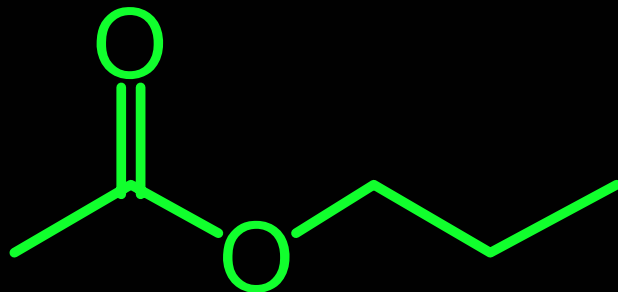
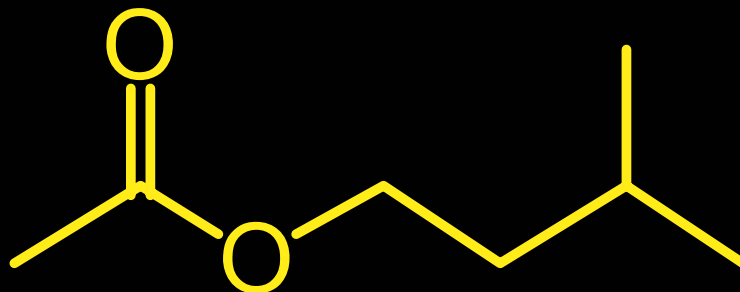


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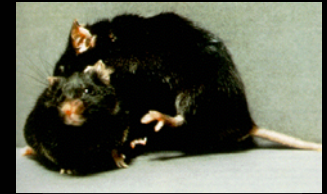
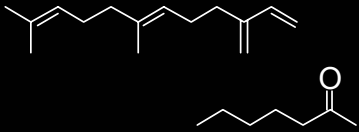
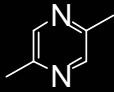
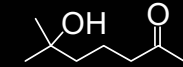
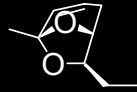
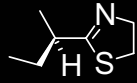
BANANA



THE OLFACTORY SYSTEM AND INSTINCTIVE BEHAVIORS



PHEROMONES



AGGRESSION



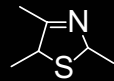
MATERNAL BEHAVIOR



SEXUAL BEHAVIOR

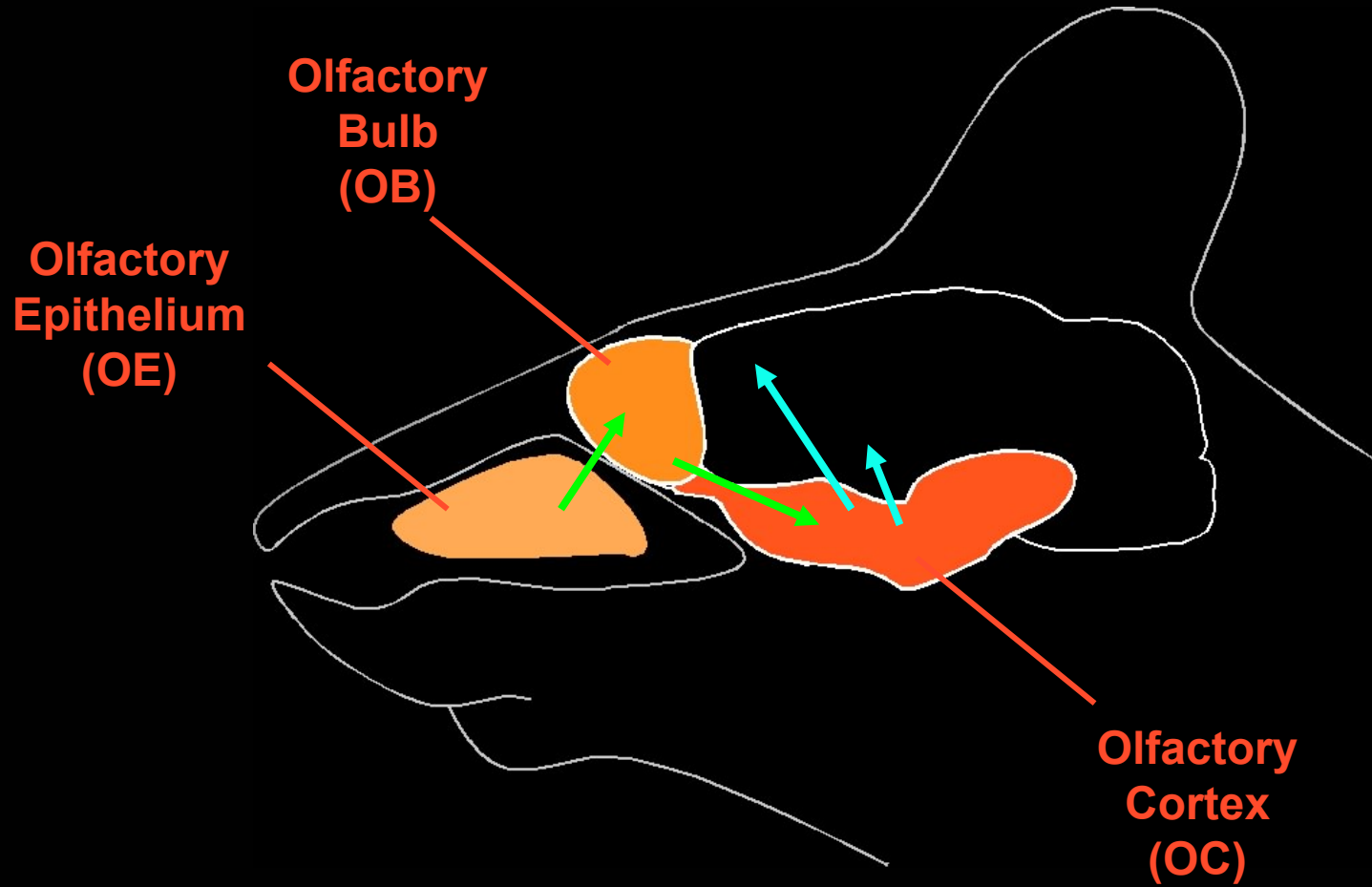


PREDATOR ODORS

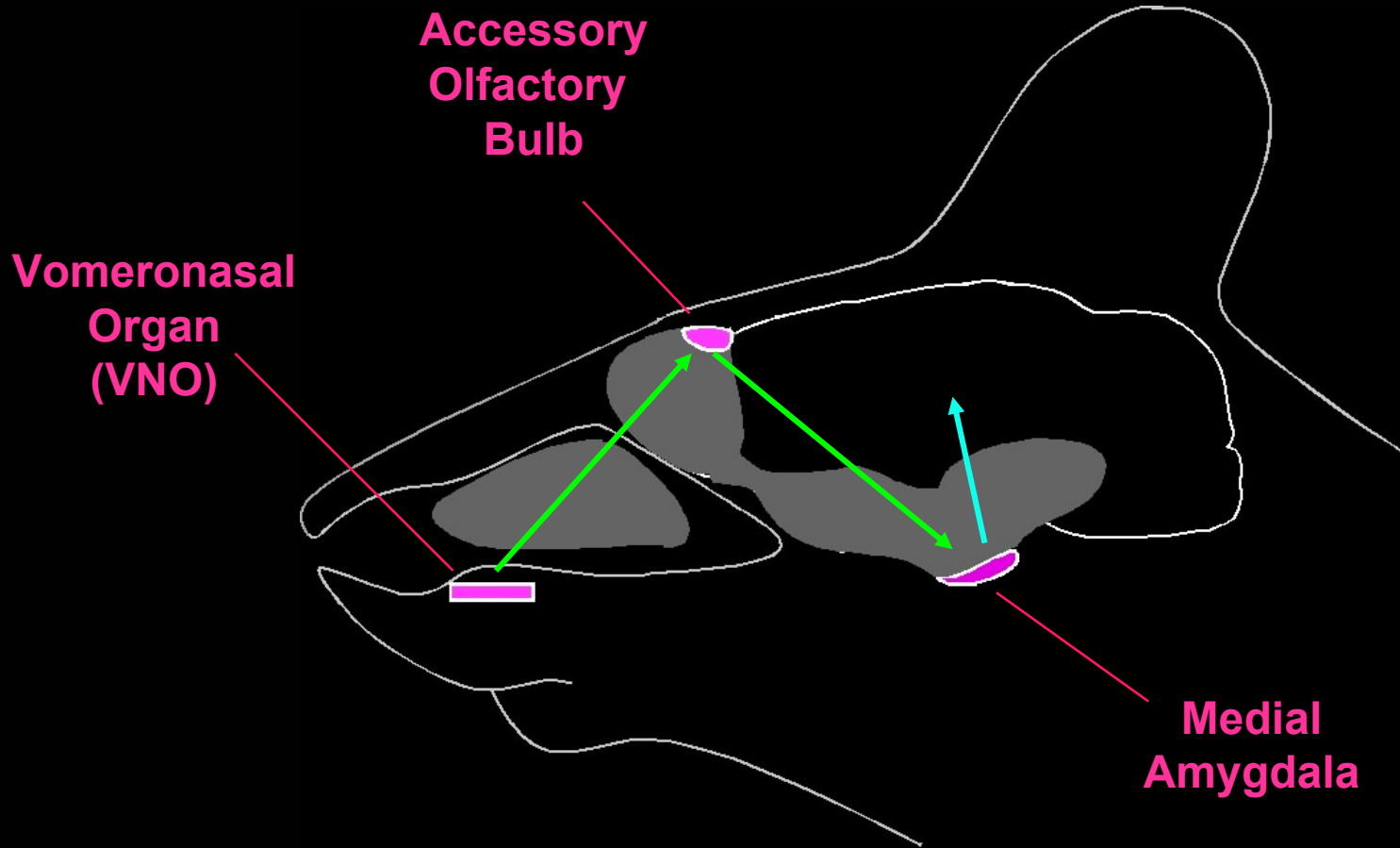


FEAR

THE OLFACTORY PATHWAY

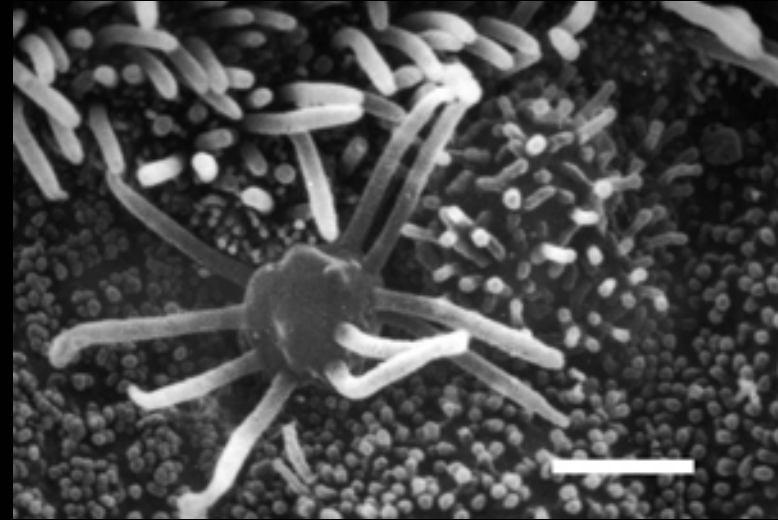


THE VOMERONASAL PATHWAY



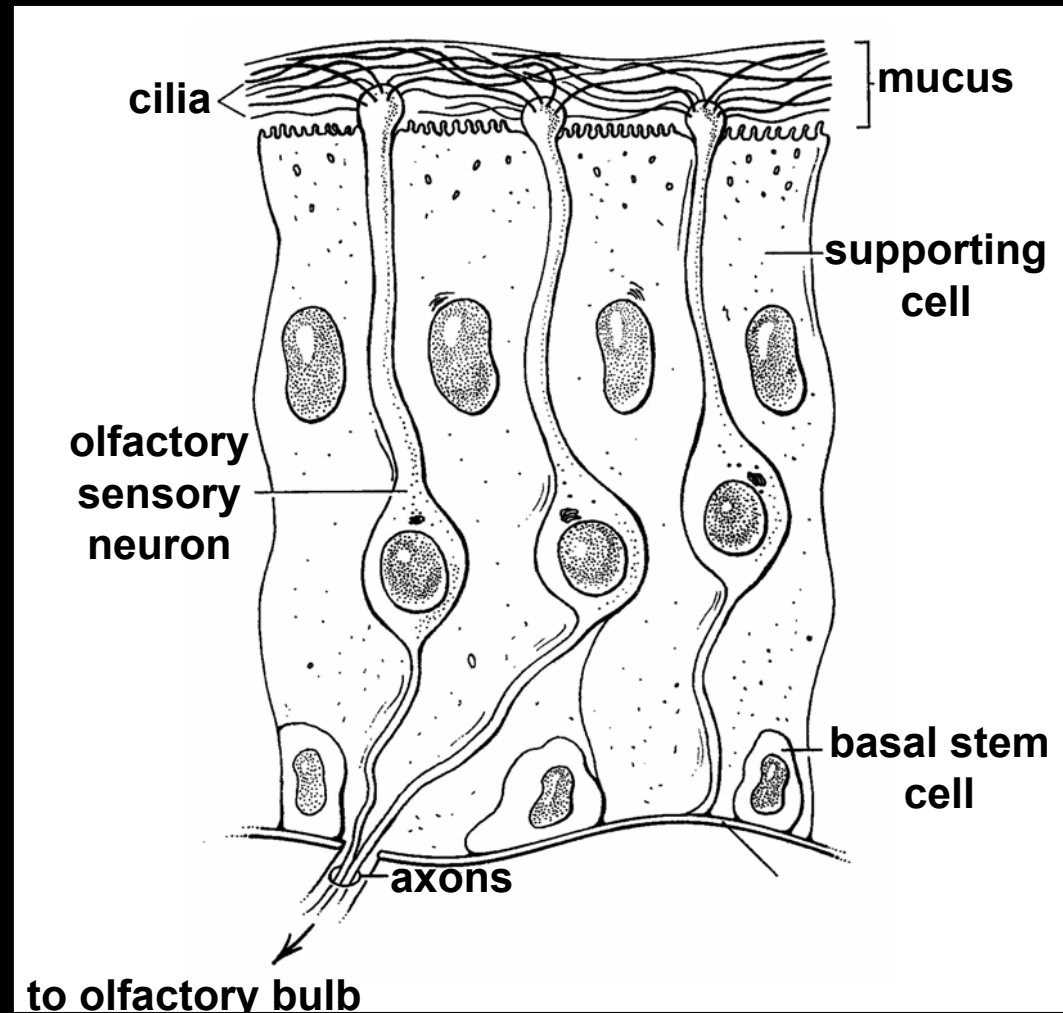
THE OLFACTORY EPITHELIUM

CILIA

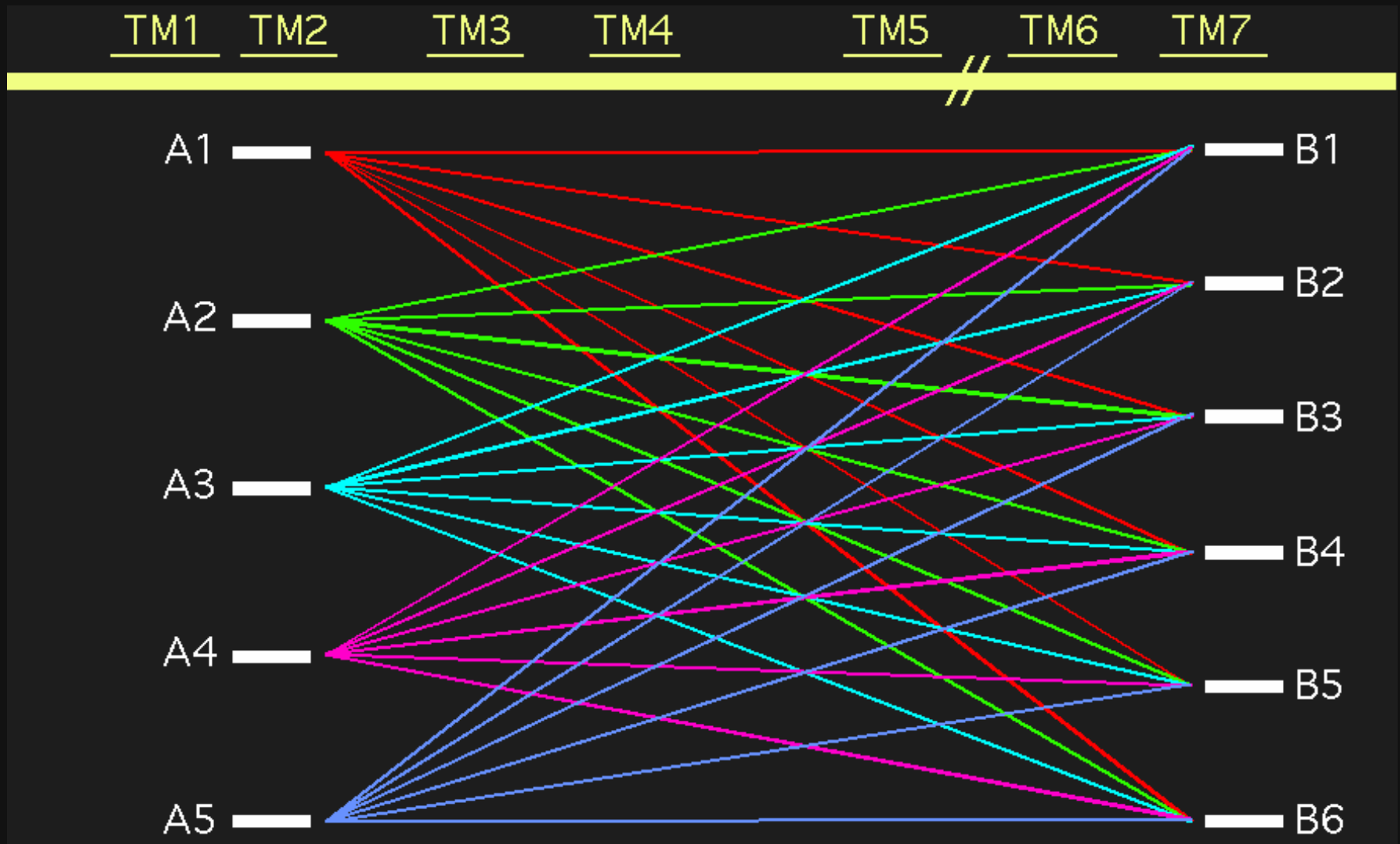


B. Menco, 1997

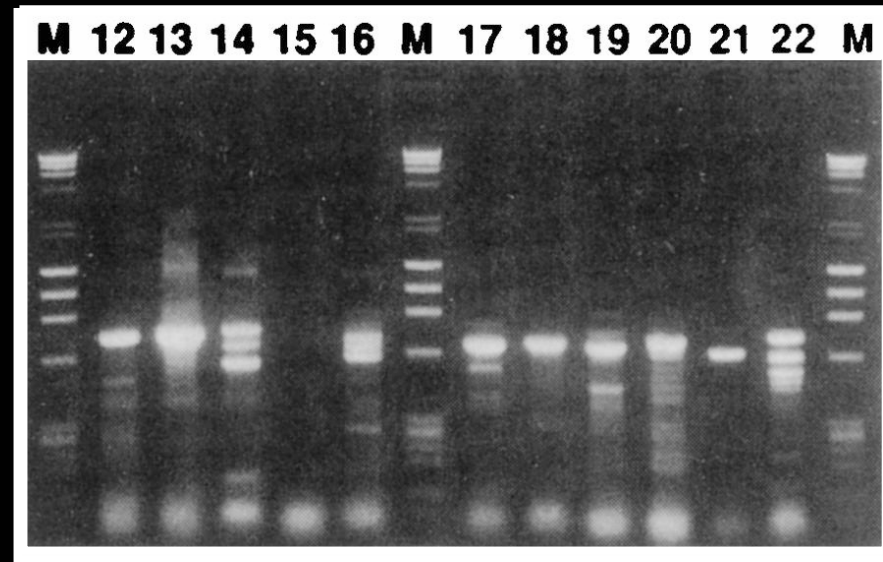
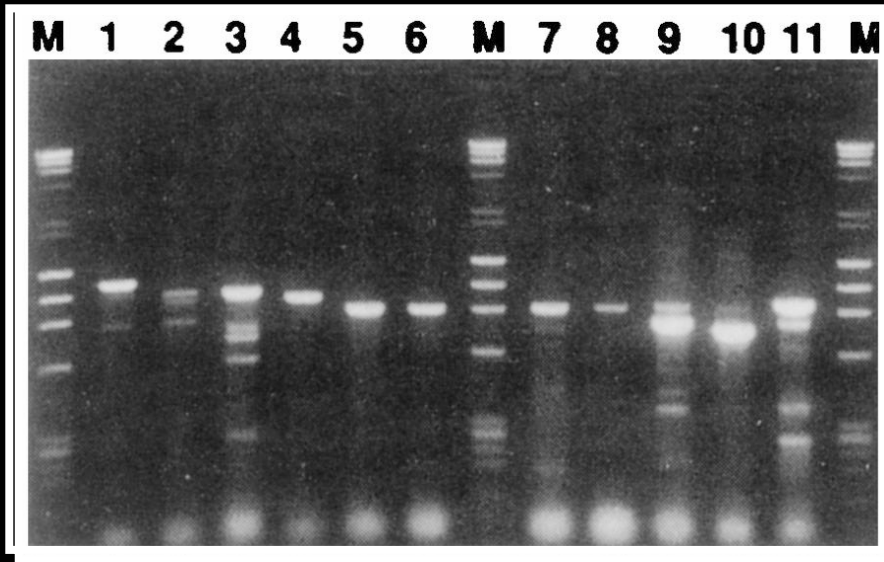
STRUCTURE



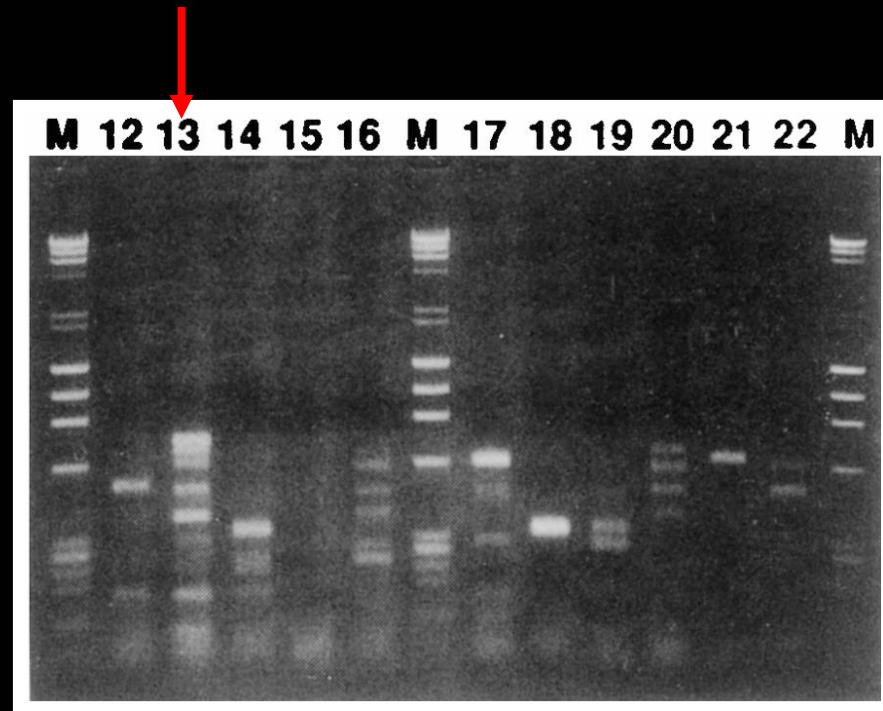
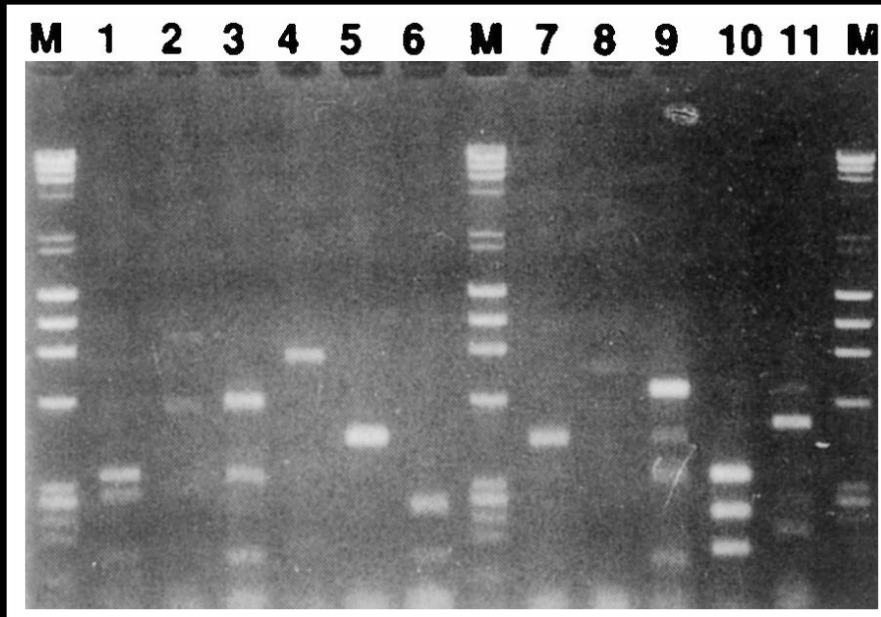
THE SEARCH FOR ORs: combinatorial PCR



PCR PRODUCTS



PCR PRODUCTS + RESTRICTION ENZYME



TEN OLFACTORY RECEPTORS

1 2

```

F3      MDSSNRTRYSEFLLLGfVENKDLQPLIYGLFLSMYLVTVIGNISIIVAIISDPCLHTPMYFFLSNLSFVDICFISITVPKML 82
F5      MSSTNQSVTEFLLGLSRQPQQQLLFLLLIMYLATVGNLLIILAIGTDSRLHTPMYFFLSNLSFVDYCFSSSTVYPKVL 82
F6      MAWSTGQNLSTPGPFILLGFPGRSMRIGLFLFLVMYLLTVGNLAIISLVGAHRCLQTPMYFFLCNLSFLEIWFTTACVPKTL 85
F12     MESGNSTRRFSSFFLLGFTENPOLHFLIFALFLSMYLVTVGNLLIIMAIITQSHLHTPMYFFLANLSFVDICFTSTIIPKML 83
I3      MN--NQFTITQFLLGLPIPEEHQHLFYALFLVMYLTTLGNLLIIIVLVQLDSQLHTPMYLFSLNLSFSDLCFSSVTMPKLL 80
I7      MERRNHSGRVSEFYLLGFPAPAPLRVLLFFLSLLXYVLTENMLIIIAIRNHPTLHKPMYFFLANMSFLEIYWVTVTIPKML 83
I8      MN--NKTVITHFLLGLPIPEHQQLFFALFLIMYLTTLGNLLIIIVLVQLDSHLHTPMYLFSLNLSFSDLCFSSVTMLKLL 80
I9      MTRRNQTAISQFFLLGLPPPEYQHLFYALFLAMYLTTLGNLLIIILILLDSHLHTPMYLFSLNLSFADLCFSSVTMPKLL 82
I14     MTGNQTLILEFLLGLPIPSEYHLFYALFLAMYLTIIIGNLLIIIVLRLDSHLHMPMYLFSLNLSFSDLCFSSVTMPKLL 82
I15     MTEENQTVISQFLLFLPIPEHQHVFYALFSLMYLTTVGNLLIIILILLDSHLHTPMYLFSLNLSFSDLCFSSVTMPKLL 82
    
```

3 4

```

F3      ---VNIQTQNNVITYAGCITQIYFFLLFVELDNFLLTIMAYDRVVAICHPMHYTVIMNYKLCGGFLVLVSWIVSVLHALFQSLMM 163
F5      ----ANHILGSQAISFSGLTQLYFLAVFGNMDNFLLAVMSYDRVFAICHPHYTTKMRQLCVLLVVGSWVYVANMNCLLHILLM 163
F6      ---ATFAPRGGVISLAGCATQMYFVFLSGCTEYFLLAVMAYDRVLAICLPLRYGGIMTPGLAMRLALGSWLCGFSAITVPATLI 166
F12     ---VNIYTQSKSITYEDCISQMCYFLVFAELGNFLLAVMAYDRVYAXCHPLCYTVIVNHRCLCILLLLLSWVISIFHAFIQSLIV 164
I3      ---QNMRSQDTSIPYGGCLAQTYFFMVFGDMESFLLVAMAYDRVVAICFPLHYTSIMSPKLCCTCLVLLLWMLTTSHAMMHTLLA 161
I7      AGFIGSKENHGQLISFEACMTQLYFFLGLGCTECVLLAVMAYDRVVAICHPHYTVIVSSRLCVQMAAGSWAGGFGISMVYVFLI 168
I8      ---QNIQSQVPSISYAGCLTQIFFLLFGYLGNFLLVAMAYDRVVAICFPLHYTNIMSHKLCCTCLLVFWIMTSSHAMMHTLLA 161
I9      ---QNMQSQVPSIPYAGCLAQIYFFLFFGDLGNFLLVAMAYDRVVAICFPLHYMSIMSPKLCVSLVVLWVLTTFHAMLHTLLM 163
I14     ---QNMQSQVPSISYTGCLTQLYFFMVFGDMESFLLVAMAYDRVVAICFPLRYTTIMSTKFCASLVLLLWMLTMTTHALLHTLLI 163
I15     ---QNMQSQVPSIPFAGCLTQLYFYLYFADLESFLLVAMAYDRVVAICFPLHYMSIMSPKLCVSLVVLWVLTTFHAMLHTLLM 163
    
```

5 6

```

F3      LALPFCTHLEIPHYFCEPNQVIQLTCSDAFLNDLVIIYFTLVLLATVPLAGIFYSYFKIYSSICAISSVHGKYKAFSTCASHLSVY 248
F5      ARKSFCADNMIPHFFCDGTPLKLSGSDTHNELMLILTEGAVVMYTPFVCILISYIHTCAVLRVSSPRGGKSFSTCGSHLAVV 248
F6      ARLSFCGSRVINHFFCDISPWIVLSCDTQVVELVSFGIAFCVILGSCGITLVSYAYIITTIKIPSAARGHRRAFSTCCSHLTVV 251
F12     LQLTFCGDVKIPHFFCELNQLSQTCSDNFPSHLIMNLVPMYLAISFSGILYSYFKIYSSIHSISTVQGGKYKAFSTCASHLSIV 249
I3      ARLSFCENNVYLNHFFCDLVLLKLACSDTYINELMIFIMSTLLIIPFLLIVMSYARISSILKVPSTOGICKVSTCGSHLSVY 246
I7      SRLSYCGPNTINHFFCDVSPLLNLSCTDMSTAEELDFVLAIFILLGLPSVTGASYMAITGAVMRIPSAAGRHKAFSTCASHLTVV 253
I8      ARLSFCENNVLLNHFFCDLVLLKLACSDTYVNELMIHIMGVIIIVIPFVLIVISYAKIISSILKVPSTQSIHKVSTCGSHLSVY 246
I9      ARLSFCEDSVIPHYFCDMSTLLKVACSDTHDNELAIFILGGPIVVLFPFLIIIVSYARIVSSIFKVPSSQSIHKAFSTCGSHLSVY 248
I14     ARLSFCEKNYILHFFCDISALLKLSGSDIYVNELMIYILGGLIIIPFLLIVMSYVRIFFSILKFPISQDIYKVFSTCGSHLSVY 248
I15     ARLSFCADNMIPHFFCDISPLKLSGSDTHVNELVIFVMGGLVIVIPFVLIIVSYARVVASILKVPVSRGIIHKIFSTCGSHLSVY 248
    
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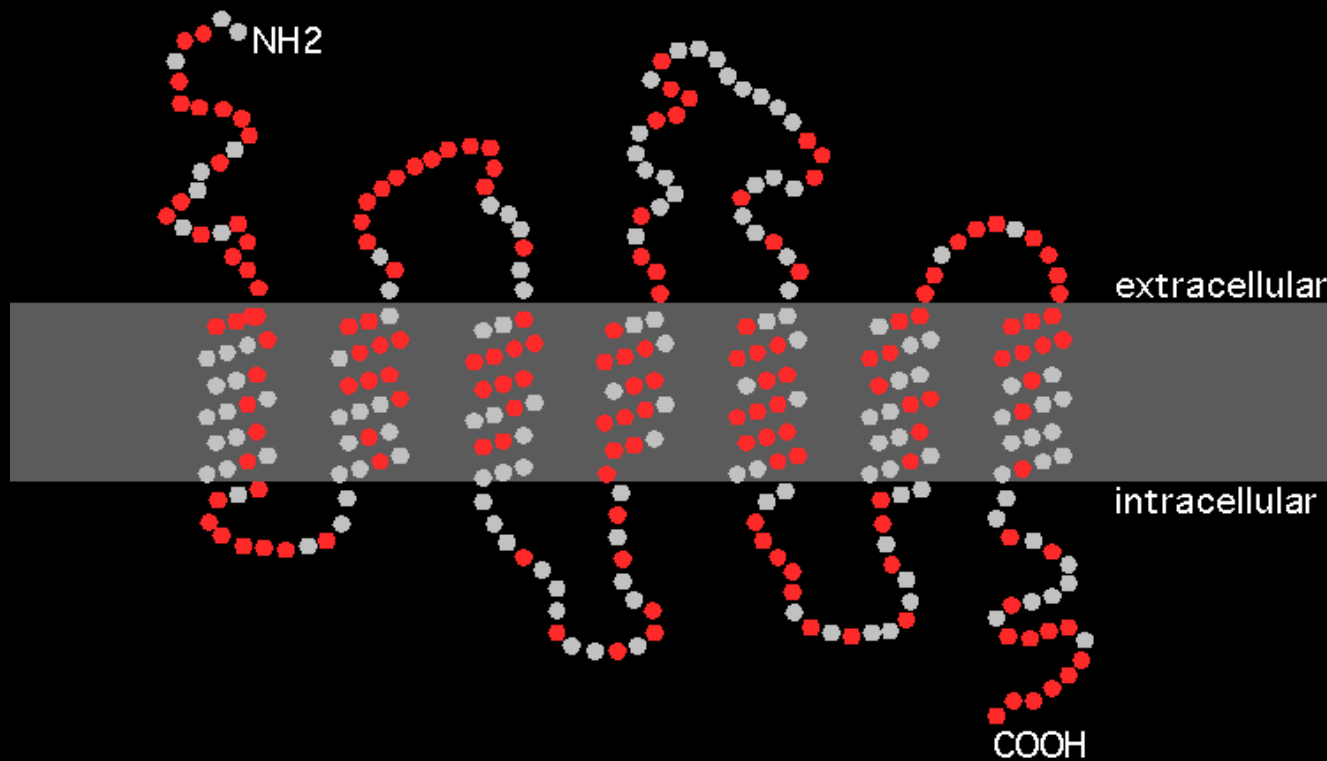
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F3      SLFYCTGLGVYLSAANNSSQASATASVMYTVVTPMVPNPFYISLRNKDVKSVLKKTLCCEEVIRSPPSLLHFFLVLCHLPCFIFCY 333
F5      CLFYGTVIAYVFNPSSSHLAGRDMAAAVMYAVVTPMLNPFYISLRNSDMKAALRKVLAMRFPKQ 313
F6      LIWYGSTIFLHYRTSVESLDTKAITVLTNTIIVTPVLPNPFYITLRNKDVKEALRRTYKGG 311
F12     SLFYSTGLGVYVSSAYVQSSHSASASVMYTVVTPMVPNPFYISLRNKDVKRALERLLEGCKVHHWTG 317
I3      SLFYGTIIGLYLCPAGNNSTVKEMVMAMMYTVVTPMLNPFYISLRNRDMKRALIRVICSMKITL 310
I7      IIFYAASIFIYARPKALSAFDTNKLVSYLYAVIVPLFNPIIYCLRNQDVKRALRRTLHLAQDQEANTKNGSKIG 327
I8      SLFYGTIIGLYLCPSGDNFSLKGSAMAMMYTVVTPMLNPFYISLRNRDMKDALIRVTCSSKISLPW 312
I9      SLFYGTIIGLYLCPANNSTVKETVMSLMYTMVTPMLNPFYISLRNRDIKDALKIMCKKQIPSF 314
I14     TLFYGTIFGIYLCPSGNNSTVKEIAMAMMYTVVTPMLNPFYISLRNRDMKRALIRVICTKKISL 312
I15     SLFYGTIIGLYLCPANNSTVKEIAMAMMYTVVTPMLNPFYISLRNRDMKEALIRVLCCKKITFCL 314
    
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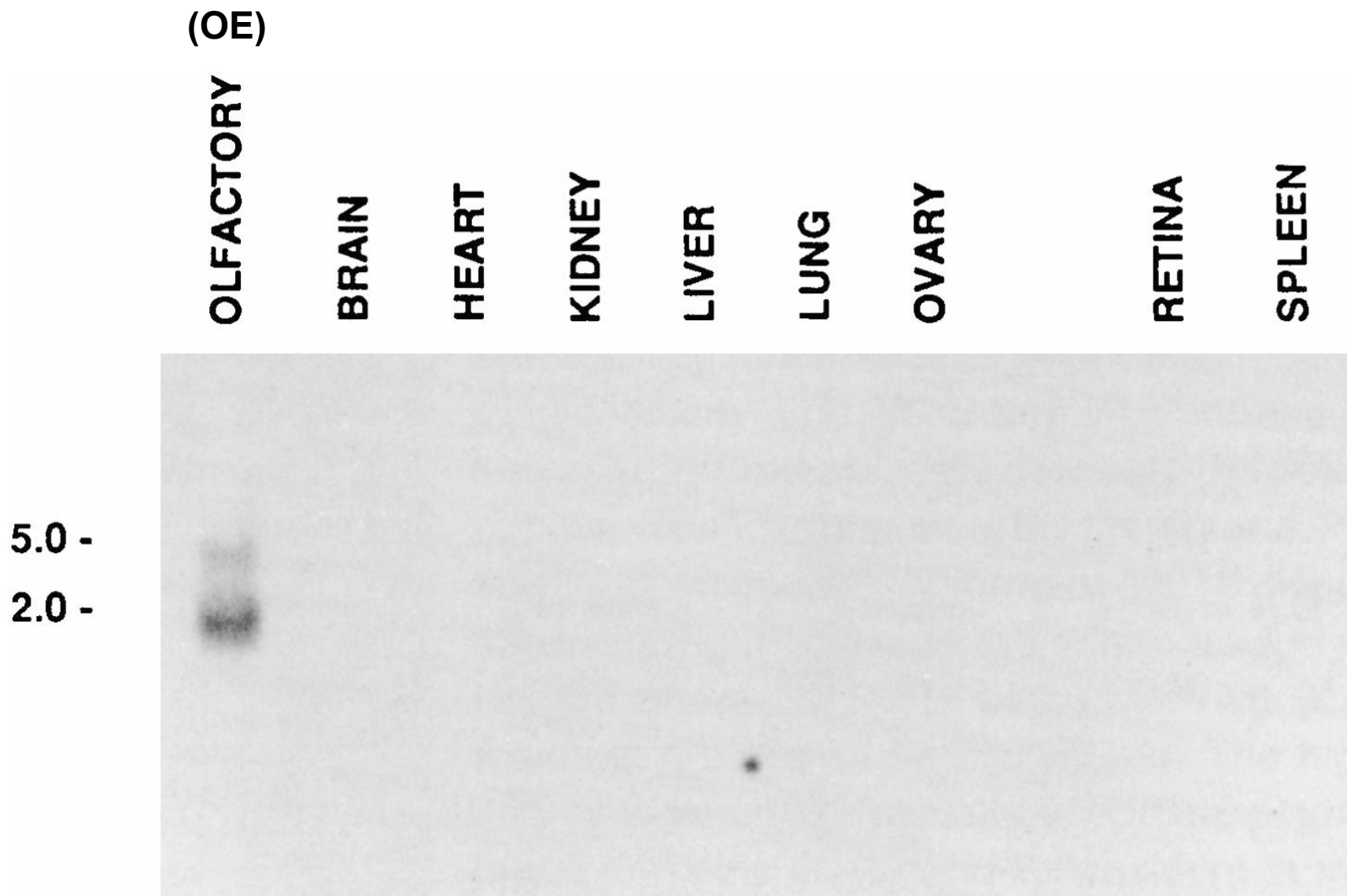
NOVEL MOTIFS IN OLFACTORY RECEPTORS

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F3	MDSSNRTRYSEFLLLGFFVENKDLQPLIYGLFLLSMYLVTVIGNISIIIVAIISDPC	LHT	PMYFFL	SNLSFVDICFISITV	PKML 82					
F5	MSSTNQSSVTEFLLGLSRQPQQQLLFLLLFLIMYLATVGLNLLIILAIGTDSR	LHT	PMYFFL	SNLSFVDYCFSSSTV	PKVL 82					
F6	MAWSTGQNLSTPGPFILLGFPGRSMRIGLFLFLVMYLLTVVGNLAIISLVGAHRC	LOT	PMYFFL	CNLSFLEIWFTTACV	PKTL 85					
F12	MESGNSTRRFSSFFLLGFTENPOLHFLIFALFLLSMYLVTVLGNLLIIMAIITQSH	LHT	PMYFFL	ANLSFVDICFTSTI	PKML 83					
I3	MN--NQFTITQFLLGLPIPEEHQHLFYALFLVMYLTTLGNLLIIVLVQLDSQ	LHT	PMYFL	SNLSFSDLCFSSVT	MPKLL 80					
I7	MERRNHSGRVSEFYLLGFPAPAPLRVLLFFLSLLXYVLVTENMLIIIAIRNHPT	LHK	PMYFFL	ANMSFLEIYWVTV	IPKML 83					
I8	MN--NKTVITHFLLGLPIPEHQQLFFALFLIMYLTTLFGLNLLIIVLVQLDSH	LHT	PMYFL	SNLSFSDLCFSSVT	MLKLL 80					
I9	MTRRNQTAISQFFLLGLPPPEYQHLFYALFLAMYLTTLGNLLIILILLDSH	LHT	PMYFL	SNLSFADLCFSSVT	MPKLL 82					
I14	MTGNQTLILEFLLGLPIPSEYHLLFYALFLAMYLTIIIGNLLIIVLVRLDSH	LHM	PMYFL	SNLSFSDLCFSSVT	MPKLL 82					
I15	MTEENQTVISQFLLFLPIPSEHQHVFYALFLLSMYLTTLGNLLIILILLDSH	LHT	PMYFL	SNLSFSDLCFSSVT	MPKLL 82					
		3		4						
F3	---VNIQTQNNVITYAGCITQIYFFLLFVELDNFLLTIMAY	DRYVAIC	HPMHYTVIMNYK	LCGFLVLVSWIVSVLHALF	QSLMM 163					
F5	----ANHILGSQAISFSGLTQLYFLAVFGMNDNFLLAVMSY	DRFVAIC	HPLHYTTKMRQL	LCVLLVVGSMVYVANMNC	LHILLM 163					
F6	----ATFAPRGGVISLAGCATQMYFVFLSGCTEYFLLAVMAY	DRYLAIC	LPLRYGGIMTPG	LAMRLALGSWLCGFSAITV	PATLI 166					
F12	---VNIYTQSKSITYEDCISQMCVFLVFAELGNFLLAVMAY	DRYVAXC	HPCLYTVIVNHR	LCILLLLLSWVISIFHAF	IQSLIV 164					
I3	----QNMRSQDTSIPYGGCLAQTYFFMVFGDMESFLLVAMAY	DRYVAIC	FPLHYTSIMSPK	LCTCLVLLWMLTTSHAM	MHTLLA 161					
I7	AGFIGSKENHGQLISFEACMTQLYFFLGLGCTECVLLAVMAY	DRYVAIC	HPLHYPVIVSSR	LCVQMAAGSWAGGFGIS	MVFLI 168					
I8	----QNIQSQVPSISYAGCLTQIFFFLLFGYLGNFLLVAMAY	DRYVAIC	FPLHYTNIMSHK	LCTCLLLVFWIMTSSHAM	MHTLLA 161					
I9	----QNMQSQVPSIPYAGCLAQIYFFLFFGDLGNFLLVAMAY	DRYVAIC	FPLHYMSIMSPK	LCVSLVYLSWVLTTFHAM	LHTLLM 163					
I14	----QNMQSQVPSISYTGCLTQLYFFMVFGDMESFLLVAMAY	DRYVAIC	FPLRYTTIMSTK	FCASLVLLWMLTMT	HALLHTLLI 163					
I15	----QNMQSQVPSIPFAGCLTQLYFYLYFADLESFLLVAMAY	DRYVAIC	FPLHYMSIMSPK	LCVSLVYLSWVLTTFHAM	LHTLLM 163					
		5		6						
F3	LALPFCTHLEIPH	YFC	PNQVIQLT	CSDAFLNDL	LVIIYFTLVLLATVPLAGIFY	SY	FKIVSSICA	AISSVHGKYK	AFSTCASHLSVY	248
F5	ARKSFCADNMIPH	FFC	DGTPLLKLS	CSDTHLNE	LMILTEGAVVMYTFVFCIL	ISY	IHITCAVLRVSSPRGGWKS	FSTCGSHLAVV	248	
F6	ARLSFCGSRVINH	FFC	DISPWIVLS	CTDTQVVEL	VSFGIAFCVILGSCGITLV	SY	AYIITTIKIPSARGRHR	FSTCSSLHTVY	251	
F12	LQLTFCGDVKIPH	FFC	ELNQLSQT	CSDNFP	SHLIMNLVPYMLAAISFSGILY	SY	FKIVSSIHSISTVQGGKYK	FSTCASHLSIV	249	
I3	ARLSFCENNVYLN	FFC	DLFVLLKLA	CSDTYINEL	LMIFIMSTLLIIPFFLIVM	SY	ARISSILKVPSTOGICKY	FSTCGSHLSVY	246	
I7	SRLSYCGPNTINH	FFC	DVSPLLNLS	CTDMSTAE	ELTDFVLAIFILLGPLSVTGAS	YMAITGAVMRIPSAAGRHK	AFSTCASHLTVY	253		
I8	ARLSFCENNVLLN	FFC	DLFVLLKLA	CSDTYVNE	LMIHIMGVIIIVIPFVLIV	SY	AKIISSILKVPSTQSIHKV	FSTCGSHLSVY	246	
I9	ARLSFCEDSVIPH	YFC	DMSTLLKVA	CSDTHDNE	LAIFILGGPIVVLFPLLIIV	SY	ARIVSSIFKVPSSQSIHK	AFSTCGSHLSVY	248	
I14	ARLSFCEKNYILH	FFC	DISALLKLS	CSDIYVNE	LMIYILGGLIIIPFFLIVM	SY	VRIFFSILKFPISQDIYKY	FSTCGSHLSVY	248	
I15	ARLSFCADNMIPH	FFC	DISPLLKLS	CSDTHVNE	LVIFVMGGLVIVIPFVLII	IVSY	ARVVASILKVPVSRGIHKI	FSTCGSHLSVY	248	
		7								
F3	SLFYCTGLGVYLS	SSAANNSSQAS	ATASVMYTVV	TPMVNPF	FIYSLRN	KDVKSVLKKT	LCEEVIRSP	PLLHFFLV	LCHLPCF	IFCY 333
F5	CLFYGTVIAYVF	NPSSSHLAGR	DMAAAVMYAV	TPMLNPF	FIYSLRN	SDMKAALR	KVVLAMR	FPSPKQ		313
F6	LIWYGSTIFLH	VRTSVES	LDLTKAITV	LNTIVT	PVLNPF	FIYTLRN	KDYKEAL	RRTVKGK		311
F12	SLFYSTGLGVYV	SSAYVQSS	SHSAA	SASVMYTVV	TPMLNPF	FIYSLRN	KDVKRAL	ERLLEGNCKV	VHHWTG 317	
I3	SLFYGTIIIGLYL	CPAGNNSTV	KEMVMAMMYTVV	TPMLNPF	FIYSLRN	DMKRAL	IRVIC	SMKITL 310		
I7	IIFYAASIFIY	ARPKALSA	FDTNKLVS	YLYAVI	PLFNPI	IYCLRN	QDVKRAL	RRTLHLA	QDQEANTK	NGSKIG 327
I8	SLFYGTIIIGLYL	CPSGDNF	SLKGS	AMAMMYTVV	TPMLNPF	FIYSLRN	DMKQAL	IRVTC	SKKISLPW 312	
I9	SLFYGTIIGLYL	CP	SANNSTV	KETVMSLMY	TMVTPMLNPF	FIYSLRN	RIKDALE	IMCKKQ	IPSFL 314	
I14	TLFYGTIFGIYL	CP	SGNNSTV	KETIAMAMMYTVV	TPMLNPF	FIYSLRN	DMKRAL	IRVICT	KKISL 312	
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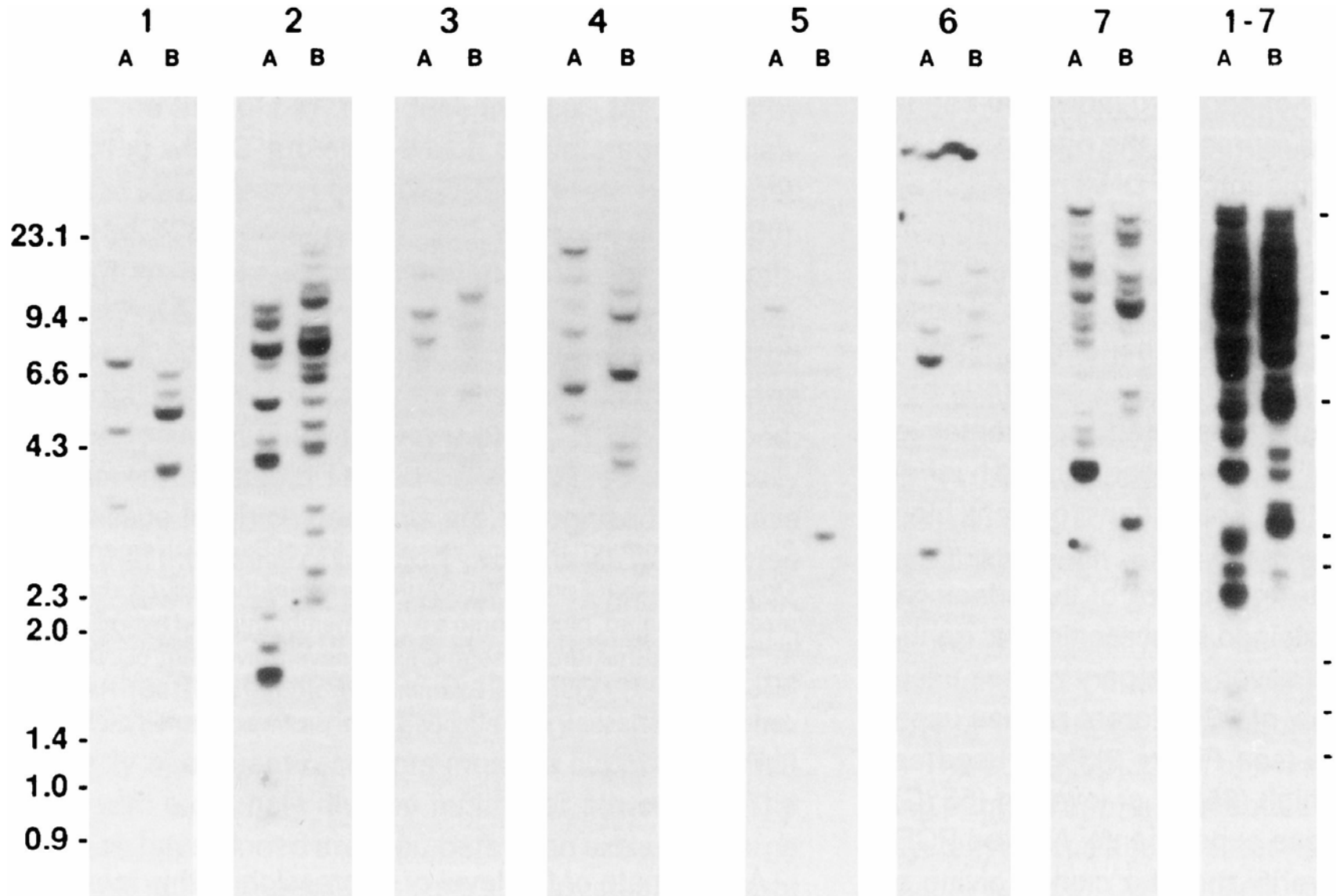


● hypervariable residues

OR GENES: EXPRESSION IN OLFACTORY EPITHELIUM



OR GENES: A MULTIGENE FAMILY



Cell, Vol. 65, 175–187, April 5, 1991, Copyright ©1991 by Cell Press

A Novel Multigene Family May Encode Odorant Receptors: A Molecular Basis for Odor Recognition

Linda Buck* and Richard Axel*†

*Department of Biochemistry and Molecular Biophysics

†Howard Hughes Medical Institute

College of Physicians and Surgeons

Columbia University

New York, New York 10032

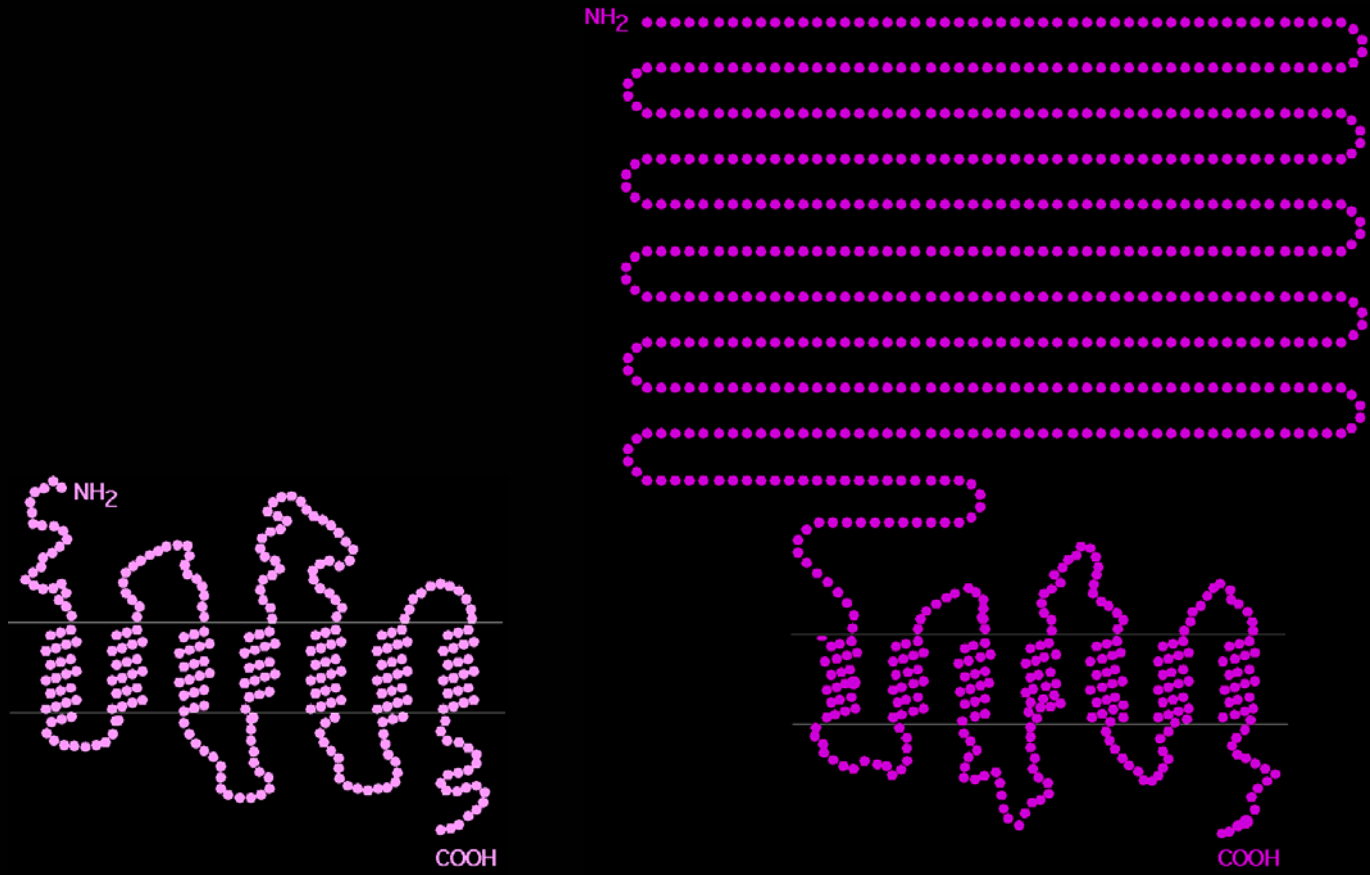
THE OR GENE FAMILY IN HUMAN AND MOUSE

	Human	Mouse
Total OR genes	638	1209
Intact OR genes	363	910
Pseudogenes	275	299
% pseudogenes	43	25

CHROMOSOMAL LOCATIONS OF HUMAN OR GENES



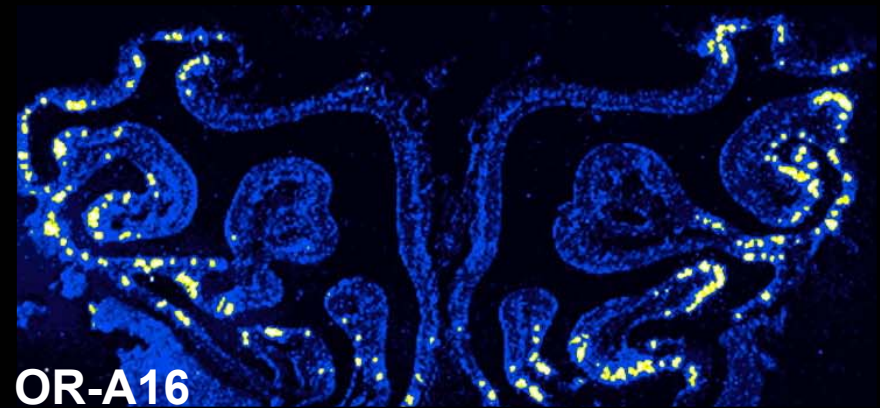
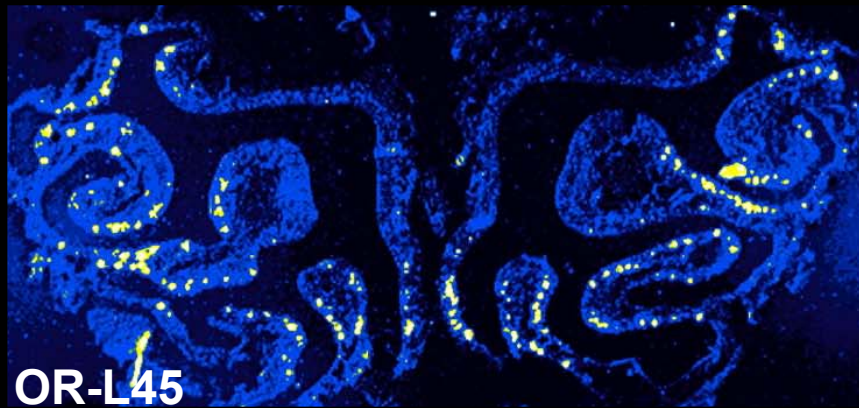
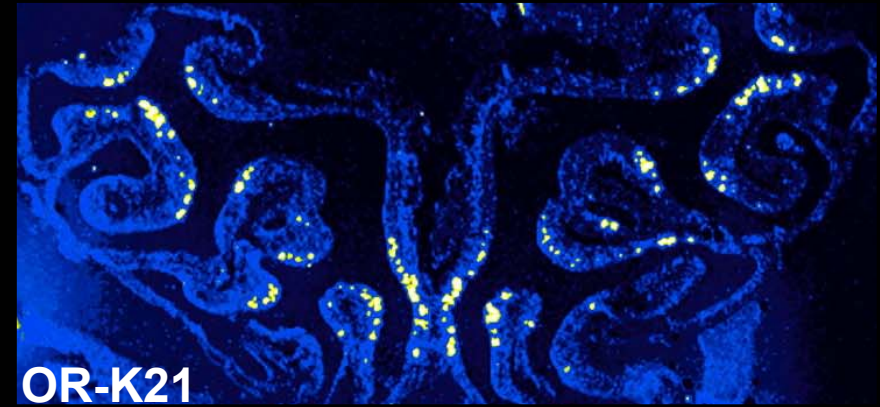
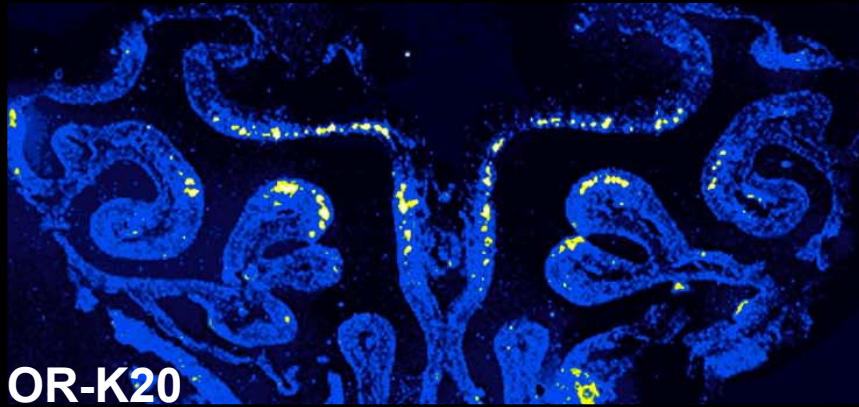
CANDIDATE PHEROMONE RECEPTORS IN THE VOMERONASAL ORGAN



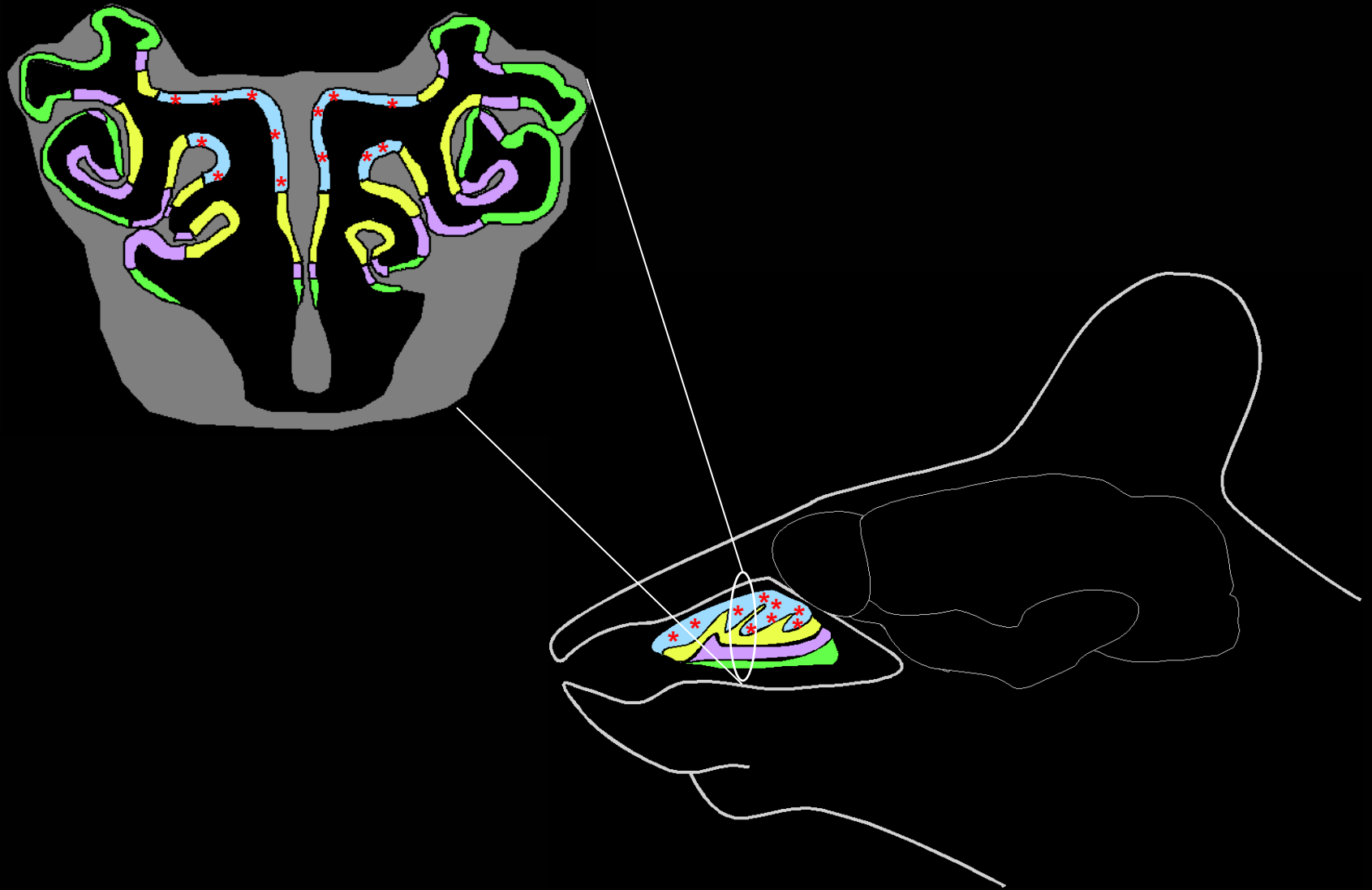
V1Rs
(~120)

V2Rs
(~140)

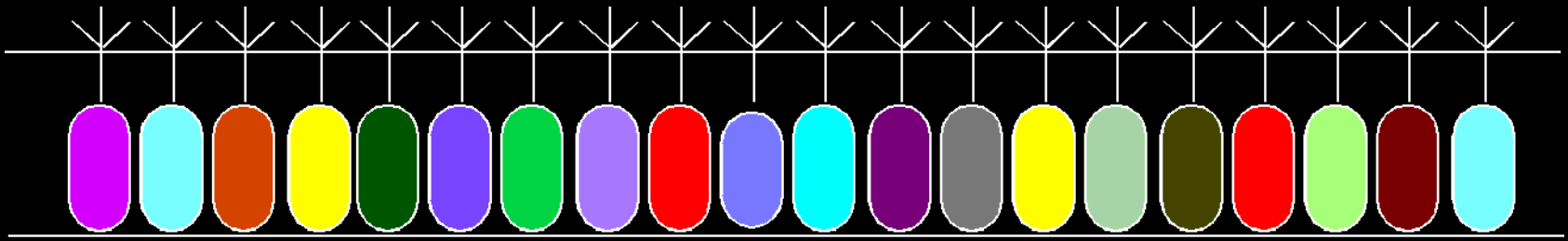
PATTERNS OF OR GENE EXPRESSION IN OLFACTORY EPITHELIUM



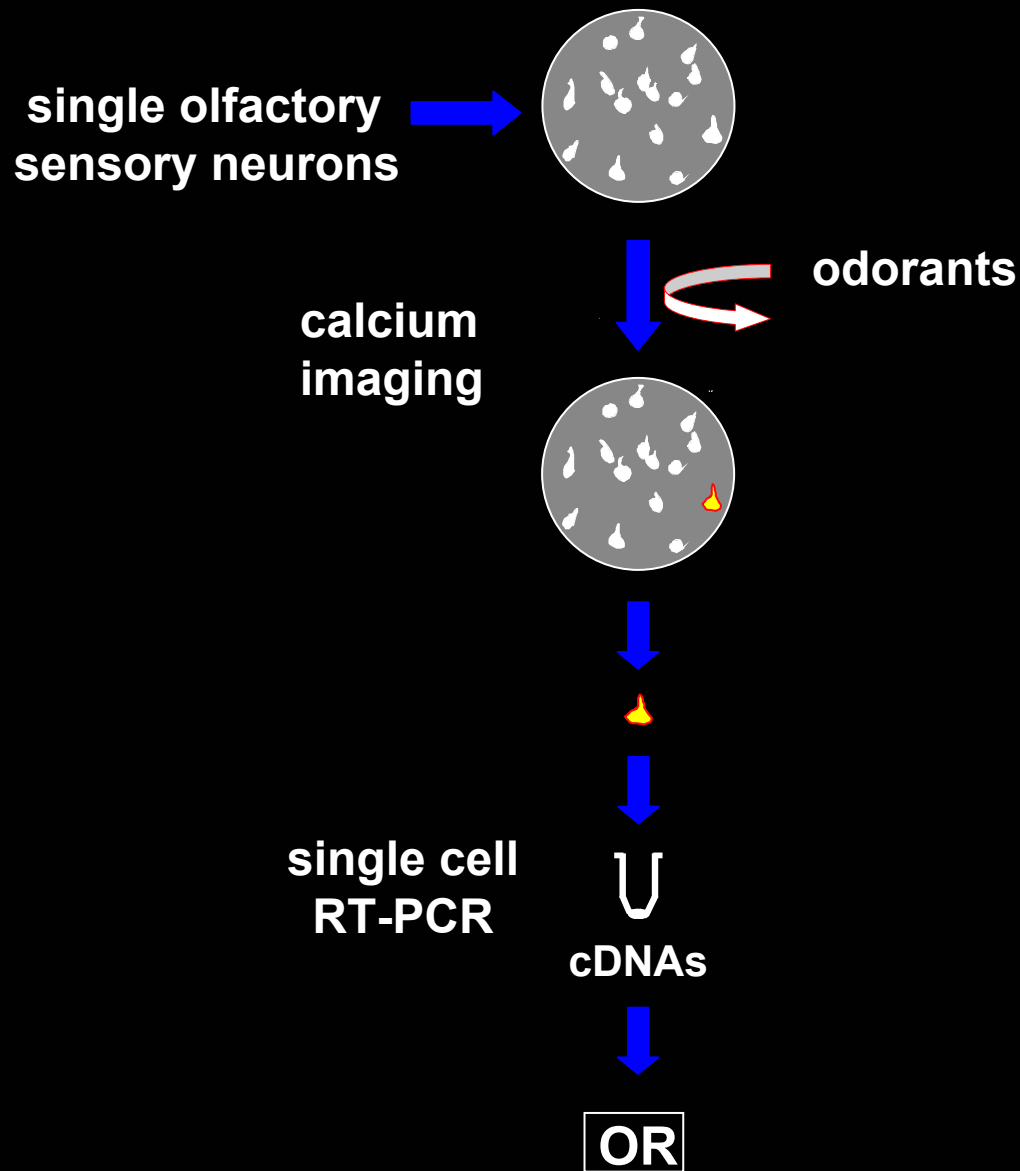
EXPRESSION ZONES IN THE OLFACTORY EPITHELIUM




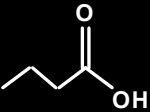
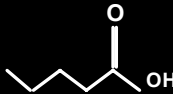
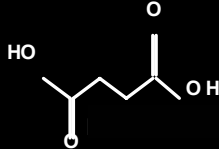

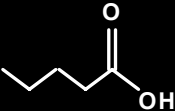
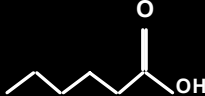
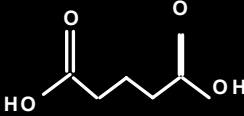

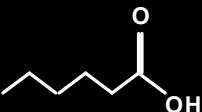
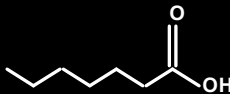
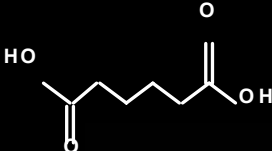












OLFACTORY EPITHELIUM: A MOSAIC OF NEURONS EXPRESSING DIFFERENT ORs



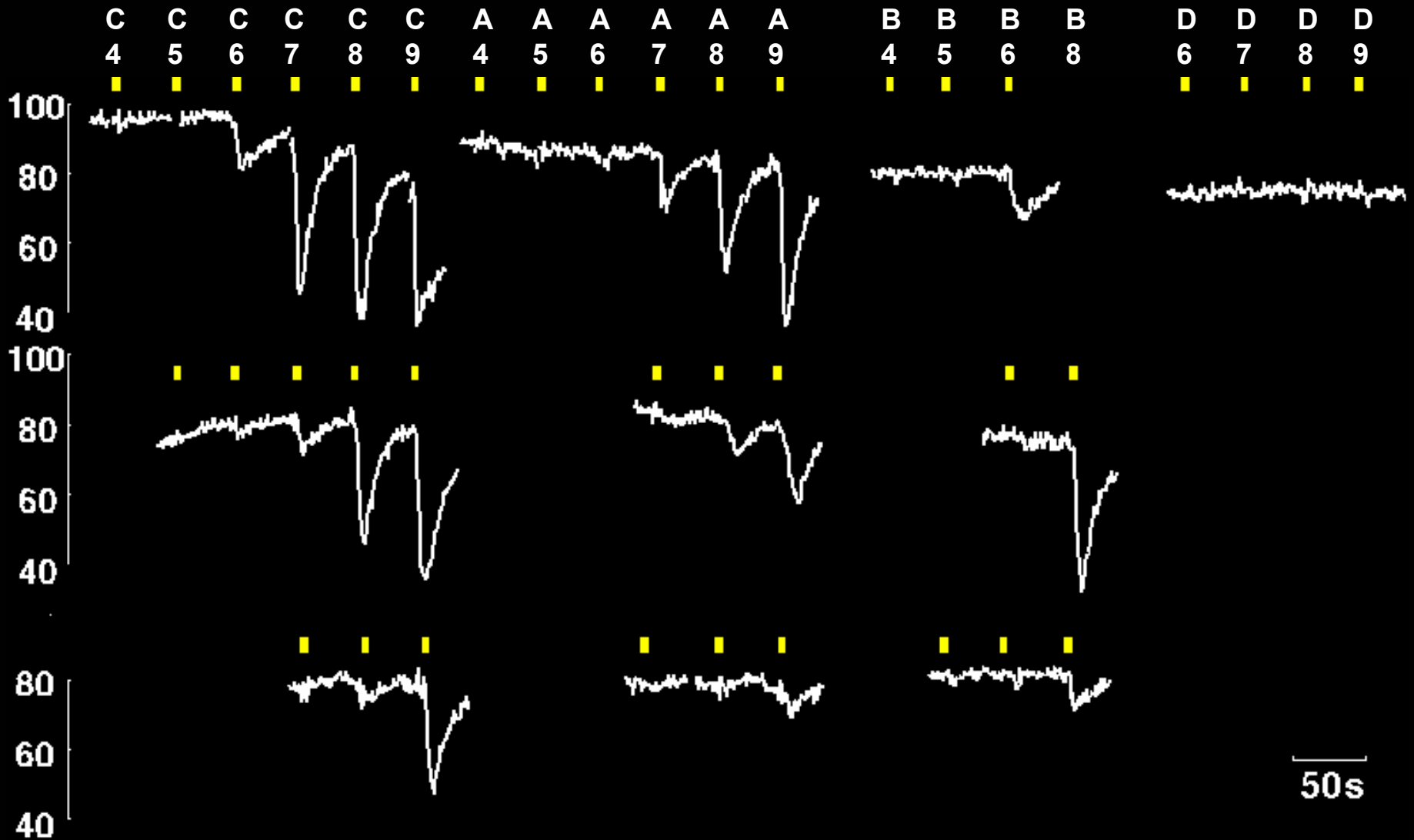
IDENTIFICATION OF ORs FOR SPECIFIC ODORANTS



TEST ODORANTS

#carbon atoms	alcohols	carboxylic acids	bromocarboxylic acids	dicarboxylic acids
4			Br 	
5			Br 	
6			Br 	
7			Br 	
8			Br 	
9			Br 	

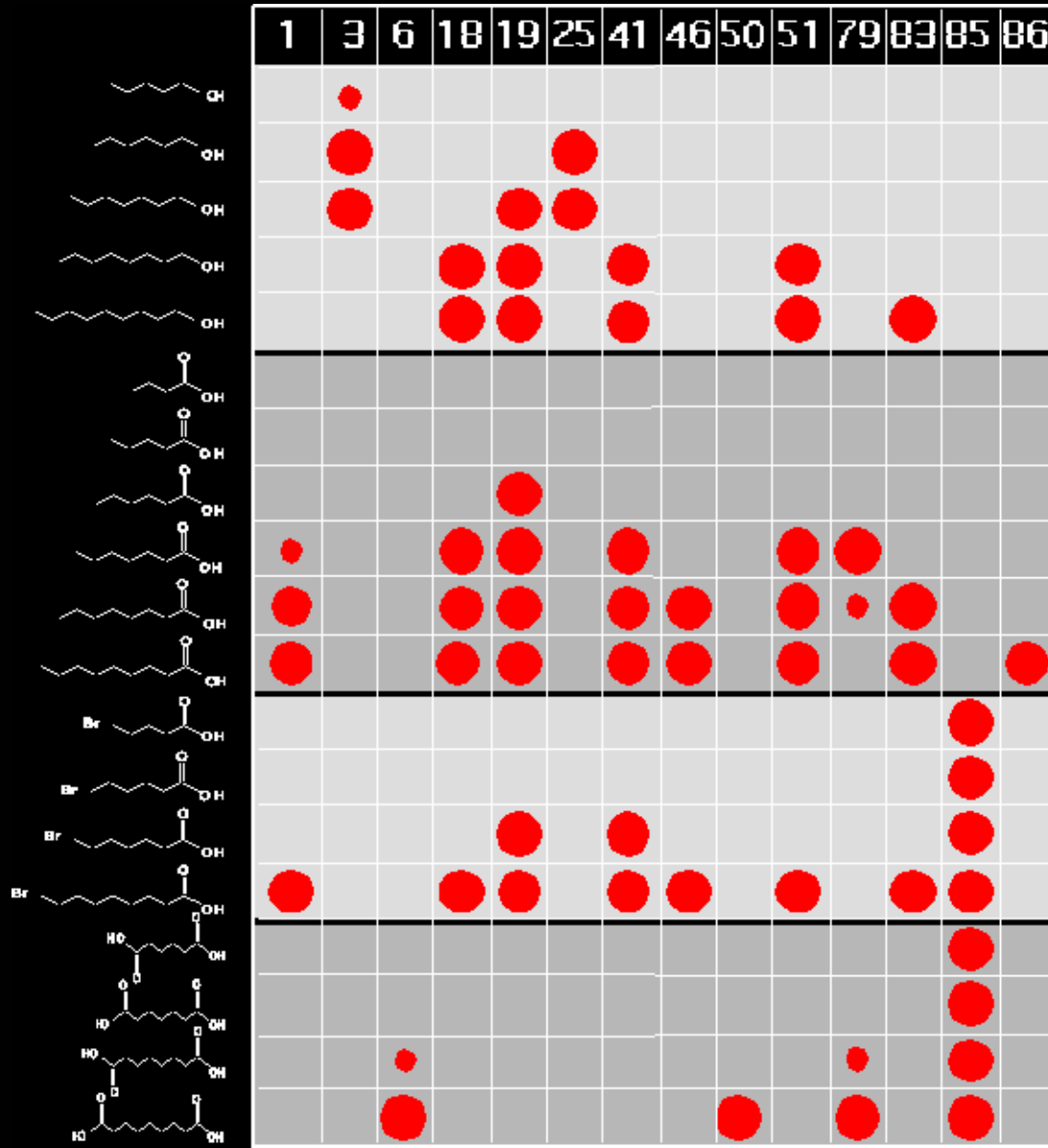
RESPONSES OF ONE NEURON TO ODORANTS



ODORANTS ARE DETECTED BY COMBINATIONS OF ORS

ODORANT

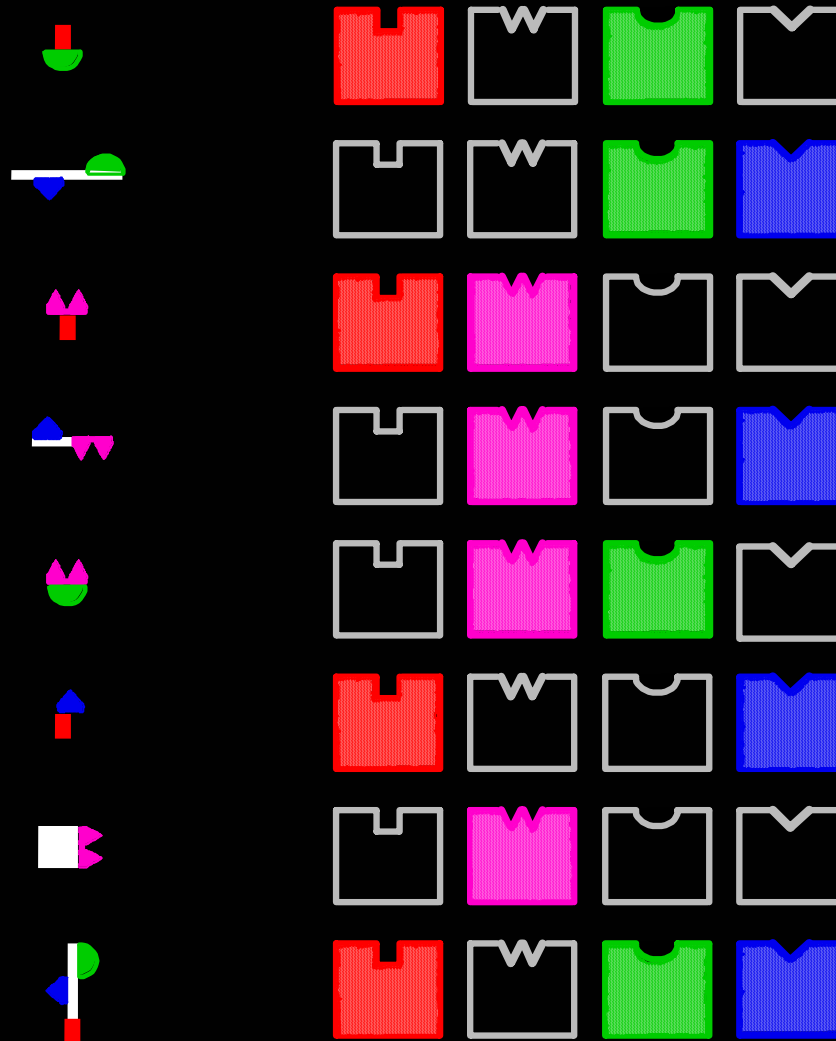
ODORANT RECEPTOR



COMBINATORIAL RECEPTOR CODES FOR ODORS

ODORANTS

RECEPTORS



RECEPTOR CODES AND PERCEPTION

ODORANT RECEPTOR

1 3 6 18 19 25 41 46 50 51 79 83 85 86

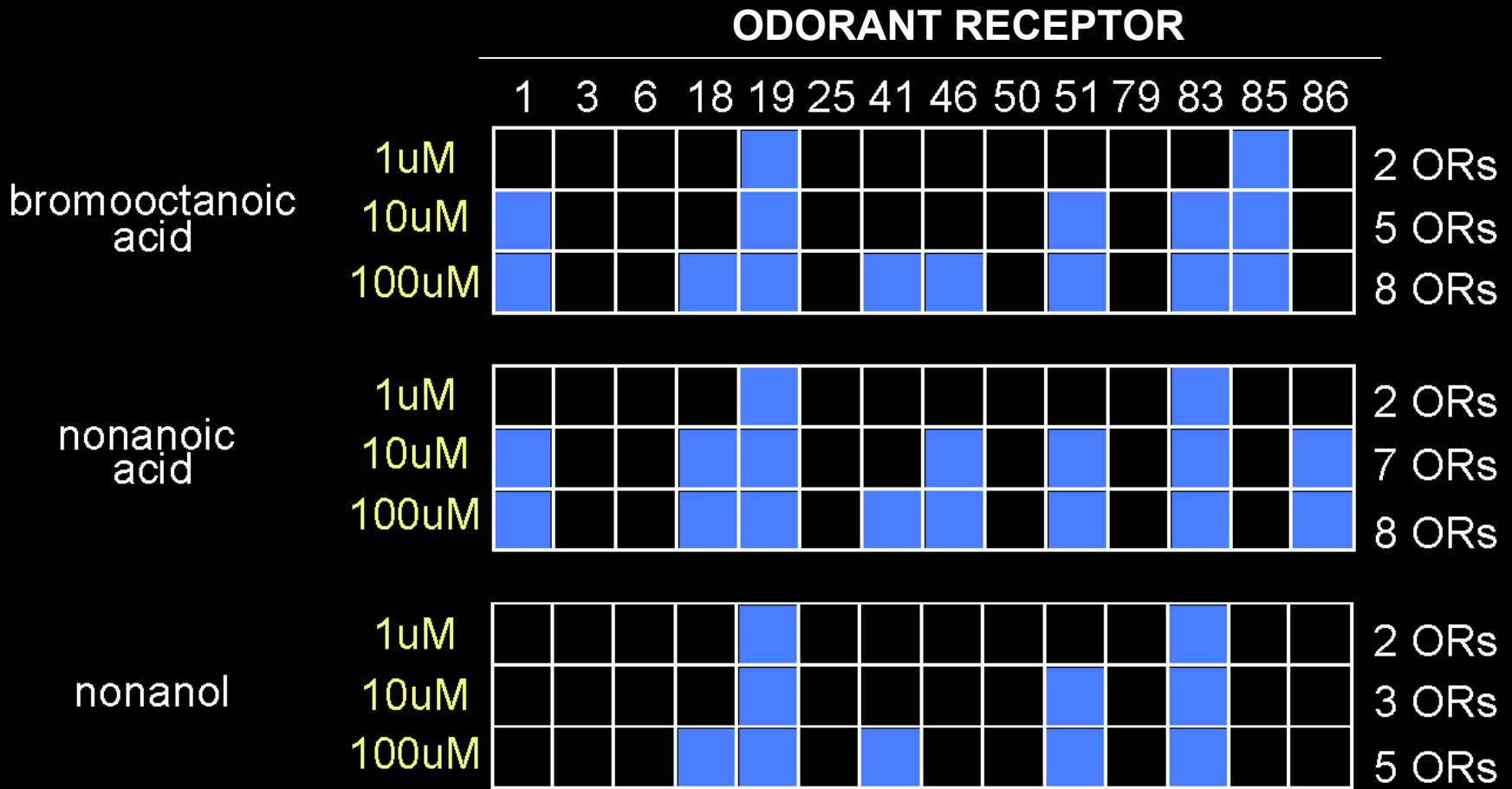
Hexanoic Acid					■										rancid, sour, goat-like
Hexanol		■				■									sweet, herbal, woody

Heptanoic Acid	■			■	■		■			■	■				rancid, sour, sweaty
Heptanol		■			■	■									violet, sweet, woody

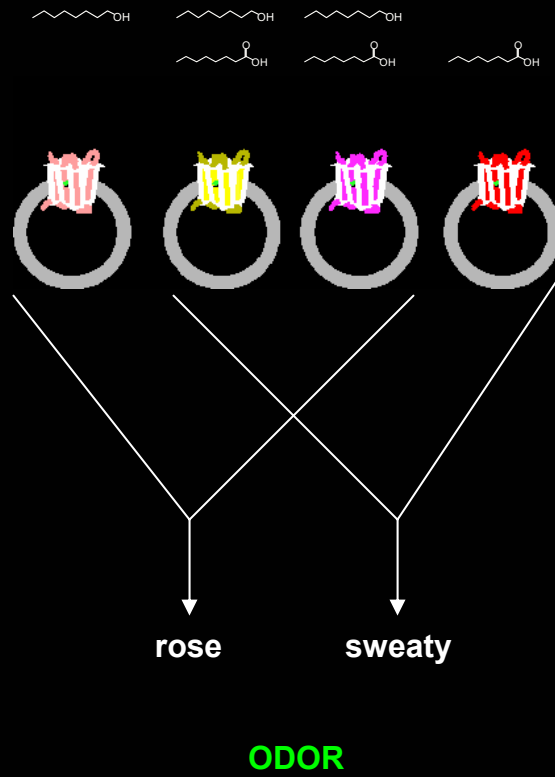
Octanoic Acid	■			■	■		■	■		■	■	■			rancid, sour, repulsive
Octanol				■	■		■			■					sweet, orange, rose

Nonanoic Acid	■			■	■		■	■		■		■		■	waxy, cheese, nut-like
Nonanol				■	■		■			■		■			fresh, rose, oily floral

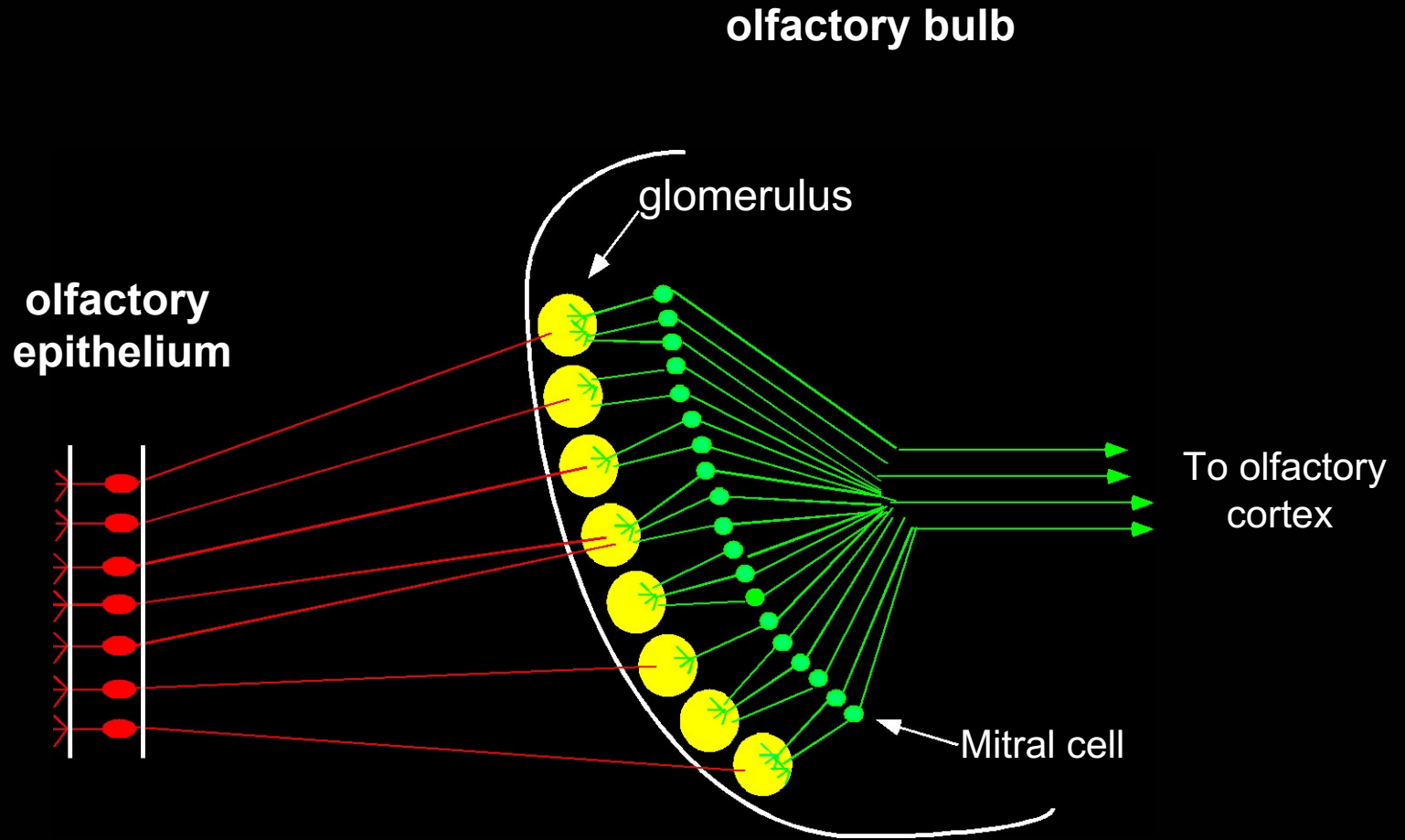
RECEPTOR CODES: THE EFFECT OF CONCENTRATION



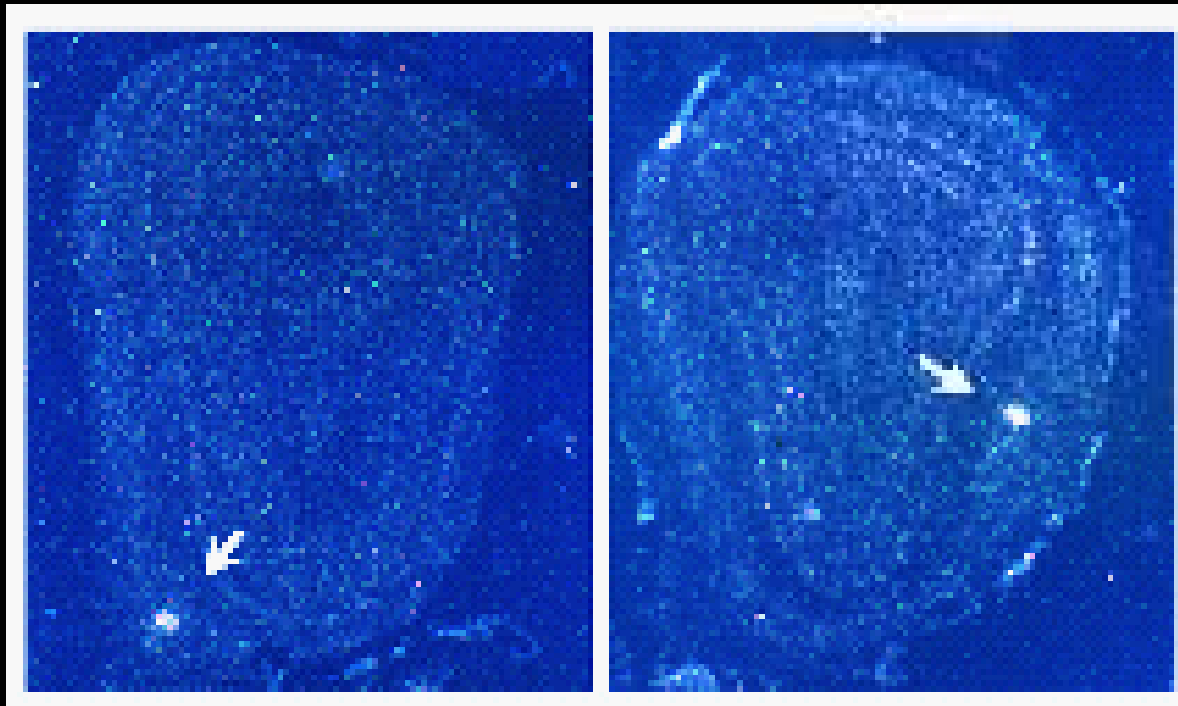
ODORANTS



THE OLFACTORY BULB



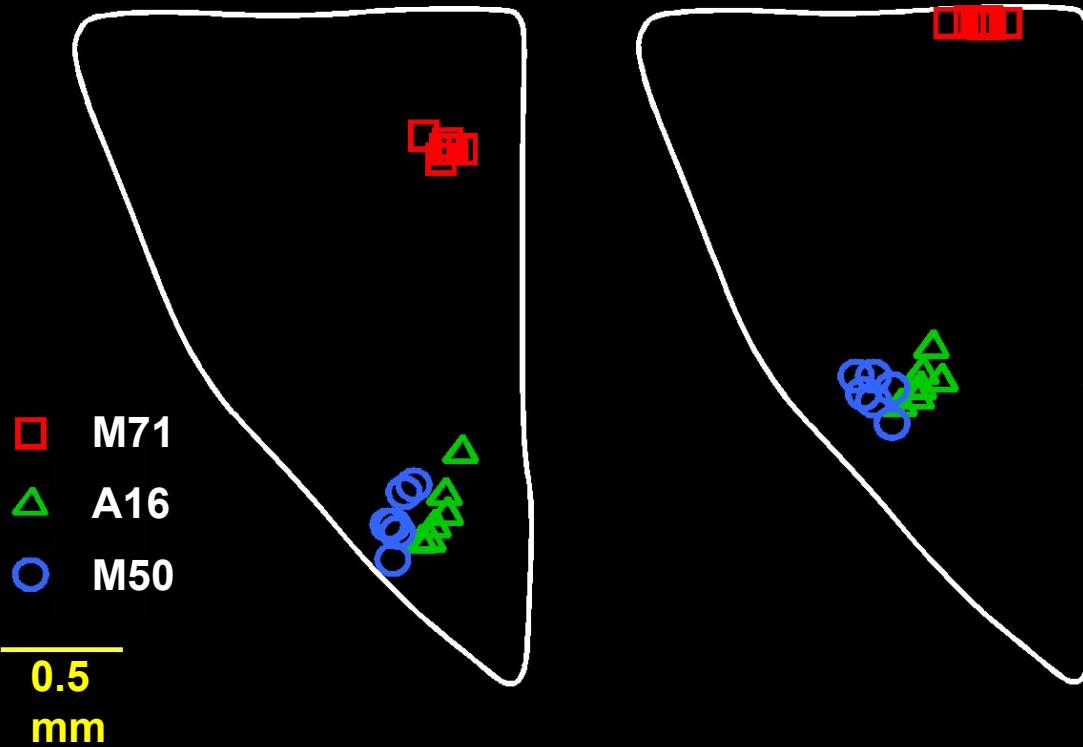
AXONS OF NEURONS WITH THE SAME OR CONVERGE IN OLFACTORY BULB



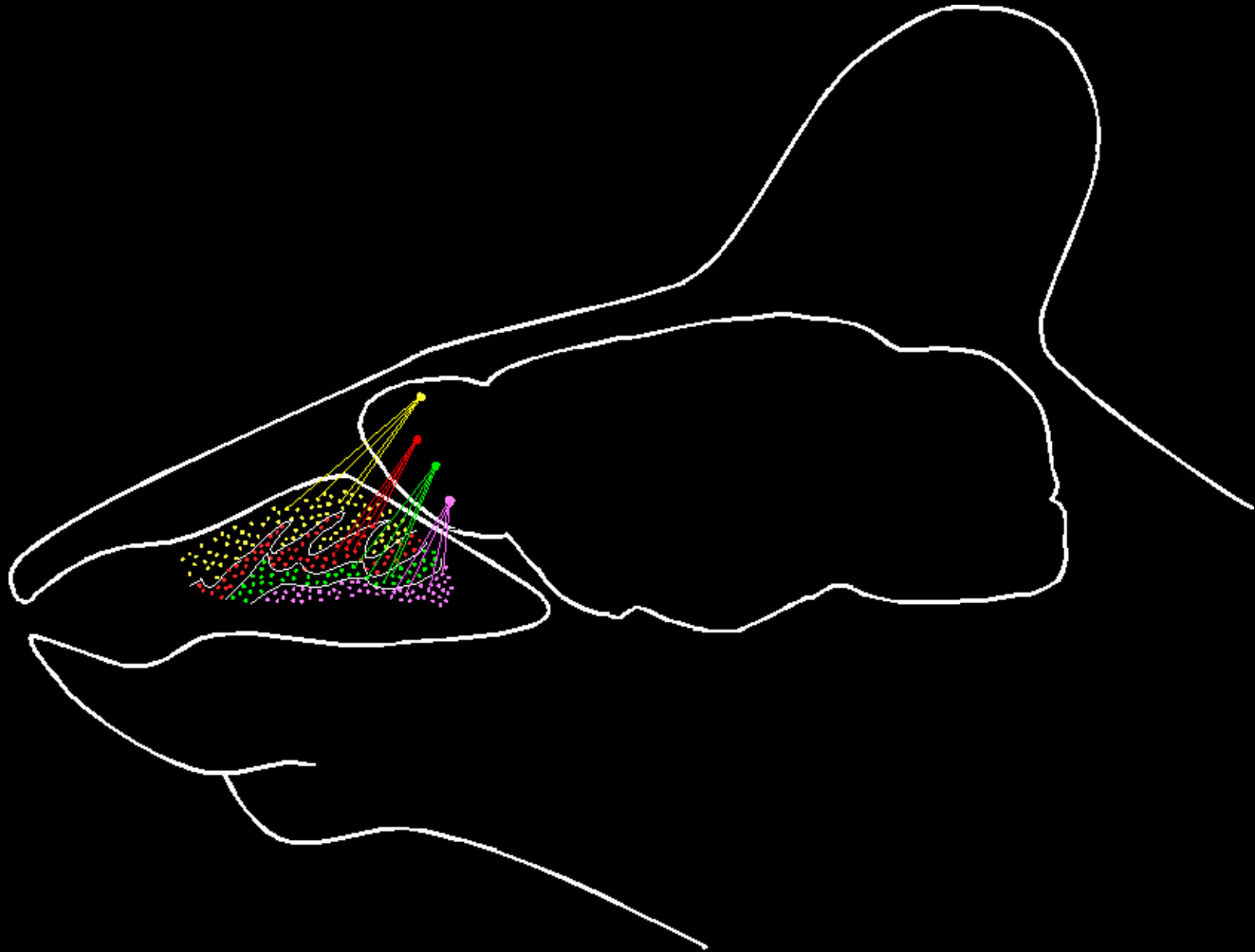
OR-SPECIFIC GLOMERULI IN THE OLFACTORY BULB

medial
olfactory bulb

lateral
olfactory bulb



A STEREOTYPED MAP OF OR INPUTS IN THE OLFACTORY BULB



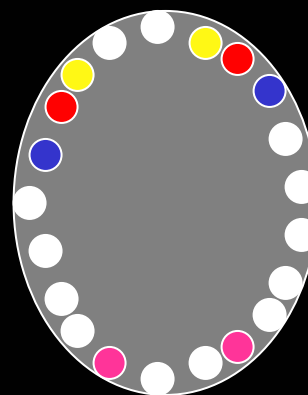
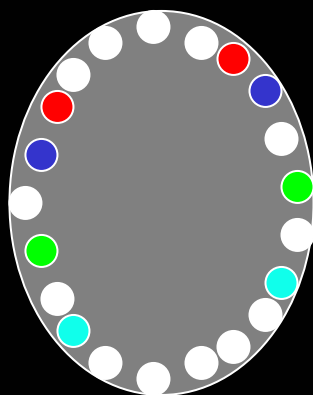
ODOR CODING IN OLFACTORY EPITHELIUM AND BULB



OE



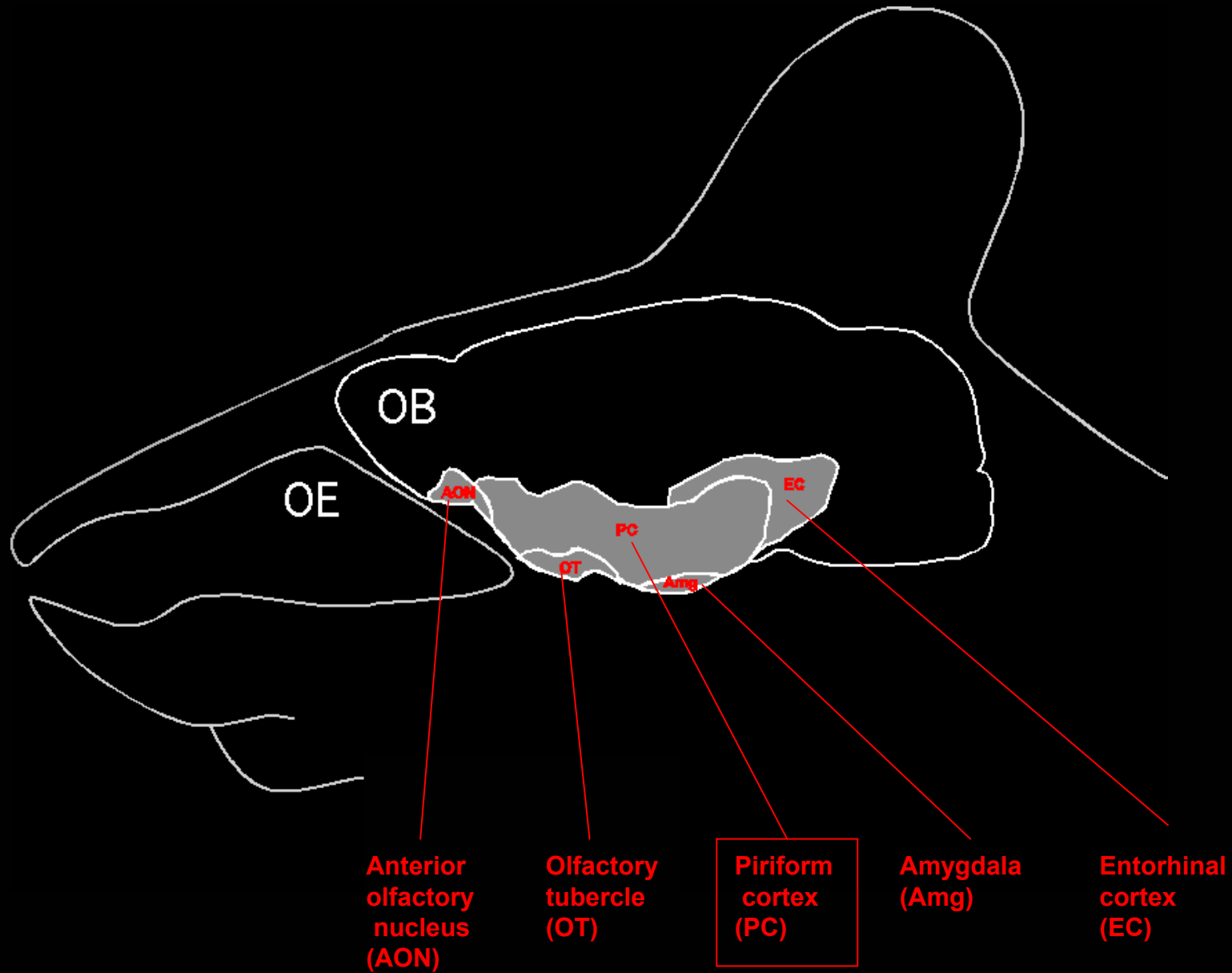
OB



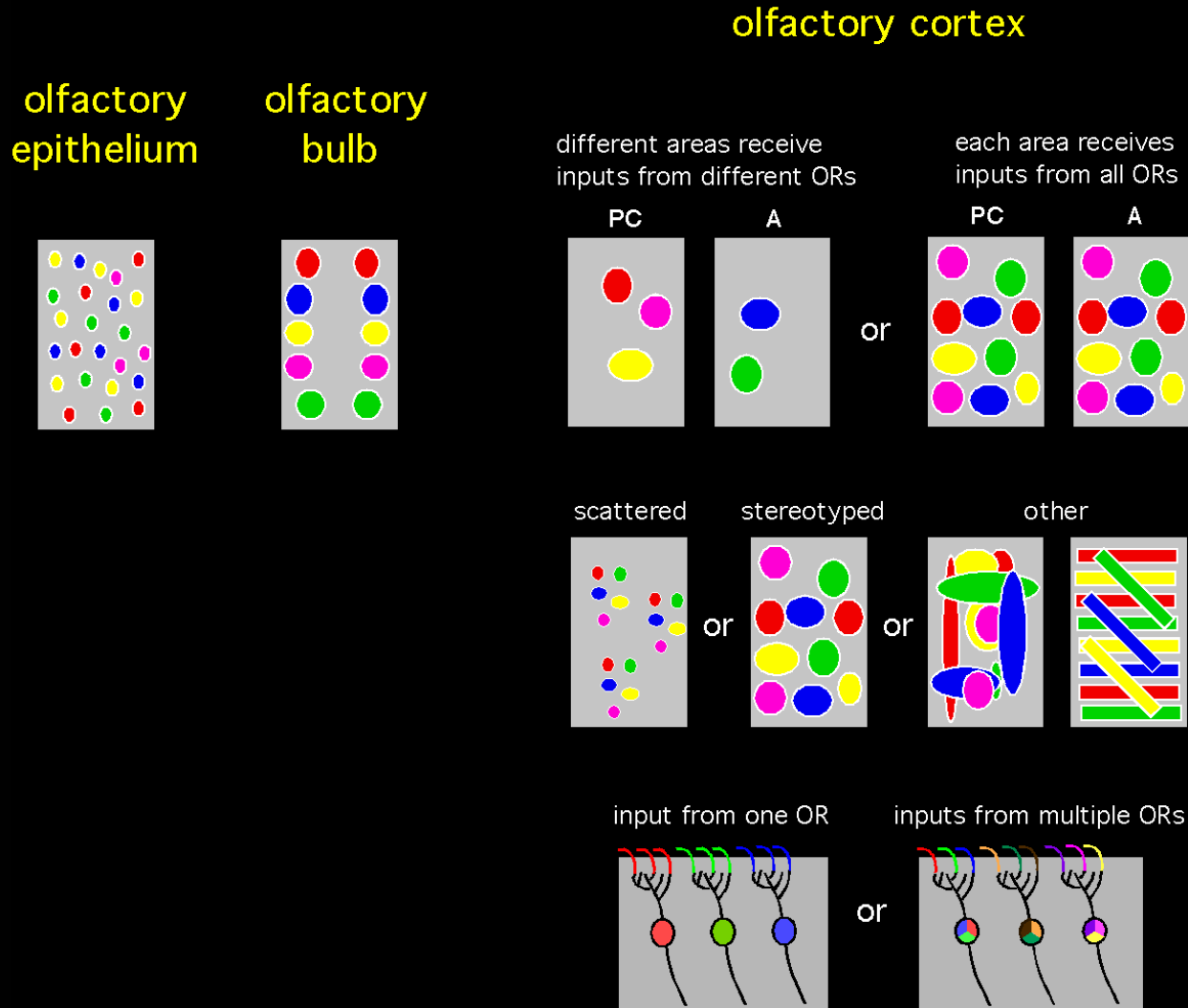
ROSE

RANCID

THE OLFACTORY CORTEX



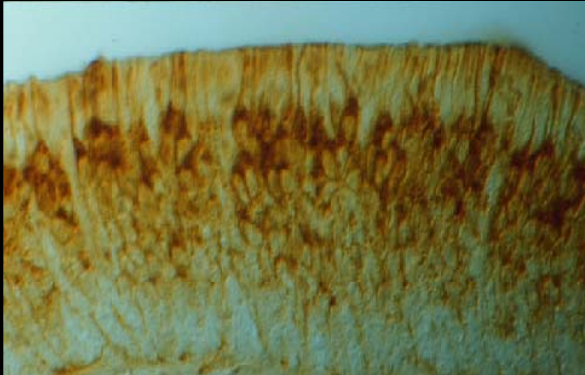
HOW ARE OR INPUTS ORGANIZED IN THE CORTEX?



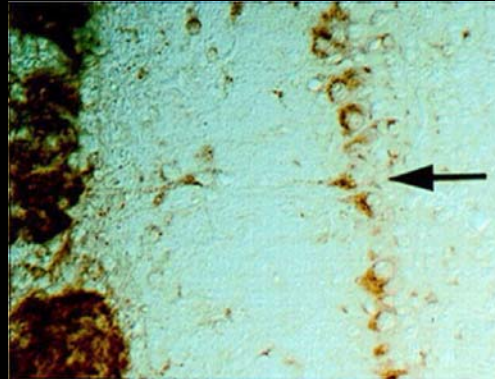
BARLEY LECTIN: A GENETIC TRANSNEURONAL TRACER



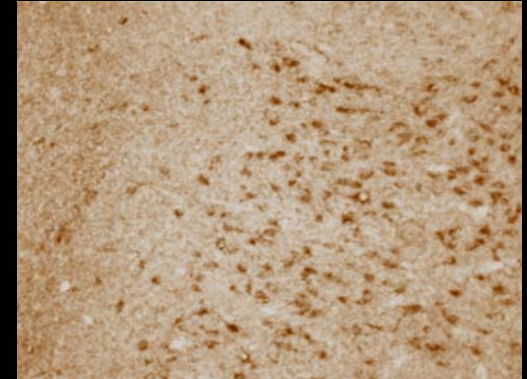
PompBL mice



olfactory
epithelium



olfactory
bulb



olfactory
cortex

COEXPRESSION OF BL WITH A SINGLE OR GENE

M5iBL mice



gene

M50iBL mice



mRNA

protein

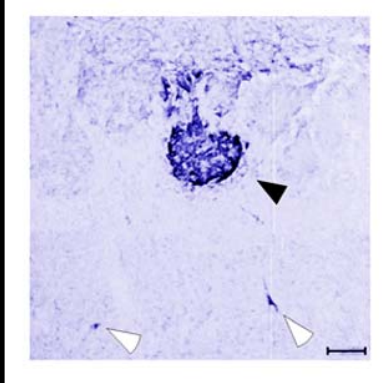
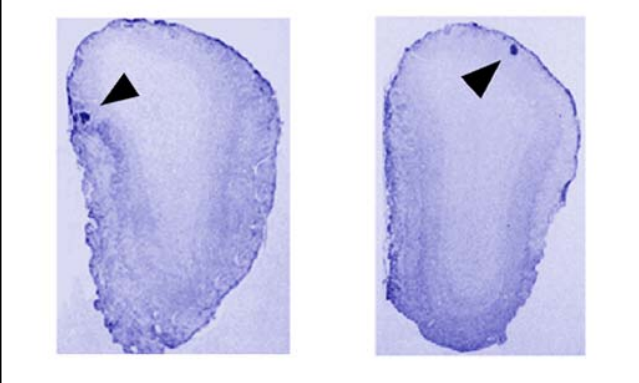
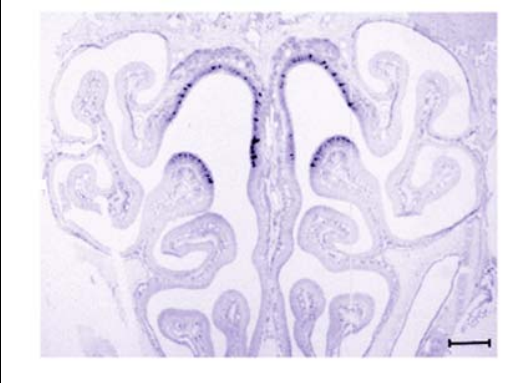
BL IN THE OLFACTORY EPITHELIUM AND OLFACTORY BULB

olfactory epithelium

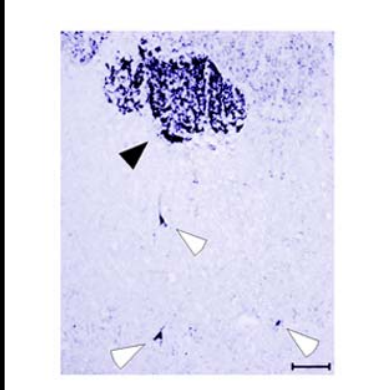
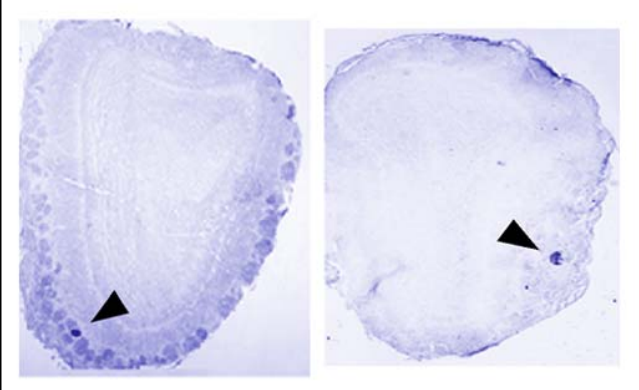
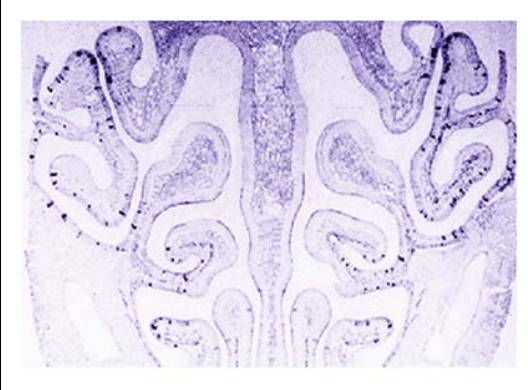
olfactory bulb

olfactory bulb relay neurons

M5iBL

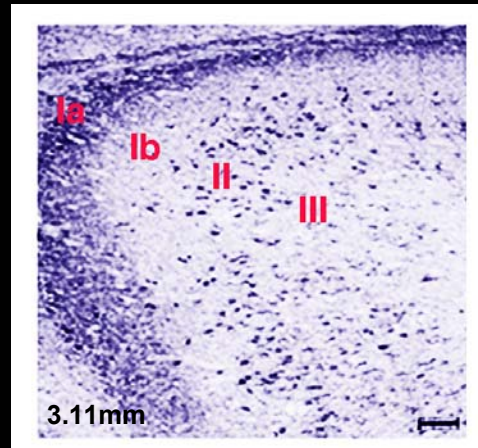


M50iBL

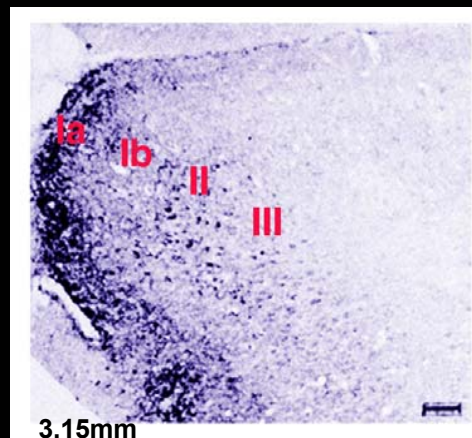


BL IN OLFACTORY CORTEX

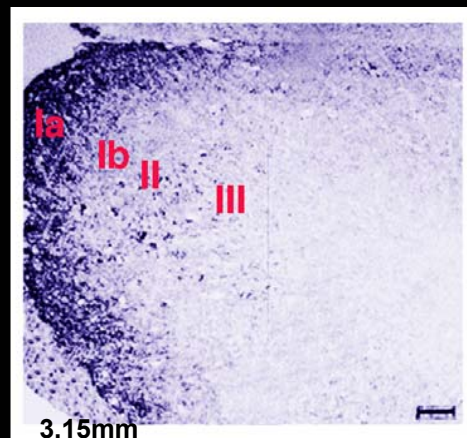
PompBL



M50iBL-#1

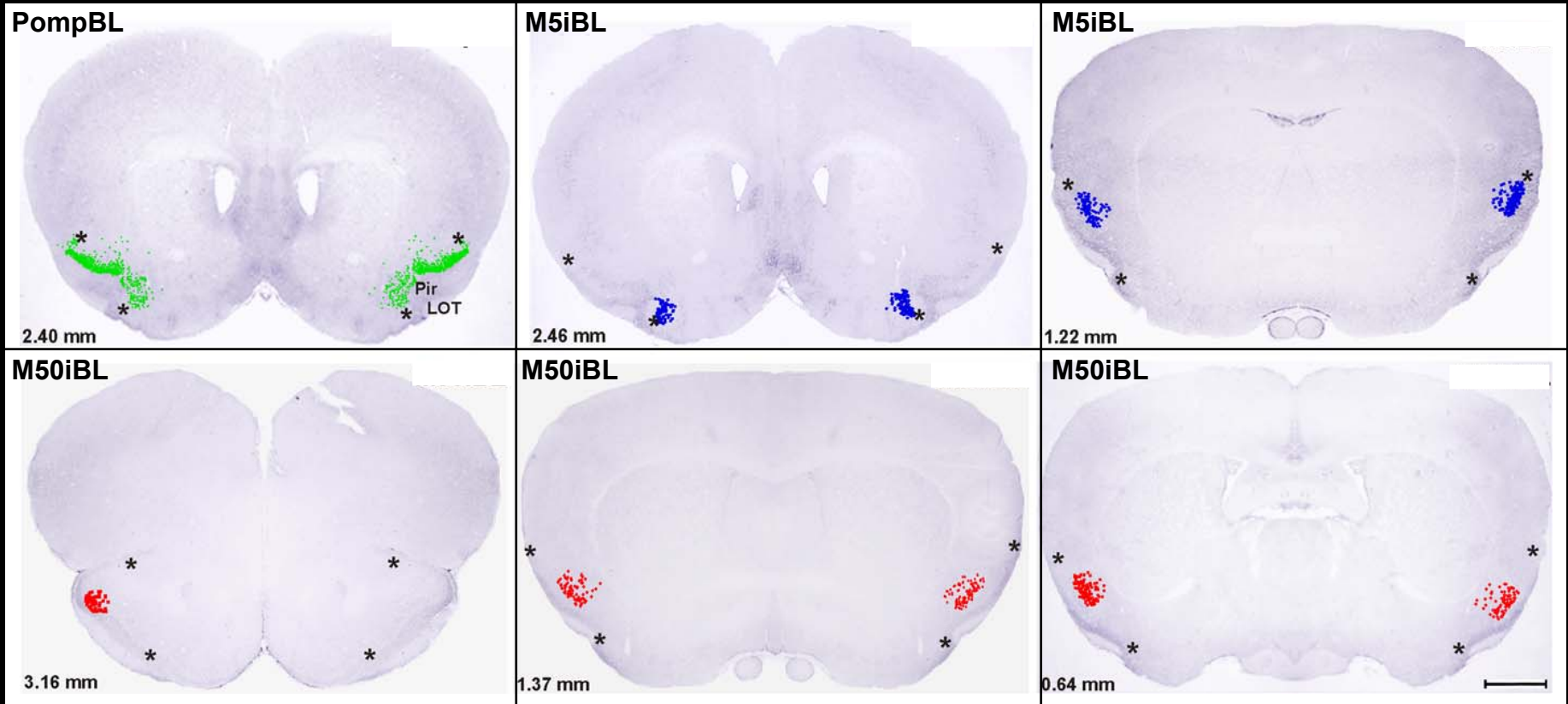


M50iBL-#2



CLUSTERS OF BL+ CORTICAL NEURONS IN M5iBL AND M50iBL MICE

anterior piriform cortex



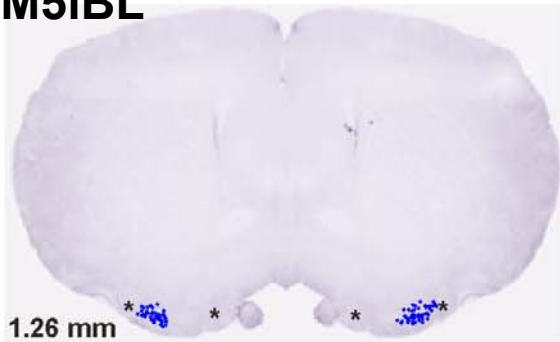
CLUSTERS OF BL+ CORTICAL NEURONS IN M5iBL AND M50iBL MICE

olfactory tubercle

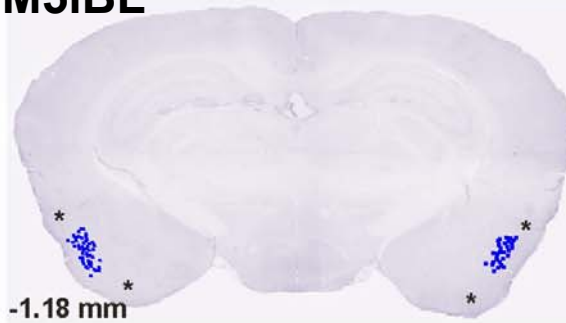
posterior piriform cortex

lateral entorhinal cortex

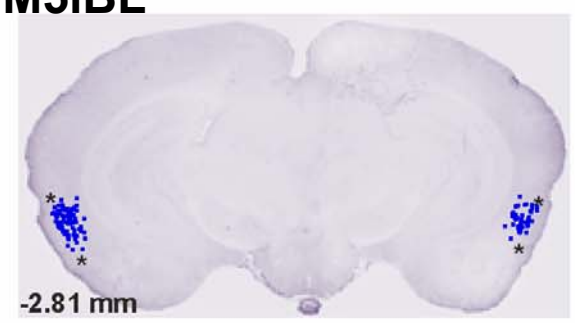
M5iBL



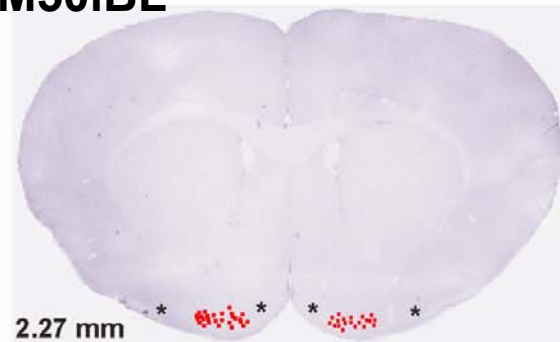
M5iBL



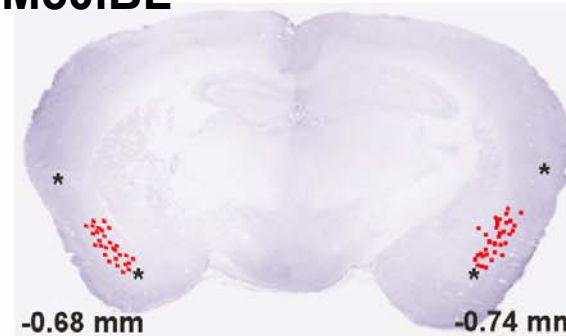
M5iBL



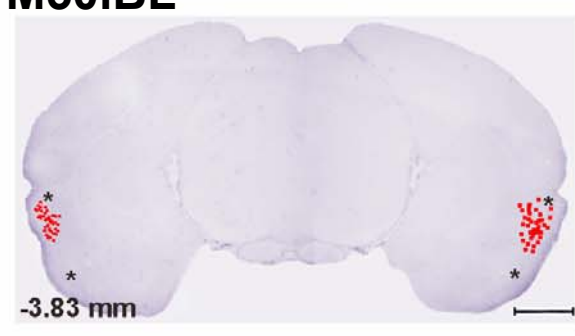
M50iBL



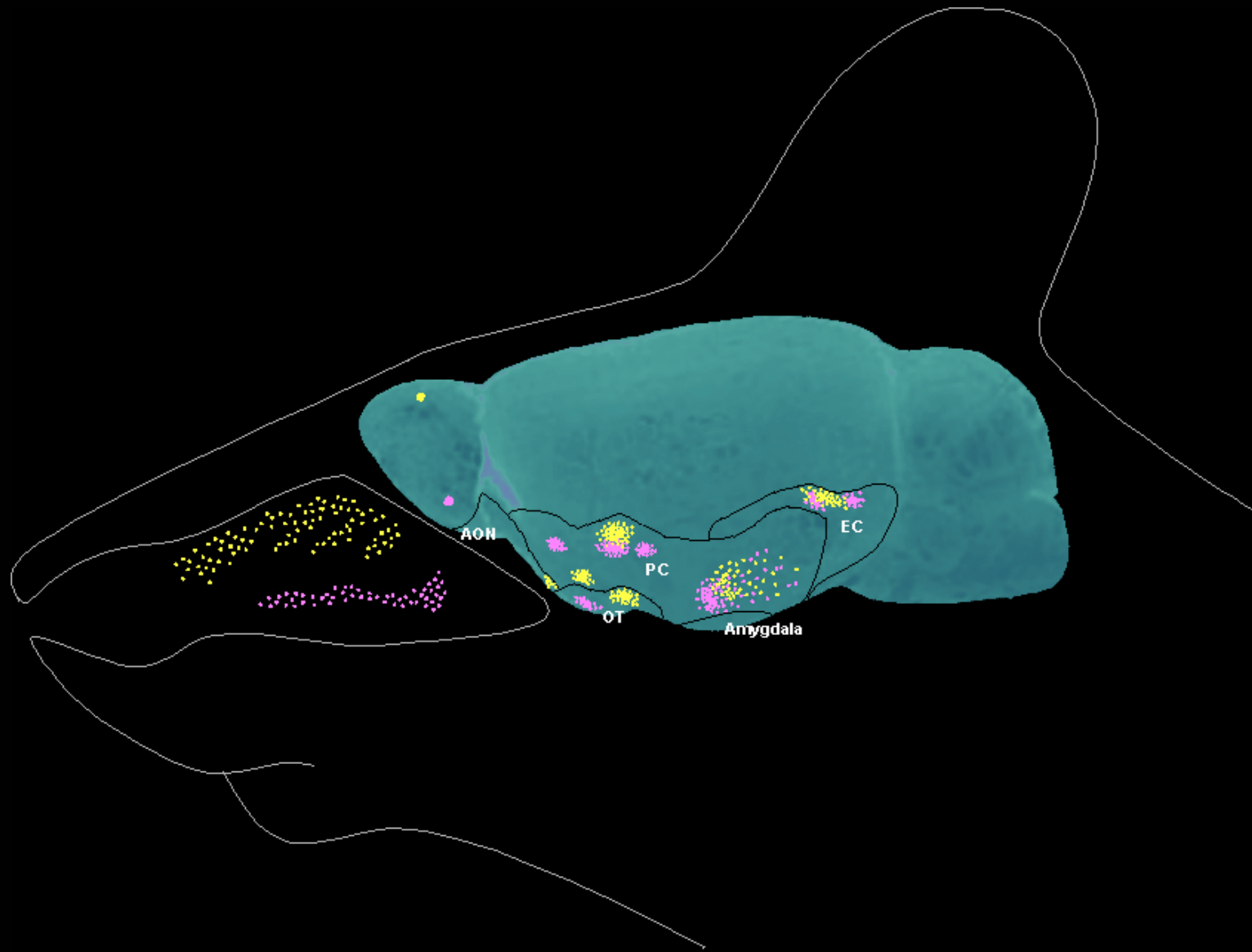
M50iBL



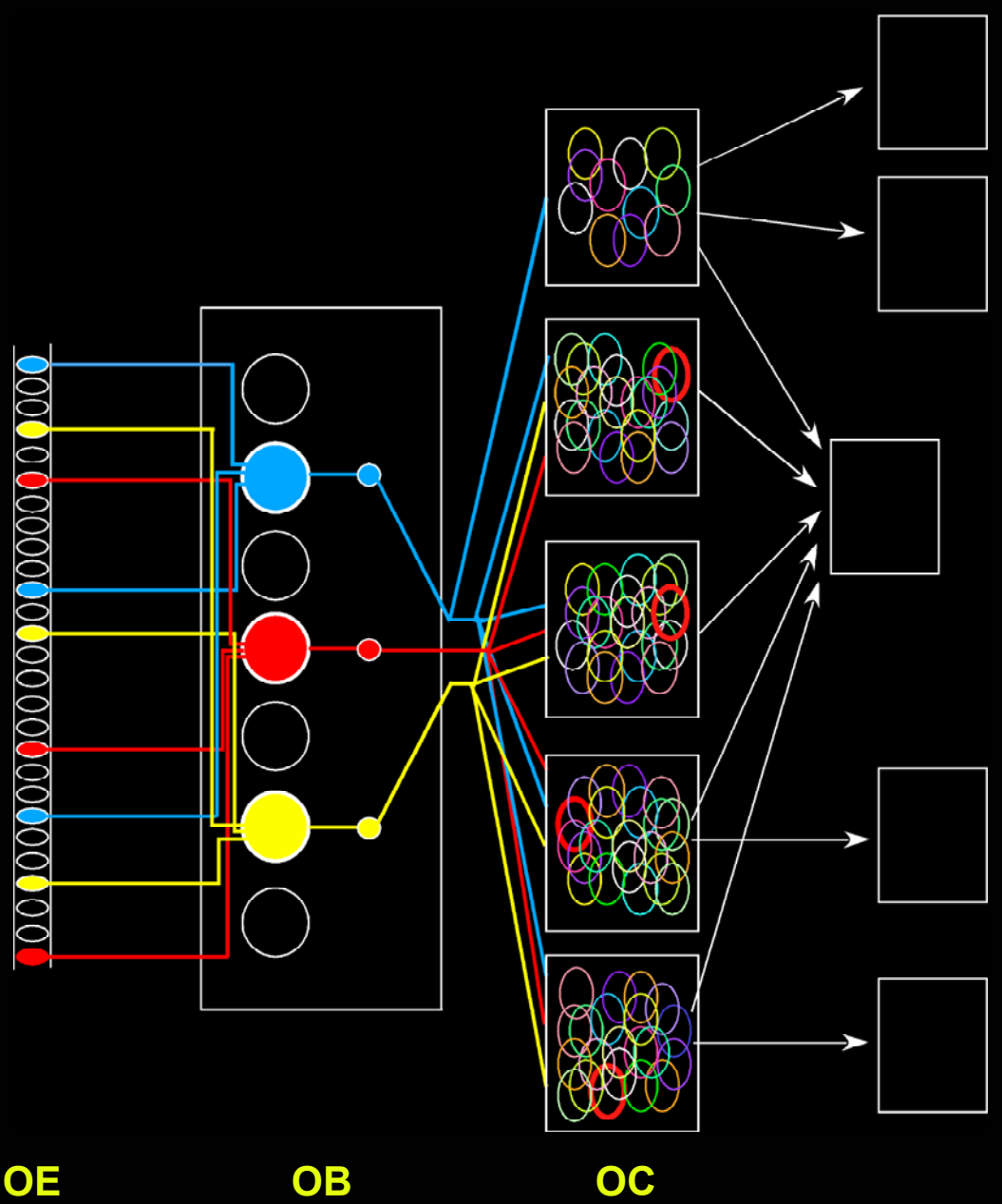
M50iBL



A STEREOTYPED MAP OF OR INPUTS IN OLFACTORY CORTEX



DIVERGENCE AND PARALLEL PROCESSING OF OR INPUTS



BL+ NEURONS IN ANTERIOR PIRIFORM CORTEX

PERCENT OF AREA OCCUPIED BY BL+ CLUSTERS

M5iBL: 5.7%

M50iBL: 4.2%

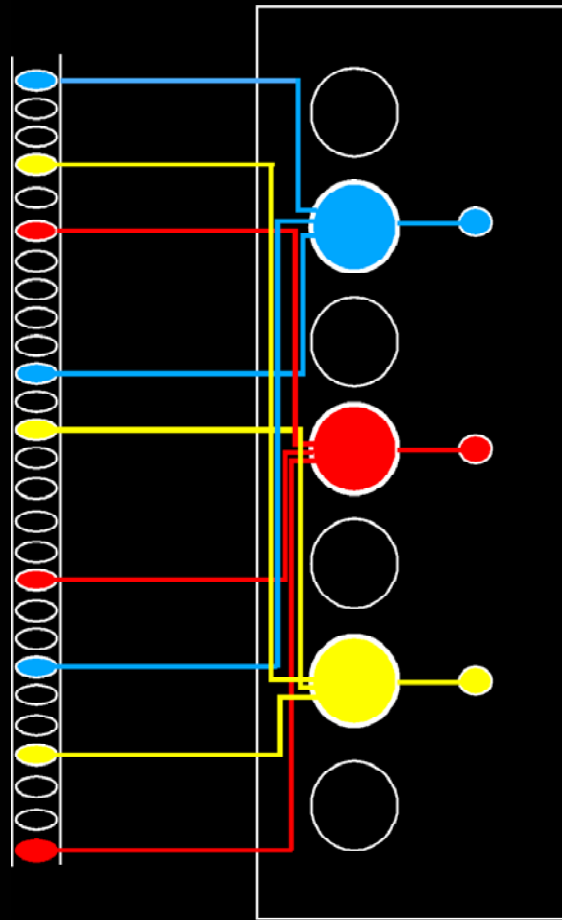
NUMBER OF BL+ NEURONS

PompBL: 179,570 ±3935

M50iBL: 4390 ±179 (2.4% of PompBL)

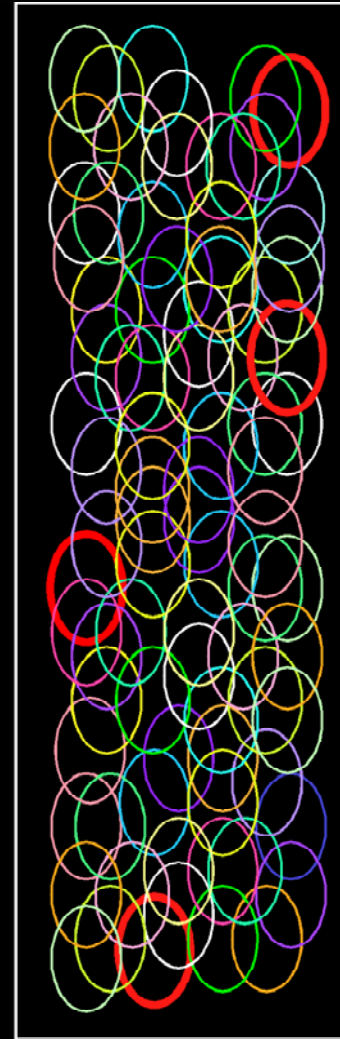
M5iBL: 6570 ±217 (3.7% of PompBL)

INPUTS FROM DIFFERENT ORS OVERLAP IN CORTEX



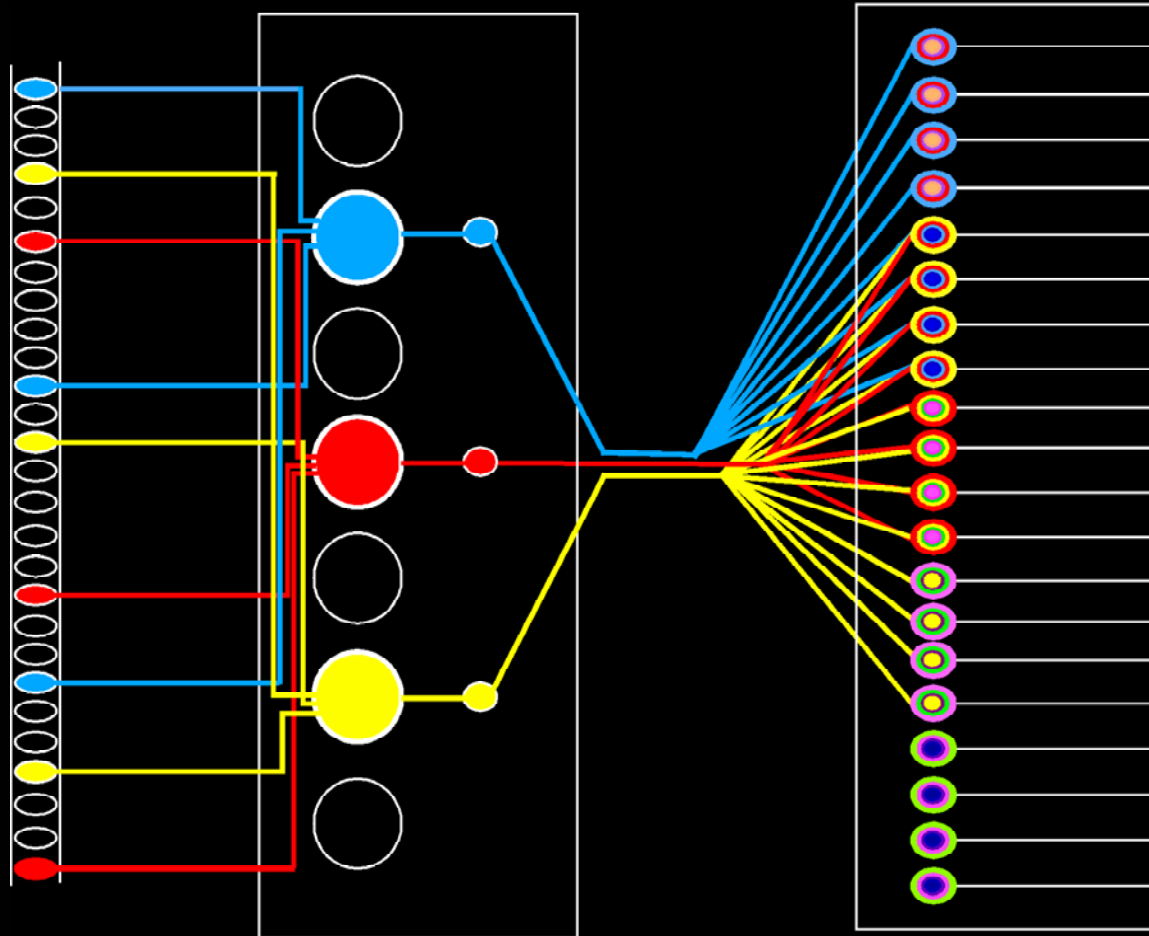
OE

OB



OC

INPUTS FROM DIFFERENT ORS ARE COMBINED IN SINGLE CORTICAL NEURONS

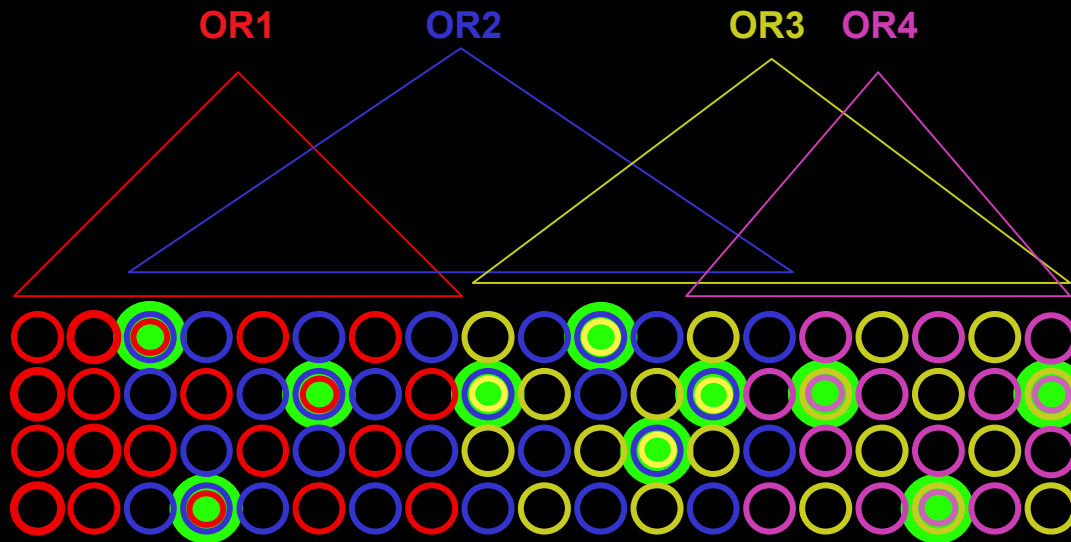
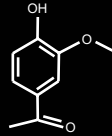


OE

OB

OC

MODEL: CORTICAL NEURONS AS COINCIDENCE DETECTORS



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Junzo Hirono**