Competition-based model of pheromone component ratio detection in the moth

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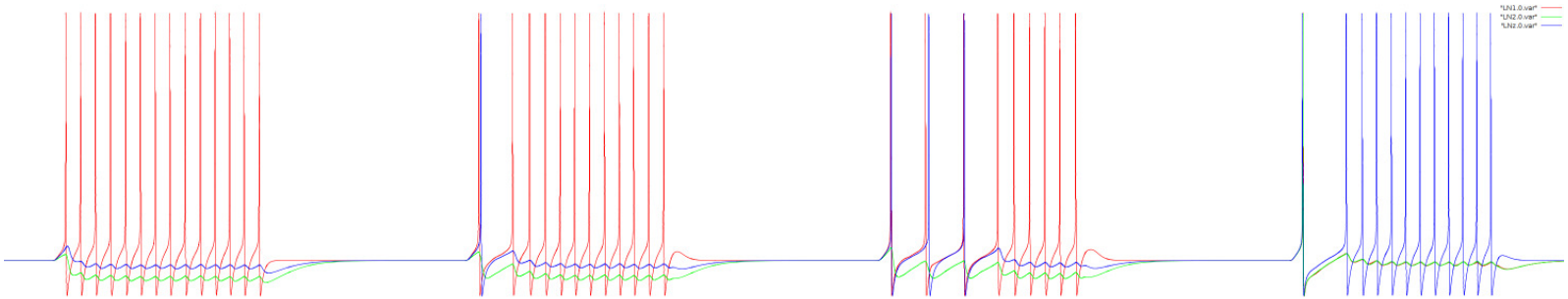


Overview

Observations:

- pheromones often come as a blend of two or more components;
- components can be agonistic, antagonistic — in different roles for different species;
- where agonistic, ratio is often important;

Problem:

- is known structure of the MGC capable of ratio recognition?
- if it is, how accurate can it be?

Ratio recognition performance in the wild

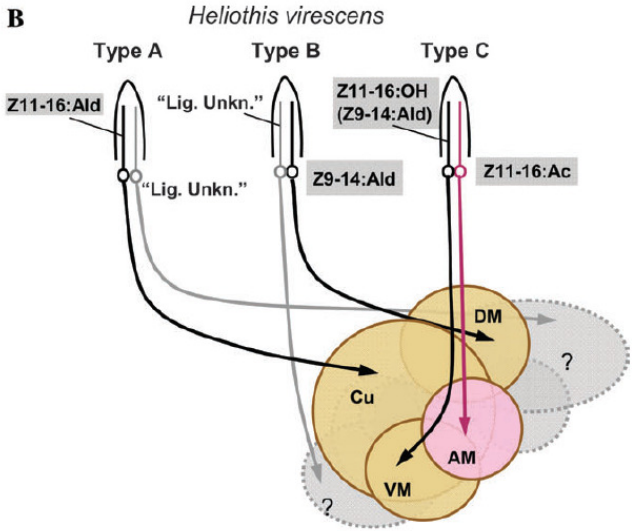
Table 1. Percentage success of *Heliothis virescens* males in performing 4 sequential behaviors in response to a series of synthetic binary pheromone mixtures containing the most important constituents of the conspecific female blend: 1 µg Z11-16:AL (100%) and varying amounts of Z9-14:AL relative to Z11-16:AL. Maximal 'upwind flight' and 'source contact' were attained between 5% and 50% Z9-14:AL.

Treatment	*N*	Take flight	Cast	Upwind flight	Contact source
+0.1% Z9-14:AL	72	86% b	13% c	0% c	0% c
+1.0% Z9-14:AL	75	97% a	29% b	7% bc	1% c
+5.0% Z9-14:AL	74	99% a	46% ab	20% a	16% ab
+15% Z9-14:AL	69	100% a	61% a	32% a	29% a
+50% Z9-14:AL	68	99% a	54% a	26% a	16% ab
+100% Z9-14:AL	76	93% ab	43% ab	18% ab	10% b

[1]

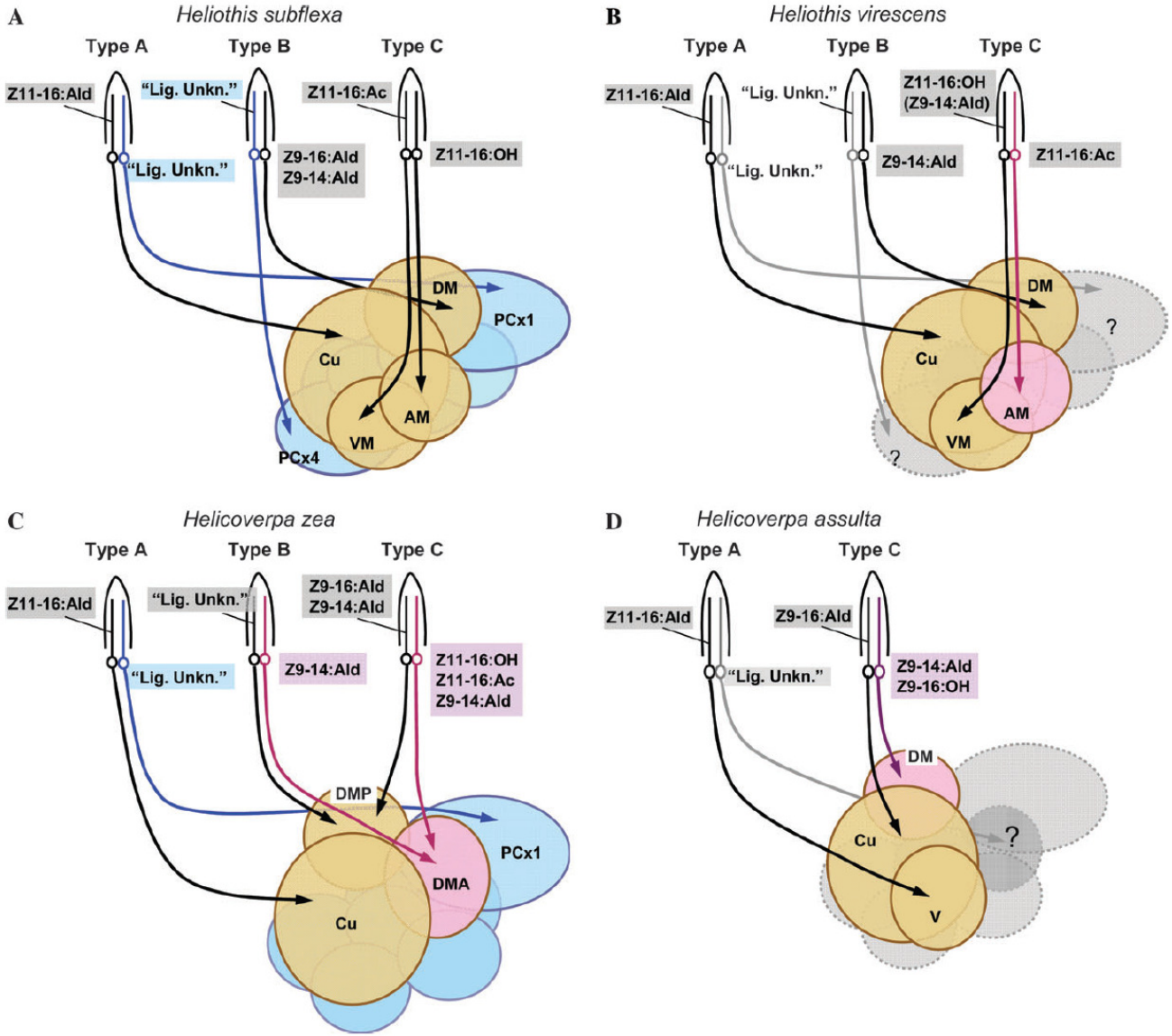
[1] Vickers et al. *J Comp Physiol* **169**:275–80, 1991.

Structure of the moth MGC in *Heliothis virescens*



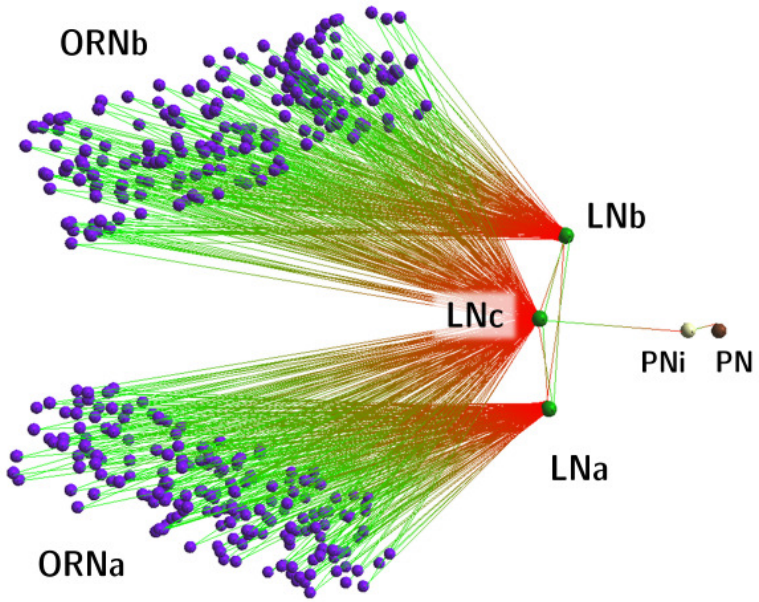
[2] Lee et al. *Chem Senses* **31**:821-34, 2006.

Structure of the moth MGC in *Heliothis* spp



[3] Lee et al. *Chem Senses* **31**:821-34, 2006.

Proposed abstraction for a basic ratio recognition unit



- All connections except ORN-LN are inhibitory;
- LNc will fire if stimulation from ORNs groups is presented in the right 'target ratio' and if g on inter-LN connections are optimal for that ratio;
- PNi and PN are spontaneously oscillating, thus removing the signal amplitude component from LNc.

Experimental protocol: Odour presentation

- Poisson oscillators as source of stimulation (ORNs): $\lambda \propto \log\ c$;

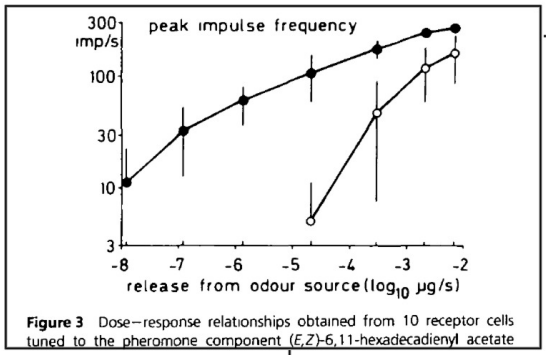


Figure 3 Dose–response relationships obtained from 10 receptor cells tuned to the pheromone component (*E,Z*)-6,11-hexadecadienyl acetate

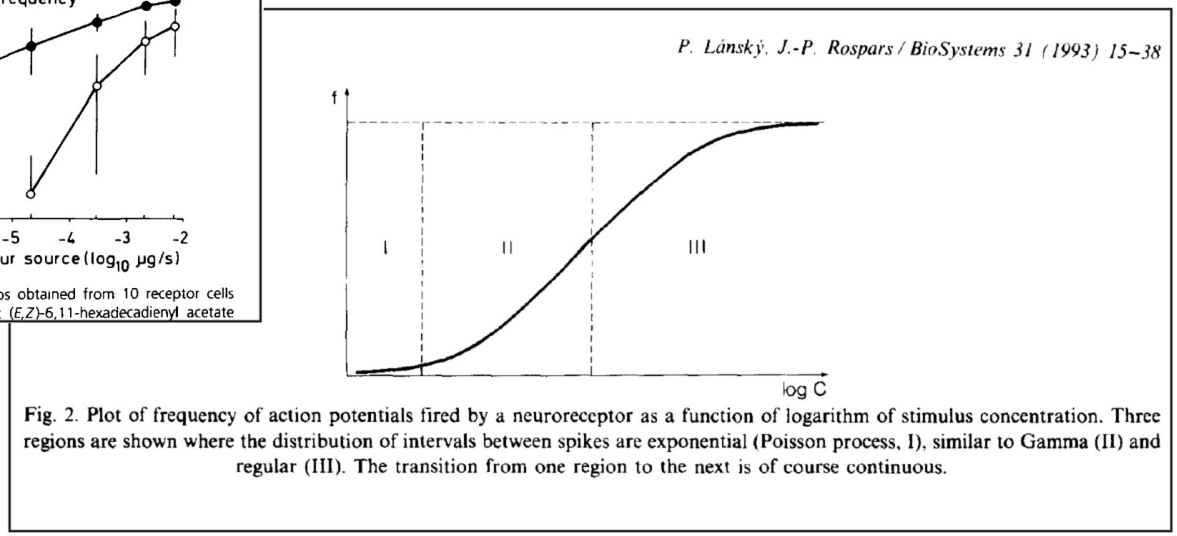


Fig. 2. Plot of frequency of action potentials fired by a neuroreceptor as a function of logarithm of stimulus concentration. Three regions are shown where the distribution of intervals between spikes are exponential (Poisson process, I), similar to Gamma (II) and regular (III). The transition from one region to the next is of course continuous.

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- ORNs grouped, with a certain convergence rate;
- Stimulus presentation for 250 msec, spaced by 250 msec intervals;
- $\lambda_{i+1} = \lambda_i\, 1.3^i$ ($\lambda_0 \ldots \lambda_9$ thus covering around one log unit);
- Cost function (CF) defined as spike density of the PN at midpoint of stimulus presentation.
- 10×10 intensity pairs λ_i *vs* λ_j, in a matrix.

[4] Kaissling *Chem Senses* **21**:257–68, 1996 (left); Lánský & Rospars *BioSystems* **31**:15–38, 1993 (right).

Experimental protocol: Cost function & target profiles

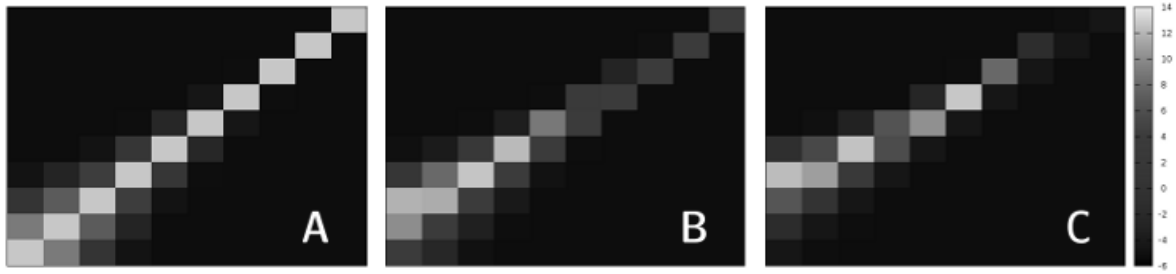


Figure: The weight matrix for the conductance-based setup. Individual weights are $\underline{r}_{i,j} = a\,(\exp\frac{-(C_i - C_j - \ln R)^2}{b^2} - c)$ for the ratio R of 1:1 (**A**), 1:3 (**B**) and 1:9 (**C**), where $C_i = 2 \times 1.3^i$ and $a = 18$, $b = 1.25$ and $c = 0.3$.

- A careful selection of c is key for the CF minimization.

Experimental protocol: Parameters of the model

Synaptic strength	ORN-LN convergence rate		
	200	500	1000
ORN-LNsp			
ORN-LNgen			
LNsp-LNgen			
LNsp-LNsp			
LNgen-LNsp			

Resulting parameters

Synaptic strength	ORN-LN convergence rate		
	200	500	1000
ORN-LNsp	0.0234	0.0341	0.0196
ORN-LNgen	0.0133	0.0235	0.0130
sp:gen	1.76	1.45	1.51
LNsp-LNgen	0.1849	0.1693	0.0738
LNsp-LNsp	0.1848	0.4749	0.0823
LNgen-LNsp	0.1840	0.1199	0.0516

Parameters most affecting cost function

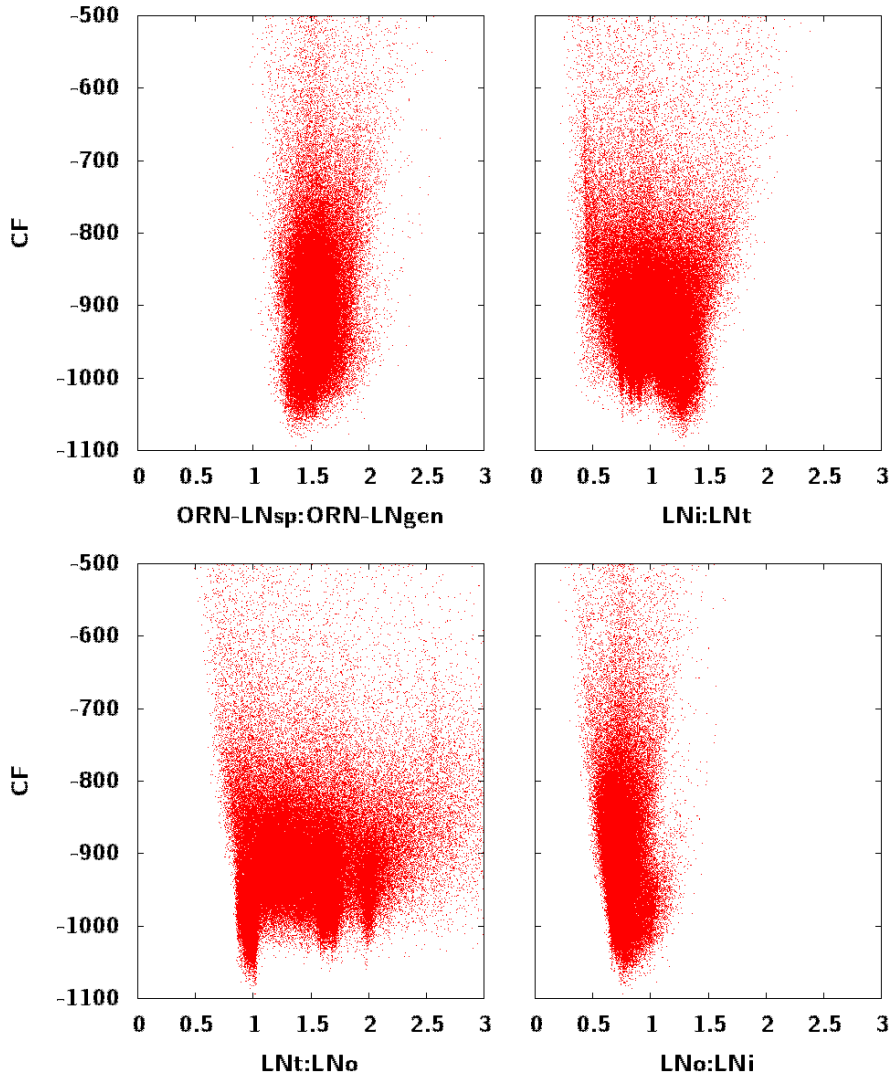
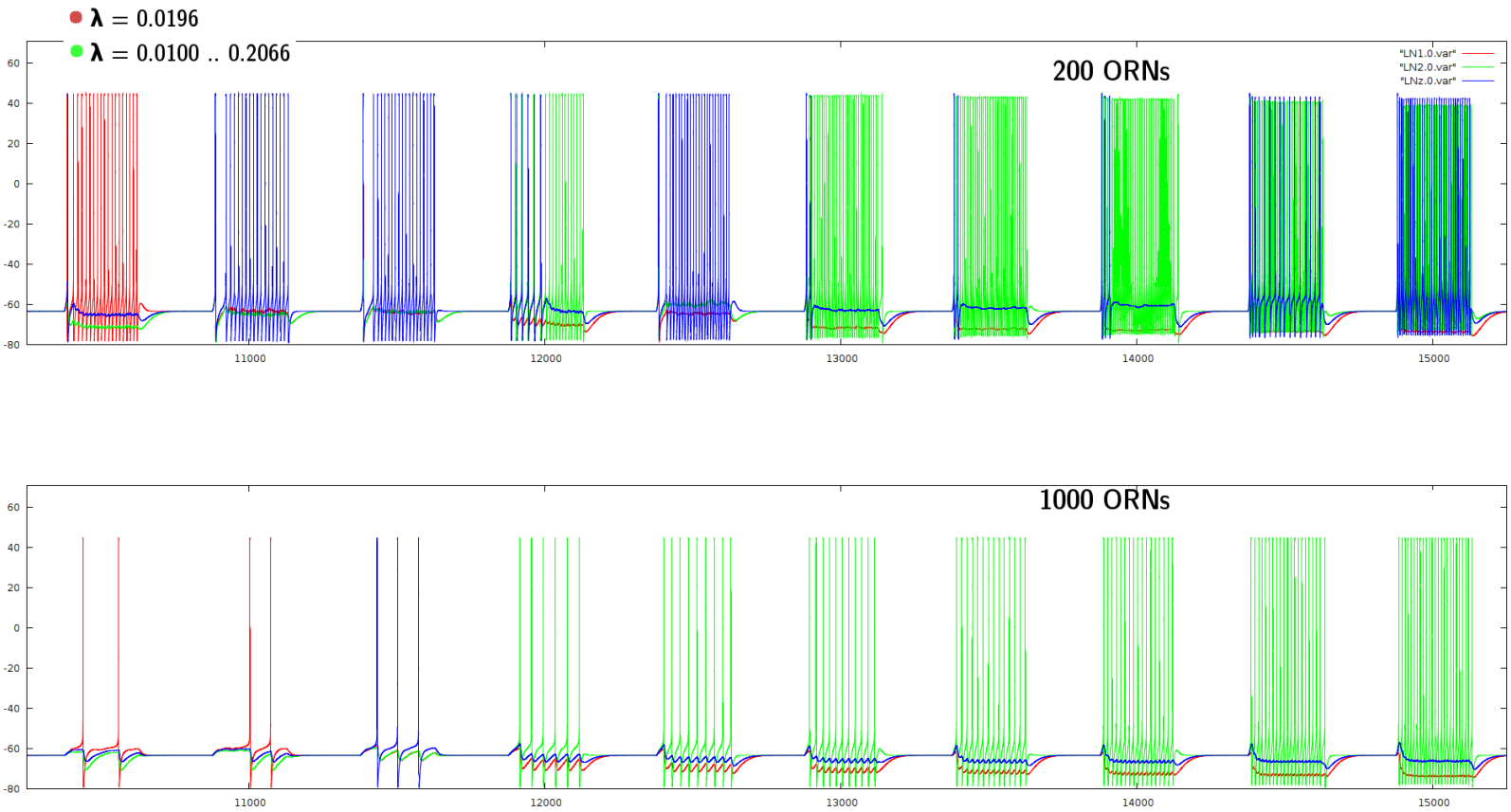


Figure: ORN:LN = 1000, $n = 159,515$.

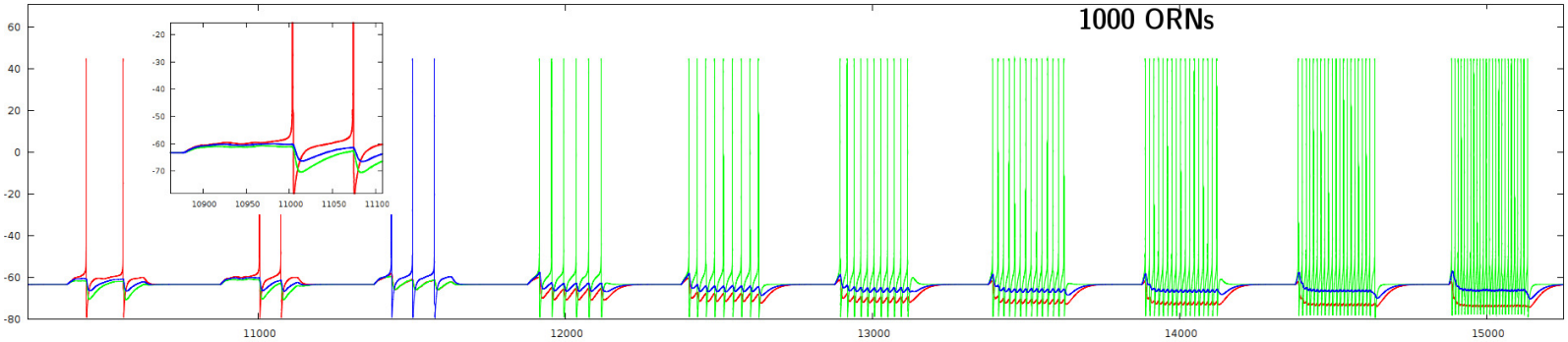
Investigating error causes

- Low ORN-LN convergence rate causes false, or spurious, spikes;
- Spurious spikes prevent a locked LN from yielding.

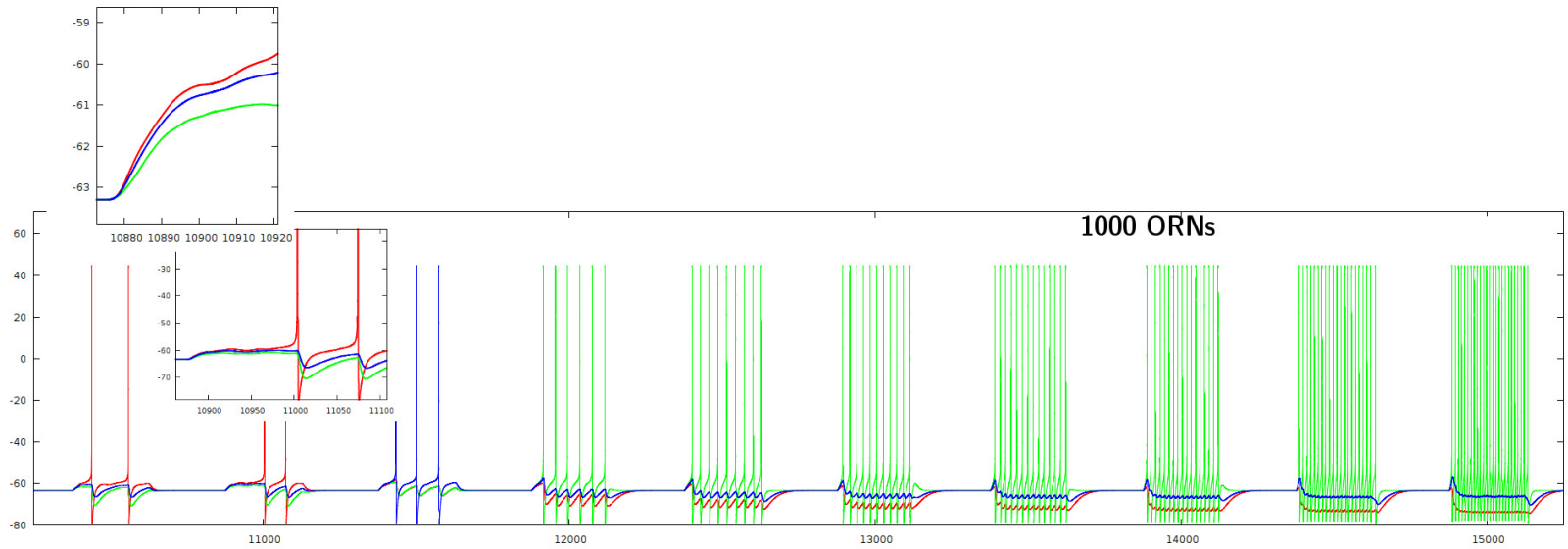
Phasic phenomena: spurious spikes disrupting "target acquisition"



Phasic phenomena: spurious spikes disrupting "target acquisition"



Phasic phenomena: spurious spikes disrupting "target acquisition"



- **Replace native membrane potential E with instantaneous spiking rate F, thus doing away with any phasic events and try to elicit the true competition.**

Finding the optimal convergence rate

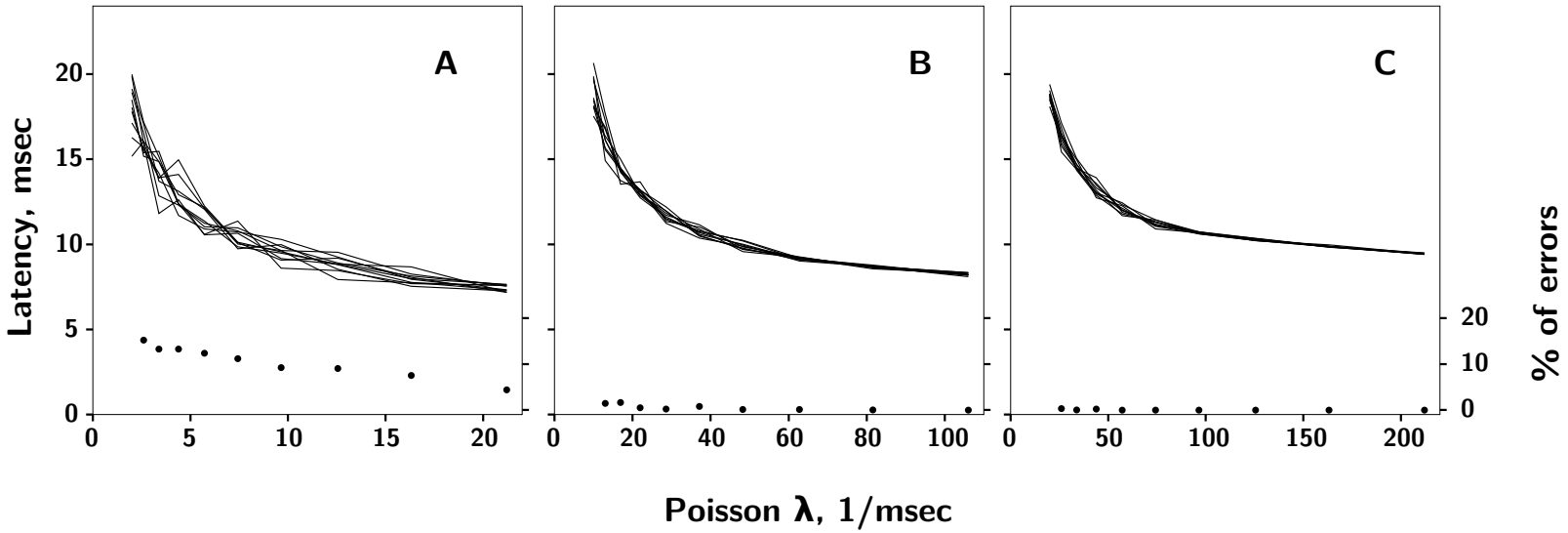


Figure: The HH neuron spiking latency as a function of rate λ of Poisson oscillators, and the distribution of errors in the λ bins, for different numbers of oscillators simultaneously exciting it: 200, 500 and 1000 (**A**–**C**; only 10 trials shown). An error is counted for a given λ bin i when $l(\lambda_i) < l(\lambda_{i+1})$.

Reduction of HH neurons to a rate-based representation (1)

The $\alpha\beta$ synapse

$$\frac{dS}{dt} = \begin{cases} \alpha\left(1 - S(t)\right) - \beta\, S(t) & \text{if } t - t_{\text{spike}} \le t_{\text{rel}}, \\ -\beta\, S(t) & \text{otherwise} \end{cases} \tag{1}$$

$$I_{\text{syn}} = g_{\text{syn}}\, S\,(E_{\text{pre}} - E_{\text{syn}}), \tag{2}$$

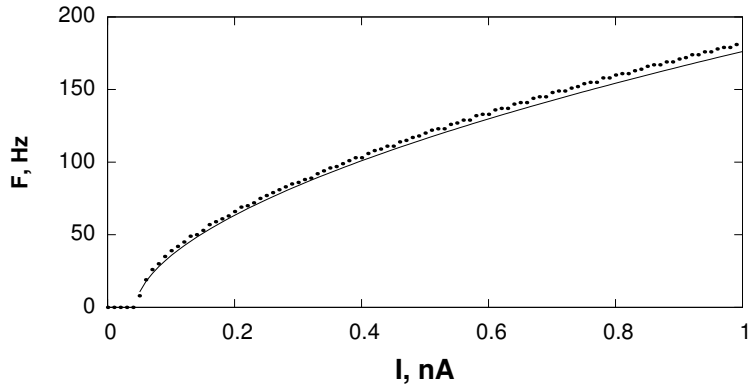


Figure: $F = a\,(I_{syn} - I_0)^r$, where $I_0 = 0.0439\,\text{nA}$, $a = 0.185$ and $r = 0.564$.

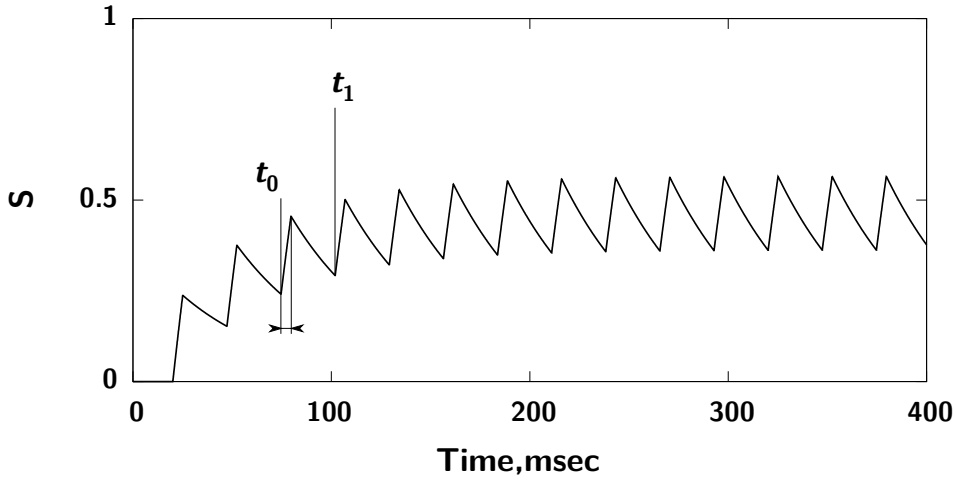
$$\frac{dS}{dt} = \begin{cases} \alpha - \beta\, S(t) & \text{if } t - t_{\text{spike}} \le T, \\ -\beta\, S(t) & \text{otherwise} \end{cases} \tag{3}$$

which we want to reduce to a form $dS/dt = -\beta\, S + \gamma$.

Reduction of HH neurons to a rate-based representation (2)

Let t_0 be a time where spike occurs and $t_1 = t_0 + 1/F$, and assume $1/F > T$. Then,

$$\begin{aligned} S(t_0 + T) &= \frac{\alpha + \left(S(t_0)\,\beta - \alpha\right) e^{-\beta\,T}}{\beta} \\ &= \frac{\alpha}{\beta}\,(1 - e^{-\beta\,T}) + S(t_0)\,e^{-\beta\,T} \end{aligned} \tag{4}$$



And, for the decay part,

$$\begin{aligned} S(t_1) &= S(t_0 + T)\,e^{-\beta\,(\frac{1}{F} - T)} \\ &= \frac{\alpha}{\beta}\,(1 - e^{-\beta\,T})\,e^{-\beta/F + \beta\,T} + S(t_0)\,e^{-\beta/F} \end{aligned} \tag{5}$$

Reduction of HH neurons to a rate-based representation (3)

Remembering that $S(t_1)$ can be reached in a single step via a similar function with γ, we can, after bringing the solution of $dS/dt = -\beta\, S + \gamma$ for $S(t)$ to the form similar to (4), equate

$$S(t_1) = \frac{\gamma}{\beta}(1 - e^{-\beta/F}) + S(t_0)\, e^{-\beta/F} \tag{6}$$

Removing the common term $S(t_0)\, e^{-\beta/F}$ from (5) and (6) produces

$$\frac{\alpha}{\beta}\,(1 - e^{-\beta\, T})\, e^{-\beta/F+\beta\, T} = \frac{\gamma}{\beta}(1 - e^{-\beta/F}) \tag{7}$$

simplifying the left-hand side of which and solving for γ we get

$$\gamma = \alpha\, \frac{e^{\beta\, T} - 1}{e^{\beta/F} - 1} \tag{8}$$

Resulting parameters (rate-based HH)

Synaptic strength	ORN-LN convergence rate		
	200	500	1000
ORN-LNsp	0.0104	0.1136	0.0342
ORN-LNgen	0.0087	0.0620	0.0206
sp:gen	1.20	1.83	1.66
LNsp-LNgen	0.1531	0.1373	0.0977
LNsp-LNsp	0.0848	0.1413	0.1874
LNgen-LNsp	0.0750	0.1447	0.0987

Competition in the rate-based model

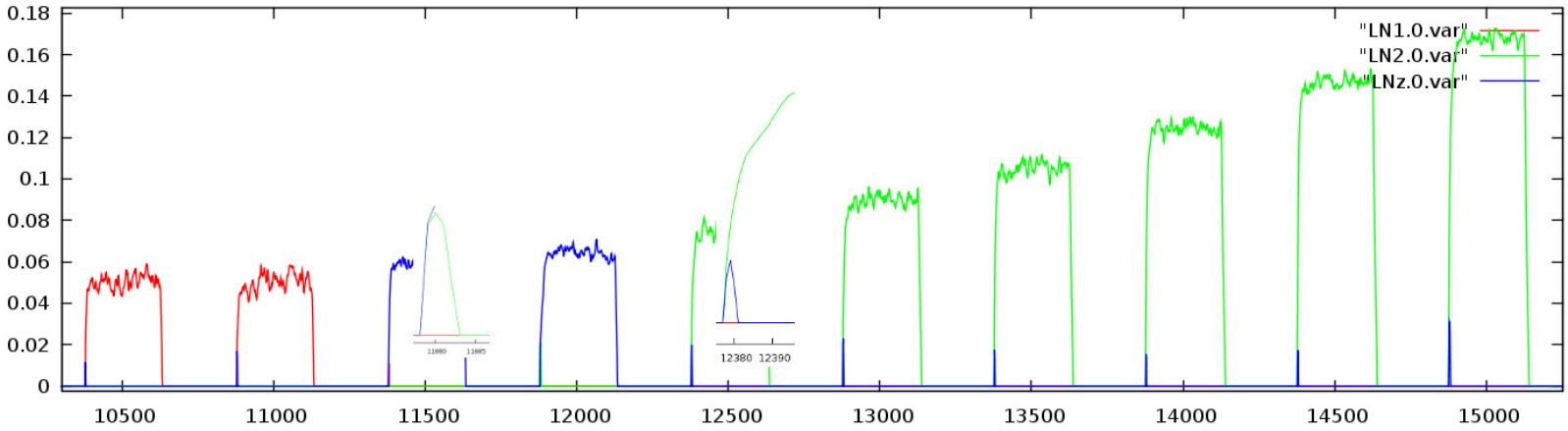
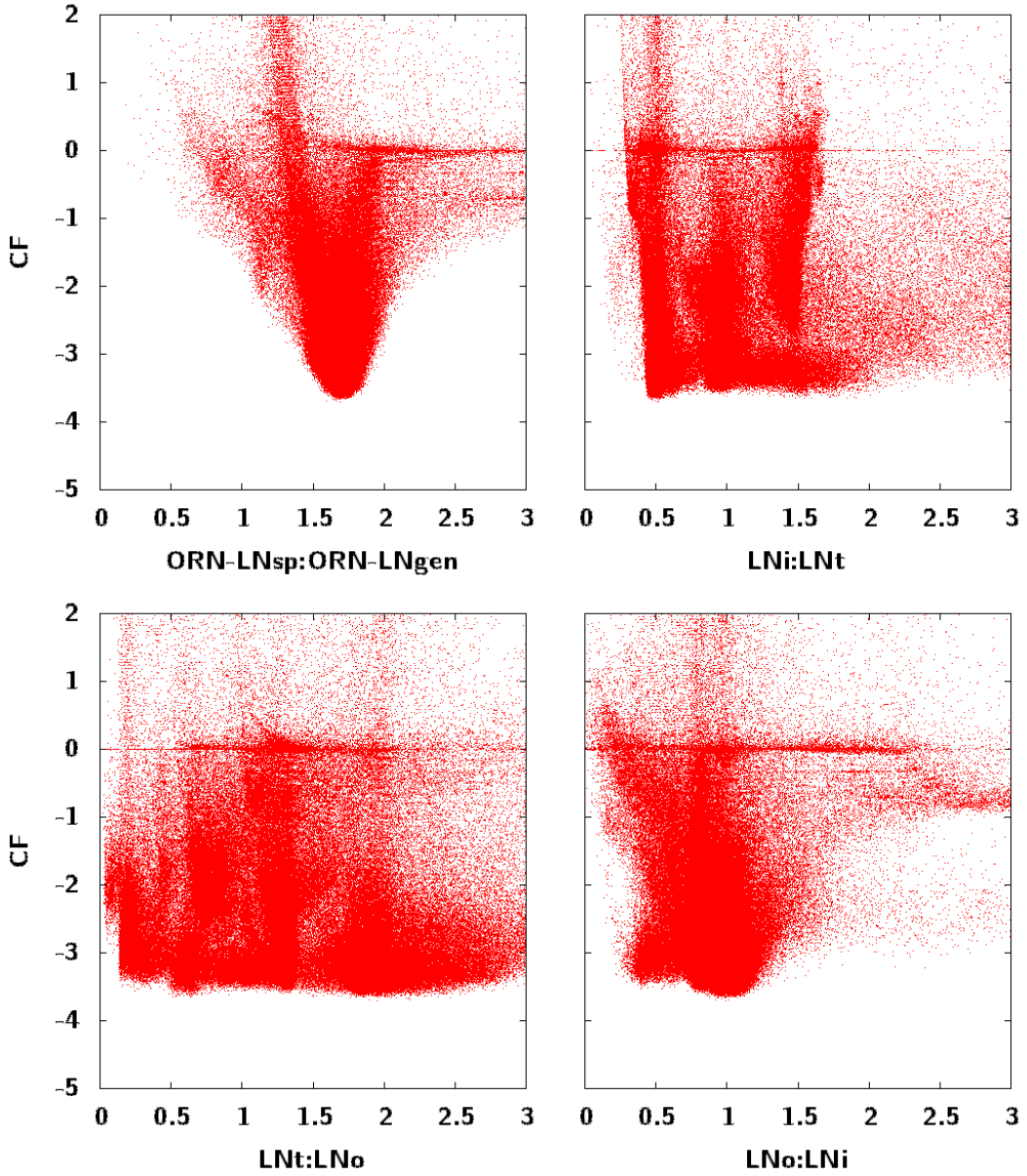


Figure: Rate-based setup, ORN-LN convergence rate 1000. Pure competition, unaffected by spikes.

Parameters *vs* cost function (rate-based)



Invariant properties of the model

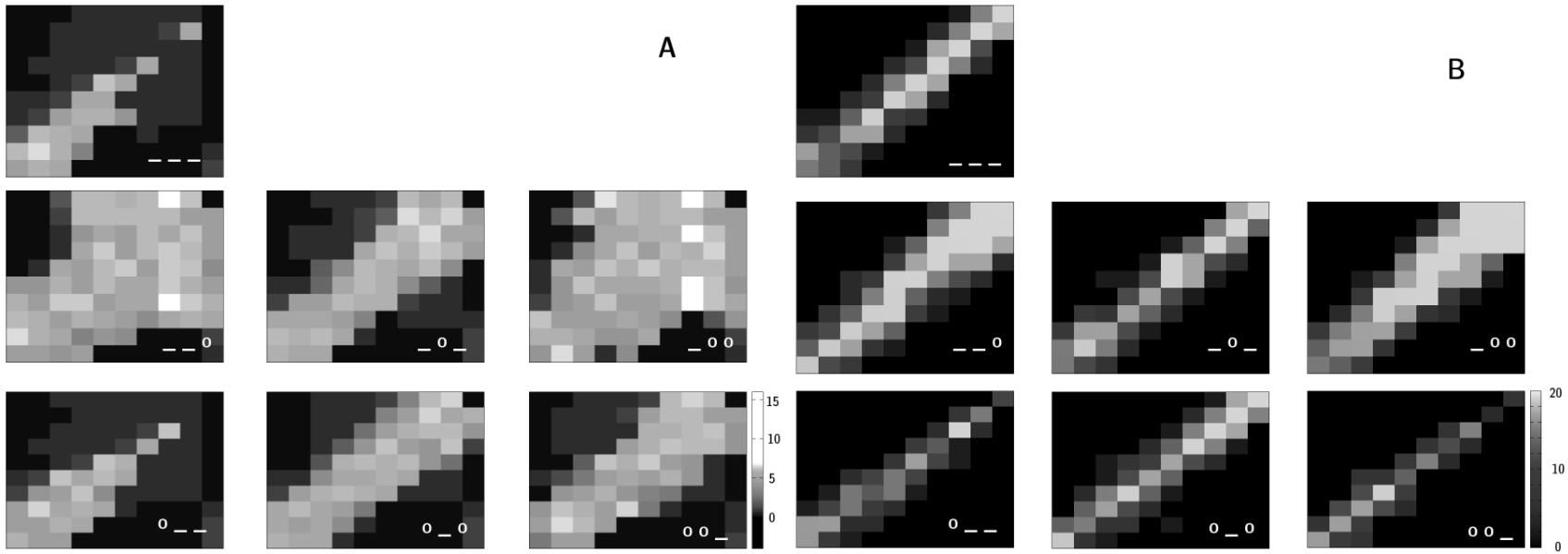


Figure: Features of the model built with original HH neurons (**A**) and with rate-based reductions (**B**). The code in each panel shows g on LNsp-LNgen, LNsp-LNsp and LNgen-LNsp connections, where **"_"** is $0.18\,\mu\mathrm{S}$ and **"o"** is $0.27\,\mu\mathrm{S}$. The x- and y-axes represent the concentration of individual component in the blend as a log of Poisson rate; squares show the SDF as a colour-coded value (A) or the average spiking rate (B). ORN-LN convergence rate used is 1000, with $g_{\mathrm{ORN-LNsp}} = 0.0371\,\mu\mathrm{S}$ and $g_{\mathrm{ORN-LNgen}} = 0.0218\,\mu\mathrm{S}$.

Non-1:1 ratios

Synaptic strength	Target ratio	
	1:3	1:9
ORN-LNsp(a)	0.0229	0.0227
ORN-LNgen(a)	0.0131	0.0140
ORN-LNsp(a)/ORN-LNsp(b)	1.0718	1.5008
ORN-LNgen(a)/ORN-LNgen(b)	1.0739	1.2929
inter-LN	0.2542	0.2041

LNi = LNo = LNt.

Conclusions

- **The ORN-LN convergence rate needs to be around 400 to reduce the incidence of spurious spikes below 5%;**
- **Inter-LN synaptic strengths are not critical in a competition-based model, except that**
- **$g_{\mathrm{LNgen-LNsp}}$ must be close to $g_{\mathrm{LNsp-LNgen}}$;**
- **HH rate-based reductions retain the features of the model, albeit much attenuated;**

(contd.)

- **New things are just those well-forgotten old things.**

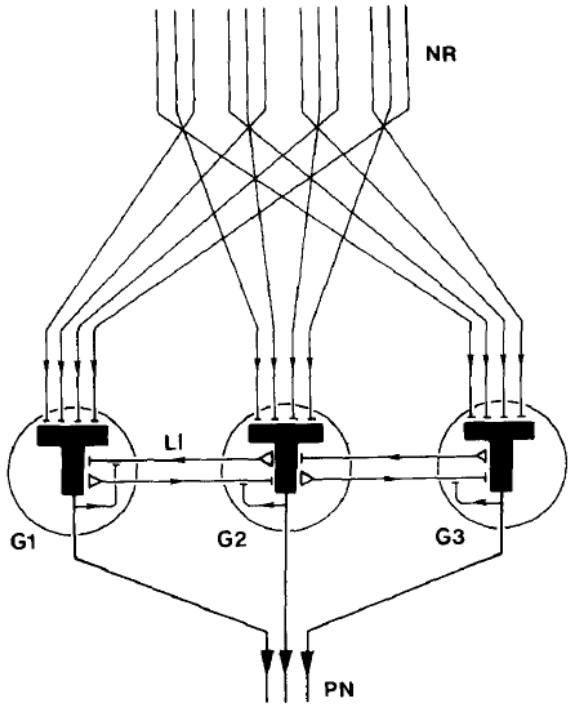


Fig. 3. Simplified circuitry of the arthropod antennal lobe and vertebrate olfactory bulb, showing the three main types of neurons and their synaptic connections. First-order input neurons NR (neuroreceptors) make excitatory synapses onto second-order (principal) neurons PN. Local inhibitory LI neurons mediate lateral inhibition and self-inhibition. All synaptic interactions in arthropods, and part of them in vertebrates, take place within distinctive subunits named glomeruli (G). All neurons and synapses are involved in intensity coding.

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Thank you

[5] Lánský & Rospars *BioSystems* **31**:15–38, 1993.