 4	Internal: widespread, high density medium intensity; External: no expression
41	Cadps2	Ca ²⁺ -dependent activator protein for secretion 2	Internal: widespread, high density medium intensity with sparse density high intensity; External: no expression
42	Grik2	glutamate receptor, ionotropic, kainate 2 (beta 2)	Internal: widespread, high density and intensity; External: no expression
43	Cacng8	calcium channel, voltage-dependent, gamma subunit 8	Internal: widespread, high density and intensity; External: scattered, medium-high density high intensity
44	Cpne7	copine VII	Internal: widespread, high density and intensity; External: scattered, scattered-medium density, high intensity
45	Cacna1g	calcium channel, voltage-dependent, T type, alpha 1G subunit	Internal: widespread, medium-high density and intensity; External: scattered medium density, medium intensity

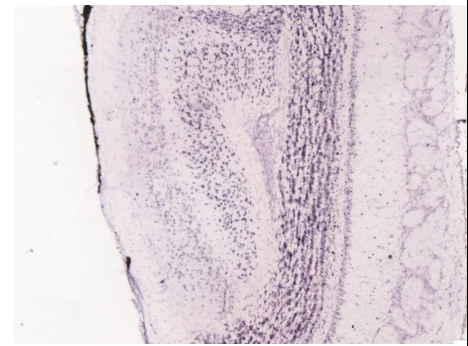
[27.2310015N21Rik](#)



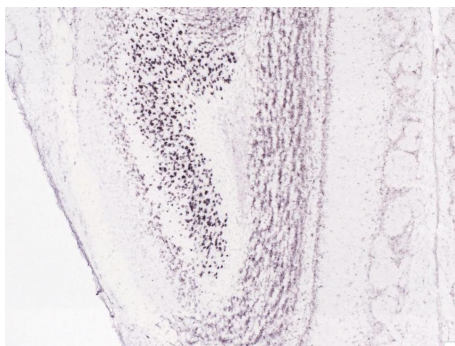
[28.Cpne8](#)



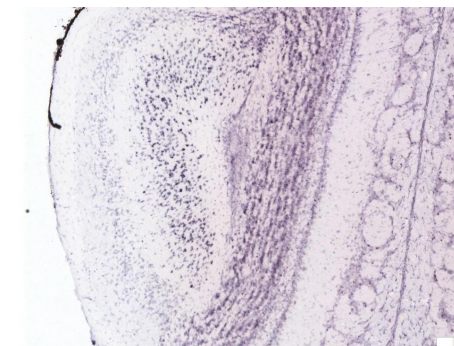
[29.A830018L16Rik](#)



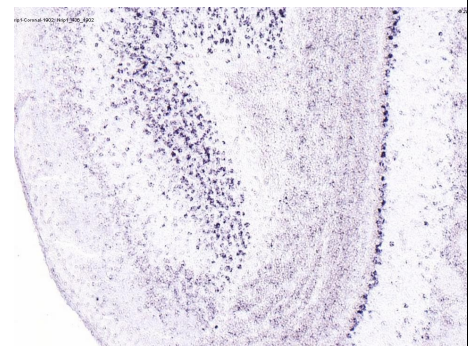
[30.Slitrk4](#)



[31.St3gal1](#)

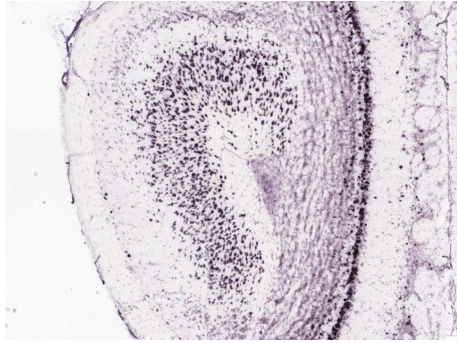


[32.Nrip1](#)

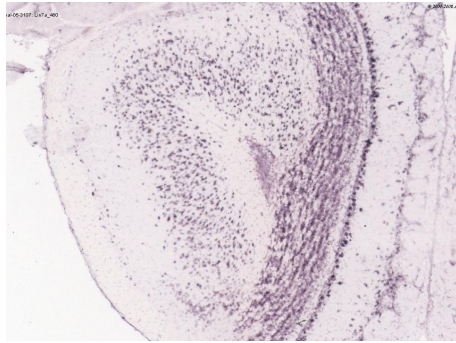


Preferential Expression in Internal Nuclei

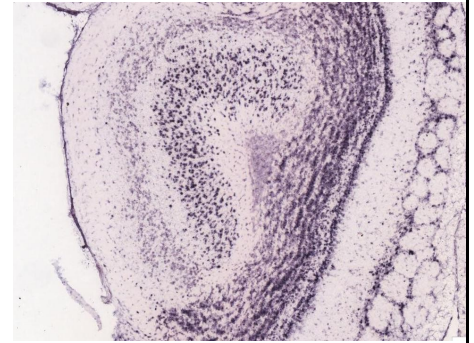
[33.Tpbq](#)



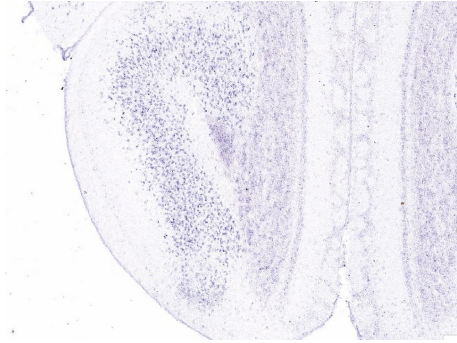
[34.Lin7a](#)



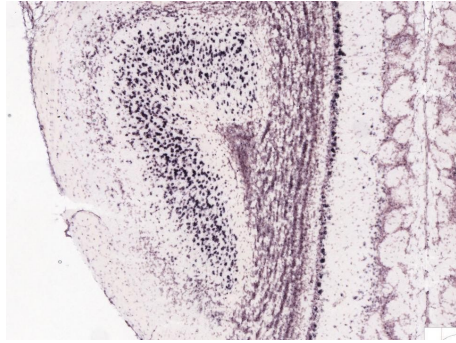
[35.Homer2](#)



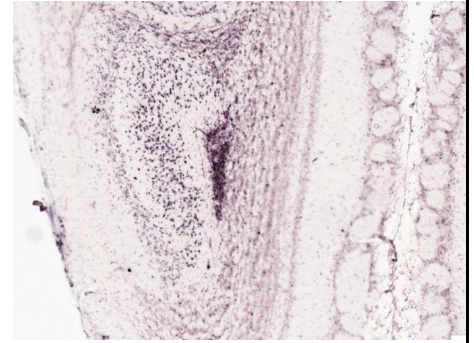
[36.Fzd3](#)



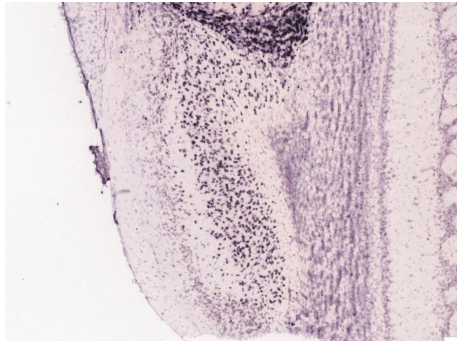
[37.Pvrl1](#)



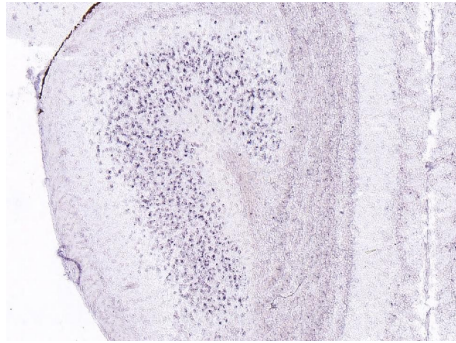
[38.Slit1](#)



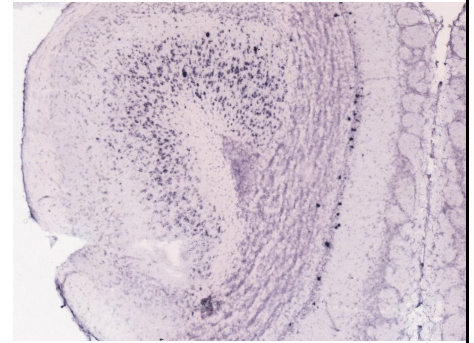
[39.Syt17](#)



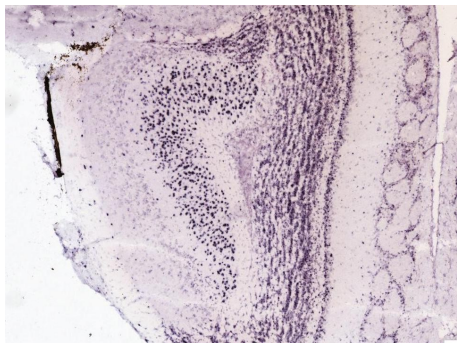
[40.Trpc4](#)



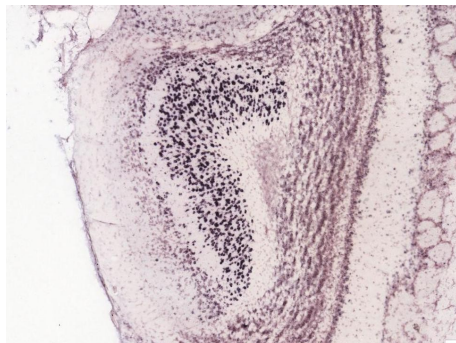
[41.Cadps2](#)



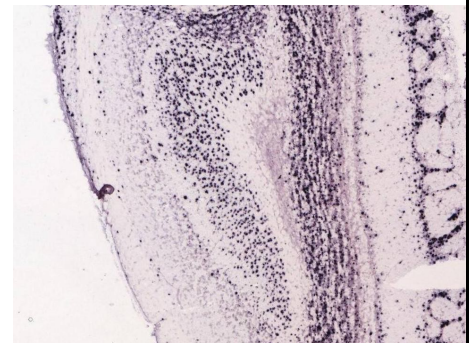
[42.Grik2](#)



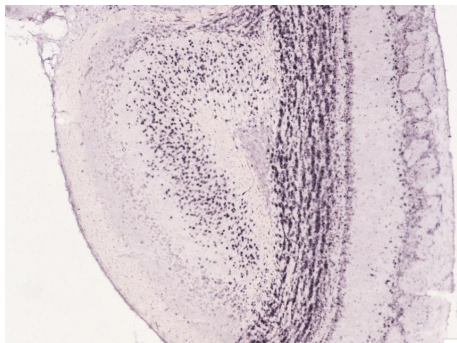
[43.Cacng8](#)



[44.Cpne7](#)



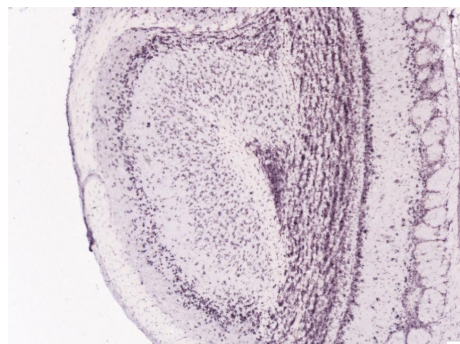
[45.Cacna1g](#)



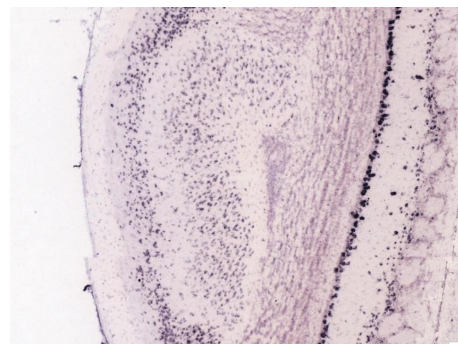
Preferential Expression in the External Nucleus

46	Shb	src homology 2 domain-containing transforming protein B	Internal: widespread, low density and intensity; External: widespread, high density medium intensity
47	3632451O06Rik	RIKEN cDNA 3632451O06 gene	Internal: widespread, medium density and intensity; External: widespread, high density and intensity
48	Slc6a15	solute carrier family 6 (neurotransmitter transporter), member 15	Internal: widespread, medium density low intensity; External: widespread, high density medium intensity
49	Inhba	inhibin beta-A	Internal: widespread, low-medium density and intensity; External: widespread, high density medium intensity
50	2810439F02Rik	RIKEN cDNA 2810439F02 gene	Internal: widespread, medium-high density low intensity; External: high density medium intensity

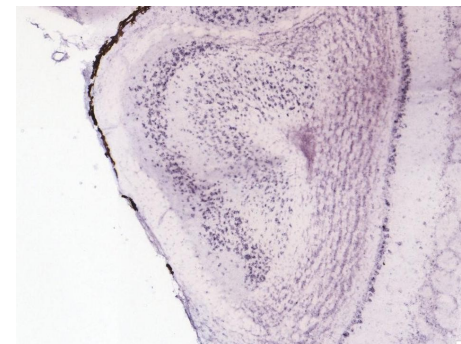
[46.Shb](#)



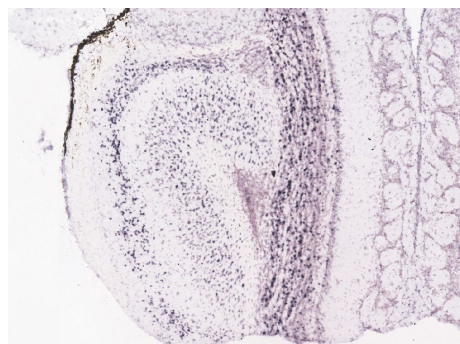
[47.3632451O06Rik](#)



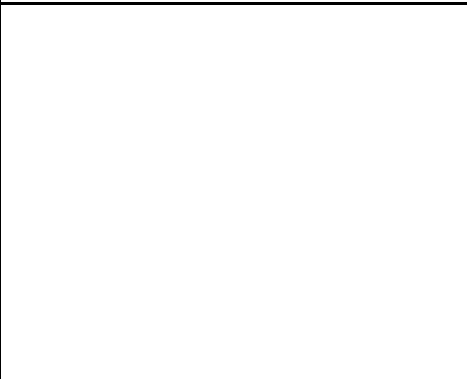
[48.Slc6a15](#)



[49.Inhba](#)



[50.2810439F02Rik](#)



Correlated Expression:

The ABA coronal set contains many genes of known scientific interest as well as genes exhibiting combinatorial or unique expression patterns. A correlation analysis of all available ABA coronal experiments (4376) was performed by comparing the expression value of the AON to expression values in other regions of the brain. Following [image analysis](#), the data values for each experiment were mapped to a 3-D reference brain at (200 μ m)³ voxel resolution. Then, each voxel was assigned a single expression value based on the product of density and intensity of expression. Values from all 4376 experiments were computed, and the likelihood of co-expression between any two voxels or regions are reported as a Pearson's correlation coefficient.

For the purposes of determining correlated expression between the AON and other brain regions, expression values from all voxels within the AON were aggregated to form a single expression value. Two types of comparisons were then made. First, the aggregate expression values of the AON and those of other anatomically defined regions (~200 structures) were compared within the 3-D reference brain (structure vs. structure; table below). Second, a color map was then generated to display the correlation between the AON and each of the ~53,000 voxels of the reference volume (structure vs. voxel; correlation map on the following page).

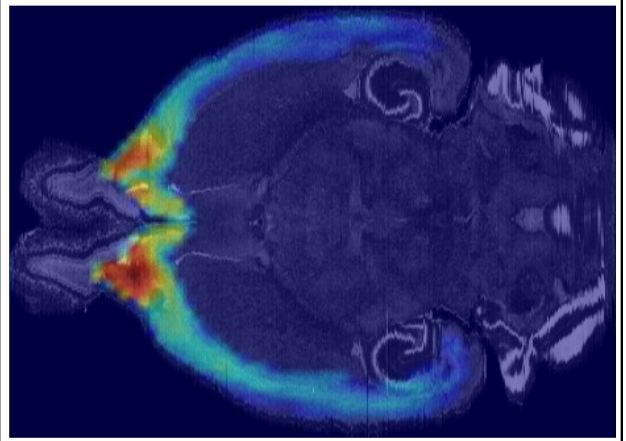
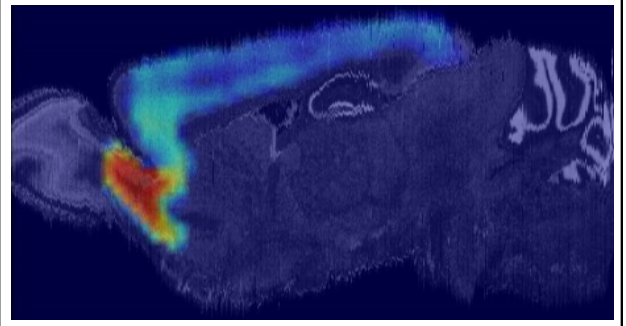
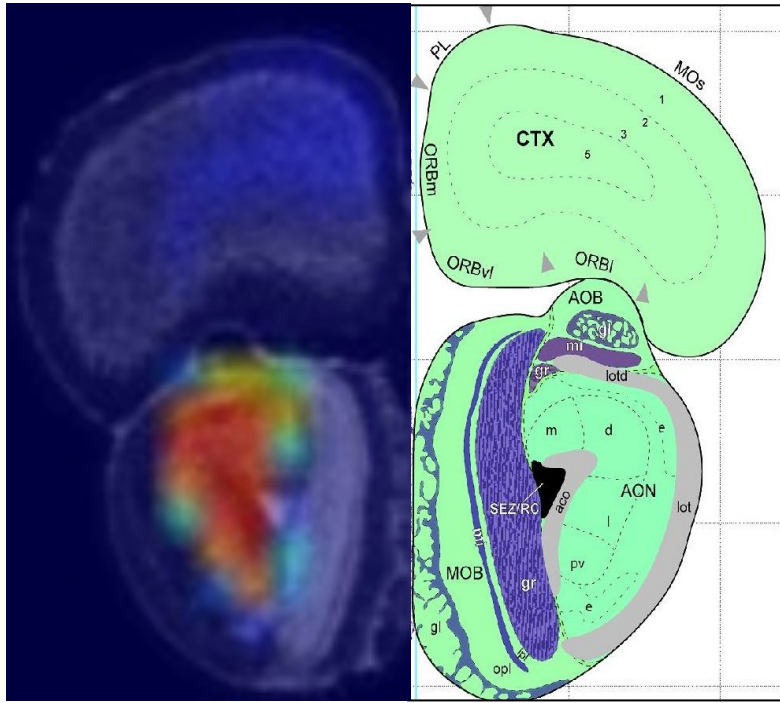
STRUCTURE vs. STRUCTURE

The expression value of the AON was compared to expression values for all other defined atlas regions. Degree of correlation is displayed as a comparative fraction, with self-correlation = 1.000. Correlation between the AON and macro/parent-structures are presented, as well as correlation between the AON and the 25 highest ranking substructures. The most highly correlated macro/parent-structures don't always contain the 25 top most correlated substructures. Columns match the Allen Reference Atlas palette.

Correlation of AON with macro structures:		Correlation of AON with substructures:	
Macro Structure	Correlation	Substructure	Correlation
OLF (Olfactory areas)	0.974188	Anterior olfactory nucleus (AON)	1
STR (Striatum)	0.869359	Taenia tecta (TT)	0.966882
PAL (Pallidum)	0.872437	Orbital area, ventrolateral part (ORBv)	0.954103
CTX (Cerebral cortex)	0.946192	Orbital area (ORB)	0.953238
HY (Hypothalamus)	0.83285	Agranular insular area (AI)	0.952739
TH (Thalamus)	0.841705	Agranular insular area, ventral part (AIV)	0.95268
HIP (Hippocampal region)	0.909955	Agranular insular area, dorsal part (AID)	0.949764
RHP (Retrohippocampal formation)	0.944842	Orbital area, ventrolateral part, layer 2/3 (ORBv2/3)	0.948738
P (Pons)	0.843421	Dorsal peduncular area, layer 2/3 (DP2/3)	0.94832
MY (Medulla)	0.808188	Endopiriform nucleus (EP)	0.947085
CB (Cerebellum)	0.704506	Orbital area, medial part (ORBm)	0.946804
		Agranular insular area, ventral part, layer 2/3 (AIV2/3)	0.946694
		Infralimbic area, layer 2/3 (ILA2/3)	0.946478
		Dorsal peduncular area (DP)	0.946232
		Infralimbic area (ILA)	0.944842
		Cerebral cortex, layer 2 (CTX2)	0.944784
		Orbital area, lateral part (ORBv)	0.943528
		Gustatory areas (GU)	0.943483
		Agranular insular area, dorsal part, layer 2/3 (AID2/3)	0.94324
		Endopiriform nucleus, dorsal part (EPd)	0.942981
		Agranular insular area, posterior part (AIP)	0.9422
		Endopiriform nucleus, ventral part (EPv)	0.941694
		Orbital area, ventrolateral part, layer 5 (ORBv5)	0.941319
		Agranular insular area, ventral part, layer 5 (AIV5)	0.941169
		Agranular insular area, dorsal part, layer 5 (AID5)	0.939676

STRUCTURE vs. VOXEL:

Correlation between the AON and all other $(200\mu\text{m})^3$ voxels in the brain. Degree of correlation assessed for each voxel is provided visually (lower value = the correlation value of the 25th ranked substructure reported on the previous page) using the "jet" color scale at rostrocaudal levels throughout the brain.

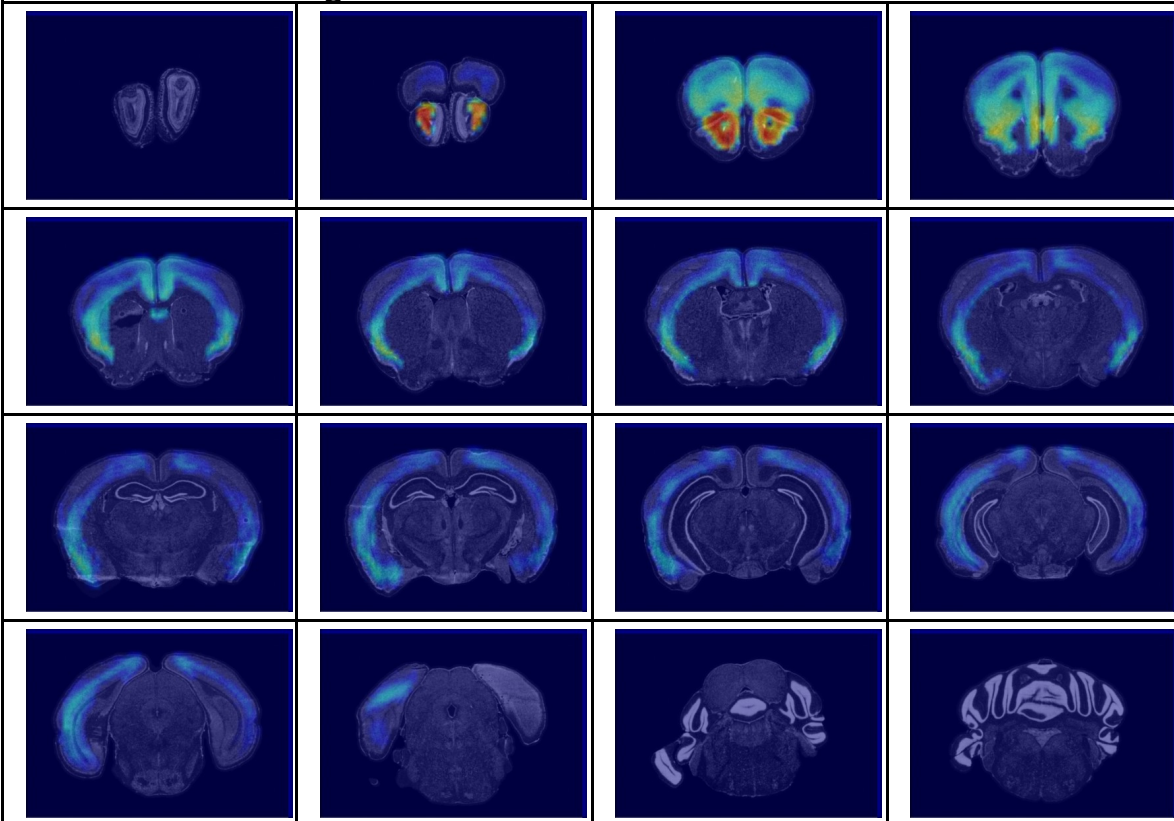


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Coronal series through brain:



Gene Ontology (GO) Analysis:

GO TABLE:

Below is an ontological analysis of the 50 Select Genes, using [DAVID](#) Bioinformatics Resources. The functional terms that follow were returned using these constraints:

Category	Definition	Constraints
P-value	Probability that the term is over-represented in this 50 Select Genes list relative to the mouse genome	when $p \leq 0.05$
Gene Count	The minimum number of genes that must fall into an ontological category to be considered a group	5 genes per term group
GO Level	The level of functional specificity for GO functional categories: Molecular Function (mf), Biological Process (bp) and Cellular Components (cc)	Level GO_All
# of DAVID IDs	Number of unique DAVID gene IDs from user's input list	49 DAVID gene IDs / 50 input genes

Date of table completion: February 2008

GO Category	GO Term	Gene Count	% of Genes	p-value
GOTERM_BP_ALL	neurogenesis	6	12.24%	4.12E-04
GOTERM_BP_ALL	neuron differentiation	5	10.20%	0.002440215
GOTERM_BP_ALL	nervous system development	6	12.24%	0.006042327
GOTERM_BP_ALL	establishment of localization	15	30.61%	0.006877538
GOTERM_BP_ALL	localization	15	30.61%	0.007417478
GOTERM_BP_ALL	system development	6	12.24%	0.008597943
GOTERM_BP_ALL	metal ion transport	5	10.20%	0.011755501
GOTERM_CC_ALL	extracellular region	14	28.57%	0.016735434
GOTERM_CC_ALL	extracellular space	13	26.53%	0.016878012
GOTERM_BP_ALL	cell differentiation	7	14.29%	0.017498944
GOTERM_CC_ALL	plasma membrane	11	22.45%	0.020723188
GOTERM_BP_ALL	ion transport	6	12.24%	0.025329619
GOTERM_BP_ALL	cation transport	5	10.20%	0.028233226

Glynn Dennis Jr., Brad T. Sherman, Douglas A. Hosack, Jun Yang, Michael W. Baseler, H. Clifford Lane, Richard A. Lempicki. "DAVID: Database for Annotation, Visualization, and Integrated Discovery." *Genome Biology*. 2003 4(5): P3.

ANTERIOR OLFACTORY NUCLEUS Summary:

Anatomy

- The AON is comprised of external (AONe), dorsal (AONd), lateral (AONI), medial (AONm) and posteroventral (AONpv) subnuclei. The cells of the external nucleus are distinctly separate from those of the more difficult to distinguish internal nuclei.
- In the coronal plane, the AON emerges within the posterior portion of the main olfactory bulb (MOB); it remains until the appearance of the nucleus accumbens.
- In the sagittal plane, the AON appears just lateral to the junction of the MOB and the rest of the brain, and remains present until the midline; it is located just caudal to the MOB and rostro-dorsal to the piriform cortex.

Expression Patterns of the 50 Select Genes

- The most common expression pattern seen in the AON is widespread expression throughout the entire nucleus.
- A subset of genes show either preferential expression in the external nucleus or preferential expression in the internal nuclei.

Correlation

- Gene expression in the AON correlated strongly with expression in olfactory and cortical areas situated close to the AON. This included the dorsal peduncular areas and orbital and agranular insular cortices.
- Distinct correlation was also noted throughout the piriform cortex and in layers two/three and five of the cerebral cortex.
- Individual voxel analysis revealed correlation with portions of the amygdala as well.

We encourage you to reply with any comments or questions by email to [!Annotation@alleninstitute.org](mailto:Annotation@alleninstitute.org). To further explore the gene expression data and analytical tools referred to in this report, please access our genome-wide data set at brain-map.org.

Other Tools:

NEUROBLAST:

Many of the 50 genes listed in this report can be used to explore the NeuroBlast tool. This unique mining tool works seamlessly from within brain-map.org to produce a list of genes that share similar expression patterns to any gene in the coronal data set. Search for and select any gene, then select one of several brain regions from the NeuroBlast drop-tab to explore a ranked list of similarly expressed genes for that region.

To learn more about this function, please refer to the [NeuroBlast white paper](#).

BRAIN EXPLORER:

To compare gene expression levels across anatomical structures in 3-D detail, download the [Brain Explorer](#) desktop application. This program is used to view gene expression in 3-D view (coronal, sagittal, horizontal and everywhere in between) across all brain structures and allows for simultaneous viewing of multiple expression profiles.

The NeuroBlast spatial homology function and an anatomic search tool are also available from within Brain Explorer to allow the user to search for and visualize genes with similar expression patterns.