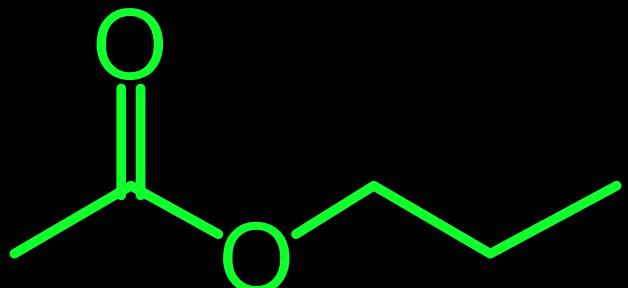
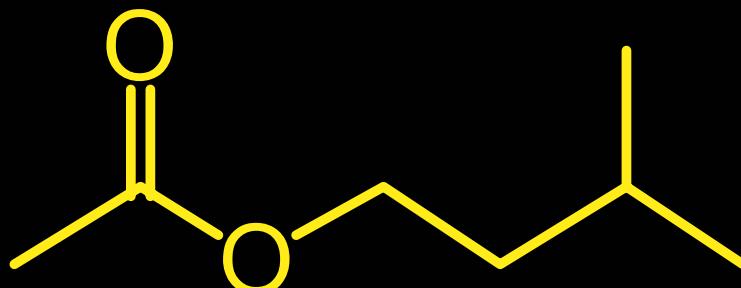


**PEAR**



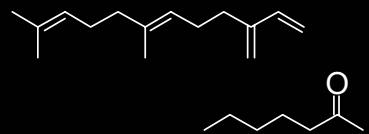
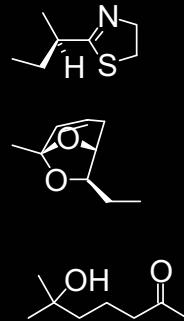
**BANANA**



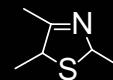
# THE OLFACTORY SYSTEM AND INSTINCTIVE BEHAVIORS



PHEROMONES



PREDATOR ODORS



AGGRESSION



MATERNAL BEHAVIOR

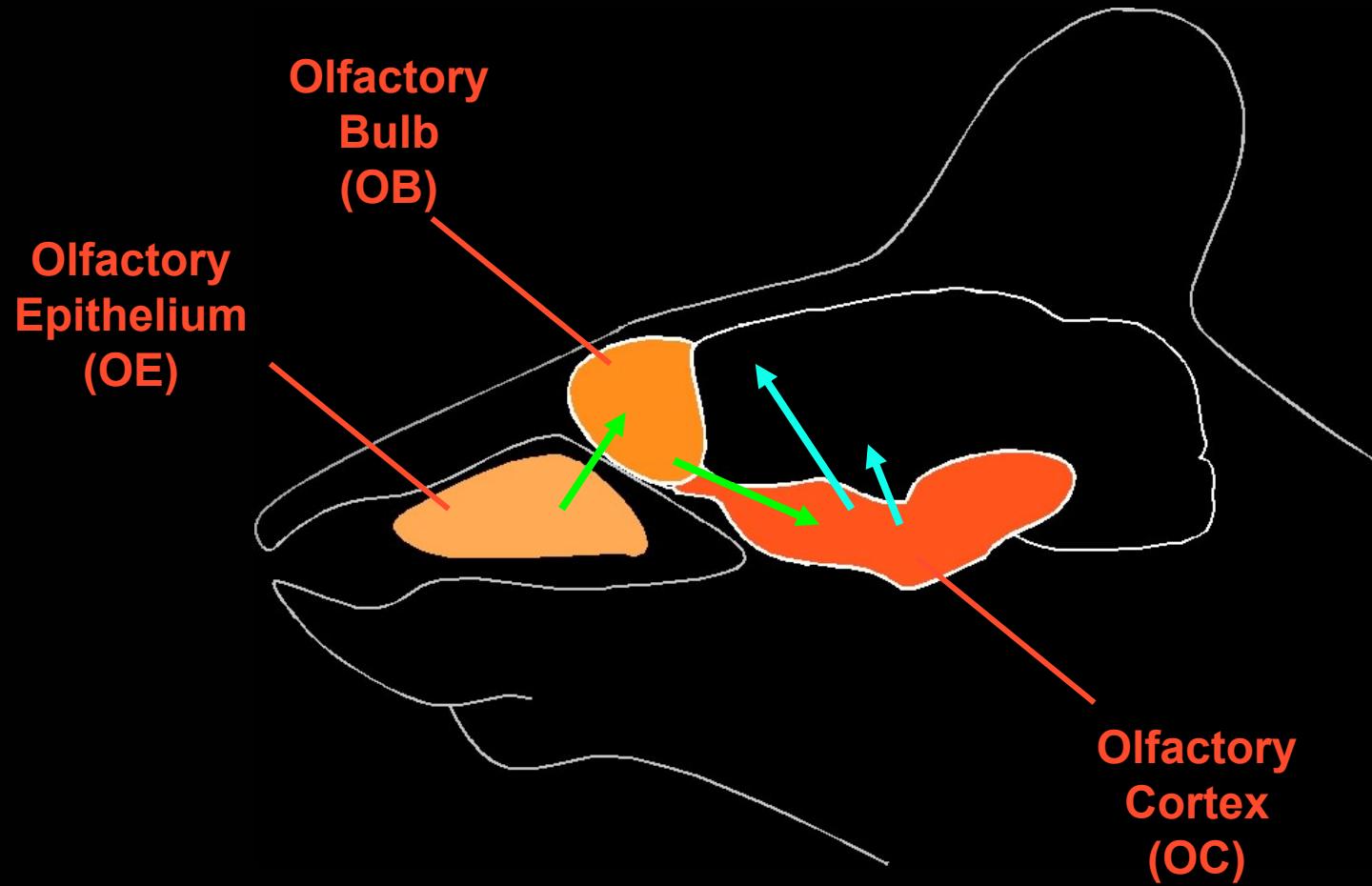


SEXUAL BEHAVIOR

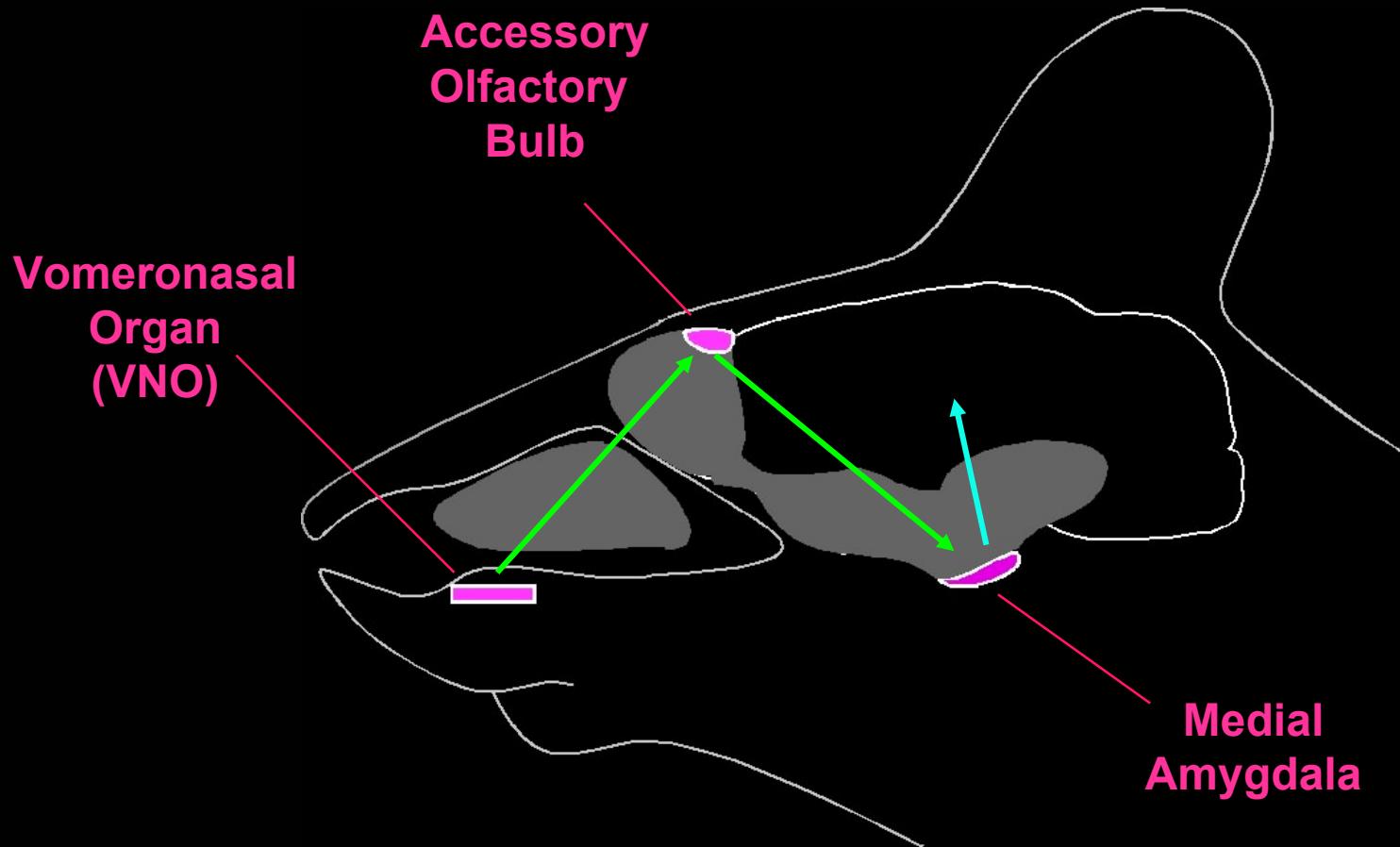


FEAR

# THE OLFACTORY PATHWAY

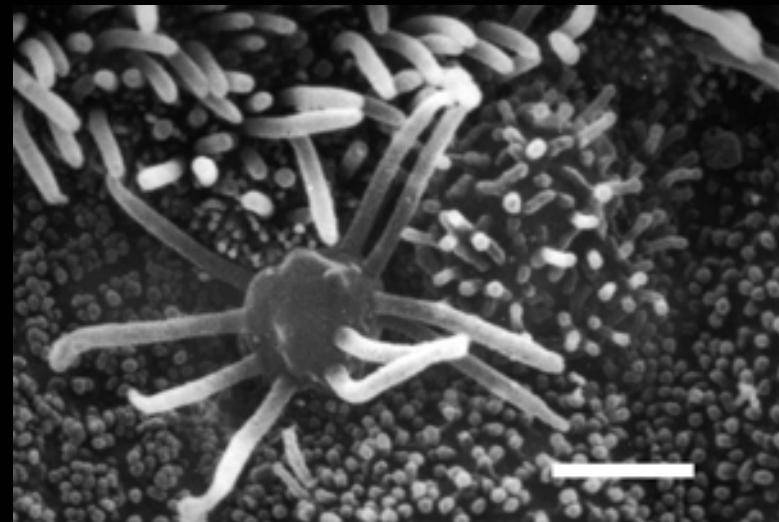


# THE VOMERONASAL PATHWAY



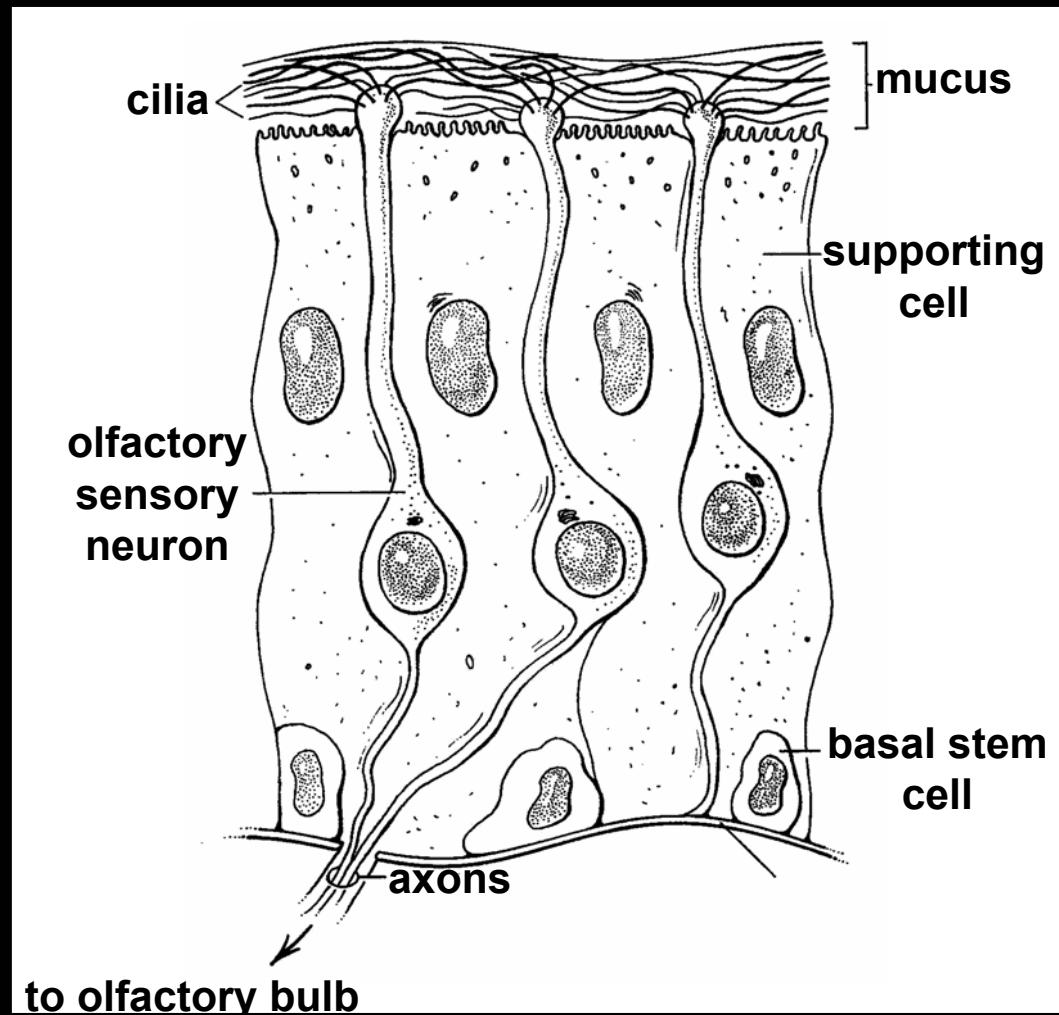
# THE OLFACTORY EPITHELIUM

CILIA

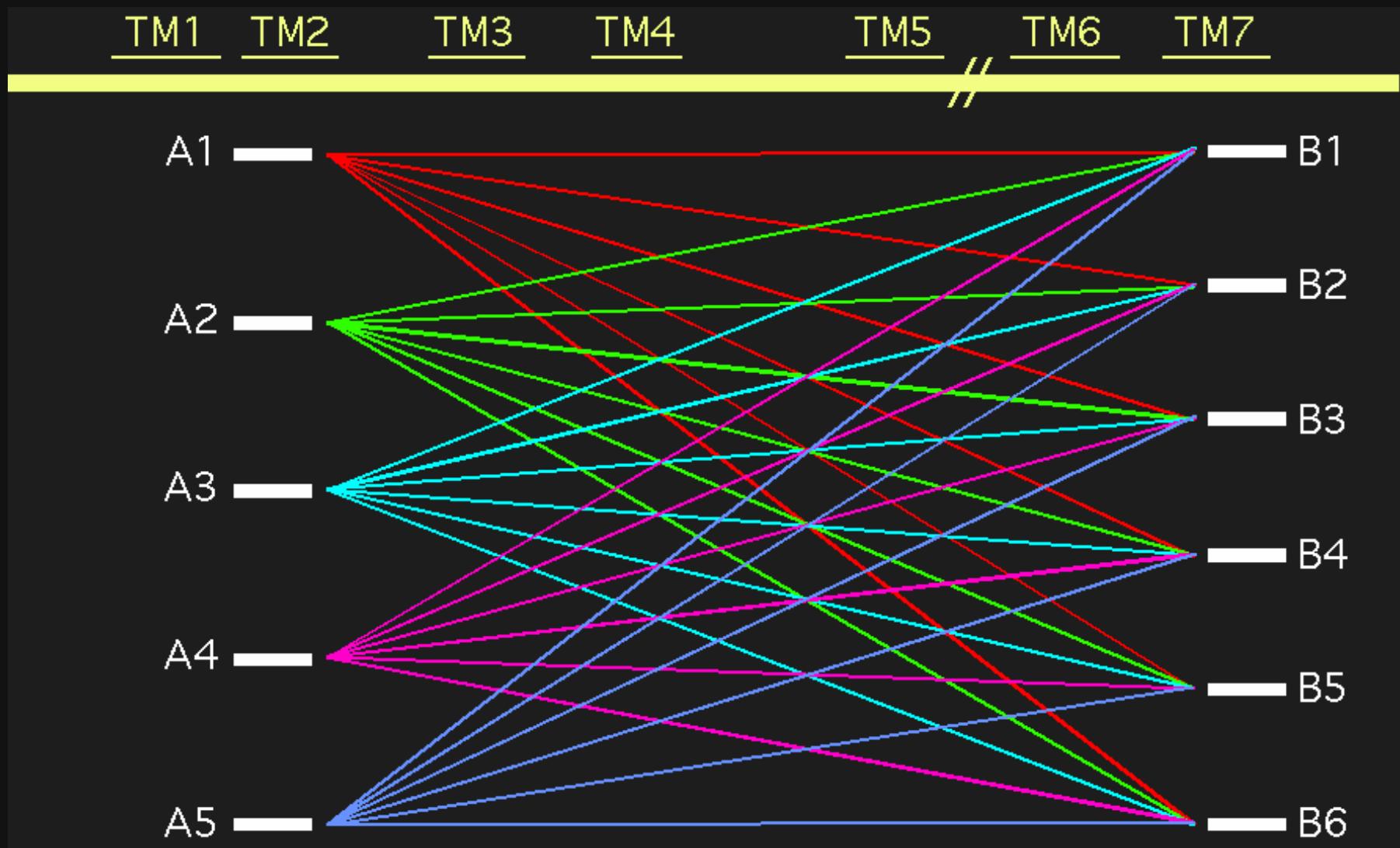


B. Menco, 1997

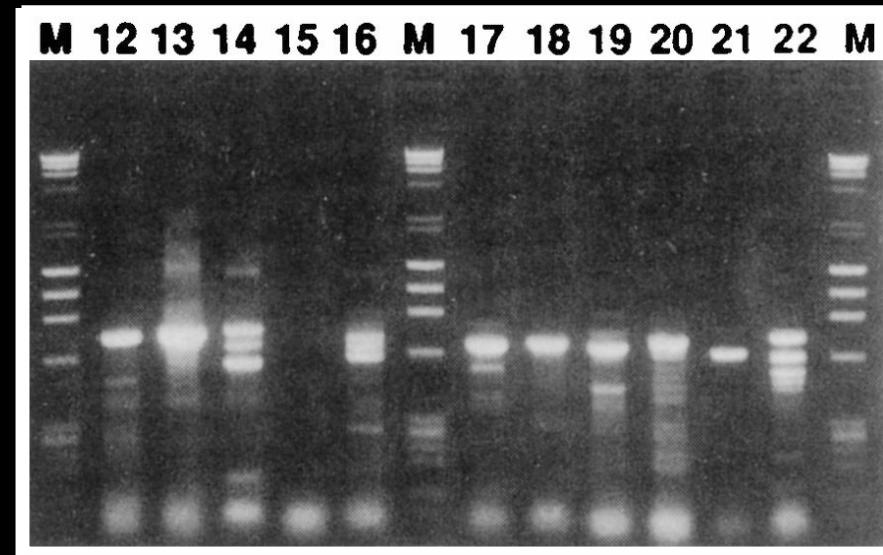
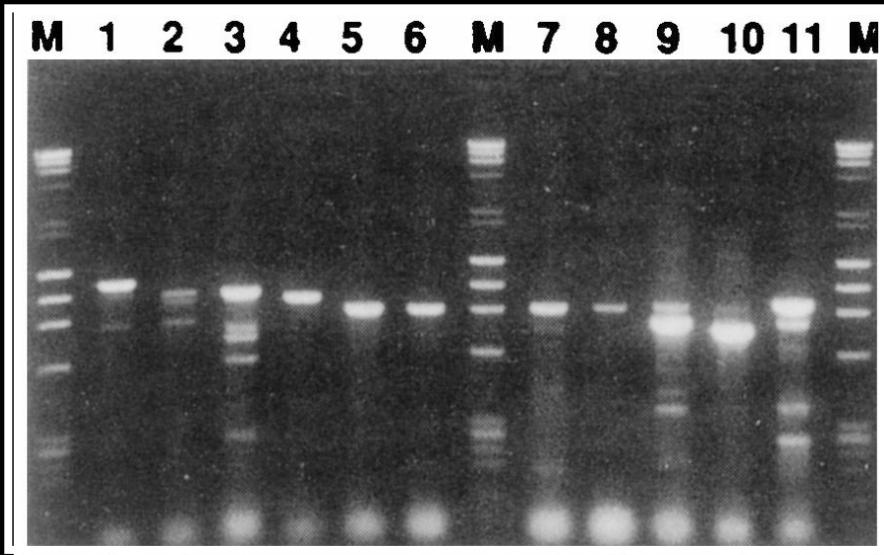
STRUCTURE



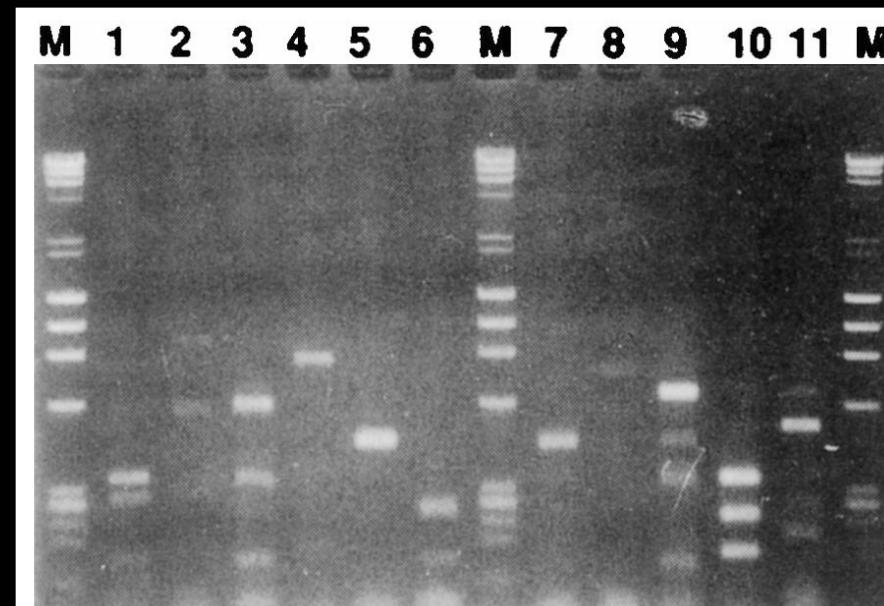
# THE SEARCH FOR ORs: combinatorial PCR



## PCR PRODUCTS



## PCR PRODUCTS + RESTRICTION ENZYME

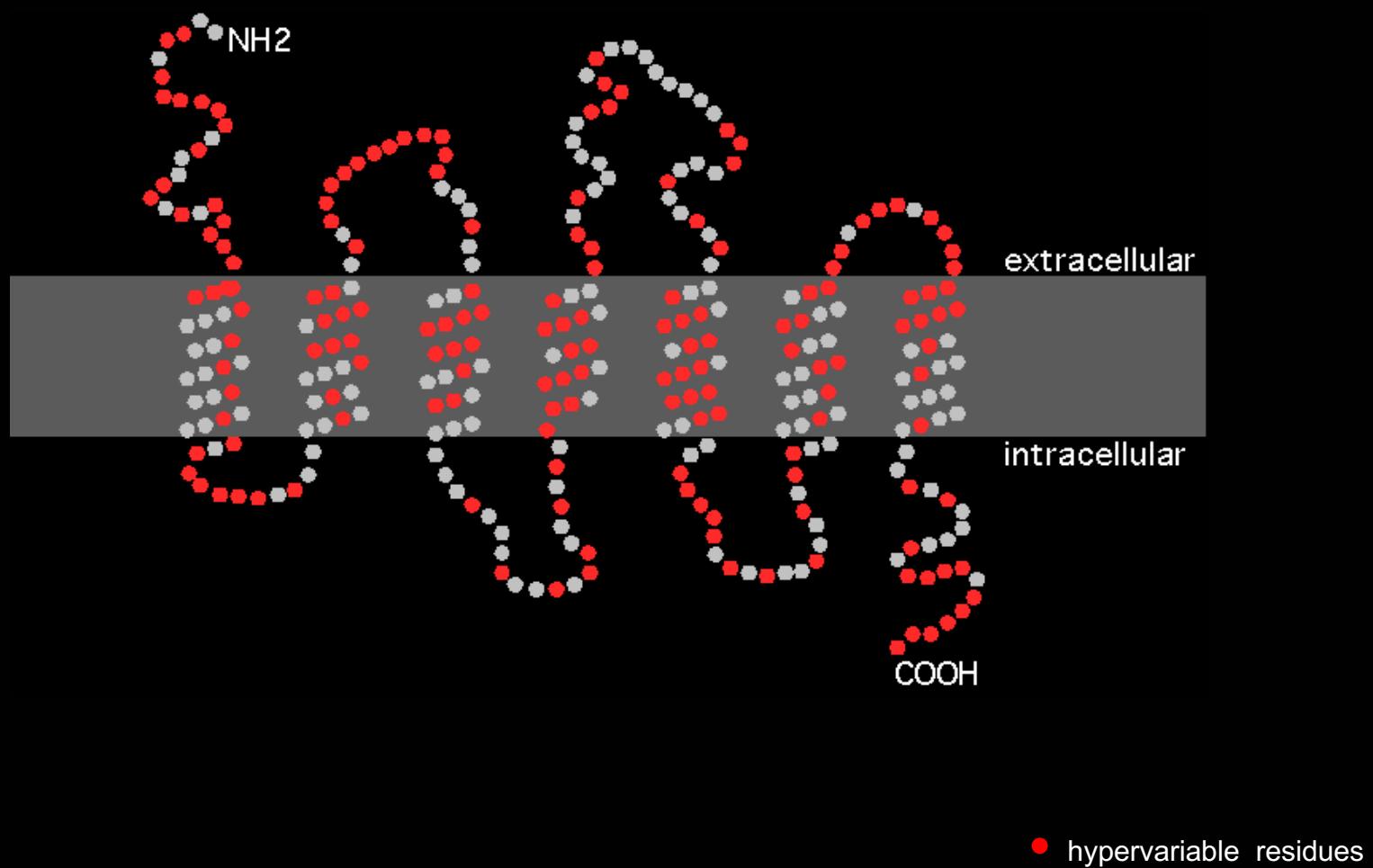


# TEN OLFACTORY RECEPTORS

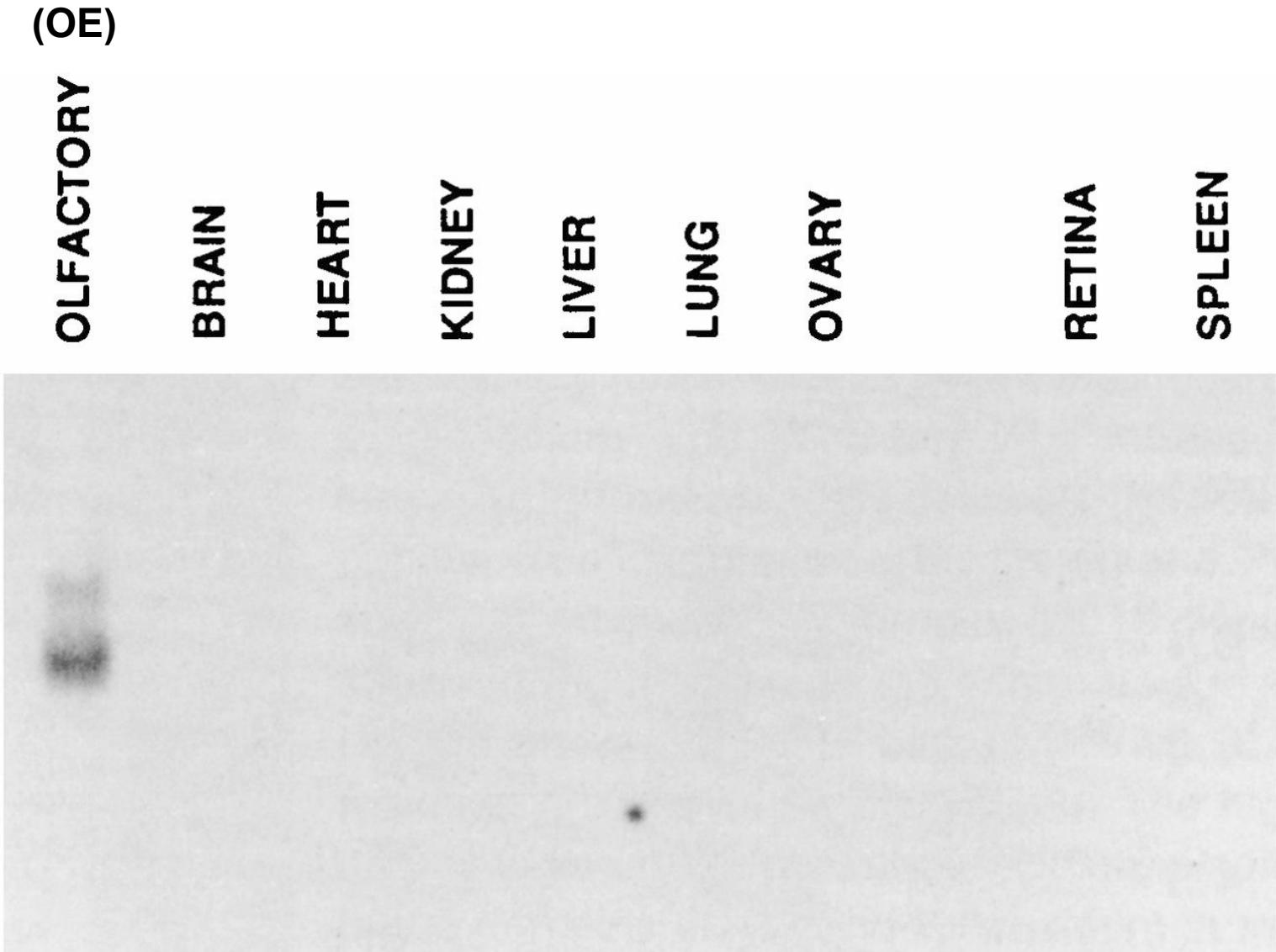
		1	2	
F3	MDSSNRTRVSEFLLLGFVENKDLQPLIYGLFLSMYLTVIGNISIIYVAISDPCLHTPMYFFLSNLSFV	DICFISTTVPKML	82	
F5	MSSTNQSSYTEFLLLGLSRQPQQQQQLLFLFLIMYLATVLGNLIIILAIGTDSRLHTPMYFFLSNLSFV	DVCFSSTTVPKVL	82	
F6	MAWSTGQNLSLTPGPFIALLGFPGRPSMRIGLFLFLIMYLTVIGNLAIISLVGAHRCLOTPMYFFLCNLNFLEI	IWFTTACVPKTL	85	
F12	MESGNSTRRFSFFLLGFTENPQLHFLIFALFLSMYLTVLGNLIIIMAIIQSHLHTPMYFFLANLSFV	DICFTSTIPKML	83	
I3	MN--NQTFITQFLLLGLPIEEHQHLFYALFLVMYLTTILGNLIIIVLVLQDSQLHTPMYFLFLSNLSFS	DLCFSSVTMPKLL	80	
I7	MERRNHSGRVSEFYVLLGFPAPAPLRVLLFLSLLXYVLVLTENMIIIAIRNHTLHKPMYFFLANMSFLEI	IWYVTVTIPKML	83	
I8	MN--NKTVITHFLLLGLPIPPEHQQLFALFLIMYLTTFLGNLIVVVLVQOLDLHHTPMYFLFLSNLSFS	DLCFSSVTMPKLL	80	
I9	MTRRNQTAISQFFLLGLPFPEYQHFLFYALFLAMYLTTLLGNLIIIIILLLDLSHLHTPMYFLFLSNLSFAD	DLCFSSVTMPKLL	82	
I14	MTGNNOTLILEFLLLGLPIPSEYHLLFYALFLAMYLTIILGNLIIIVLVRDLSLHHMPMYFLFLSNLSFS	DLCFSSVTMPKLL	82	
I15	MTEENQTVISQFLLLFLPIPSEHQHVFYALFLSMYLTTVLGNLIIIIILHDLHSLHHTPMYFLFLSNLSFS	DLCFSSVTMPKLL	82	
		3	4	
F3	----VNIQTQNNVITYAGCITOYIFFLLFVELDNFLLTIMAYDRYVAICHCPMHYTIVIMNYKLCGFLVLVS	WIVSVLHALFQSMM	163	
F5	----ANHILGSQAISFSGCLTQLYFLAVFGNMNDNLLAVMSYDRFVAICHPLHYTTKMTRQLCVLLVVGS	WWVANMNCLVHILLM	163	
F6	----ATFAPRGGVISLAGCATQMYFVFLSGCTEYFLLAVMAYDRYLAICLPLRYGGIMTPGLAMRLALGS	WLCGFSAITVPATLI	166	
F12	----VNIYTQSISITYEDCISOMCVFLYFAELGNFLLAVMAYDRYVAIXCHPLCYTVIHNRLCILLLLLS	WVISIFHAFIQSLIV	164	
I3	----QNMRSQDTSIPIYGGLAQTYFMMVFGDMESFLVAMAYDRYVAICFPLHYTSIMSPKLCTCLVLLL	WMLTTSSHAMHTLLA	161	
I7	AGFIGSKENHGQLISFEACMTQLYFFFGLGCTECVLLAVMAYDRYVAICHPLHYPVIVSSRLCVQMAAGS	WAGGGFISMVKVFLI	168	
I8	----QNIQSQVPSISYAGCLTQIFFFLFGFLGNFLLAVMAYDRYVAICFPLHYTNISHKLCCLLVLFW	WIMTSSHAMHTLLA	161	
I9	----QNMQSQVPSIPYAGCLQIYFLMFVGFLGNFLLAVMAYDRYVAICFPLHYMSIMSPKLCVSLVVLS	WVLTTFHAMLHTLLM	163	
I14	----QNMQSQVPSISYTGCLTQLYFFFVGDMESFLVVMAYDRYVAICFPLRYTTIMSTKFCPLHYMSIMSPK	WMLTMTHALLHTLLI	163	
I15	----QNMQSQVPSIPFAGCLTQLYFLYFADLESFLVAMAYDRYVAICFPLHYMSIMSPKLCVSLVVLS	WVLTTFHAMLHTLLM	163	
		5	6	
F3	LALPFCTHLEIPHYFCEPNQVIQLTCSDAFLNDLVIVFTLVLLATVPLAGIFYSYFKIVSSICAISSVHGKYKA	FSTCASHLSVV	248	
F5	ARKSFCADNMIPHFFCDGTPLLKSCSDTHLNELMILTEGAVVVMTPFVCLISYI	HITCAVLRVSSPRGGWKSFSTCGSHLAVV	248	
F6	ARLSFCGSRVINHFFCDISPWIVLSCDTDTQVVELVSFGIAFCVILGSCGITLVSYAYIITTIKIPSARGHRRA	FSTCASHLSIV	251	
F12	LQLTFCGDKIPHFFCELNQLSOLTCSDNFPSPHLLIMNVLPVMLAAISFSGILSYFKIVSSIHSISTVQGKYKA	FSTCASHLSIV	249	
I3	ARLSFCENNVLNNFFCDLFVLLKACSDTYINELMIFIMSTLLIIIPFLIVMSYARISSILKVPSTQGICKV	FSTCGSHLSVV	246	
I7	SRLSYCGPTNTHFFCDVSPPLLNCSDMTDFVLAIFFLGGLPSVTGASYMAITGAVMRIPSAAGRHKAFSTCASHLTV	V	253	
I8	ARLSFCENNVLNNFFCDLFVLLKACSDTYVNELMIHIMGVIIIVIPFVLIIVSYAKISSLKVPSTQSIHKVF	STCGSHLSVV	246	
I9	ARLSFCEDSVIPHYFCDMSTLLKACSDTDHNELAIFIILGGPIVVLFLIIIVSYARISSIFKVPSQSOSIHKAF	STCGSHLSVV	248	
I14	ARLSFCCEKNVILHFFCDISALLKLSCSDIYVNELMIYILGGLIIIPFLIVMSYVRIFFSILKFPSIQDIYKVF	STCGSHLSVV	248	
I15	ARLSFCADNMIPHFFCDISPLLKSCSDTHVNELVIFVMGGLVIVIPFVLIIVSYARVVASILKVPVRGIHKIF	STCGSHLSVV	248	
		7		
F3	SLFYCTGLGVYLSAANNNSSQASATASVMYTVVTPMVNPFIYSLRNKDVKSVLKTLCEEIRSPPSLLHFFLVLCHLPCFIFCY	333		
F5	CLFYGTIVIAYVNPSSSHLAGRDMAAAVMMYAVVTPMLNPFIYSLRNSDMKAALRKVLAMRFPBKQ	313		
F6	LIWYGSTIFLHVRTSVESSLDLTKAITVLTNTIVTPVLNPFIYTLRNKDVKEARLRTVKGK	311		
F12	SLFYSTGLGVVYSSAVVQSSHSAASAVMYTVVTPMLNPFIYSLRNKDVKRALERLLEGNCVHHWTG	317		
I3	SLFYGTIIGLYLCPAGNNSTVKEMVMMAMYTVVTPMLNPFIYSLRNNDMKRALIRVICSMSKIL	310		
I7	IIFYAASIFIYARPKALSAFDTNKLVSPLYAVIVPLFNPIIYCLRNQDVKRALRRTLHLAQDQEANTNGSKIG	327		
I8	SLFYGTIIGLYLCPGDNFSLKGSAMAMMYTVVTPMLNPFIYSLRNNDMKQALIRYTCSSKKISLPW	312		
I9	SLFYGTIVIGLYLCPSANSTYKETVMSLMYTMVTPMLNPFIYSLRNNDIKDALEKIMCKKQIPSFL	314		
I14	TLFYGTIFGIYLCPSGNNSTYKEIAMAMMYTVVTPMLNPFIYSLRNNDMKRALIRVICTKKISL	312		
I15	SLFYGTIIGLYLCPSANSTYKETVMAAMMYTVVTPMLNPFIYSLRNNDMKRALIRVLCKKKITFL	314		

# NOVEL MOTIFS IN OLFACTORY RECEPTORS

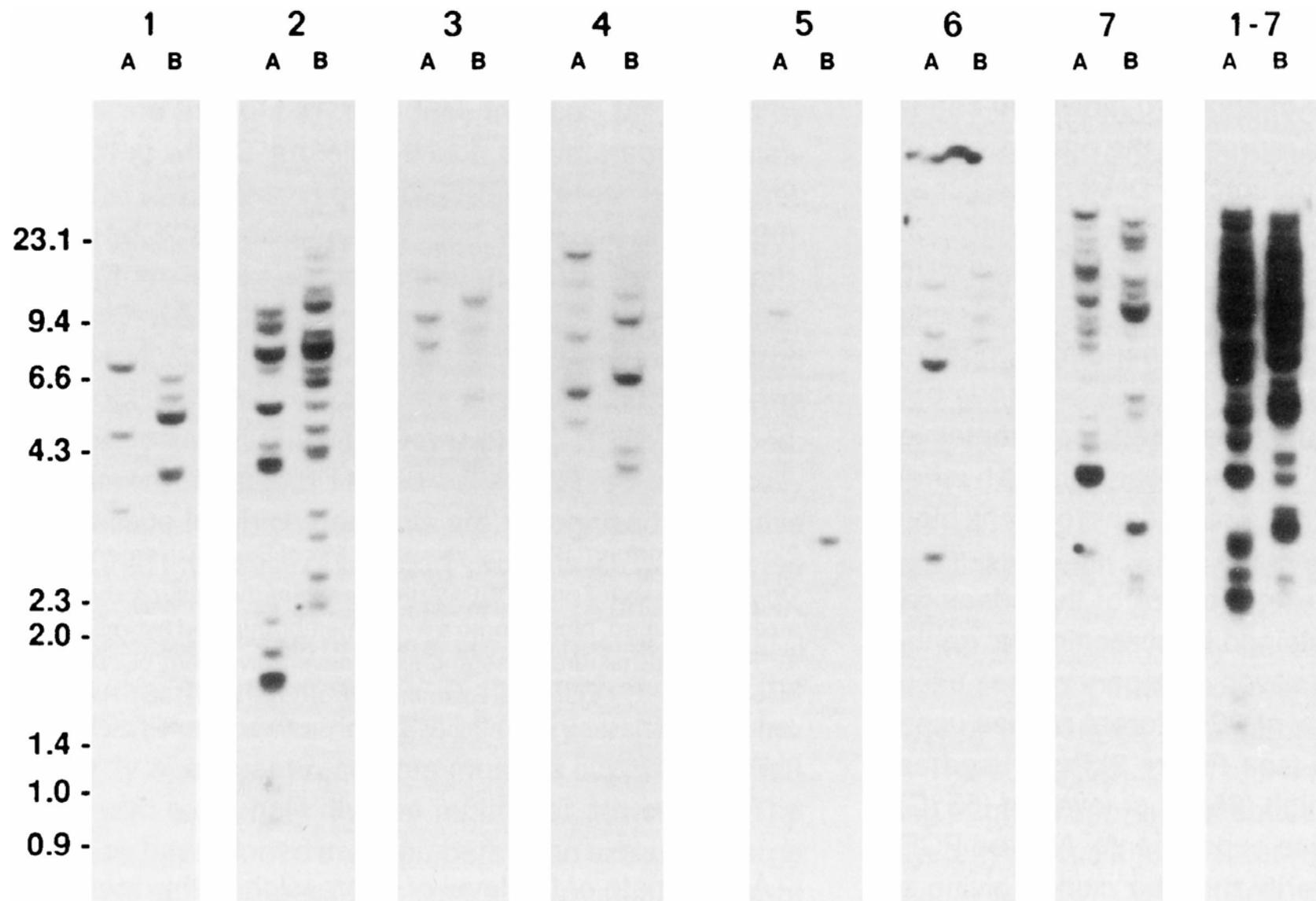
		1	2					
F3	MDSSNRTRVSEFLLLGFVENKDLQPLIYGLFLSMYLTVIGNISIIYVAISDPC	LHTPMYFFL	SNLSFYDICFISTTVPKML			82		
F5	MSSTNQSSYTEFLLLGLSRQPQQQQQLLFLLFLIMYLATVLGNLIIILAIGTDSR	LHTPMYFFL	SNLSFYDVCFSSSTTVPKVL			82		
F6	MAWSTGQNLSLTPGPFIALLGFPGRPSMRIGLFLFLMVLVYLLTVVGNLAIISLVGAHRC	LHTPMYFFL	CNLSFLEIWFTTACVPKTL			85		
F12	MESGNSTRRFSFFLLGFTENPQLHFLIFALFLSMYLTVLGNLIIIMAIIITQSH	LHTPMYFFL	ANLSFYDICFTSTIPKML			83		
I3	MN--NQTFIGQFLLLGLPIEEHQHLYFALFLVYLLTILGNLIIIVLVLQDSQ	LHTPMYFFL	SNLSFSDLCFSSVTMPKLL			80		
I7	MERRNHSGRVSEFYVLLGFPAPAPLRVLLFLSLLXYVLVLTENMIIIAIRNHP	LHTPMYFFL	ANMSFLEIWYVTVTIPKML			83		
I8	MN--NKTVITHFLLLGLPIPPEHQQLFALFLIMYLTTFLGNLIIIVLVLQDSH	LHTPMYFFL	SNLSFSDLCFSSVTMPKLL			80		
I9	MTRRNQTAISQFLLLGLPFPEYQHLYFALFLAMYLTTLLGNLIIILLLDSH	LHTPMYFFL	SNLSFADLCFSSVTMPKLL			82		
I14	MTGNNOTLILEFLLLGLPIPSEYHLLYFALFLAMYLTIILGNLIIIVLRLDSH	LHTPMYFFL	SNLSFSDLCFSSVTMPKLL			82		
I15	MTEENQTVISQFLLLFLPIPSEHQHLYFALFLSMYLTTVLGNLIIILHLDSH	LHTPMYFFL	SNLSFSDLCFSSVTMPKLL			82		
		3	4					
F3	----VNIQTQNNVITYAGCITO	IYFFLLFVELDNFLLTIMAYDRYVAIC	CHPMHYTVIMNYKLCGFLVLVSWIVSVLHALFQS	LMM		163		
F5	----ANHILGSQAISFS6CLTQLYFLAVFGNMNDNFLLAV	MSYDRFVAIC	HPLHYTTKMTRQLCVLVLVGSWVVANMNCLHILLM			163		
F6	----ATFAPRGGVISLAGCATQMYFVFLSGCTEYFLLAY	MAYDRYLAIC	LPLRYGGIMTPGLAMRLALGWSLCGFAITVPATLI			166		
F12	----VNIYTQSKSITYEDCISOMCVFLYFAELGNFLAV	MAYDRYVAIC	HPLCYTVIYNHRLCILLLLLLSWVISIFHAFIQSLIV			164		
I3	----QNMRSQDTSIPIYGGLCAQTYFMVFGDMESFLLVA	MAYDRYVAIC	FPLHYTSIMSPKLCTCLVLLLWMLTTSHAMMHTLLA			161		
I7	AGFIGSKENHGQLISFEACMTQLYFFFGLGCTECVLLAV	MAYDRYVAIC	HPLHYPVIVSSRLCQMAAGSWAGGGFGISMVKVFLI			168		
I8	----QNIQSQVPSISYAGCLTQIFFFLFGFLGNFLLVAMAYDRYVAIC	FPLHYTNIMSHKLCCLLVLVFWIMTSSHAMMHTLLA				161		
I9	----QNMQSQVPSIPYAGCLQIYFFMFVFGDMESFLLVA	MAYDRYVAIC	FPLHYMSIMSPKLCVSLLVLSWVLTTFHAMLHTLLM			163		
I14	----QNMQSQVPSISYTGCLTQLYFFFGLGDMESFLLVA	MAYDRYVAIC	FPLRYTTIMSTKFCASLWLLWMLTMTHALIHTLLI			163		
I15	----QNMQSQVPSIPFAGCLTQLYFADLESFLLVA	MAYDRYVAIC	FPLHYMSIMSPKLCVSLLVLSWVLTTFHAMLHTLLM			163		
		5	6					
F3	LALPFCTHLEIPHYFCEPNQVIQLTCSDAFLNDLVIVFTLVLLATVPLAGIFY	SY	FKIVSSICAISSVHGKYKA	FSTCASHLSVV		248		
F5	ARKSFCADNMIPHFFCDGTPLLKLS	CSDT	THLNELMILTEGAVVMVTPFVCILISY	I	HITCAVLRVSSPRGGWKS	FSTCGSHLAVV		248
F6	ARLSFCGSRVINHFFCDISPWIVLSC	CTDT	QVVELVSFGIAFCVILGSCGITLV	SY	AYIITTTIKIPSARGRHRA	FSTCSASHLTVV		251
F12	LQLTFCGDKIPHFFCDLNQSLQTC	SDNFP	PSHLLIMNLPVYMLAAISFSGLY	SY	FKIVSSIHSISTVQGKYKAF	FSTCASHLSIV		249
I3	ARLSFCENNYYLNFFCDLFVLLKACSDTYINELMIFIMSTLLIIIPFLIVM	CTDMSTAEL	DFVLAIFLGGPLSVTGASY	Y	ARISSISLKVPTQGICKVF	FSTCGSHLSVV		246
I7	SRLSYCPNTINHFFCDVSPLLNLKACSDTYVNEELMIHIMGVIIIVIPFVLI	L	VIMSYMAITGAVMRIPSAAGRHKAF	FSTCASHLTVV			253	
I8	ARLSFCENNYYLNFFCDLFVLLKACSDTYVNEELMIHIMGVIIIVIPFVLI	SY	AKISSLKVPTQSIHKVF	FSTCGSHLSVV			246	
I9	ARLSFCEDSVIPHYFCDMSTLLKACSDTHDNELAIFI	LGGPIVLPFLIIIV	SY	ARIVSSIFKVPPSSQSIHKAF	FSTCGSHLSVV		248	
I14	ARLSFCEKNVILHFFCDISALLKLCS	CSDIYVNEELMIYILGG	LIIIPFLIIIV	SY	YRIFFSILKFPSIQDIFYKV	FSTCGSHLSVV		248
I15	ARLSFCADNMIPHFFCDISPLLKLS	CSDT	HNELVIFVMGGLVIVIPFVLI	SY	ARVVASILKVPSVRGIHKIF	FSTCGSHLSVV		248
		7						
F3	SLFYCTGLGVYLSAANNSSQASATASVMYTVVT	PMVNPF	YSLRNKDVKSVLKTLCEEIRSPPSLLHFFLVLCHLPCFIFCY			333		
F5	CLFYGTIVIAYVFNPSSSHLAGRDMAAAVYAVY	PMLNPF	YSLRNSDMKAALRKVLAMRFPBKQ			313		
F6	LIWYGSTIFLHVRTSVESSLDTKAITYVLNTIVT	PVLNPF	YTLRNKDVKEARLRTVKGK			311		
F12	SLFYSTGLGVYYSSAVVQSSHAAASAVMYTVVT	PMLNPF	YSLRNKDVKRALERLLEGNCVHHWTG			317		
I3	SLFYGTIIGLYLCAGNNSTVKEMVAMM	YTVVT	PMLNPFYSLRNRMKRALIRVICS	SMKITL		310		
I7	IIFYAASIFIYARPKALSAFDNKLV	LVS	YAVIVPLFNPIIYCLRQDVKRALRRTLHLAQDQEANTNKGS	KIG		327		
I8	SLFYGTIIGLYLCPSGNFSLKGSAMAMM	YTVVT	YTVVT	PMLNPFYSLRNRMKQALIRYTC	CSKKISLPW		312	
I9	SLFYGTIIGLYLCPSANNSTYKETVMSL	MYTMV	YTVVT	PMLNPFYSLRNRDIKDALEKIMCKKQIPS	F		314	
I14	TLFYGTIFGILCPG	GNNSTYKE	IYVPLFNPIIYCLRQDVKRALIRVICT	KKISL			312	
I15	SLFYGTIIGLYLCPSANNSTYKETV	MAMM	YTVVT	PMLNPFYSLRNRMKRALIRVICKKISL			314	



# 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<sup>\*†</sup>**

**\*Department of Biochemistry and Molecular Biophysics**

**†Howard Hughes Medical Institute**

**College of Physicians and Surgeons**

**Columbia University**

**New York, New York 10032**

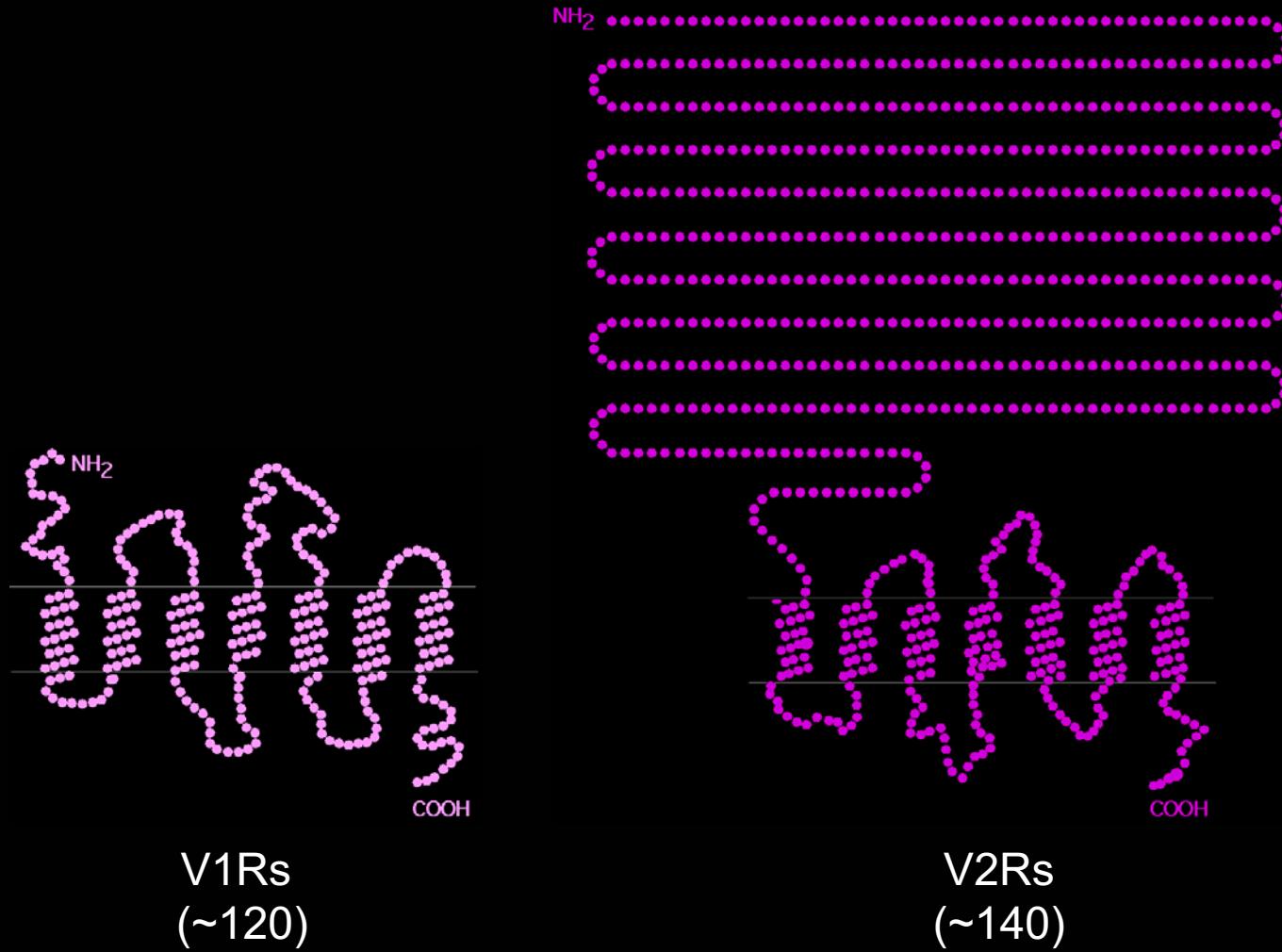
# THE OR GENE FAMILY IN HUMAN AND MOUSE

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

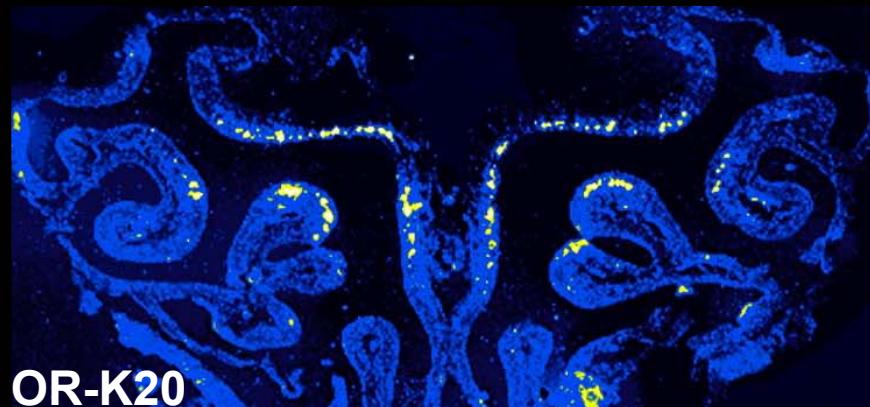
# CHROMOSOMAL LOCATIONS OF HUMAN GENES

✗

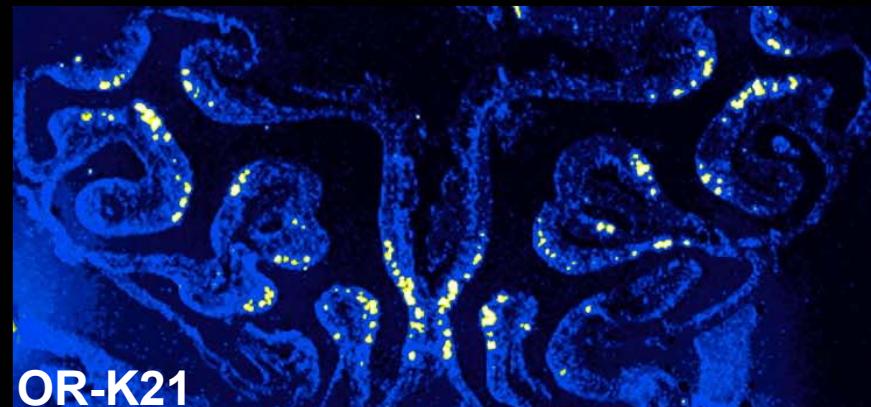
# CANDIDATE PHEROMONE RECEPTORS IN THE VOMERONASAL ORGAN



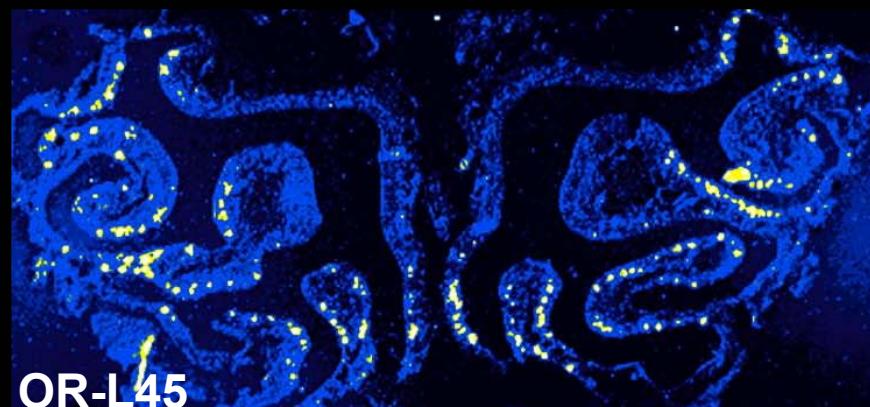
# PATTERNS OF OR GENE EXPRESSION IN OLFACTORY EPITHELIUM



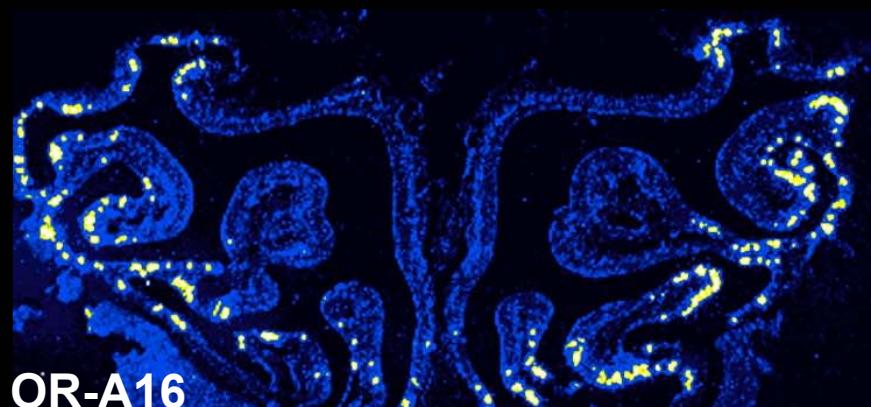
OR-K20



OR-K21

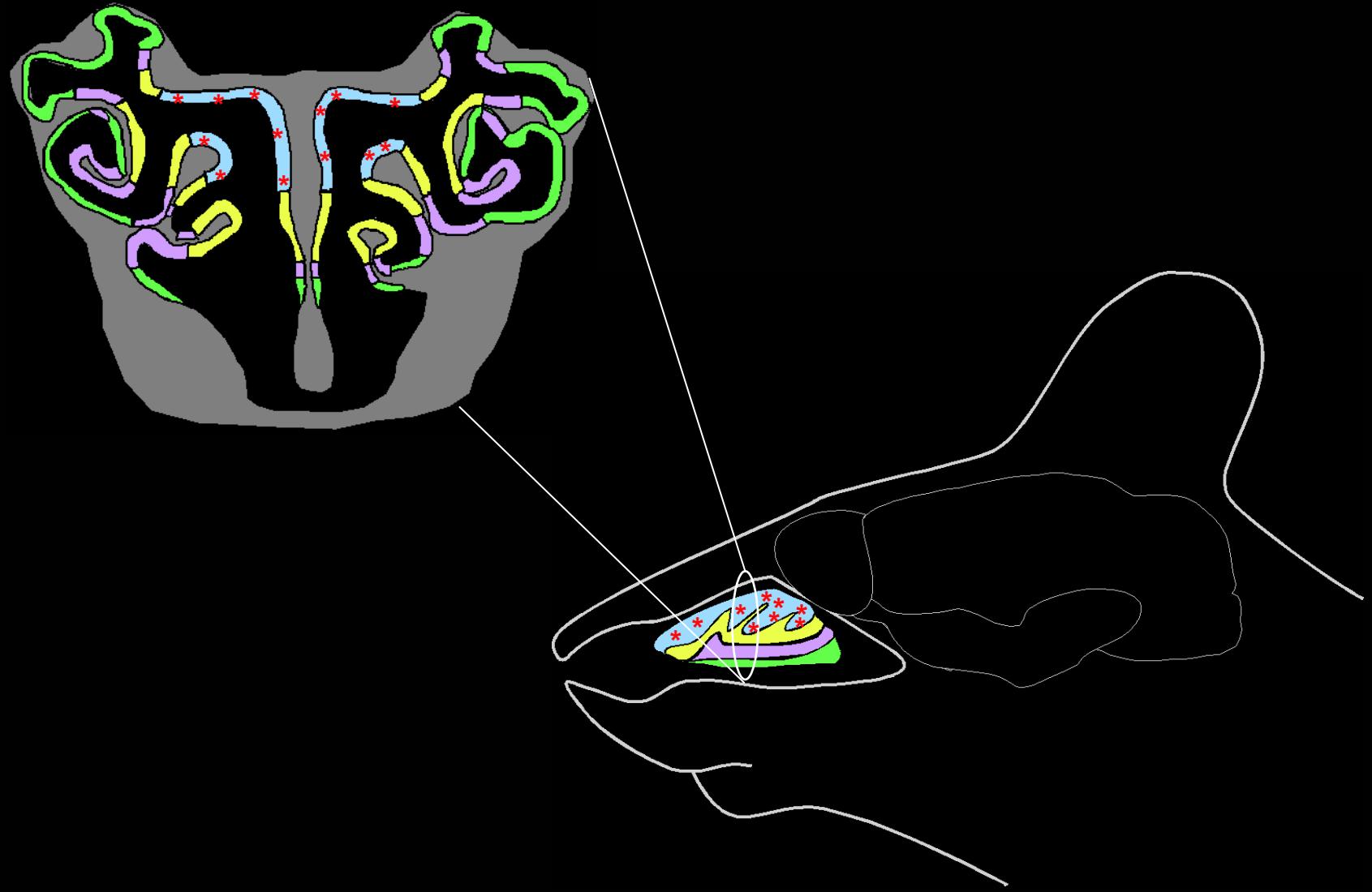


OR-L45

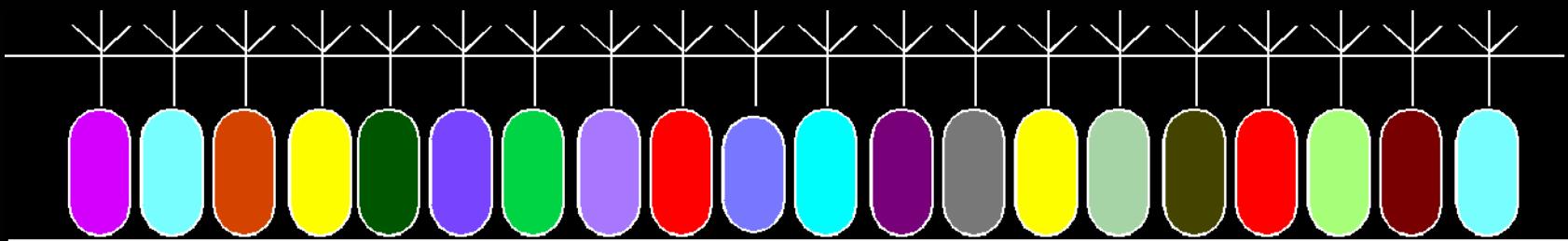


OR-A16

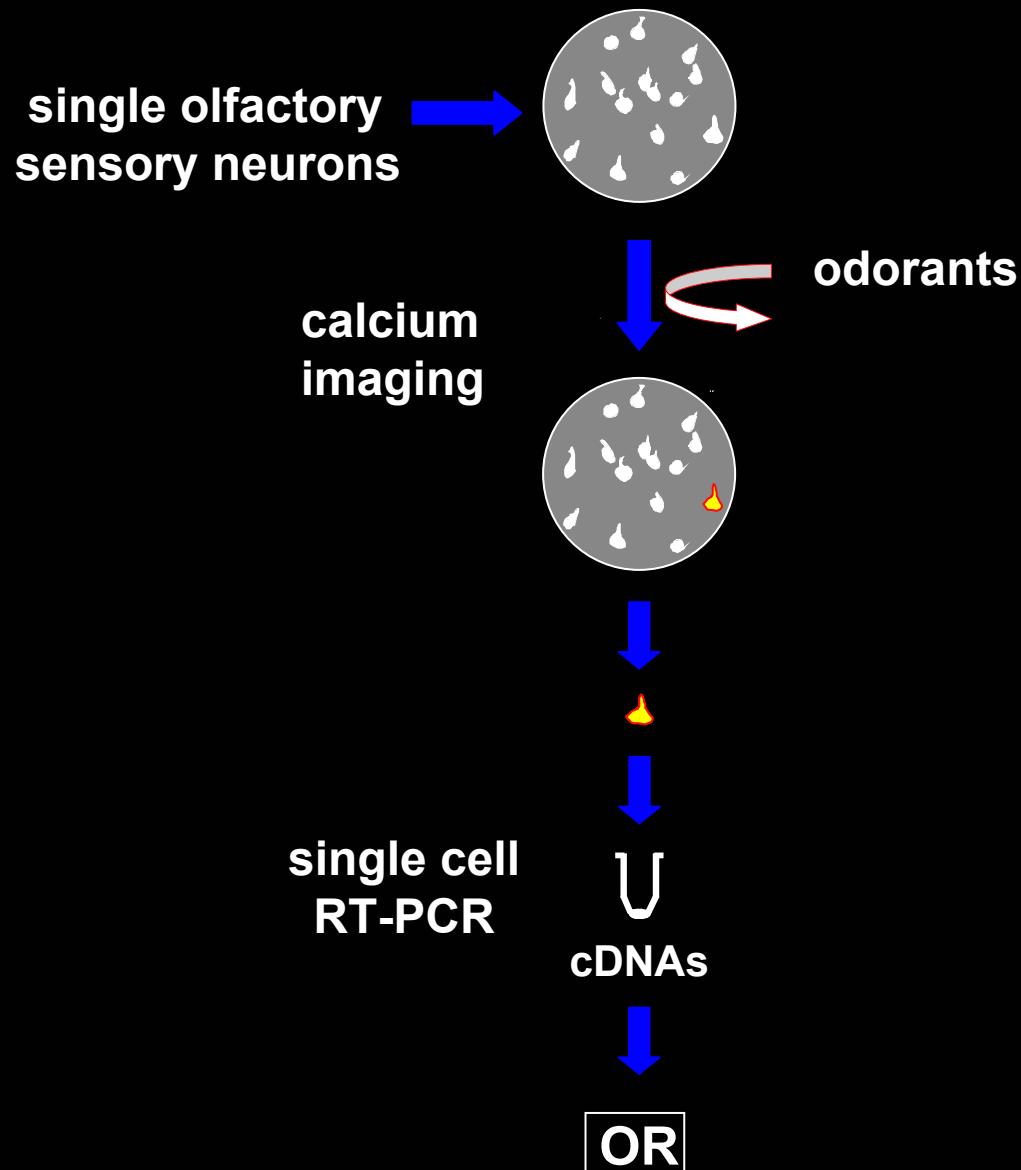
# EXPRESSION ZONES IN THE OLFACTORY EPITHELIUM



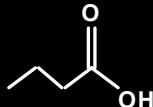
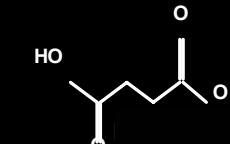
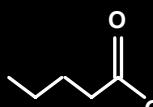
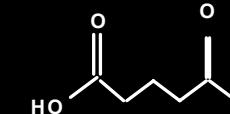
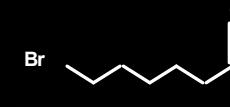
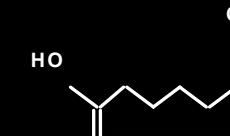
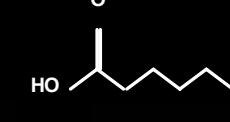
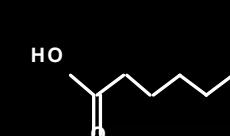
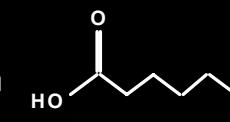
# OLFACTOORY EPITHELIUM: A MOSAIC OF NEURONS EXPRESSING DIFFERENT ORs



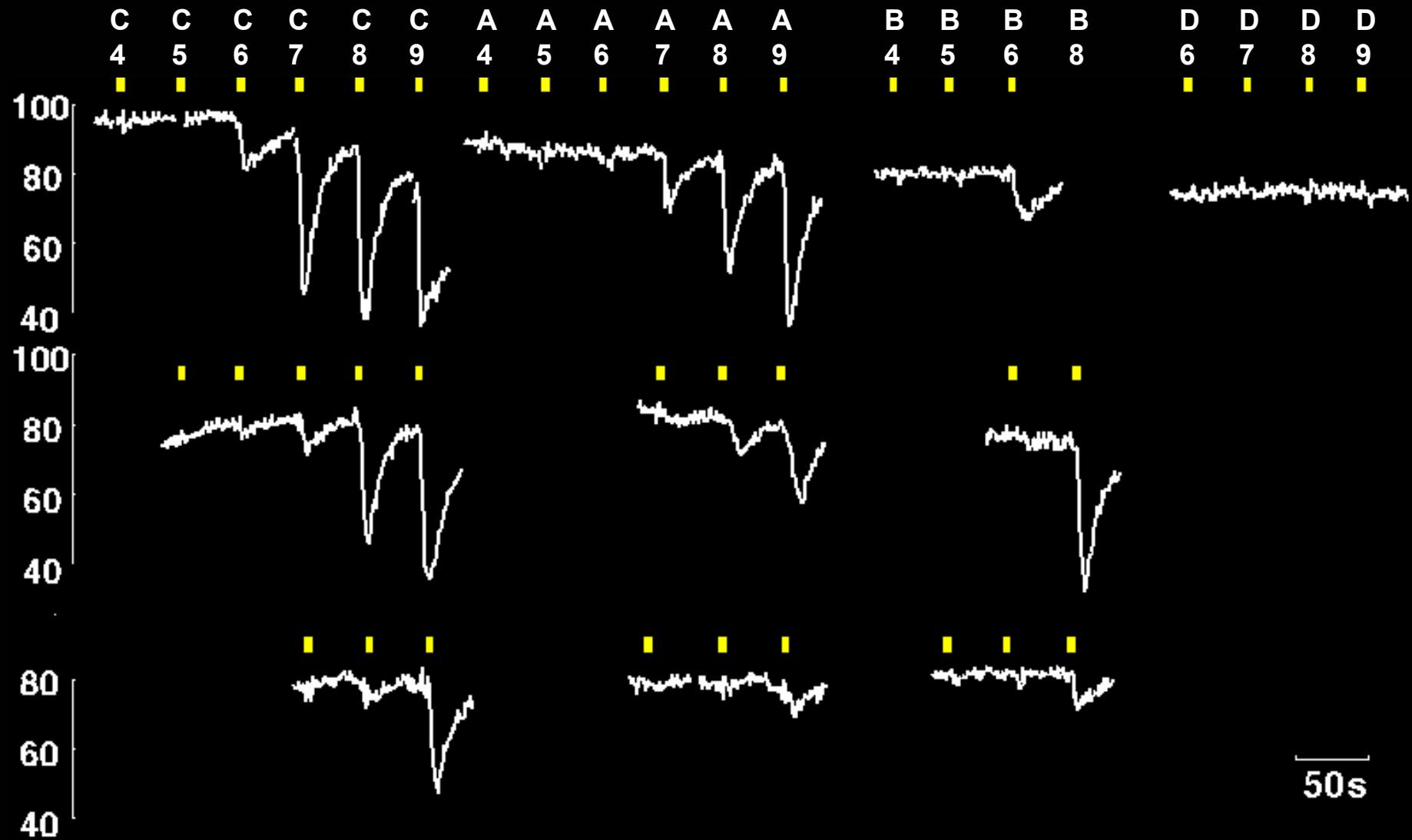
# IDENTIFICATION OF ORS FOR SPECIFIC ODORANTS



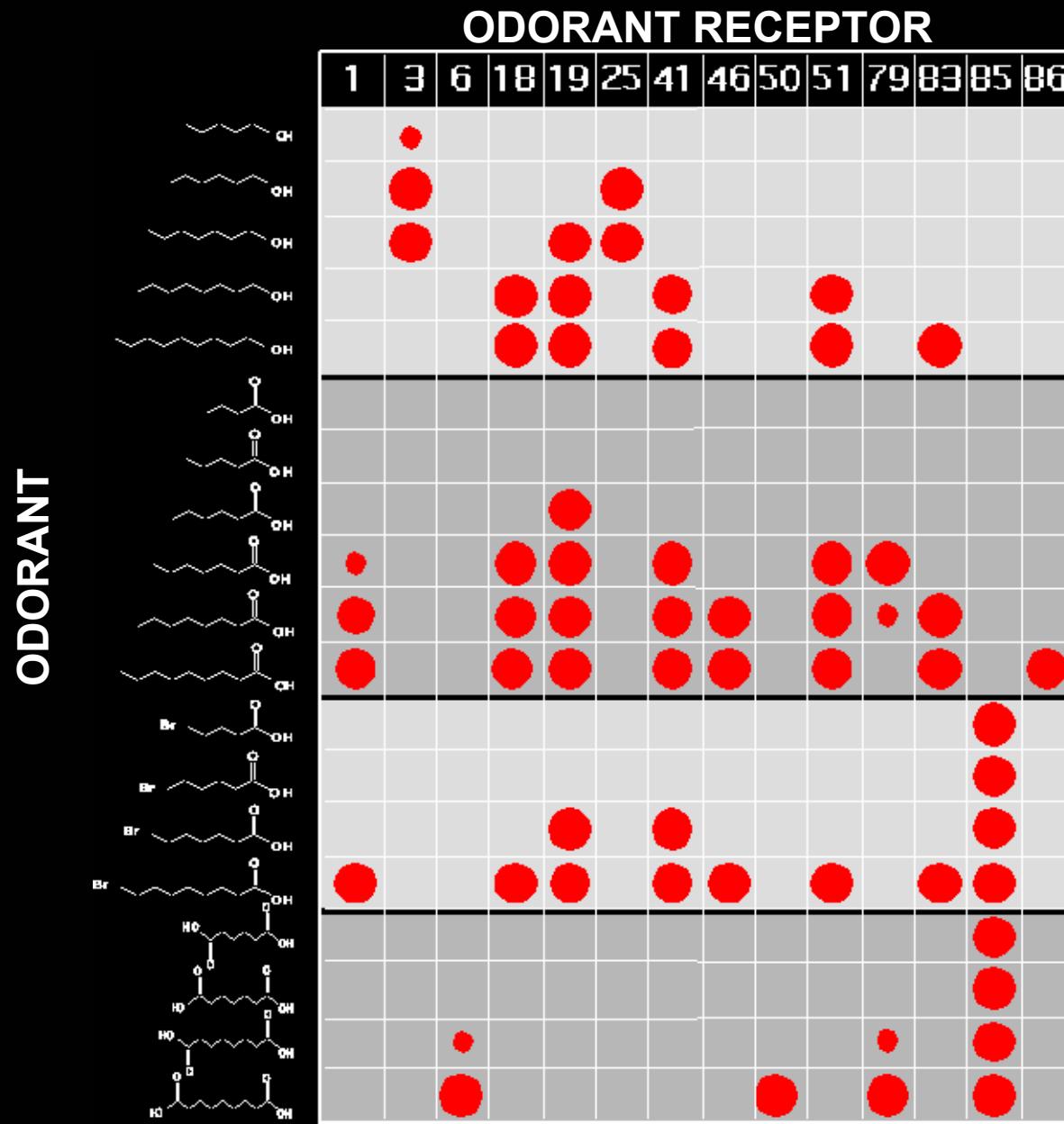
# TEST ODORANTS

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

# RESPONSES OF ONE NEURON TO ODORANTS



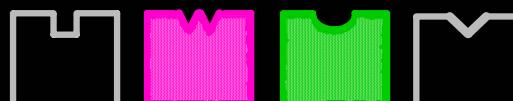
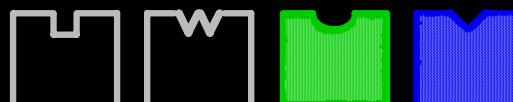
# ODORANTS ARE DETECTED BY COMBINATIONS OF ORS



# 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

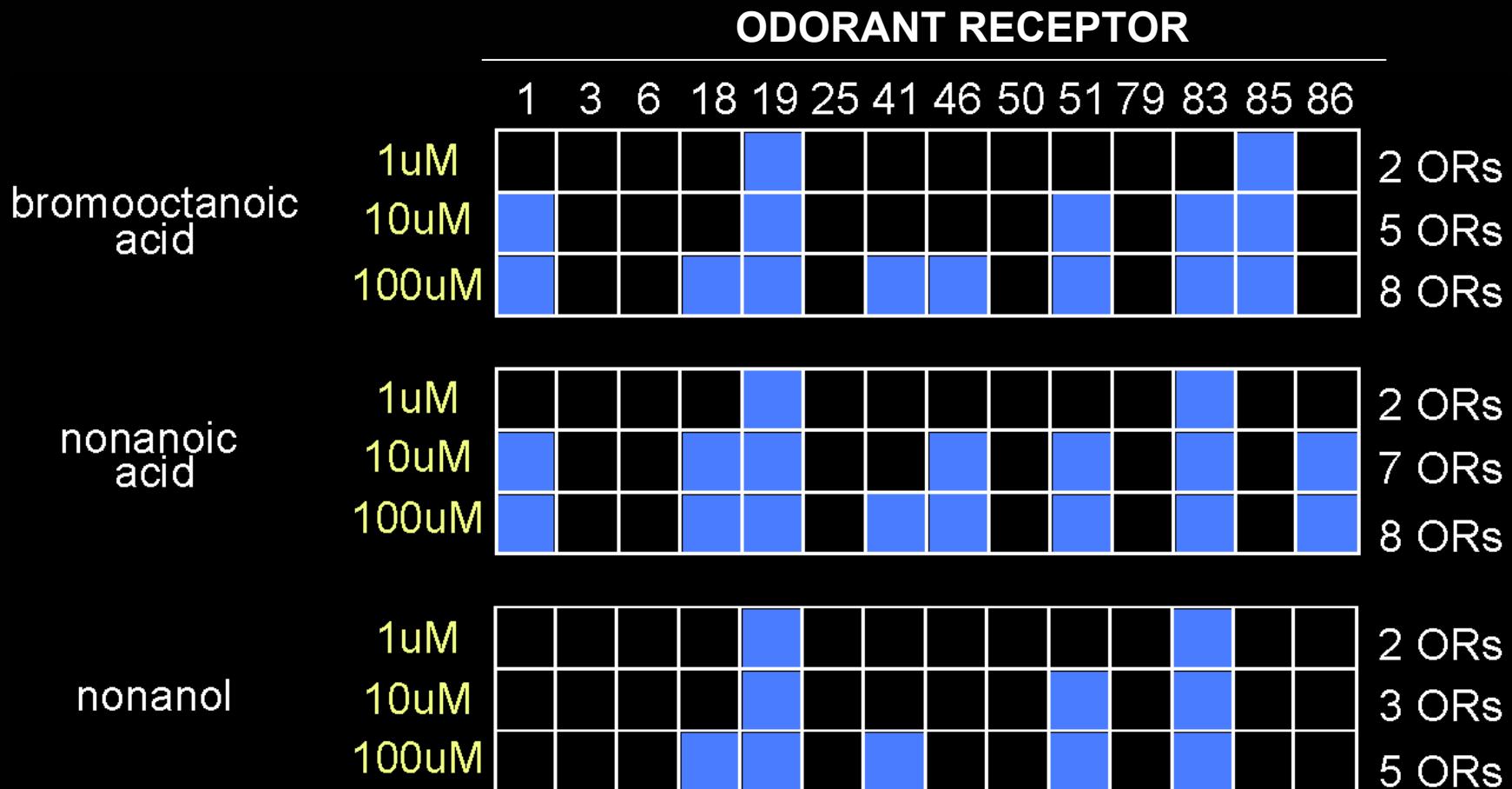
Hexanoic Acid					■										rancid, sour, goat-like
Hexanol		■				■									sweet, herbal, woody

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

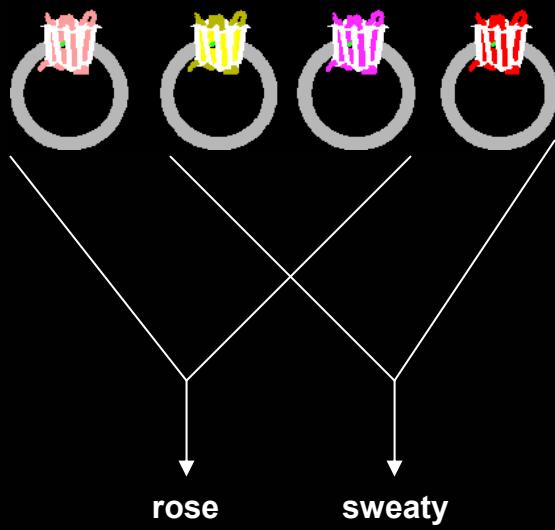
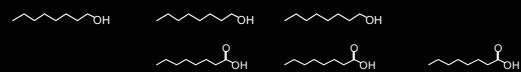
Octanoic Acid	■			■	■	■									rancid, sour, repulsive
Octanol				■	■	■									sweet, orange, rose

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

# RECEPTOR CODES: THE EFFECT OF CONCENTRATION

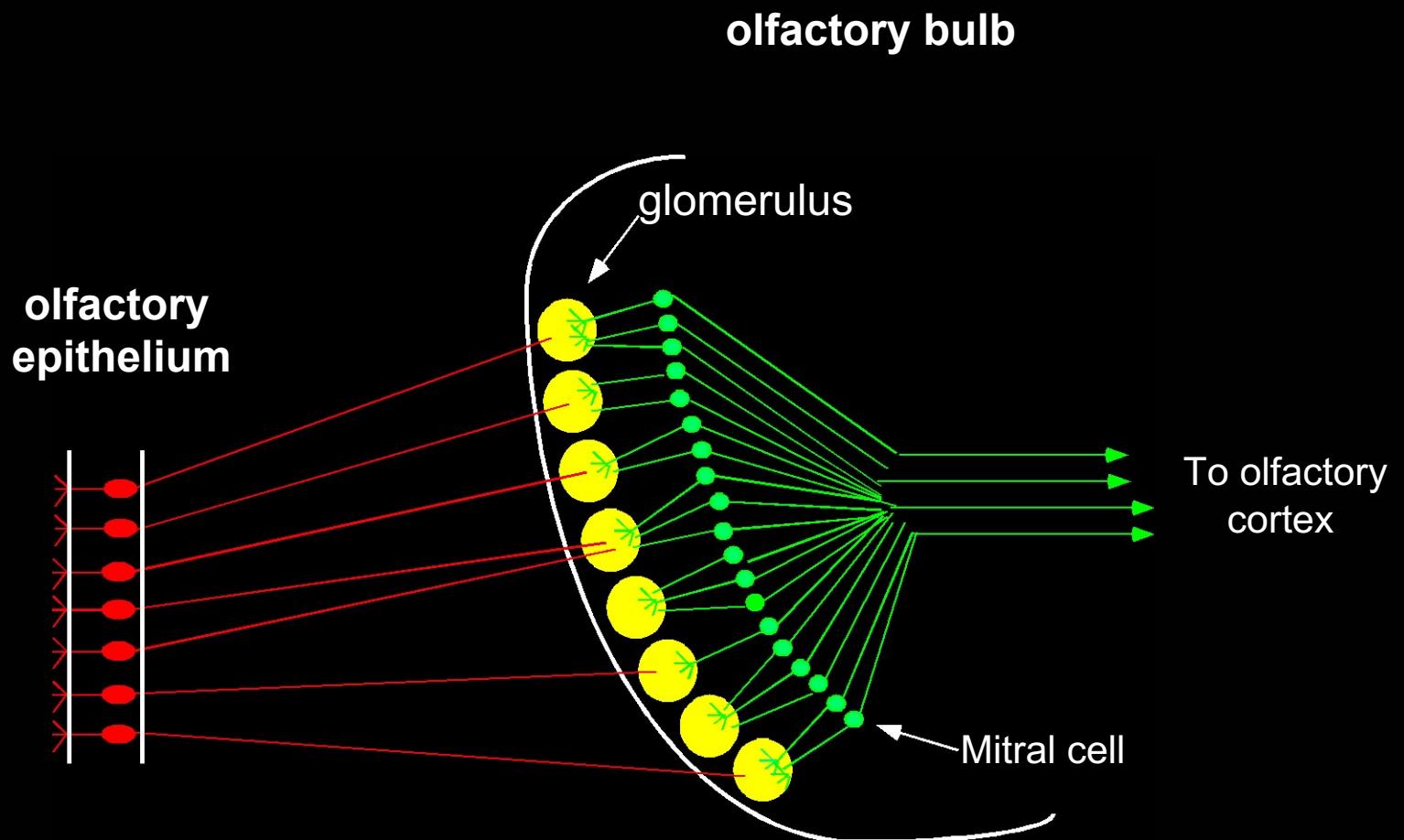


## ODORANTS

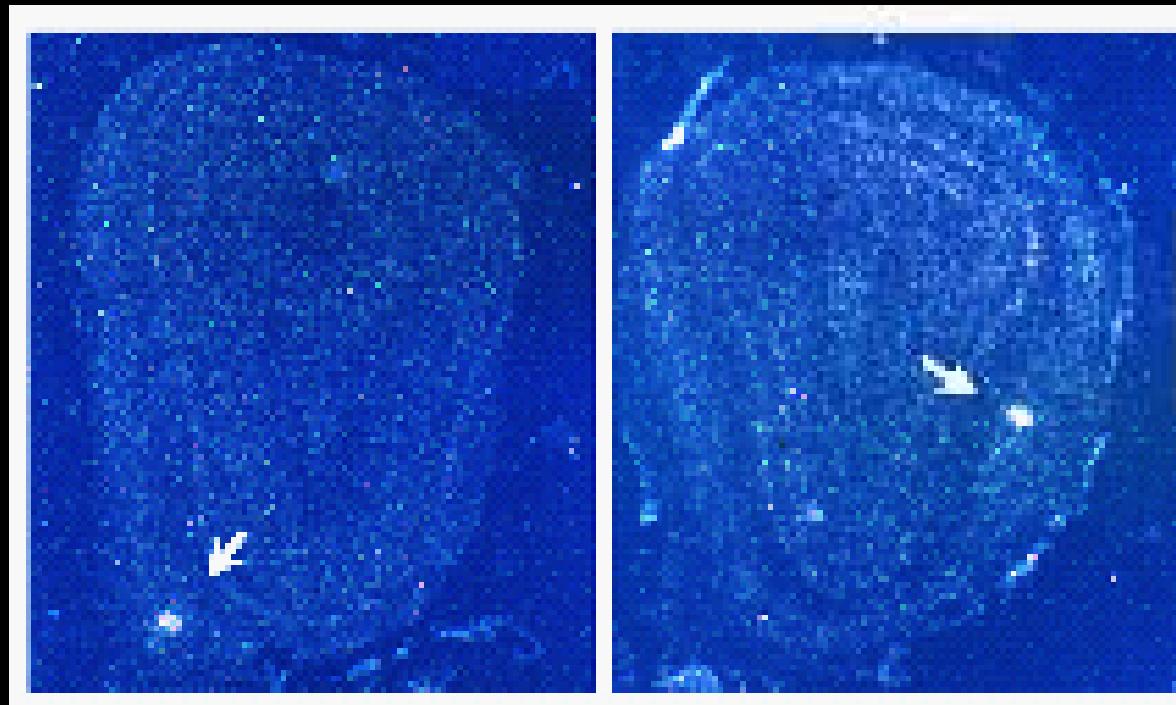


ODOR

# THE OLFACTORY BULB



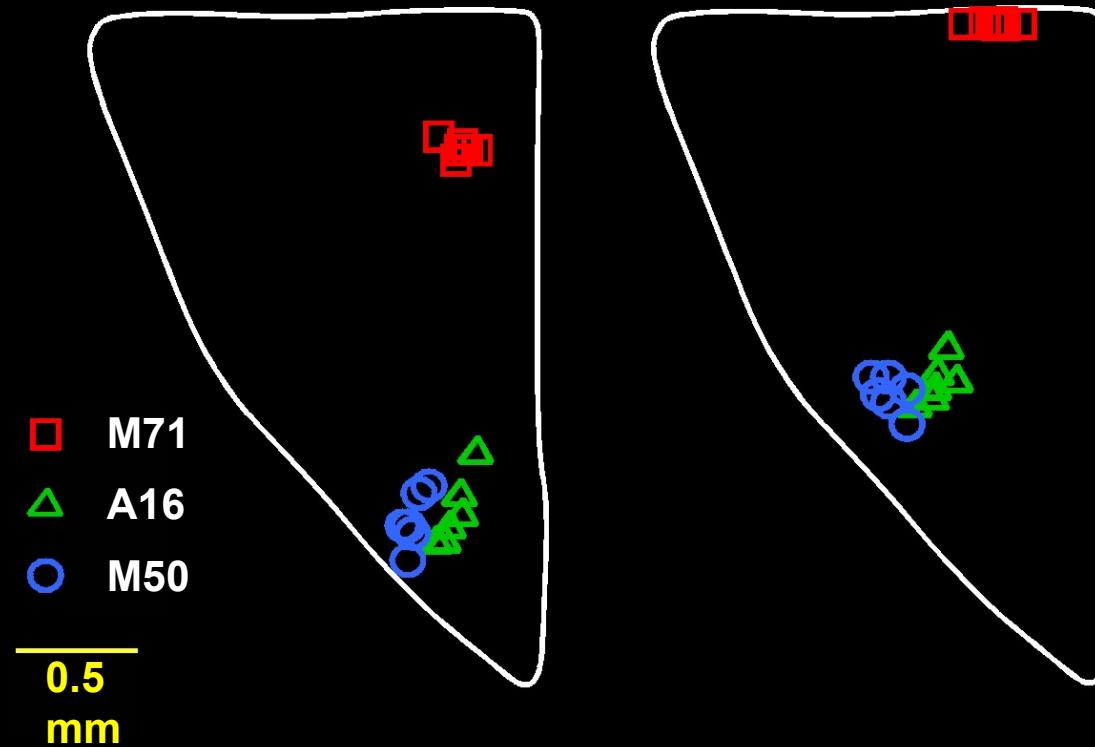
# AXONS OF NEURONS WITH THE SAME OR CONVERGE IN OLFACTORY BULB



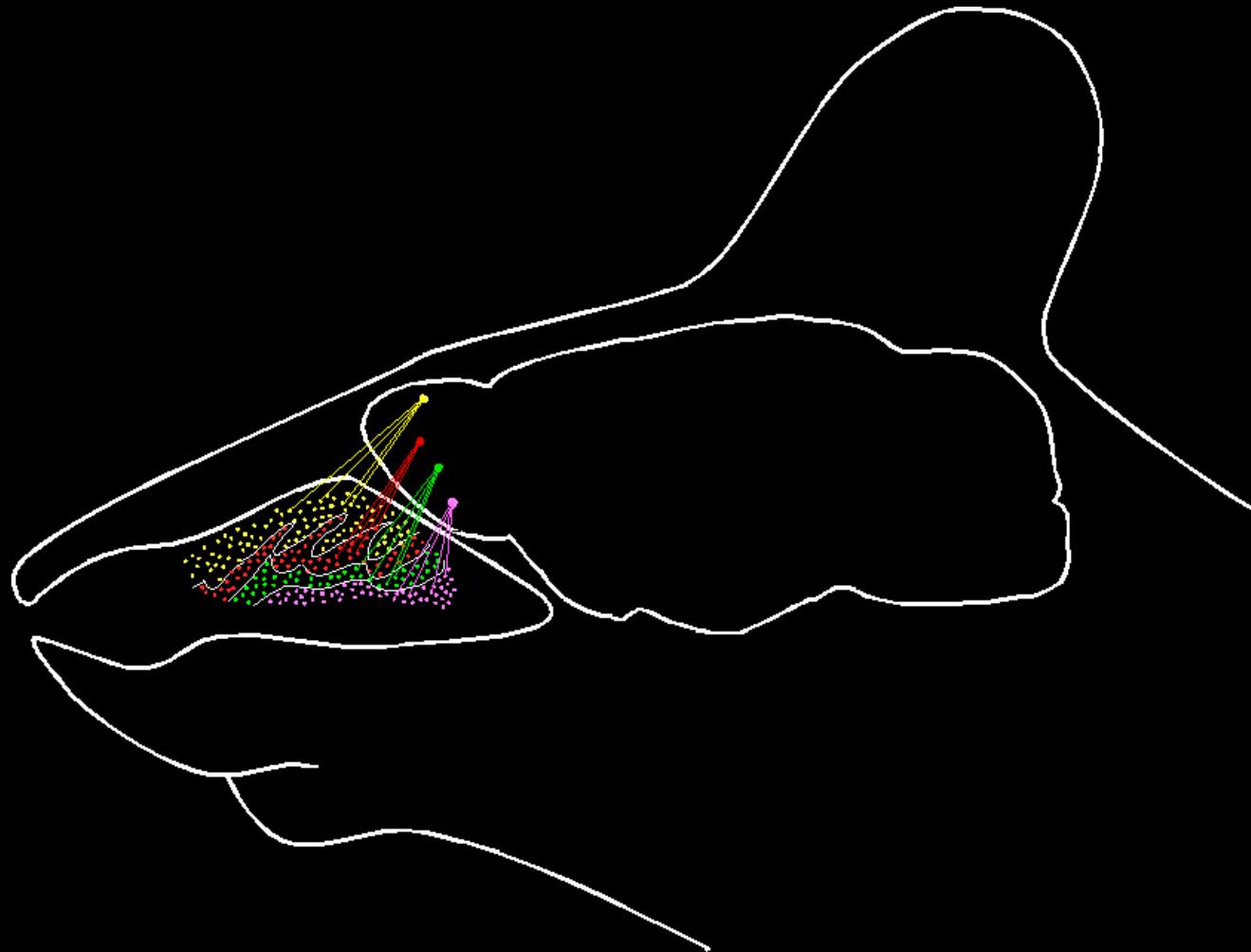
# OR-SPECIFIC GLOMERULI IN THE OLFACTORY BULB

medial  
olfactory bulb

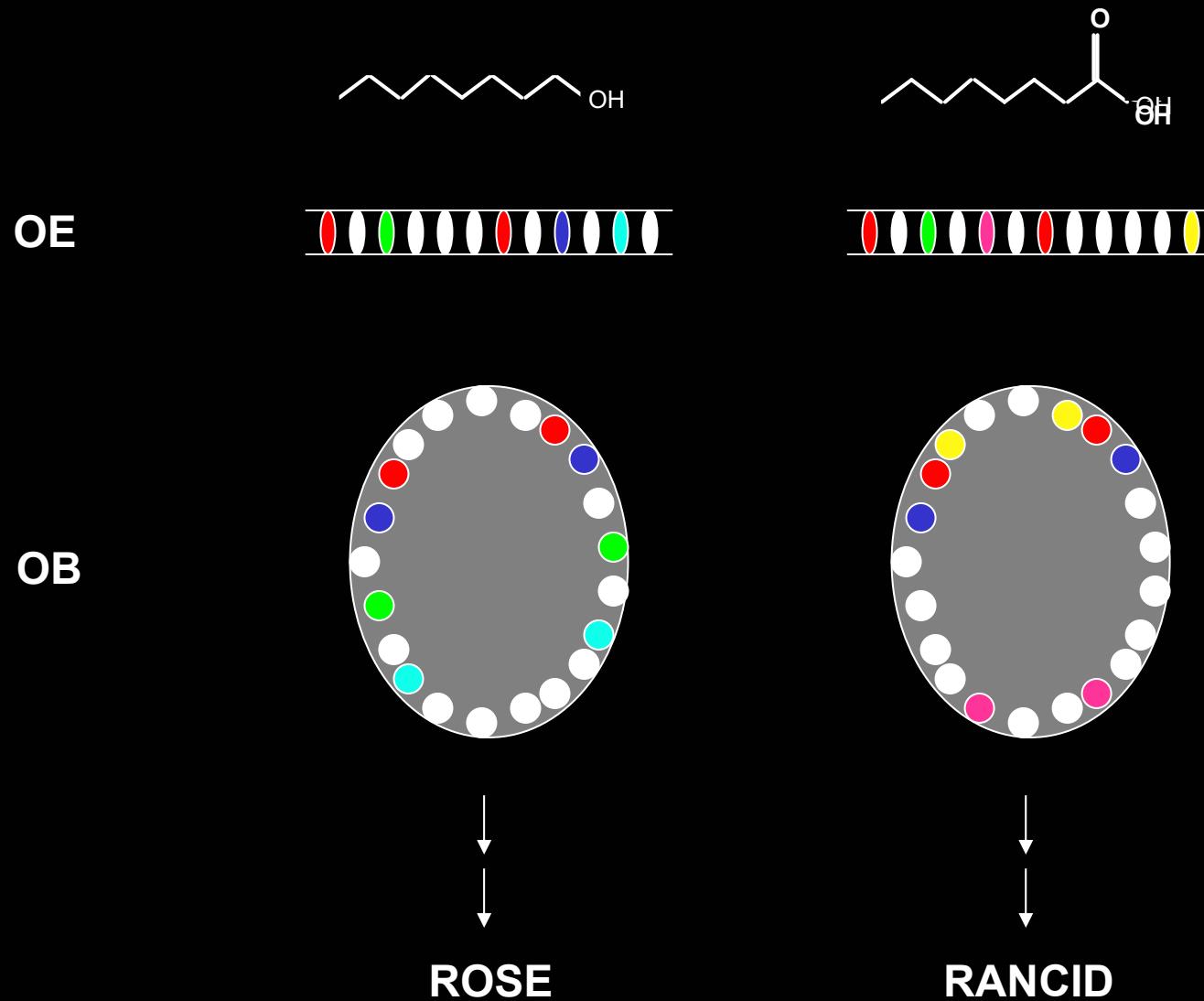
lateral  
olfactory bulb



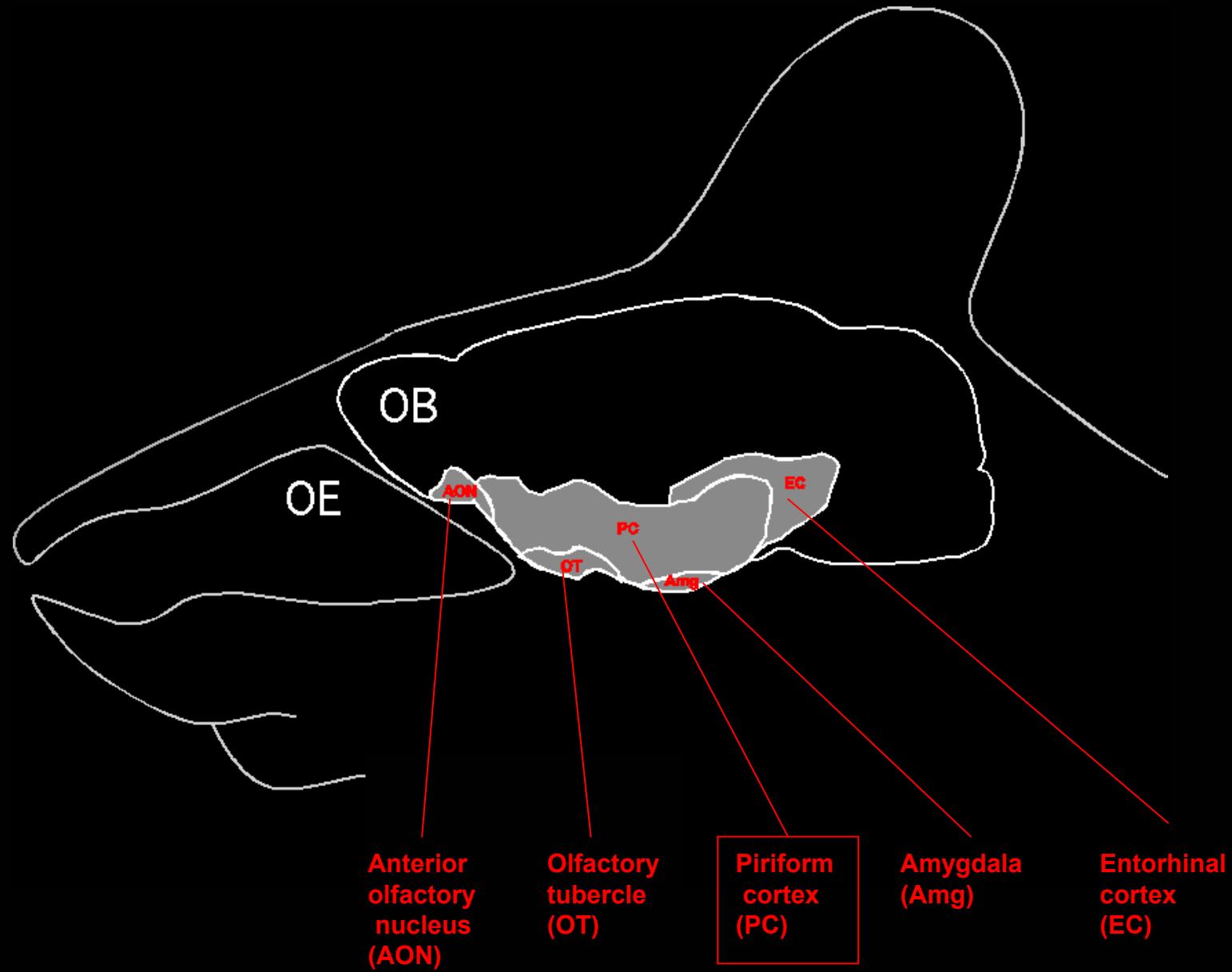
# A STEREOTYPED MAP OF OR INPUTS IN THE OLFACTORY BULB



# ODOR CODING IN OLFACTORY EPITHELIUM AND BULB



# THE OLFACTORY CORTEX

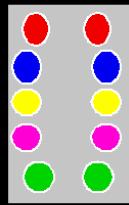


# HOW ARE OR INPUTS ORGANIZED IN THE CORTEX?

olfactory epithelium

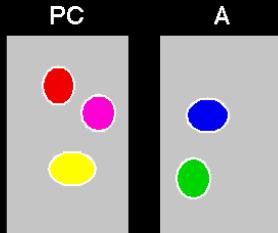


olfactory bulb

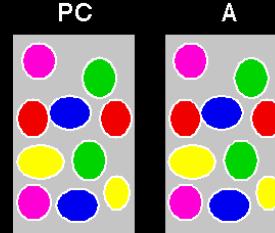


olfactory cortex

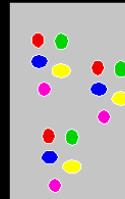
different areas receive inputs from different ORs



each area receives inputs from all ORs



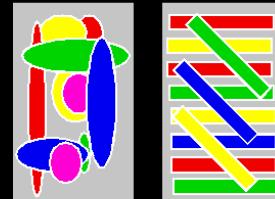
scattered



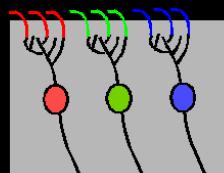
stereotyped



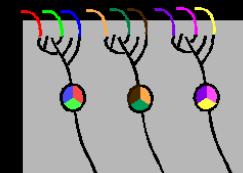
other



input from one OR



inputs from multiple ORs

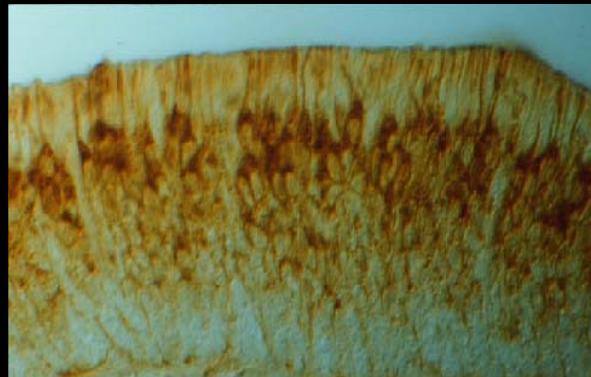


# BARLEY LECTIN: A GENETIC TRANSNEURONAL TRACER

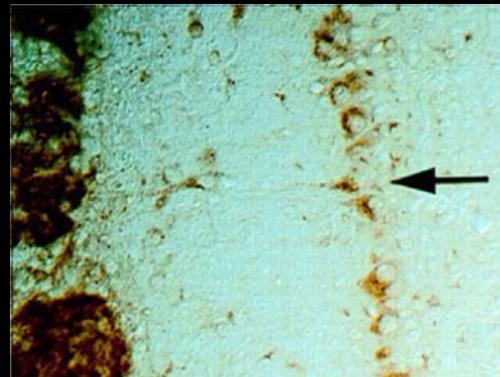


PompBL mice

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olfactory  
epithelium



olfactory  
bulb



olfactory  
cortex

# COEXPRESSION OF BL WITH A SINGLE OR GENE

**M5iBL mice**



(zone 1)



gene

M5 IRES BL



M5

BL

protein

**M50iBL mice**



(zone 4)



M50 IRES BL



M50

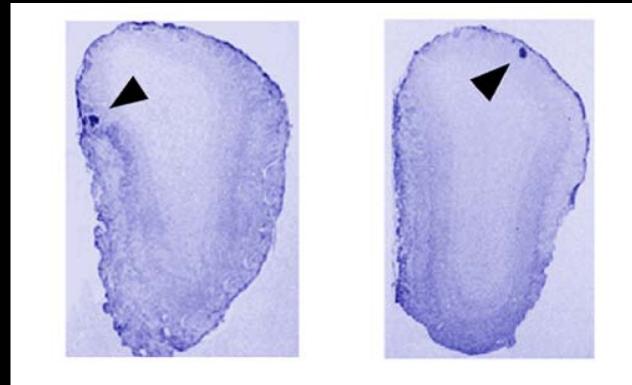
BL

# BL IN THE OLFACTORY EPITHELIUM AND OLFACTORY BULB

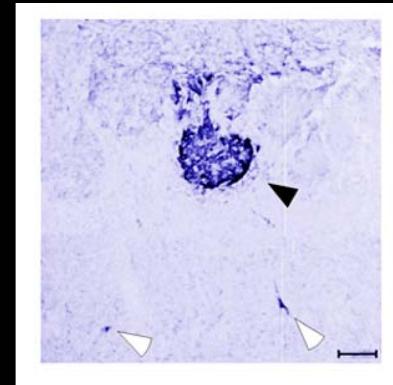
olfactory epithelium



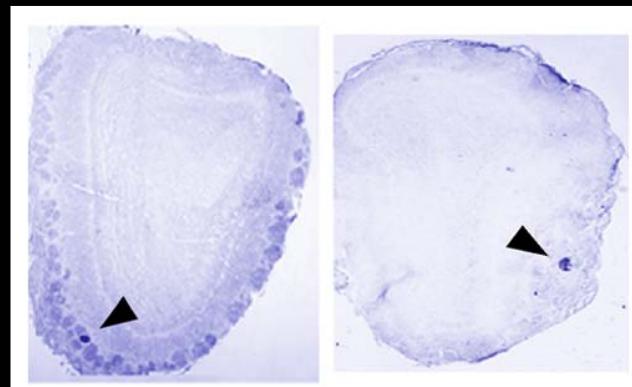
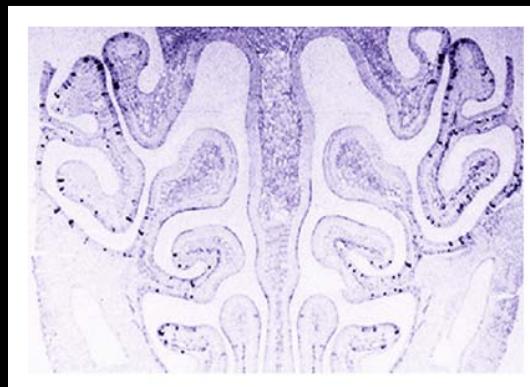
olfactory bulb



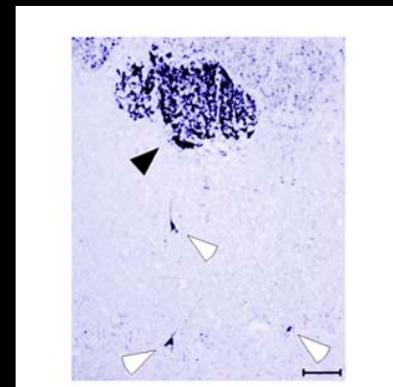
olfactory bulb  
relay neurons



M5iBL

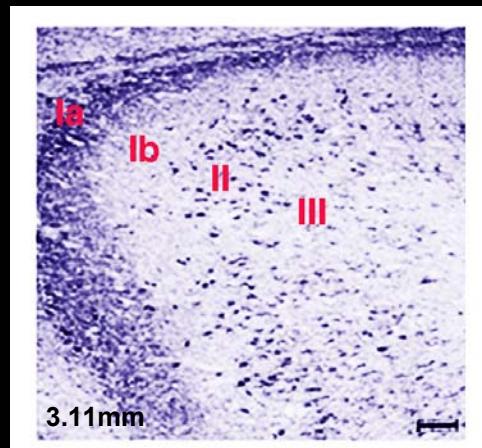


M50iBL

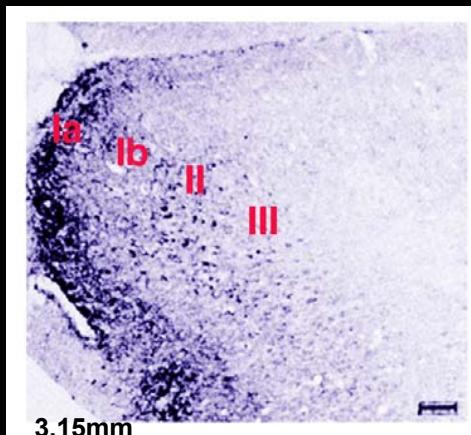


# BL IN OLFACTORY CORTEX

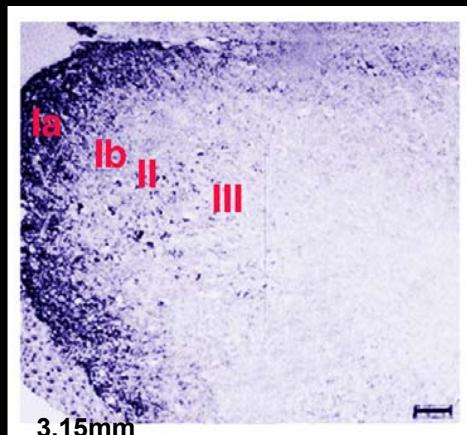
PompBL



M50iBL-#1

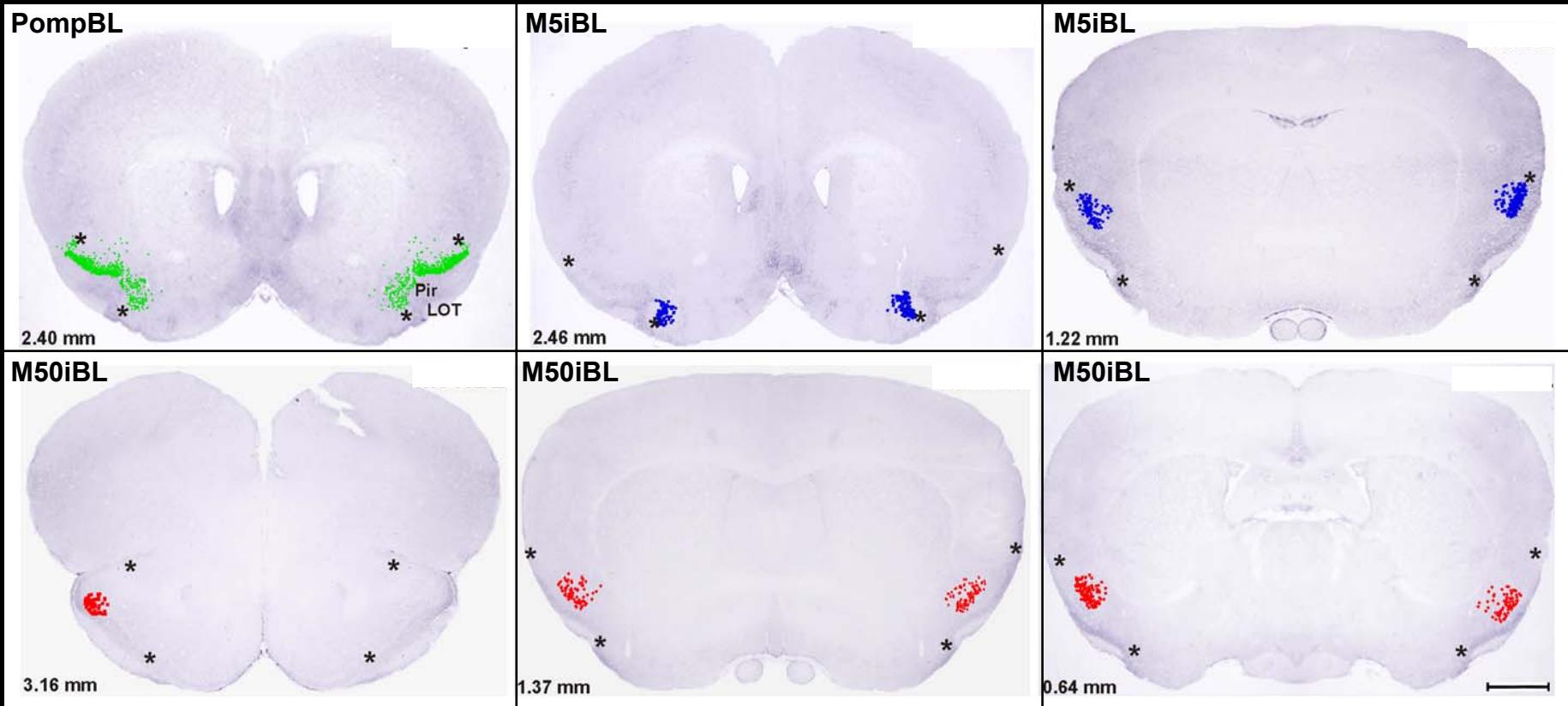


M50iBL-#2



# CLUSTERS OF BL+ CORTICAL NEURONS IN M5iBL AND M50iBL MICE

anterior piriform cortex

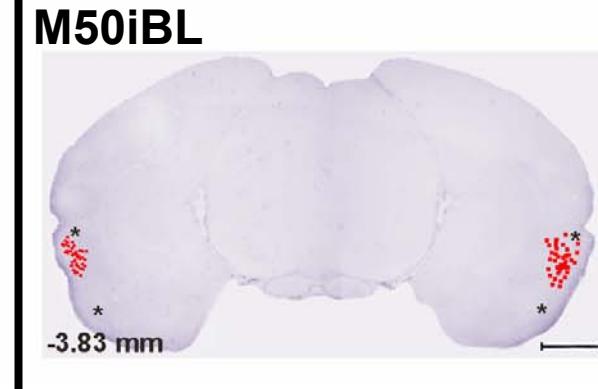
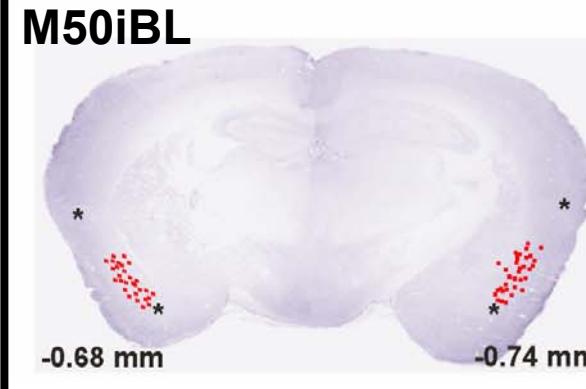
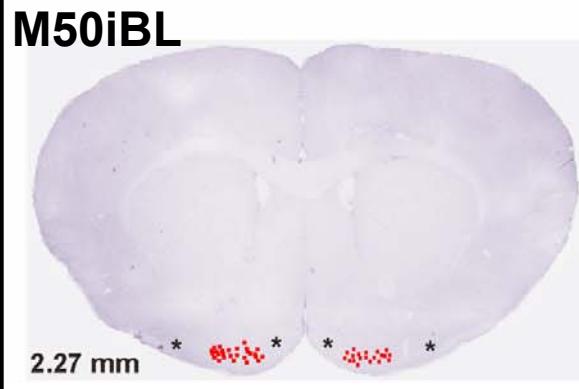
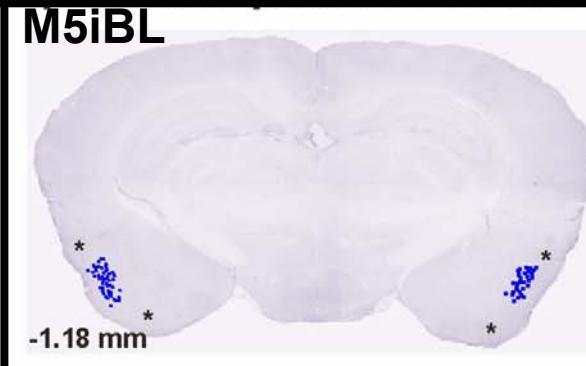
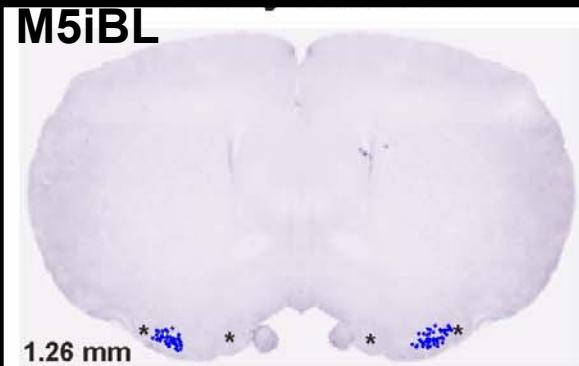


# CLUSTERS OF BL+ CORTICAL NEURONS IN M5iBL AND M50iBL MICE

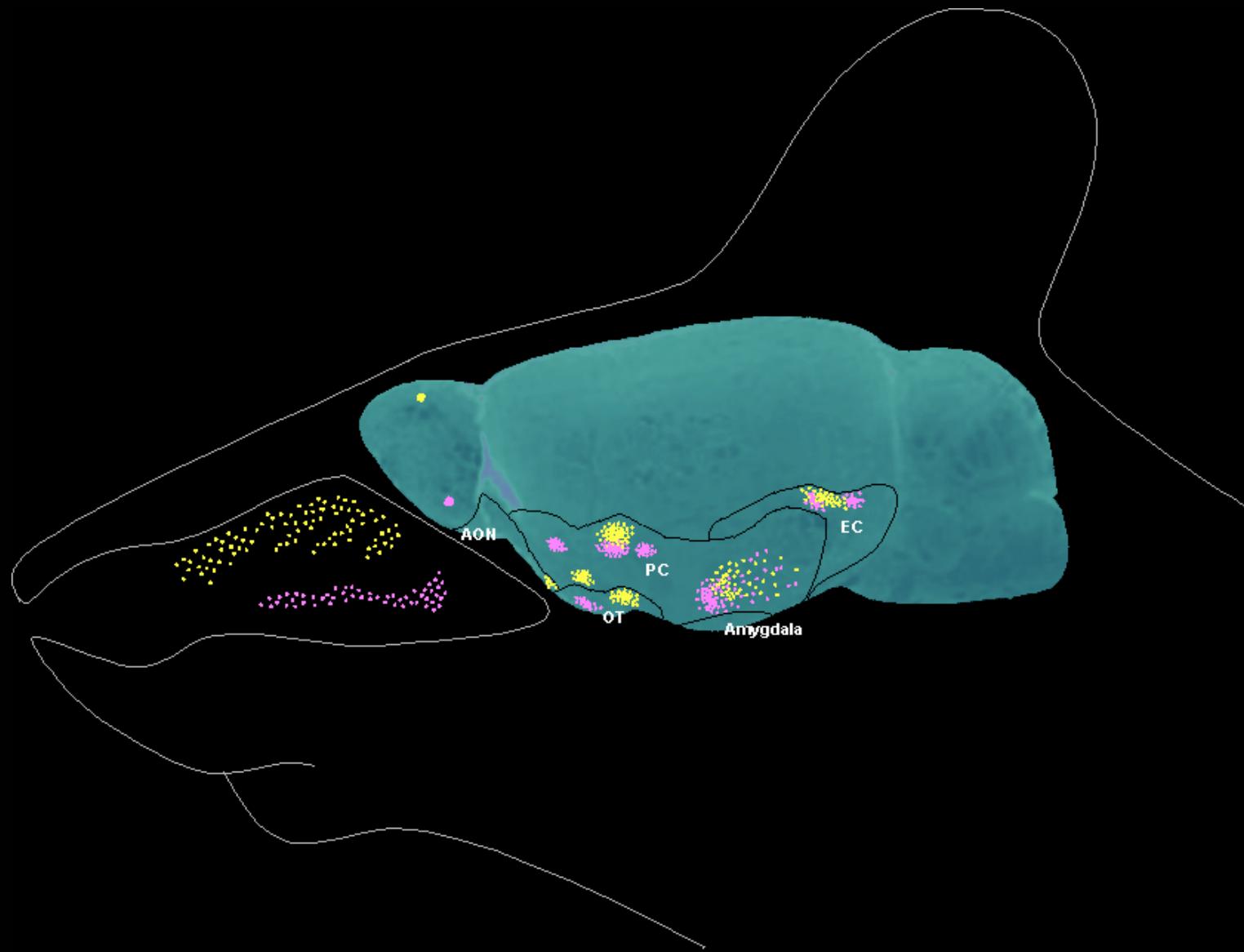
olfactory tubercle

posterior piriform cortex

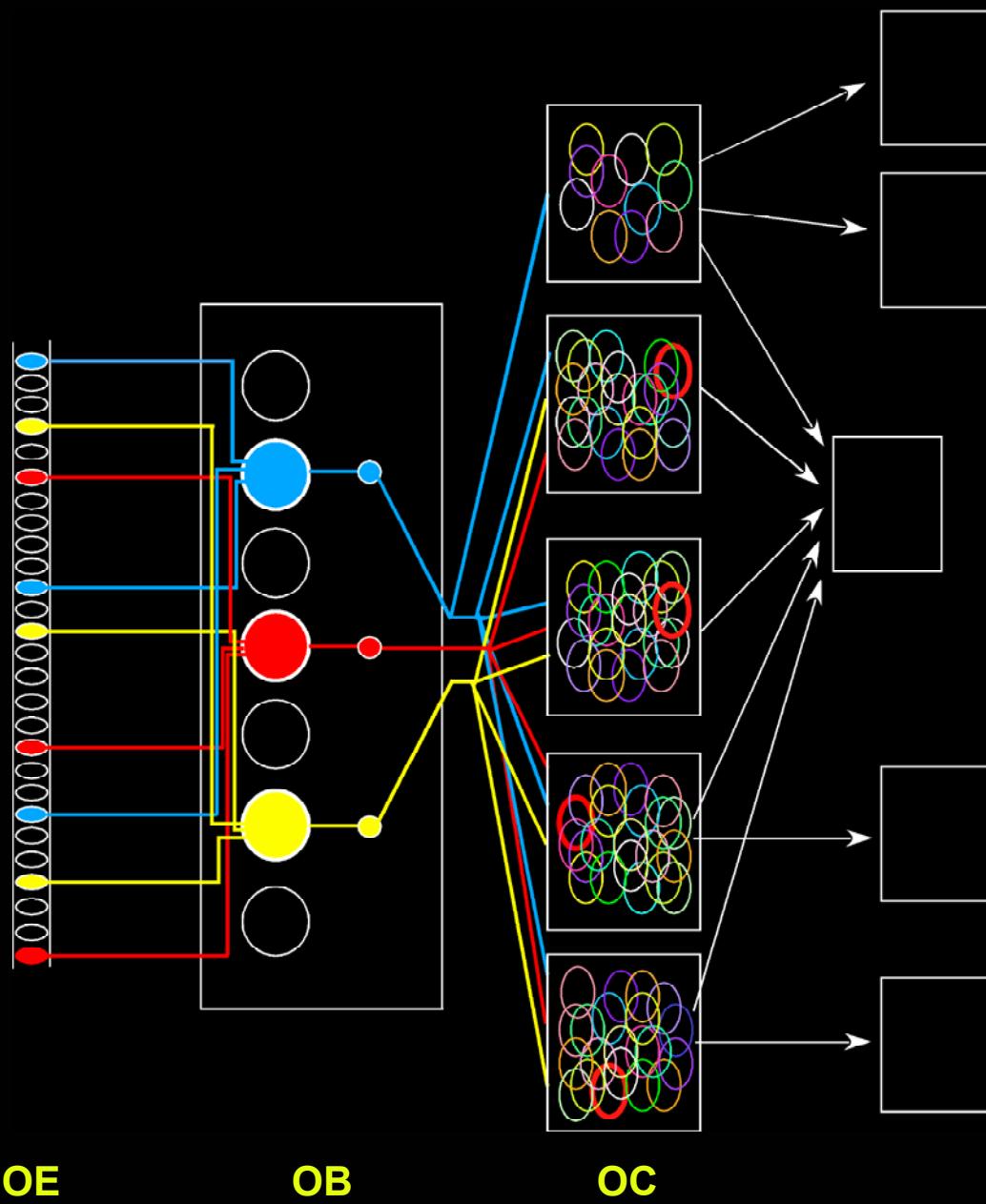
lateral entorhinal cortex



# 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%

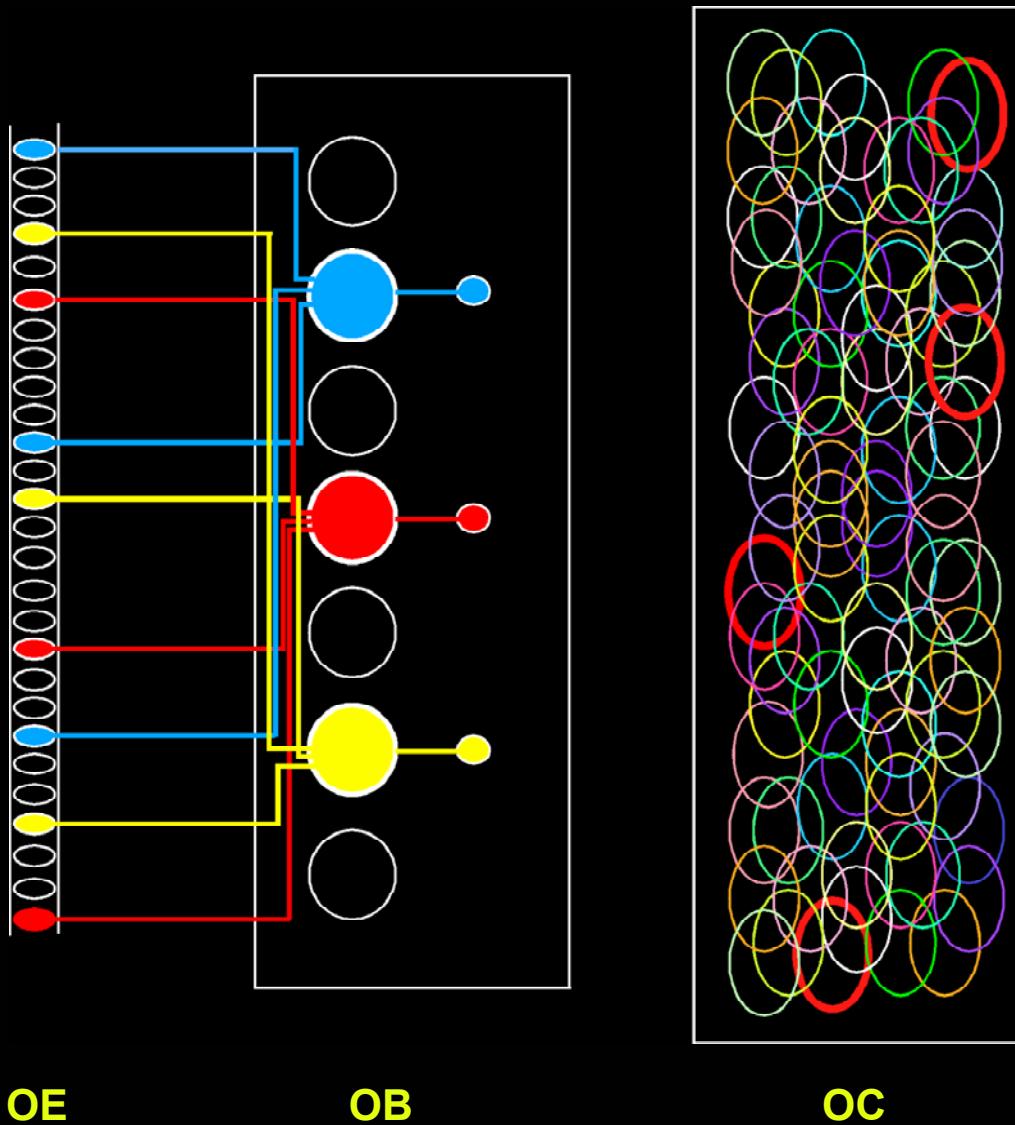
## NUMBER OF BL+ NEURONS

PompBL: 179,570  $\pm 3935$

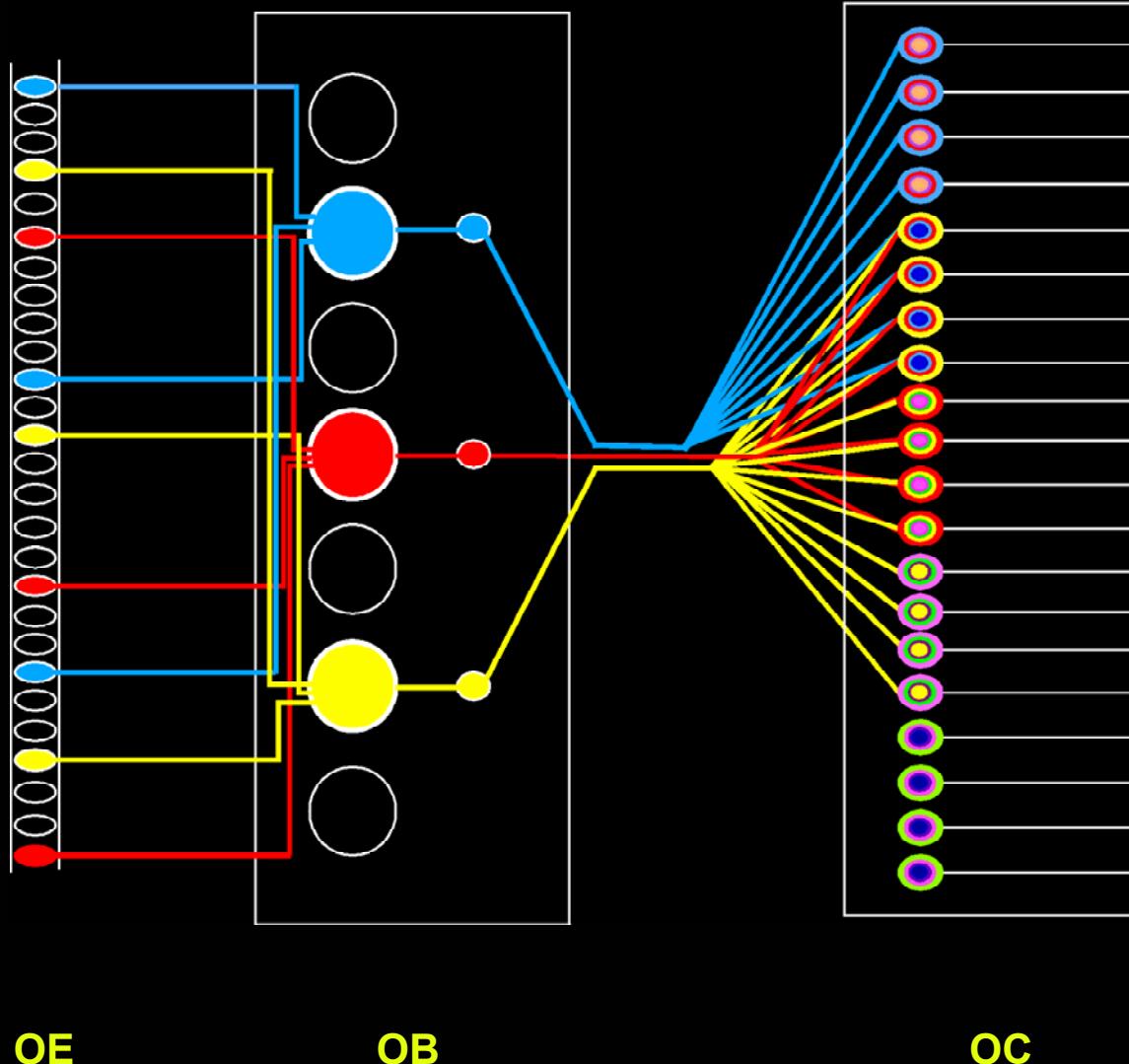
M50iBL: 4390  $\pm 179$  (2.4% of PompBL)

M5iBL: 6570  $\pm 217$  (3.7% of PompBL)

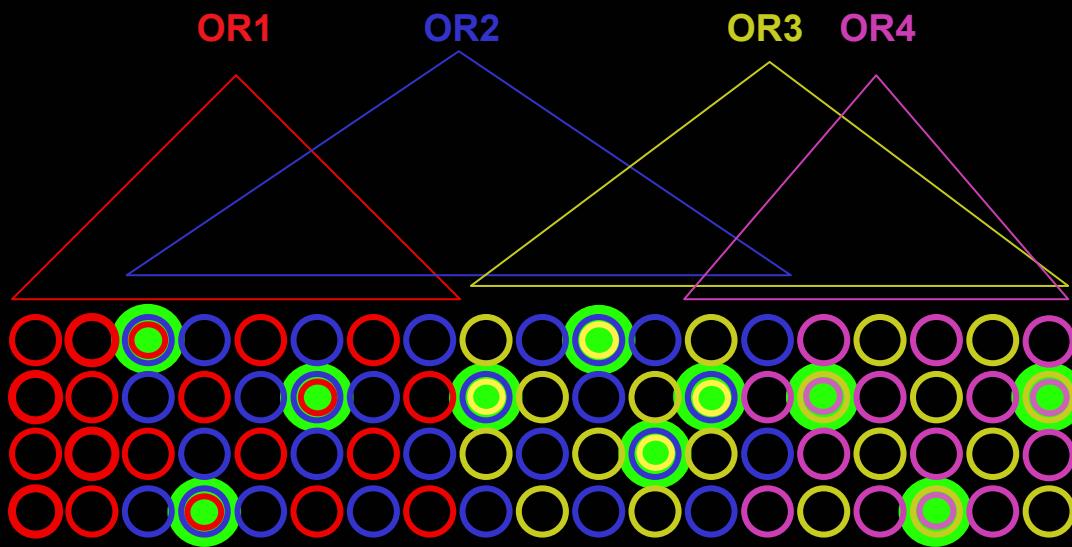
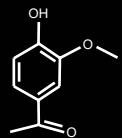
# INPUTS FROM DIFFERENT ORS OVERLAP IN CORTEX



# INPUTS FROM DIFFERENT ORS ARE COMBINED IN SINGLE CORTICAL NEURONS



# MODEL: CORTICAL NEURONS AS COINCIDENCE DETECTORS



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Junzo Hirono**