



Mixture processing in a biophysical model of the early olfactory system of honeybees

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Chemical components in Coffee Aroma

Odor component	$\mu\text{g/l}^*$	Odor component	$\mu\text{g/l}^*$
Acetaldehyde	4700	3-Hydroxy-4,5-dimethyl-2(5H)-furanone	80
Methylpropanal	760	(E)-P-Damascenone	1.6
2-Methylbutanal	870	Guaiacol	120
3-Methylbutanal	570	4-Ethylguaiacol	48
2,3-Butanedione	2100	4-Vinylguaiacol	740
2,3-Pentanedione	1600	Vanillin	210
2-Ethyl-3,5-dimethylpyrazine	17	2-Furfurylthiol	17
2-Ethenyl-3,5-dimethylpyrazine	1.0	Methional	10
2,3-Diethyl-5-methylpyrazine	3.6	3-Mercapto-3-methylbutyl formate	5.7
2-Ethenyl-3-ethyl-5-methylpyrazine	0.2	2-Methyl-3-furanthiol	1.1
3-Isobutyl-2-methoxypyrazine	1.5	3-Methyl-2-buten-1-thiol	0.6
4-Hydroxy-2,5-dimethyl-3(2H)-furanone	7200	Methanethiol	170
2(5)-Ethyl-4-hydroxy-5(2)-methyl-3(2H)-furanone	800		

*in coffee brew

Mayer et al. *Eur Food Res Technol* (2000)

Odours mix in complex plumes



Odour molecules from different sources mix and mingle with each other

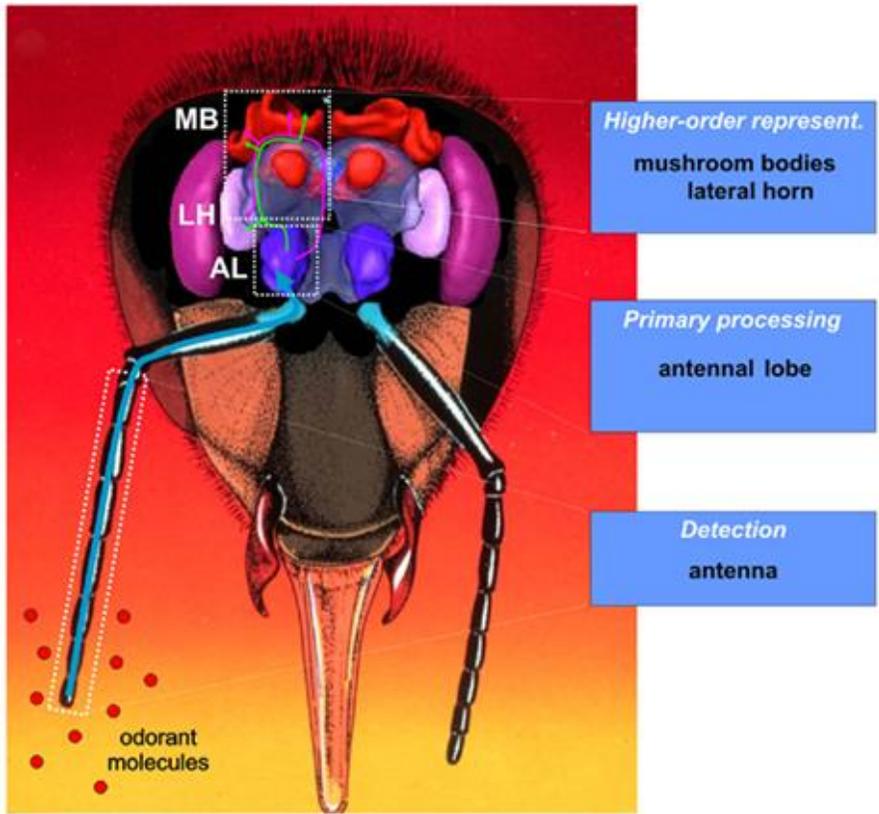
Odour plumes have distinct filaments, but with only ms delays in between

Problems of odour mixture processing

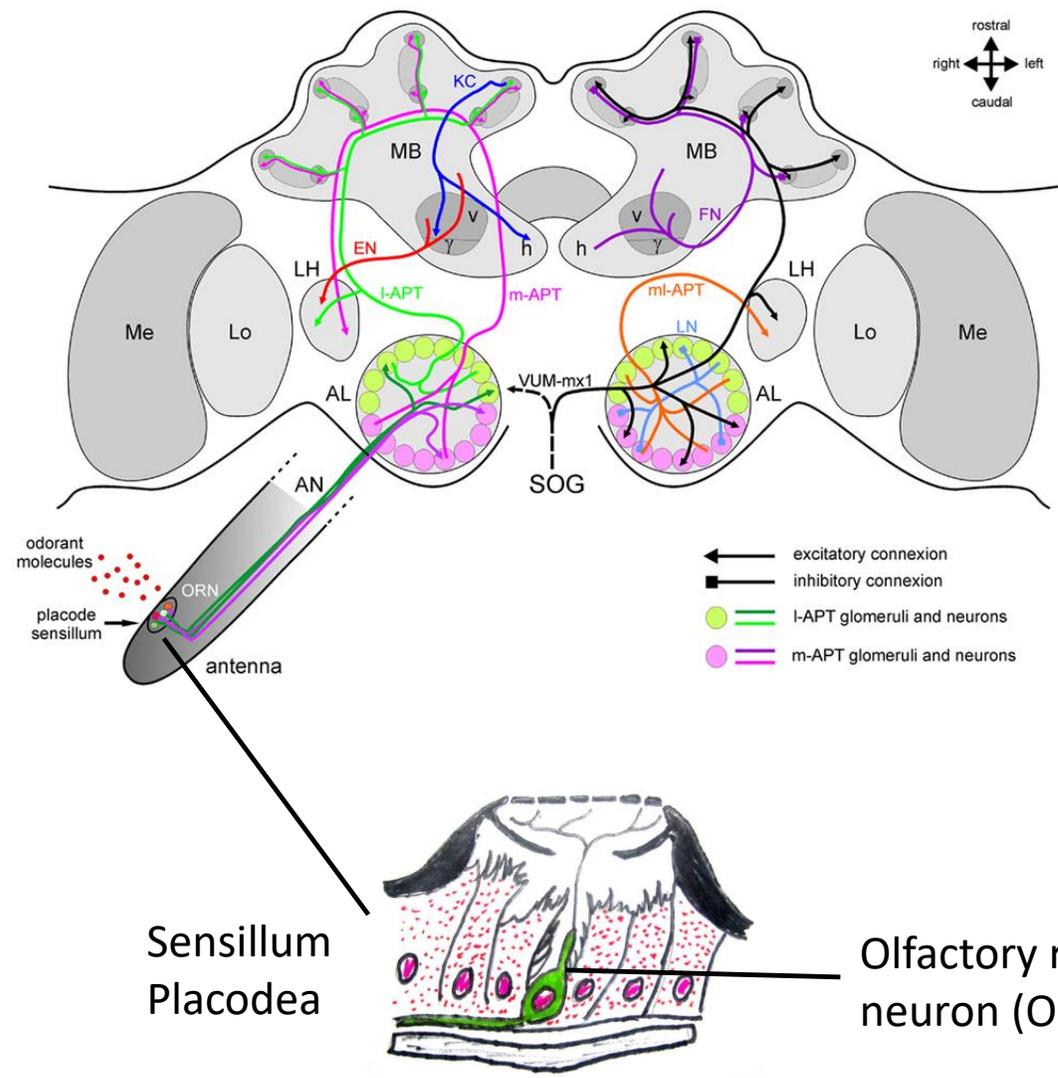
- **Information about the mixtures as a whole**
- Information about individual components in the mixtures
- How to switch between coding the whole mixture and individual components?

This talk: Is there a qualitative difference between olfactory response to mixtures of chemical compounds and a single chemical

The olfactory system of honey bees



J-C Sandoz, *Frontiers Syst Neurosci* (2011)



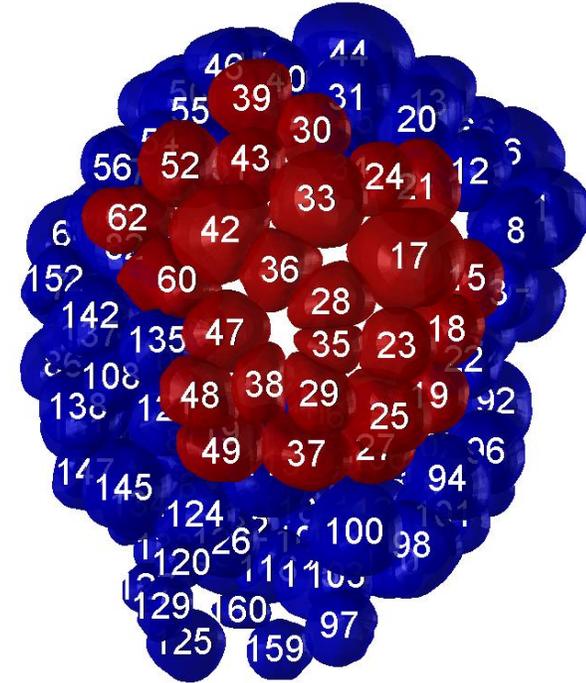
Roadmap

- Building a simple biophysical, partially data-driven model of honeybees' early olfactory system (receptors, ORNs and antennal lobe)
- Model response to single-component stimuli and comparison with experimental data
- Comparison between model response to multi and single component stimuli (**focus on receptor dynamics**), preliminary experimental evidence and its implication on coding.
- Limitation of our model and future work

Limitation when building models of animals' sensory systems

Lack of experimental data

- Low temporal and spatial resolution, e.g. Ca^{2+} imaging at glomerulus resolution
- Entire parts of the system are not observable, e.g. In honeybees, **only 30 of a total of 160 glomeruli in the antennal lobe (AL) can be routinely measured from Ca^{2+} imaging** (Galizia et al, 1999)



Antennal Lobe Atlas from
(Galizia et al, 1999)

Glomeruli which can be routinely measured

Typical modelling approaches

1. Reduced sized model
 - Problems with scaling of noise; finite size network effects; information capacity estimation
2. Model that fit to data
 - Overfitting; limited in scope; high amount of computation; large animal-to-animal variability
3. Phenomenological model
 - Hard to pinpoint relevant biophysical processes.

“Statistical bio-physical modelling”

Our model ...

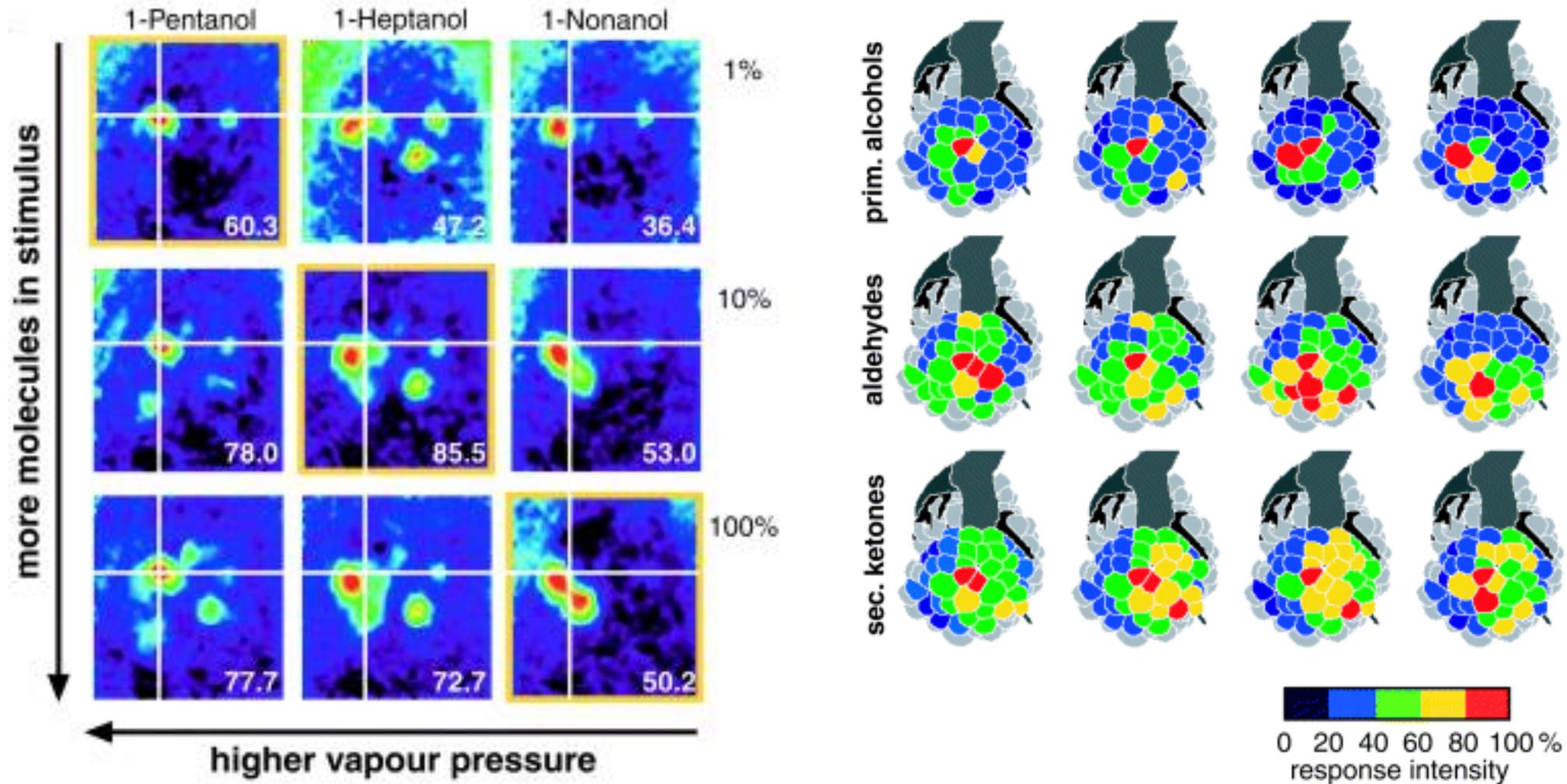
- Considers the full receptor repertoire of honeybees
- Conforms to the **statistics** of the experimental data we used
- Agrees with other experimental results not used to build it
- Is analytically tractable for most parts and otherwise requires only a small amount of computation

Our approach in building the model

1. Extrapolation of experimental ORN data (responses to 28 different types of ORNs from bath applied Ca^{2+} imaging (Galizia et al, 1999))
2. Converting the generated response patterns, which are in the form of conductance, into firing rate
3. Building a simple AL network and generating response patterns for local neurons (LNs) and projection neurons (PNs)

We used a single ORN to represent all ORNs with the same receptor type, a single PN/LN to represent all PNs/LNs in a glomerulus

Experimental data

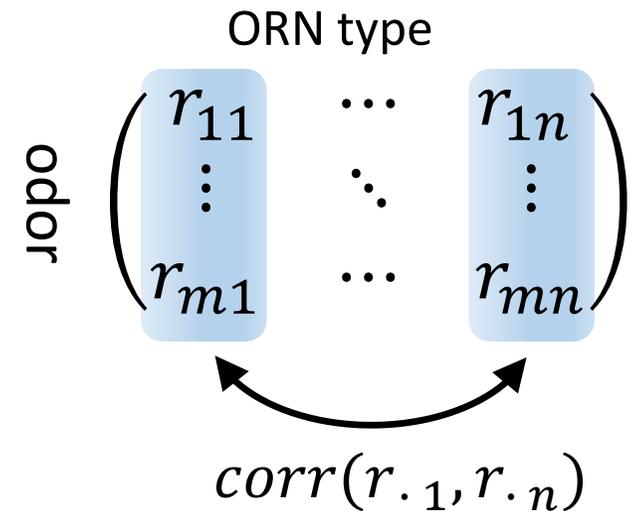


Sachse and Galizia, Eur J Neurosci (1999)

Extrapolation of experimental ORN data

Generating the asymptotic response to odours at saturating concentration

- Responses of new units generated from a combination of previously generated responses and noises, inspired by Haenicke (PhD thesis, 2015)
- Matching the **mean and variance** of the magnitude of ORN responses to different odours
- Matching the statistical distribution of **pairwise correlation between response vectors of ORN pairs**

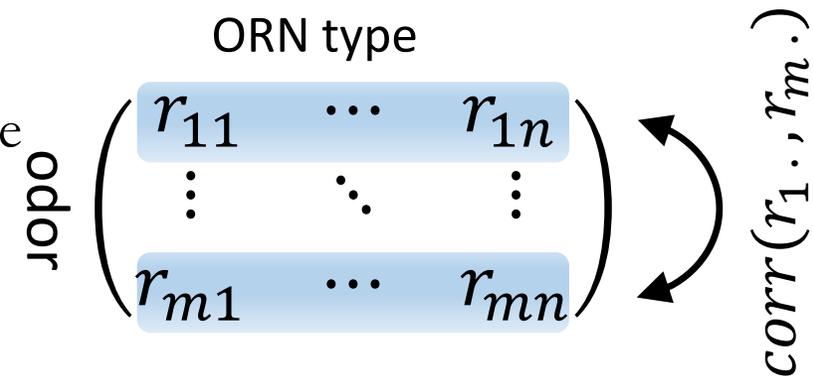


$$m = 16, n = 160$$

Extrapolation of experimental ORN data

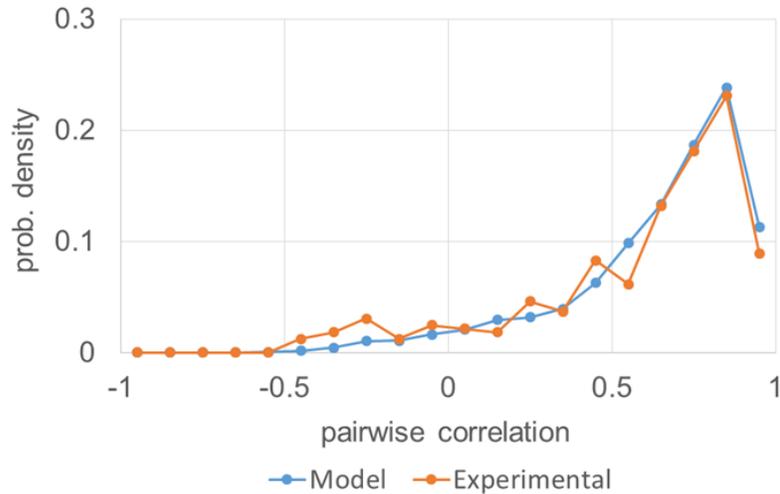
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- Matching the **mean and variance** of the magnitude of ORN responses to different odours
- Matching the statistical distribution of **pairwise correlation between response vectors of ORN pairs**
- Matching the **correlation of ORN responses patterns to different odours**, measured by normalized Euclidean distance



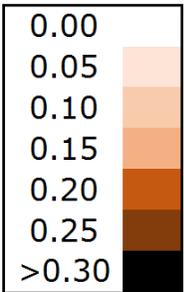
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Extrapolation of experimental ORN data

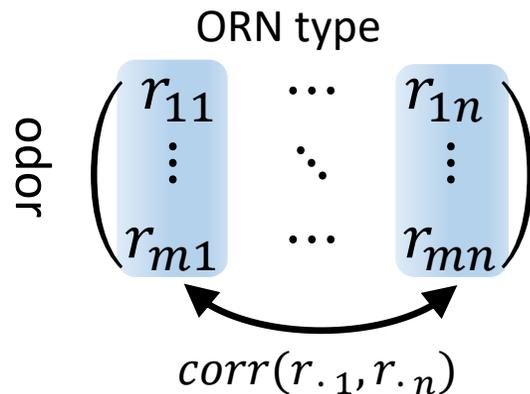


Pairwise correlation between response patterns of different ORNs

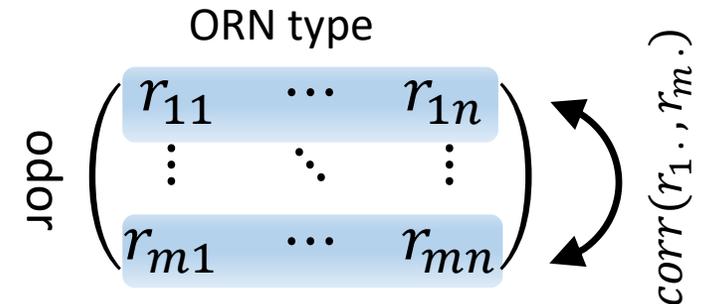
Odour	1-6 ol	1-7 ol	1-8 ol	1-9 ol	2-6 ol	2-7 ol	2-8 ol	2-9 ol	6al	7al	8al	9al	2-6 one	2-7 one	2-8 one	2-9 one
1-6 ol	0.000	0.108	0.163	0.214	0.076	0.082	0.115	0.224	0.169	0.209	0.179	0.208	0.254	0.268	0.258	0.165
1-7 ol	0.108	0.000	0.096	0.152	0.126	0.084	0.083	0.194	0.203	0.223	0.168	0.174	0.293	0.304	0.267	0.132
1-8 ol	0.163	0.096	0.000	0.072	0.155	0.156	0.138	0.126	0.255	0.269	0.186	0.182	0.350	0.361	0.324	0.121
1-9 ol	0.214	0.152	0.072	0.000	0.196	0.205	0.183	0.121	0.299	0.310	0.219	0.203	0.397	0.402	0.359	0.139
2-6 ol	0.076	0.126	0.155	0.196	0.000	0.115	0.139	0.186	0.187	0.249	0.206	0.218	0.288	0.293	0.288	0.156
2-7 ol	0.082	0.084	0.156	0.205	0.115	0.000	0.078	0.244	0.163	0.186	0.157	0.174	0.241	0.249	0.225	0.147
2-8 ol	0.115	0.083	0.138	0.183	0.139	0.078	0.000	0.238	0.163	0.181	0.123	0.130	0.234	0.239	0.205	0.100
2-9 ol	0.224	0.194	0.126	0.121	0.186	0.244	0.238	0.000	0.334	0.371	0.288	0.282	0.437	0.446	0.422	0.202
6al	0.169	0.203	0.255	0.299	0.187	0.163	0.163	0.334	0.000	0.125	0.155	0.177	0.147	0.169	0.182	0.202
7al	0.209	0.223	0.269	0.310	0.249	0.186	0.181	0.371	0.125	0.000	0.117	0.171	0.156	0.186	0.167	0.224
8al	0.179	0.168	0.186	0.219	0.206	0.157	0.123	0.288	0.155	0.117	0.000	0.099	0.211	0.233	0.201	0.139
9al	0.208	0.174	0.182	0.203	0.218	0.174	0.130	0.282	0.177	0.171	0.099	0.000	0.247	0.253	0.224	0.115
2-6 one	0.254	0.293	0.350	0.397	0.288	0.241	0.234	0.437	0.147	0.156	0.211	0.247	0.000	0.091	0.154	0.285
2-7 one	0.268	0.304	0.361	0.402	0.293	0.249	0.239	0.446	0.169	0.186	0.233	0.253	0.091	0.000	0.113	0.279
2-8 one	0.258	0.267	0.324	0.359	0.288	0.225	0.205	0.422	0.182	0.167	0.201	0.224	0.154	0.113	0.000	0.243
2-9 one	0.165	0.132	0.121	0.139	0.156	0.147	0.100	0.202	0.202	0.224	0.139	0.115	0.285	0.279	0.243	0.000



Chemical similarity of odour in **experimental** data (Galizia et al., 1999), measured by normalized Euclidean distance



Model matches statistics on both dimensions!



Receptor dynamics

$$\dot{r}_0 = k_{-1}r - (k_1c)^n r_0$$

$$\dot{r} = (k_1c)^n r_0 - k_{-1}r + k_{-2}r^* - k_2r$$

$$\dot{r}^* = k_2r - k_{-2}r^*$$

(Rospars et al, 2008)

r_0 : unbound receptor

r : bound receptor

r^* : activated receptor

Correspond to input
conductance to ORNs

k^1 (k^{-1}) and k^2 (k^{-2}) : rate of receptor (un)binding and (de)activation.

n : transduction constant

c : stimulus concentration

We sampled these variables from statistical distributions. They are **constrained by (i) the asymptotic response obtained previously (ii) statistics of dose-concentration relationship (Gremiaux, 2012) and (iii) the typical response speed of the system.**

Neuron model

- Ca^{2+} imaging data most closely related to conductance
- To obtain the firing rate of ORN, we used a **conductance based leaky integrate-and-fire (LIF) model with adaptation**

$$\tau_{\text{eff}} \frac{dV}{dt} = -V + R I_{\text{eff}} - r I_{\text{adapt}}$$

$$\tau_{\text{adapt}} \frac{dI_{\text{adapt}}}{dt} = -I_{\text{adapt}}$$

$$I_{\text{adapt}} = I_{\text{adapt}}^{\text{max}} \quad \text{at} \quad t = t_{\text{fire}}$$

Here I_{eff} is the effective input current, which depends on conductances (here described by r^*). For details please refer to Chan et al. (2016)

Rate model

- Assuming time-invariant input (constant noise and adiabatic approximation), the firing rate (at equilibrium) can be obtained analytically

$$V = V_{\text{reset}} e^{\frac{-t}{\tau_{\text{eff}}}} + I_{\text{eff}} \left(1 - e^{-\frac{t}{\tau_{\text{eff}}}} \right) - \frac{\tau_{\text{adapt}} I_{\text{adapt}}^{\text{max}}}{\tau_{\text{adapt}} - \tau_{\text{eff}}} \left(e^{-\frac{t}{\tau_{\text{adapt}}}} - e^{-\frac{t}{\tau_{\text{eff}}}} \right),$$

- The **instantaneous firing rate** can then be obtained by

$$\nu = \frac{1}{t_{\text{thres}}} + t_{\text{refract}},$$

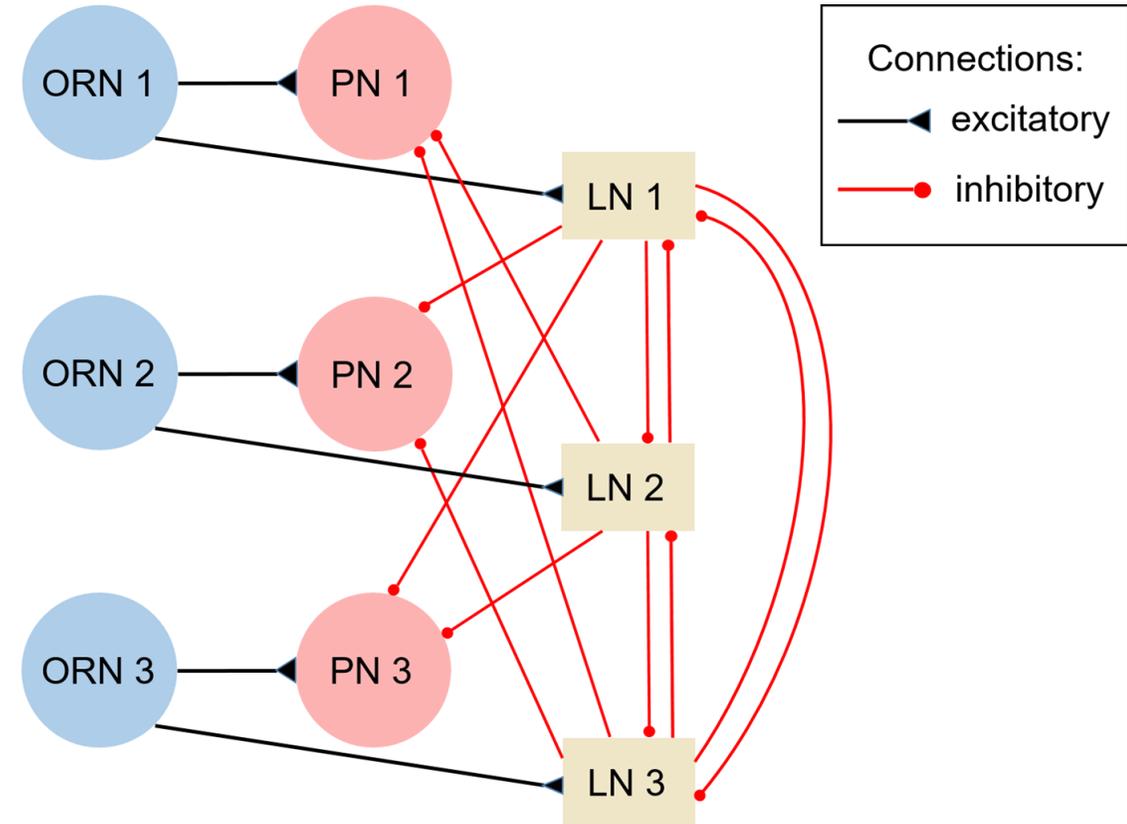
t_{thres} : time when V reaches the firing threshold

t_{refract} : absolute refractory period.

Simple AL network

- Each ORN provides one-to-one excitatory input to a single glomerulus containing a PN and an LN
- PNs and LNs both receive inhibitory input from LNs of all other glomeruli but not their own glomerulus

We used a single ORN to represent all ORNs with the same receptor type, a single PN/LN to represent all PNs/LNs in a glomerulus



Reduced AL network

AL network

LN-PN connectivity: based on the correlations between the activities of the ORNs to which they are connected, as suggested by Linster et al. (2005)

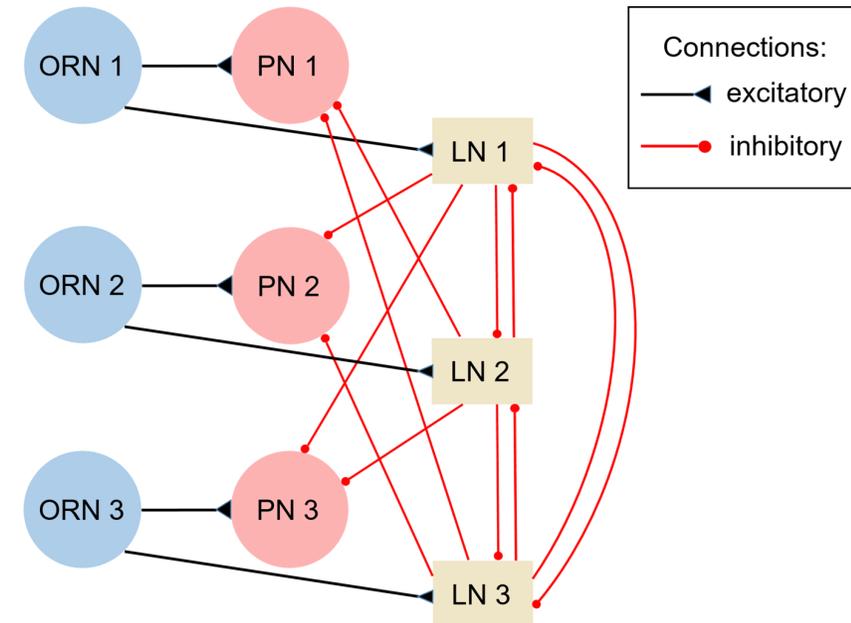
$$conn_{ij} = (1 - \delta_{ij}) [conn_b \times \xi_{unif} + H(corr_{ij}) \times corr_{ij}(1 + C\xi_{norm})]$$

δ_{ij} : Kronecker delta function

H : Heaviside step function

$conn_b$ and C : constant parameters

Firing rate of PN & LN: iteratively generated from the rate model previously described

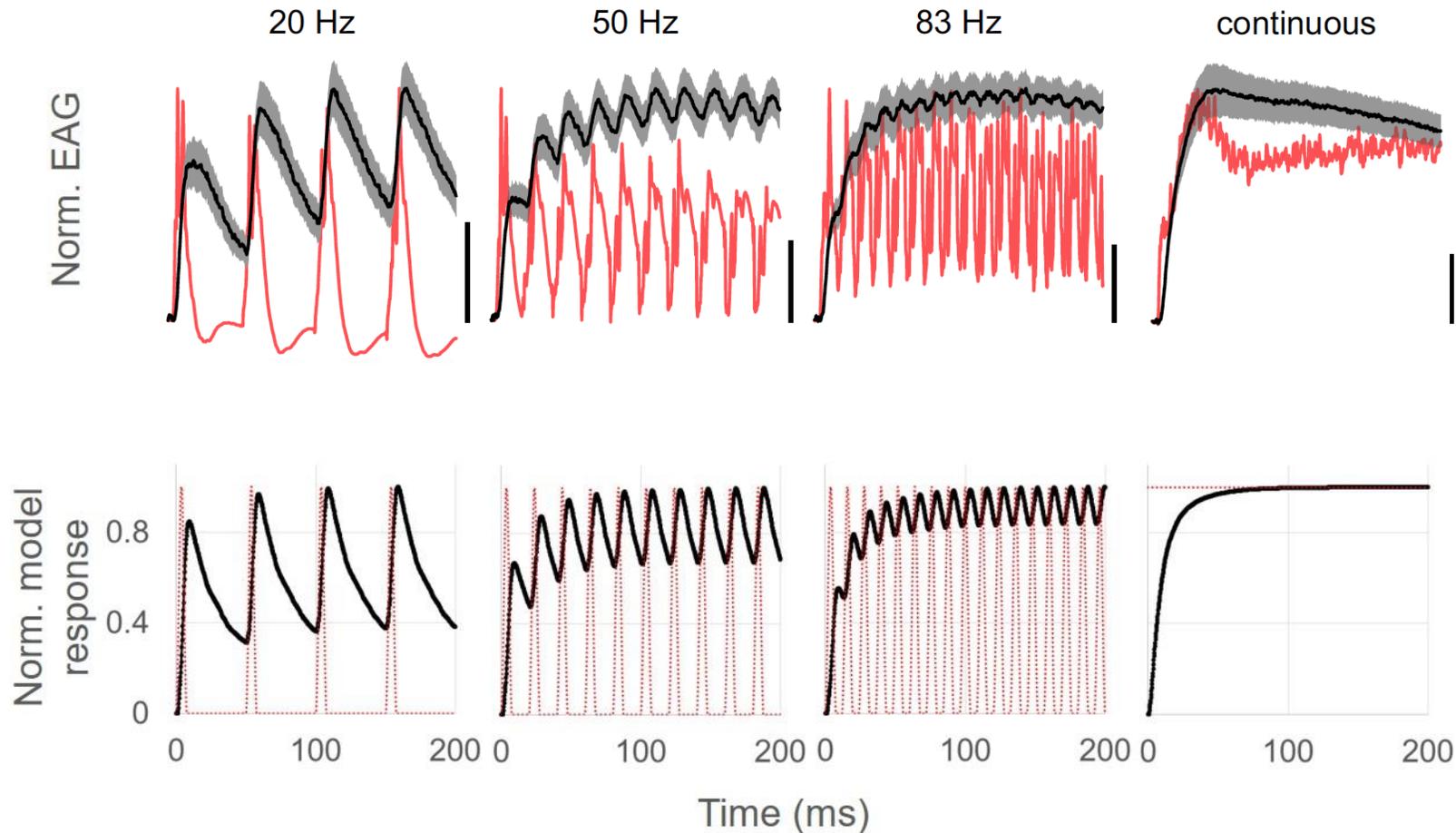


Results:

Response to single-component stimuli

- ORN Pulse tracking
- Dose-response relationship in PN
- Correlations in responses across different PNs
- ORN-PN correlations

Results (ORN pulse tracking)

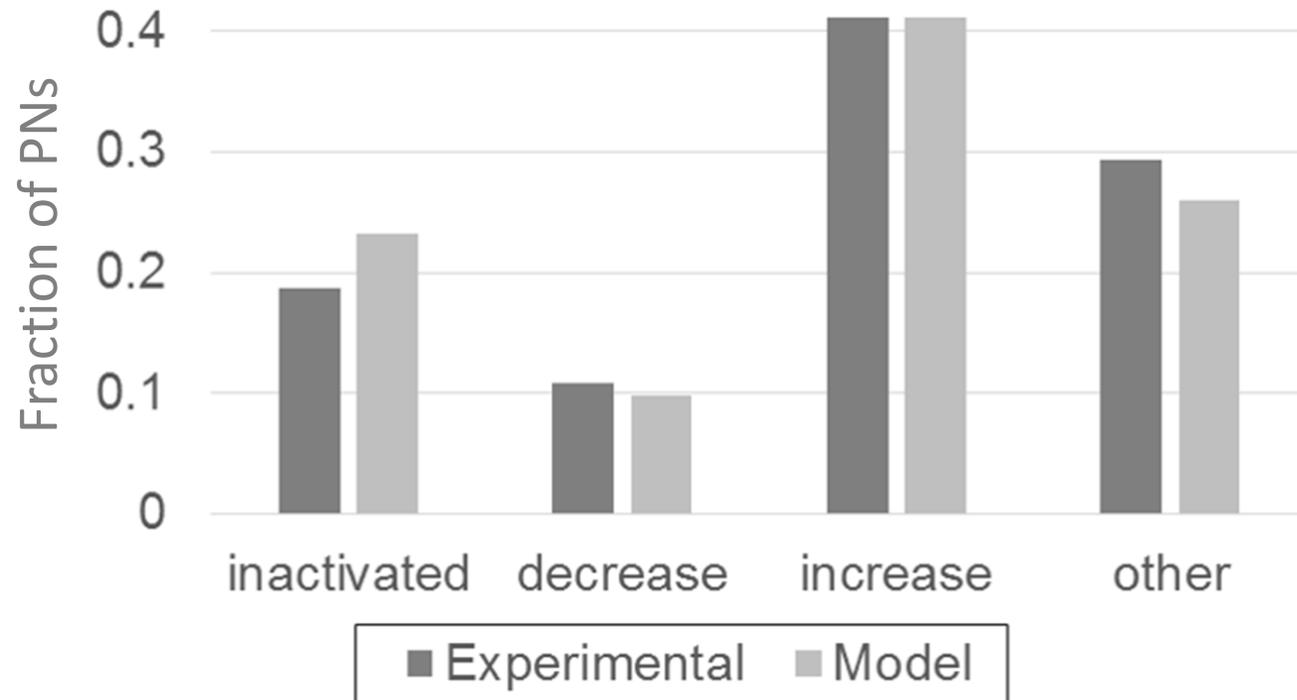


Top black: electro-antennogram recordings Syzszka et al (2014) (top, black line)

Bottom black: Average model ORN responses

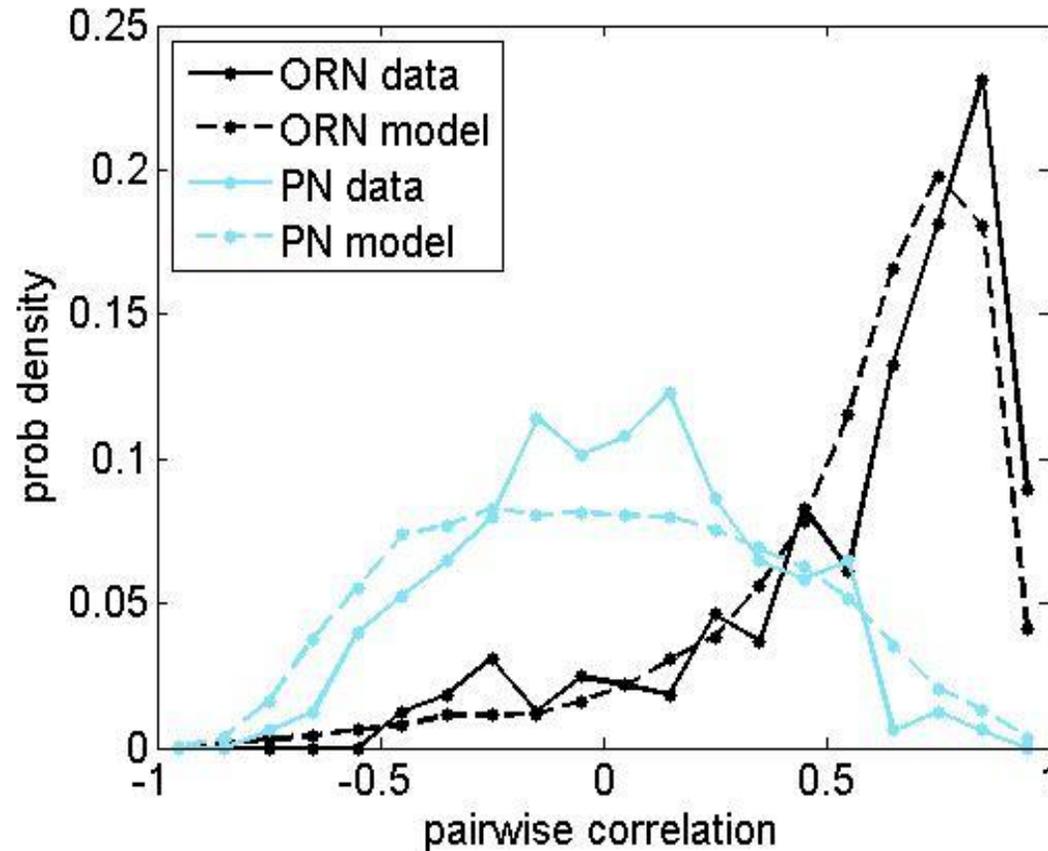
Red: concentration of odour

Results (dose-response relationship in PN)



The PN response predicted by our model show a similar statistical distribution of dose-response relationship to calcium imaging results in Ditzen (PhD thesis, 2005).

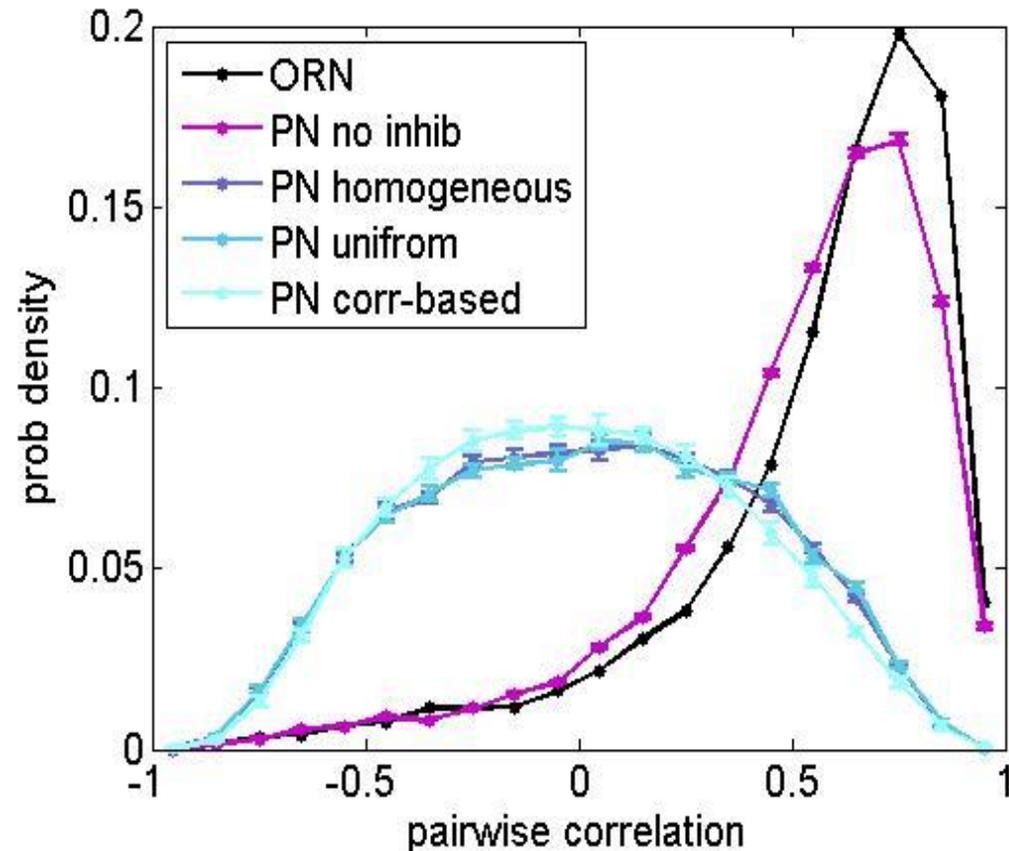
Results (dose-response relationship in PN)



Probability Density Function for pairwise correlation across response patterns observed in Ca^{2+} experiments (Galizia et al, 1999; Ditzen, 2005) and our model.

Model is fitted to the ORN distribution but not PN

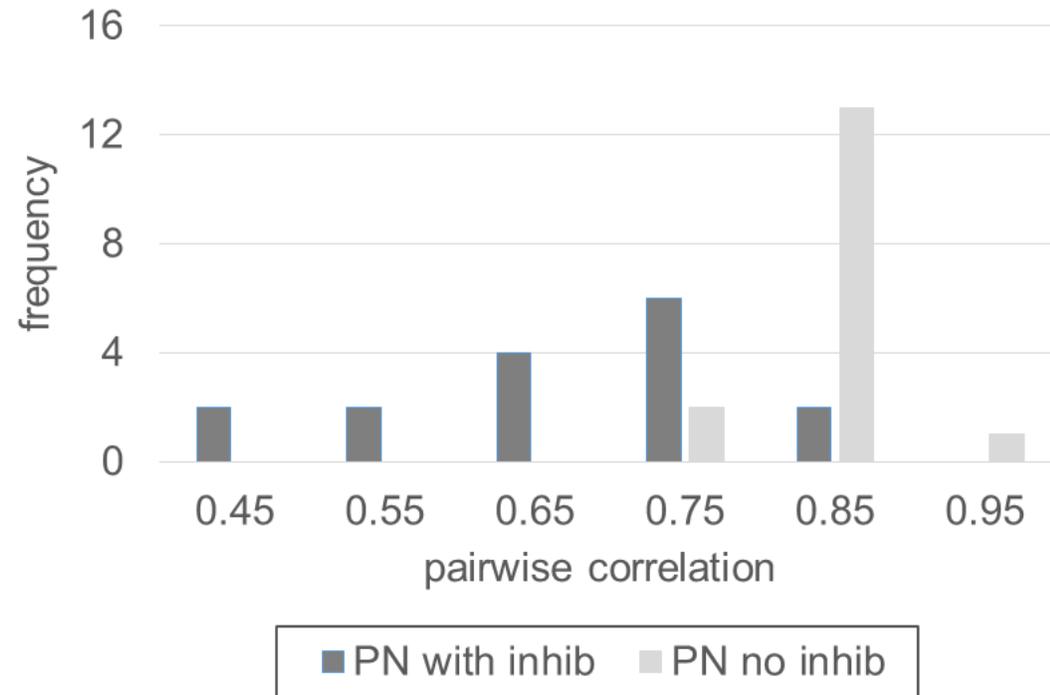
Decorrelation in PN response across different units is caused by LN-PN inhibition



LN-PN inhibition is the most significant cause of decorrelation. Structure of their connectivity matrix matters only a little.

This supports the hypothesis by Olsen and Wilson (*Nature*, 2008)

Results (ORN-PN correlations)



Statistical distribution of the pairwise correlation between the overall ORN and PN response for different odor stimuli. The average correlation is around 0.6-0.7, consistent with Deisig et al (2010).

Decorrelation is caused by both non-linearity in LIF neurons firing and LN inhibition

Results: Response to mixtures

- Equilibrium solution of **receptor dynamics** equation and the role of olfactory transduction process
- Cross-concentration correlation
- Response latency

Comparison will be made with responses to single-component stimuli

Receptor dynamics equation

For single-component:

$$\dot{r}_0 = k_{-1}r - (k_1c)^n r_0$$

$$\dot{r} = (k_1c)^n r_0 - k_{-1}r + k_{-2}r^* - k_2r$$

$$\dot{r}^* = k_2r - k_{-2}r^*$$

r_0 : unbound receptor

r : bound receptor

r^* : activated receptor

$k_i^1 (k_i^{-1})$ and $k_i^2 (k_i^{-2})$ describe the rate of (un)binding and (de)activation processes.

What about mixtures?

A possible extension?

$$\dot{r}_0 = \sum_j k_{-1}^j r_j - \sum_j \left(k_1^j c_j\right)^n r_0$$

(Rospars et al, 2008; Nowotny et al, 2013)

$$\dot{r}_i = \left(k_1^j c_j\right)^n r_0 - k_{-1}^i r_i + k_{-2}^i r_i^* - k_2^i r_i$$

$$\dot{r}_i^* = k_2^i r_i - k_{-2}^i r_i^*$$

No good! Response to mixture of identical components \neq response to single component with concentration added. Inconsistent! (Cruz and Lowe, 2013)

Our model

$$\dot{r}_0 = \sum_j k_{-1}^j r_j - \left(\sum_j k_1^j c_j \right)^n r_0$$

$$\dot{r}_i = \left(\sum_j k_1^j c_j \right)^n \frac{(k_1^i c_i)^n}{\sum_j (k_1^j c_j)^n} r_0 - k_{-1}^i r_i + k_{-2}^i r_i^* - k_2^i r_i$$

$$\dot{r}_i^* = k_2^i r_i - k_{-2}^i r_i^*$$

For each odor component, rate of binding is still proportional to their ‘effective affinity’ to receptors, but globally, the total binding rate is determined by applying the higher-order interactive effects between the odorants and receptor after taking into account of all components present

Solution to the receptor dynamics equation

- Single odor: $r^* = \frac{1}{\frac{1}{K_2'} + \frac{1}{K_{\text{eff}} c_{\text{eff}}}}$

K_{eff} : response gain to odor at low concentration

- Mixture: $r_{\text{mix}}^* = \frac{1}{\frac{1}{K_2^{\text{mix}}'} + \frac{1}{K_{\text{eff}}^{\text{mix}} c_{\text{eff}}}}$

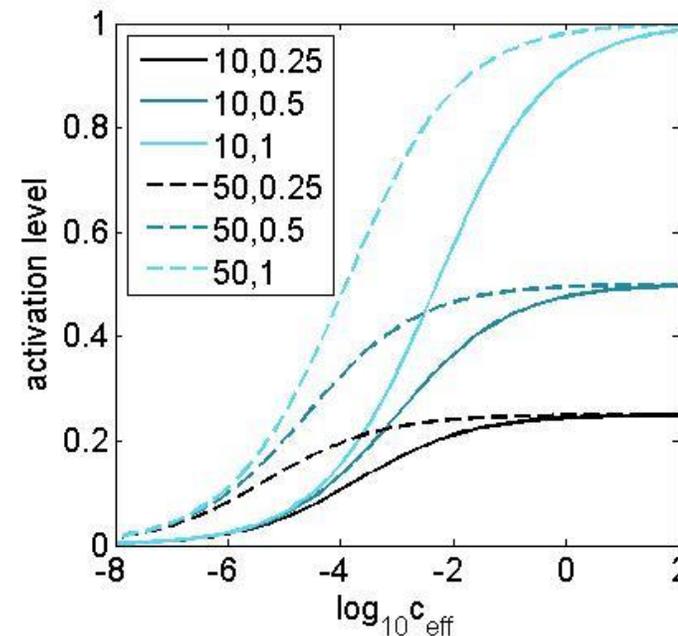
K_2' : response to odor at high concentration

$$K_1 = \frac{k_1^n}{k_{-1}}, K_2 = \frac{k_2}{k_{-2}}$$

$$K_2' = r_{\text{total}} \left(1 - \frac{1}{K_2 + 1}\right), \quad K_{\text{eff}} = r_{\text{total}} K_1 K_2,$$

$$K_{\text{eff}}^{\text{mix}} = \frac{(\sum_j k_1^j)^n}{\sum_j k_1^j} \sum_i k_{\text{eff}}^i, \quad K_2^{\text{mix}}' = \frac{1}{\sum_i \frac{p_i}{K_2^i}}, p_i = \frac{k_{\text{eff}}^i}{\sum_j k_{\text{eff}}^j},$$

$$r_{\text{mix}}^* = \sum_i r_i^*, c_{\text{eff}} = c^n$$



Legend: K_{eff}, K_2'

Assuming equal concentration for components

Response at the limit of small c_{eff}

$$r^* = K_{\text{eff}} c_{\text{eff}}$$

$$r_{\text{mix}}^* = \frac{\left(\sum_j k_1^j\right)^n}{\sum_j k_1^{jn}} \sum_i K_{\text{eff}}^i c_{\text{eff}}$$

$$\text{Let } w(n) = \frac{\left(\sum_j k_1^j\right)^n}{\sum_j k_1^{jn}}$$

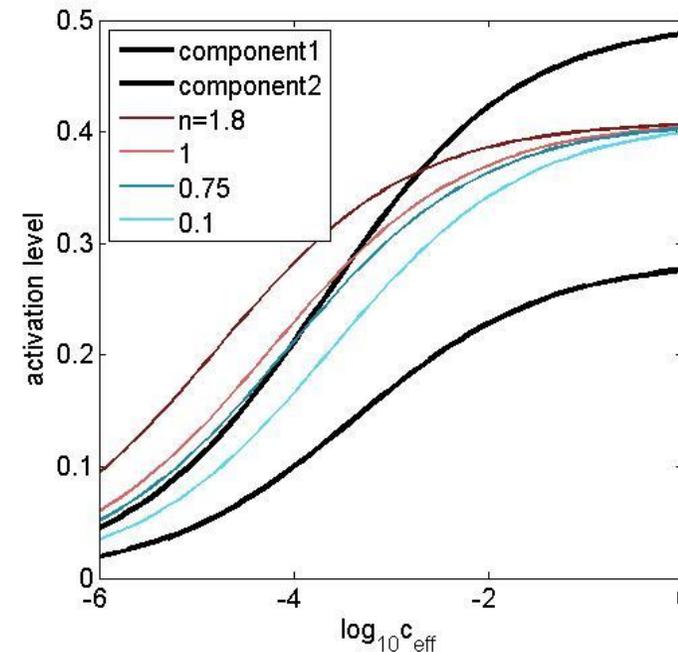
$n > 1 \rightarrow w(n) > 1 \rightarrow$ synergistic

$n = 1 \rightarrow w(n) = 1 \rightarrow$ linearly additive

$n < 1 \rightarrow w(n) < 1 \rightarrow$ hypoadditive

$$\frac{\left(\sum_j k_1^j\right)^n}{\sum_j k_1^{jn}} = \left(\frac{\left(\sum_j k_1^j\right)}{\left(\sum_j k_1^{jn}\right)^{\frac{1}{n}}}\right)^n = \left(\frac{\|k_1\|_1}{\|k_1\|_n}\right)^n$$

$\|\cdot\|_p$: L^p norm, monotonic decreasing wrt p



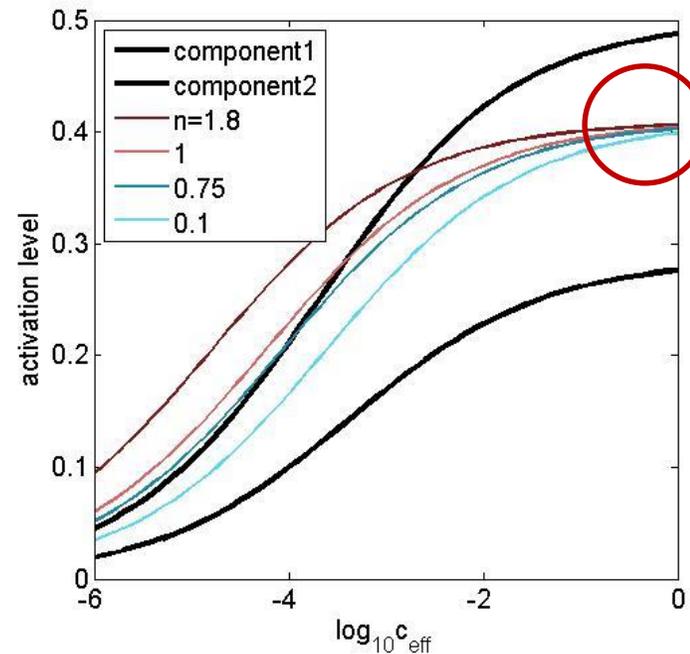
Response at the limit of large c_{eff}

$$r^* = K_2'$$

$$r_{\text{mix}}^* = K_2^{\text{mix}'} = \frac{1}{\sum_i \frac{p_i}{K_2^{i'}}$$

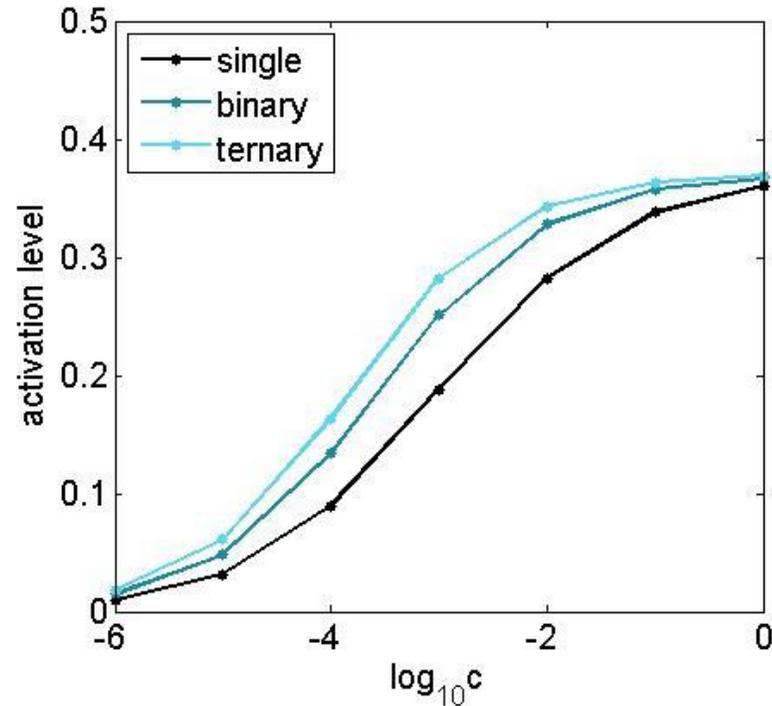
Mixture responses is a weighted harmonic mean of the response of its components

Interaction between mixtures is **dominated by the competition of the receptor site**. Effect of interaction in the transduction processes becomes negligible

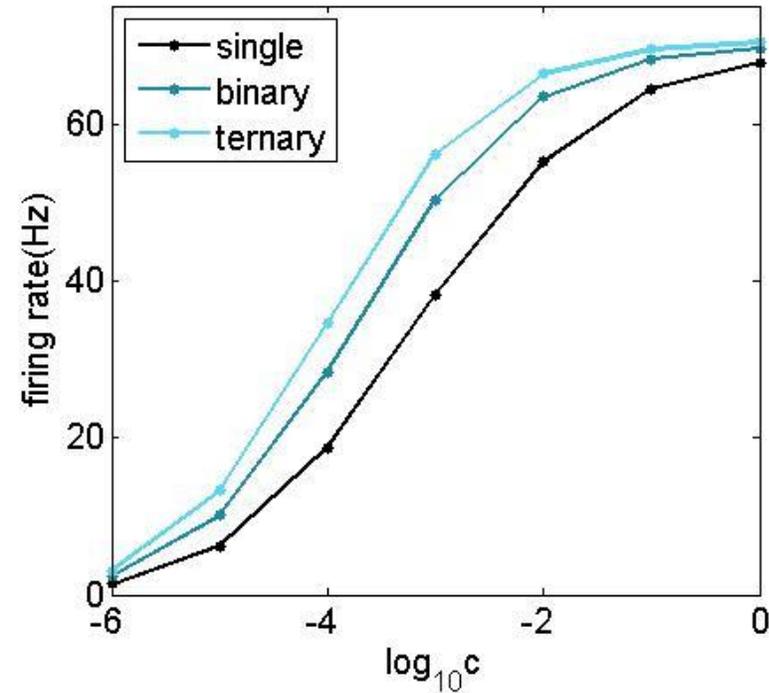


Independent of n

Simulation results: Average ORN firing rates



Activation level



Firing rate

Experimental measurements (Gremiaux et al 2012) suggests that $n < 1$ for most odor-receptor combinations. Our model generates n accordingly. Dominantly hypoadditive responses has been observed Duchamp-Viret et al (2003) and Cruz and Lowe (2013)

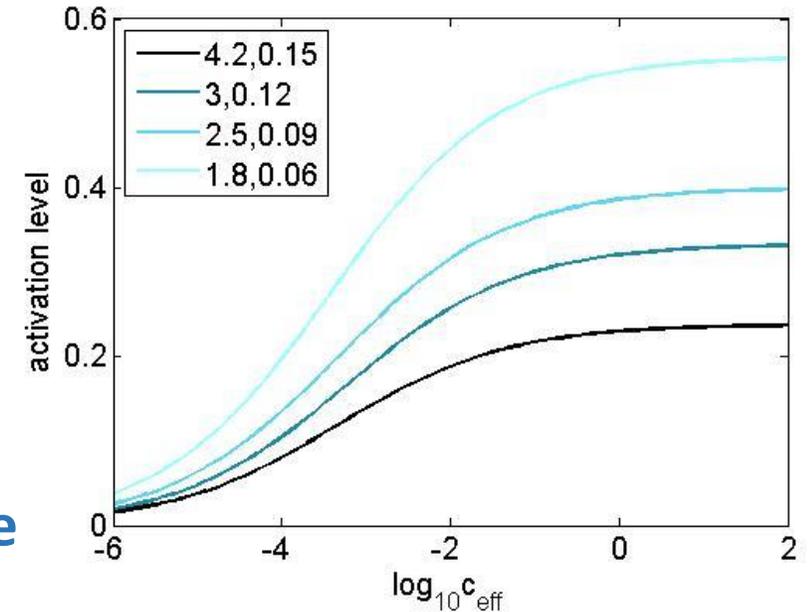
Key study 1: Cross-concentration correlation

- Look at the overall ORN response pattern at high and low stimulus concentration (same stimulus)

- Intuition:

K_2' : response to odor at high concentration

K_{eff} : response gain to odor at low concentration



K_2' and K_{eff} positively correlated

Cross-concentration correlation will be large and positive if K_2' and K_{eff} are strongly and positively correlated

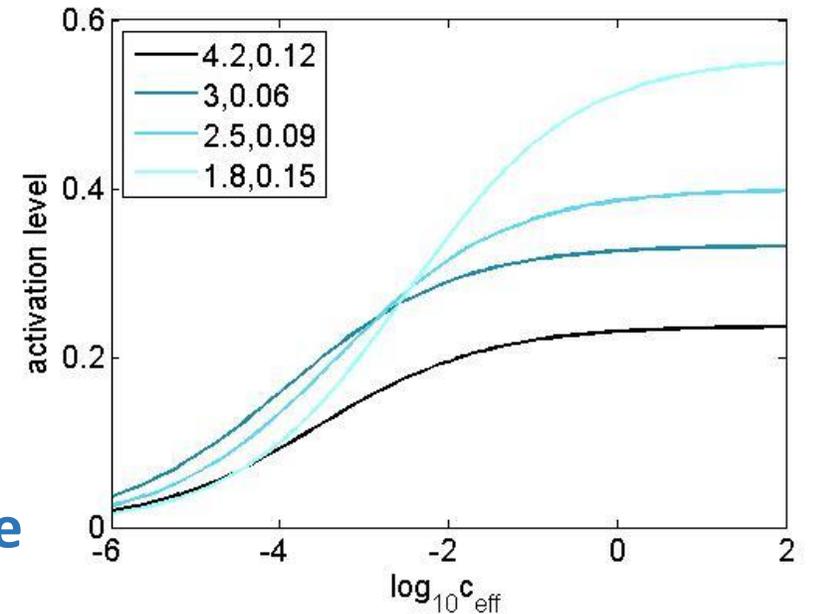
Key study 1: Cross-concentration correlation

- Look at the overall ORN response pattern at high and low stimulus concentration (same stimulus)

- Intuition:

K_2' : response to odor at high concentration

K_{eff} : response gain to odor at low concentration



K_2' and K_{eff} anti-correlated

Cross-concentration correlation will be large and positive if K_2' and K_{eff} are strongly and positively correlated

Average responses: Convert the 'K's into random variables

- Considering the entire input and receptor space: many possible odor-reception combinations.
- Each combination i can be characterized by parameters, x_{1i}, \dots, x_{ni} , which are sampled from a parameter sets x_1, \dots, x_n
- If we consider a sufficiently **large number of combinations**, the sets x_1, \dots, x_n are large and can be **assumed to be random variables** with a certain continuous probability distribution.

Can now study ensemble behaviour analytically

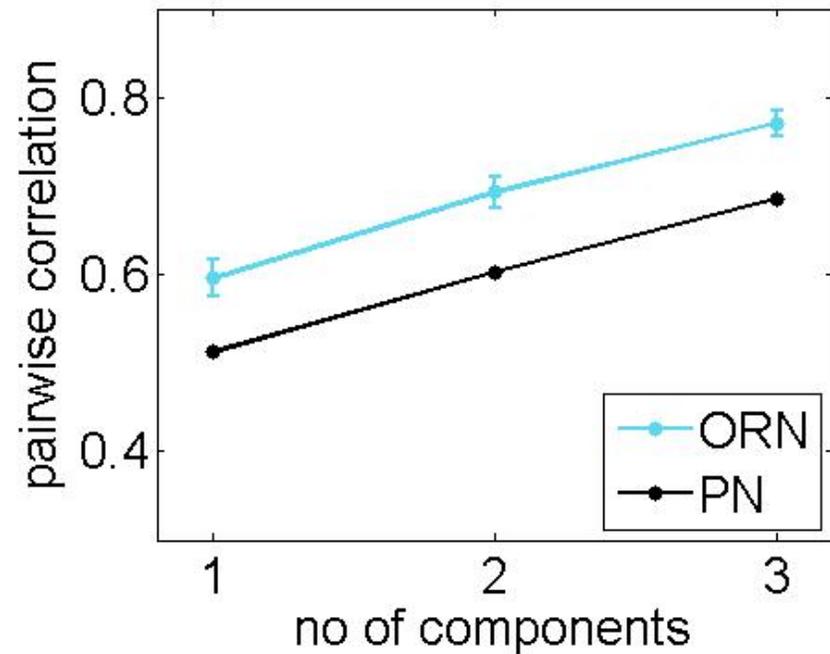
Question: Are $K_{\text{eff}}^{\text{mix}}$ and $K_2^{\text{mix}'}$ more strongly positively correlated than K_{eff} and K_2' , assuming K_1 and K_2 are independent?

Numerical experiments (binary mixtures)

Prob distribution	k_1^n (min,max)/ μ, σ	k_{-1}	K_2	Mean Δ corr	% error
K_{eff}^{mix} and $K_2^{mix'}$, and K_{eff} and K_2' ($n = 0.65$)					
Unif	(0.5,5)	(0.005,0.05)	(0.01,1)	0.061	0
Exp(unif)	(0.63,31.6)	(0.006,0.1)	(0.01,1)	0.095	0
Norm	4,1.5	0.03,0.01	0.3,0.15	0.038	0
Unif	(0.5,5)	(0.005,0.05)	(1,10)	0.06	0
Unif	(0.01,0.1)	(0.1,1)	(0.01,1)	0.061	0
Exp(unif)	(0.01,1)	(0.01,1)	(0.01,10)	0.063	0
Log(unif)	(0.095,4.61)	(0.001,0.1)	(0.01,1.1)	0.042	0
Average firing rate ($n = 0.65$)					
Unif	(0.5,5)	(0.005,0.05)	(0.01,1)	0.239	0
Exp(unif)	(0.63,31.6)	(0.006,0.1)	(0.01,1)	0.379	0
Norm	4,1.5	0.03,0.01	0.3,0.15	0.312	0
Average firing rate (variable n)					
Unif	(0.5,5)	(0.005,0.05)	(0.01,1)	0.083	0.009
Exp(unif)	(0.63,31.6)	(0.006,0.1)	(0.01,1)	0.308	0
Norm	4,1.5	0.03,0.01	0.3,0.15	0.101	0.007

Numerical experiments studying the correlation between $K_{eff,mix}$ and $K_2^{mix'}$, and cross-concentration correlation

Simulation results: Cross-concentration correlation increases with the number of components



Cross-concentration correlation of the response patterns for both ORN and PN increases with the number of components

Key study 2: Response latency

- Response latency, defined as the **timing of the 1st spike after the onset of stimuli**, is low if response at small time (after stimulus onset) is high

Transient response at the limit small c_{eff} and t

$$r^* = \frac{k_2}{k_{-2}} k_1^n r_{\text{total}} c_{\text{eff}} t$$

Assumption: $k_1^n \gg k_{-1}, K_2$
(Biologically realistic)

$$r_{\text{mix}}^* = \frac{\left(\sum_j k_1^j\right)^n}{\sum_j k_1^{j n}} \sum_i \frac{k_2^i}{k_{-2}^i} k_1^{i n} r_{\text{total}} c_{\text{eff}} t$$

Key study 2: Response latency

- Comparing the average across many combinations: $\langle r^* \rangle$
- ‘Fair’ comparison: mixtures at $c = c_0$ and single components at $c = Nc_0$

Both would have equal amount of odour molecules. Any effect observed is not due to discrepancy in no of odour molecules

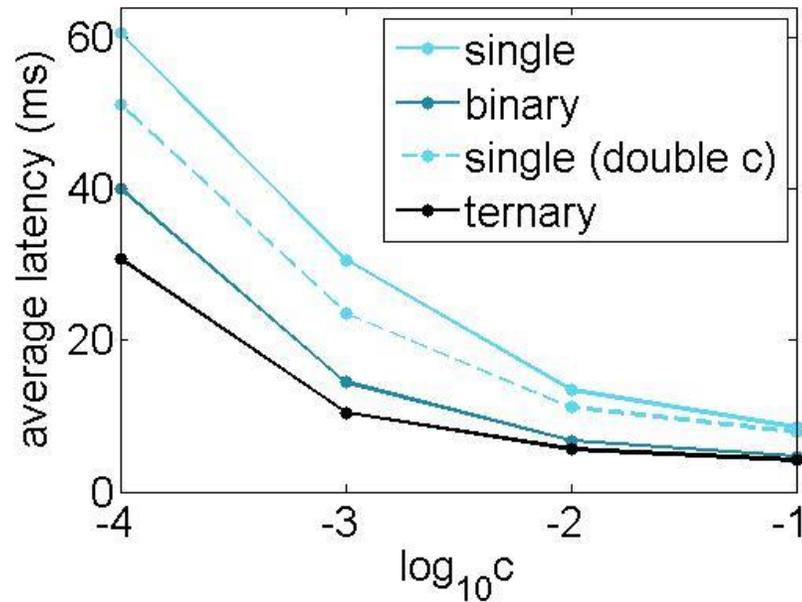
We have shown that $\langle r^*(c = Nc_0) \rangle \leq \langle r_{\text{mix}}^*(c = c_0) \rangle$ for $n \leq 1$

which implies **shorter response latency for mixtures**
at the limit of small c_{eff}

$$\begin{aligned} &\because w(n) \\ &\geq N^{n-1} \end{aligned}$$

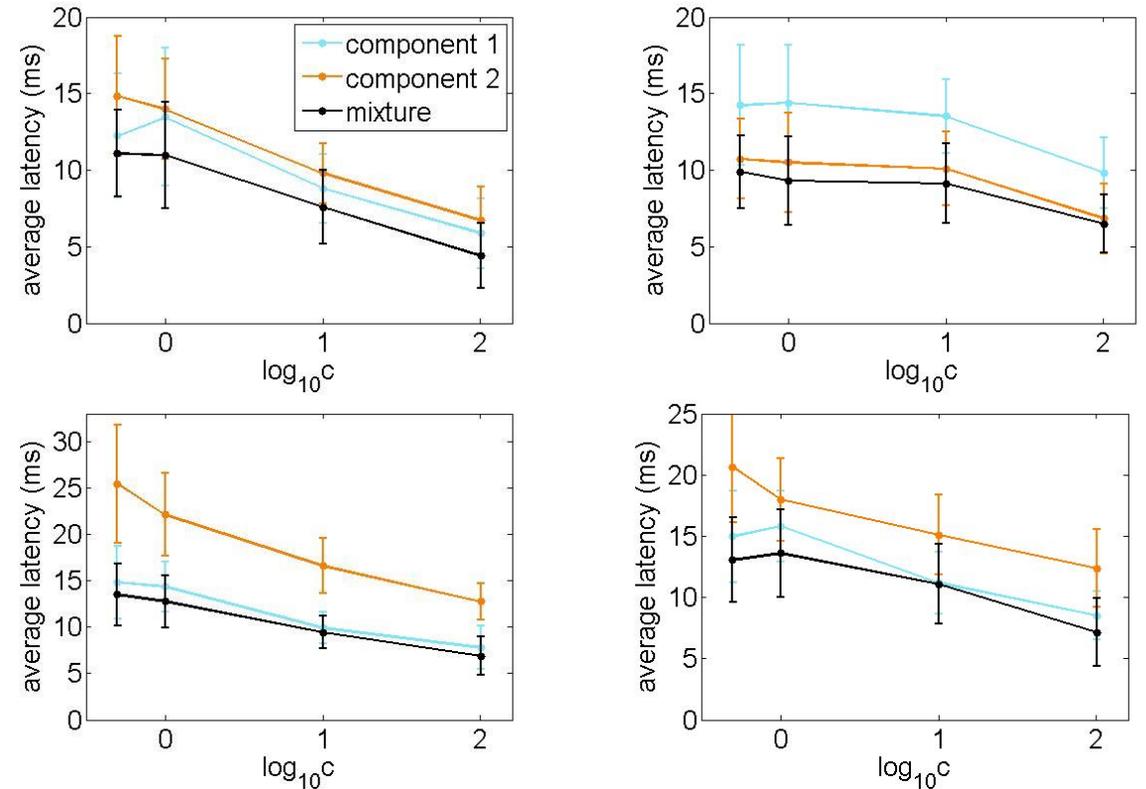
Response latency decreases with the number of components

Simulation



Response latency is smaller for mixtures at low concentration

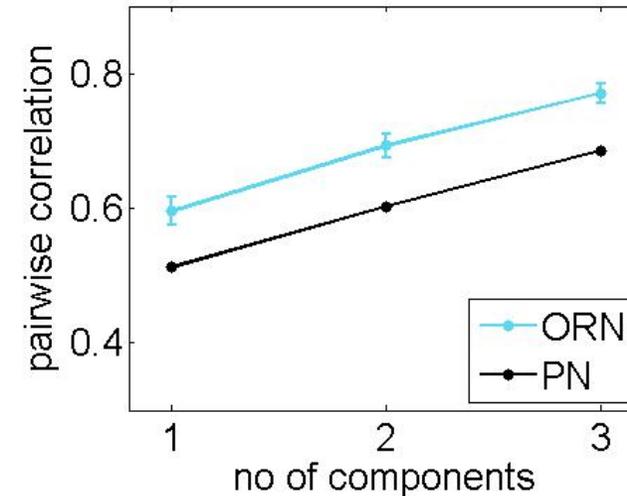
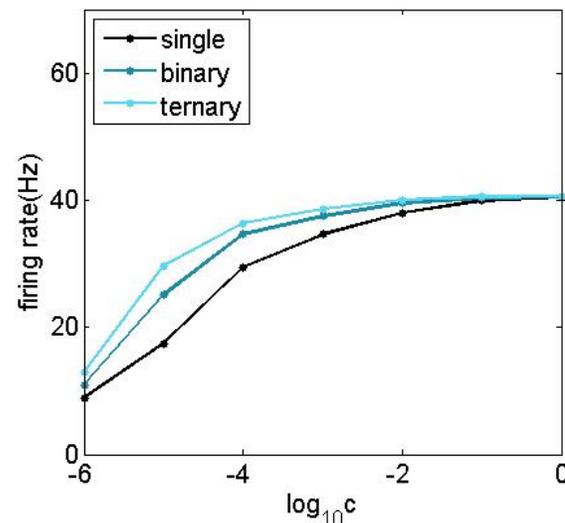
Experimental (preliminary)



Single sensillum recordings from *Drosophila* (Hersperger and Syaszka, 2017). Each panel correspond to a different odour-receptor combination.

Extension of the results

- Components with unequal concentration:** Receptor dynamics equation can still be solved. **Weighting terms would be added** to $K_{\text{eff}}^{\text{mix}}$ and $K_2^{\text{mix}'}$. **No qualitative change to the results is expected.**
- PN:** Shorter response latency for mixtures obviously still holds. Simulation results suggest that the **results** of hypoaddivitivity in mixture response and higher cross-concentration correlation **still holds**

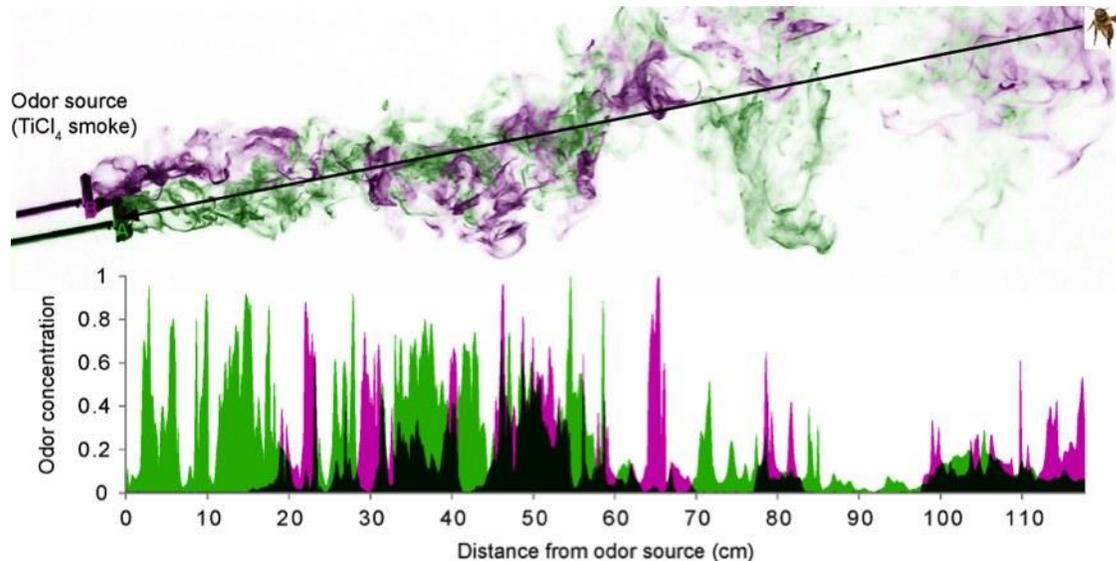


Potential wider implications

Flowers emit complex mixtures. Why?

Our work suggests:

- **Reduced latency** allows **faster coding** for weak stimuli
- **Concentration-invariant identity coding** helps to recognize odours which insects encounter in **largely varying concentrations because of air turbulence**



Time series of concentration of odour received by honey bees under natural conditions

Limitation of our model

- No inhibitory response: limitation of Ca^{2+} imaging. Can be incorporated into the model if required.
- Assumptions in firing rate calculation: Adiabatic approximation (lack of temporal filter for input fluctuation). No stochasticity in the system.

Note: We are now developing a method to obtain response latency and its variability analytically under more realistic conditions.

- Receptor equations: Are there other possible interactions between odour molecules and receptors? Or between different ORN types?

Problems of mixture coding

- Mixtures as a whole
- Individual components in the mixtures

Question: In general, when do we want to treat a mixture as a whole and when do we want to decipher the individual components in a mixture?

We want to group odour from the same source together!

A problem of odour segregation by honeybees



Chemical A

Chemical B

Bush 1



Chemical A&B

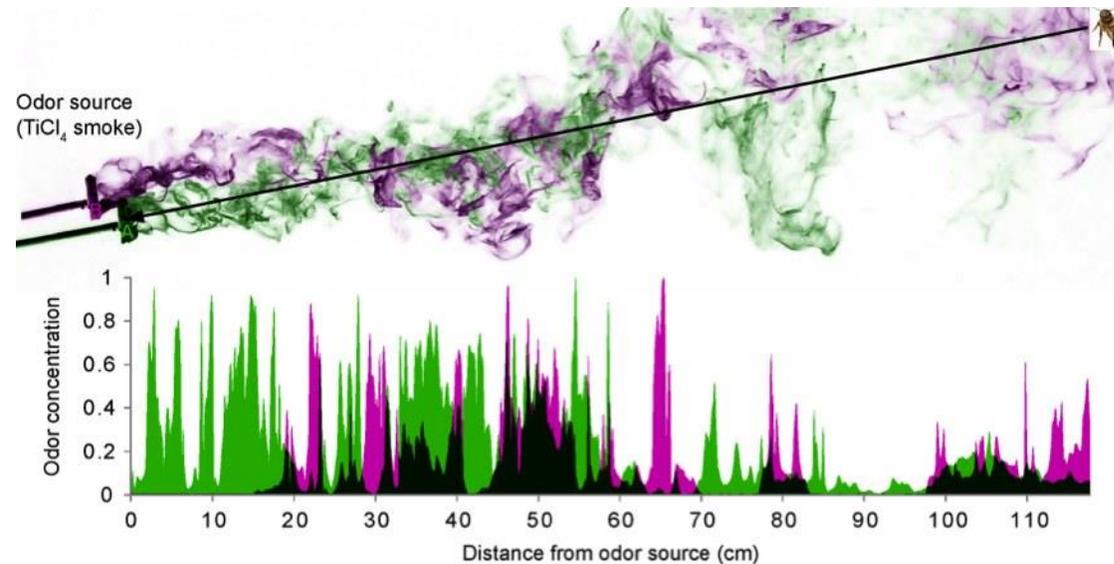
Bush 2

Can bees perform the task?



Difference between coherent and incoherent mixtures

- Odours are transmitted in plumes in which their concentration is significantly higher than in the surroundings



- Odours in coherent mixtures are present in the same plumes and hence their **concentrations co-fluctuate with time**

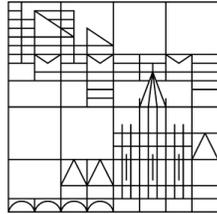
General question: How does a neural network discriminate between correlated and uncorrelated signals?

A possible answer: Using temporally correlated excitation and inhibition to modulate firing of neurons

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Our work is now on BioRxiv :

Mixtures are more salient stimuli in olfaction. BioRxiv 163238;
doi: <https://doi.org/10.1101/163238>



<http://www.odor-objects.org>

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Thank you for your attention!