Transient Dynamical Processing in the Moth Macroglomerulus

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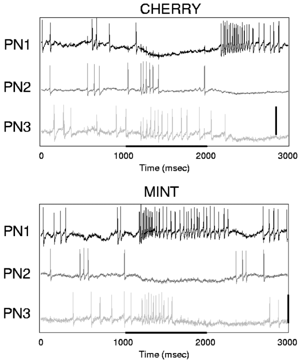
This Talk

- The Dynamics of Olfaction.
- Nonlinear Dynamical Frameworks.
- The Model.
- Critical Dynamics in the MGC.
- Conclusions and Future Work.

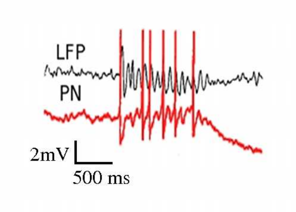
The Dynamics of Invertebrate Olfaction



The dynamics of the *general olfactory system* in locust are thought to arise from two distinct processes:

- Slow multiphasic rate patterning (order 500ms).
- Return to a baseline after odour subsides.
- Arise from LN's connected through slow GABA$_B$ synapses.

The Dynamics of Invertebrate Olfaction



- Relatively fast but transient local field potential (LFP) oscillations (periods of order 50ms).
- Reflect synchronisation of PN spiking events.
- Mediated by fast GABA$_A$ synapses.

The Dynamics of the MGC

- Slow patterning observed in the MGC.
- Whether there are significant oscillations in the LFPs is still unclear.
- Perfusing the bee with picrotoxin and blocking synchronisation had only a weak affect on cognitive performance.
- Suggest the primacy of rate patterning even in general olfaction?
- Here we focus on the rate dynamics of the system as mediated by the GABA_B synapses.

Phenomena of Interest

	Responses patterns summary
+	Excitatory response (tonic)
+/-	**Excitation (burst) / Inhibition ('classic PN response')**
+/- -	Excitation (burst) / long inhibition
+ +/-	Excitation (long burst, tonic) / Inhibition
-/+	Inhibition / Excitation
-/+/-	Inhibition / Excitation / Inhibition
+/-/+	**Excitation (burst) / Inhibition / Excitation (tonic)**
-	Inhibition

Question:

- What kind of rate dynamics could account for this *multiphasic profile* and its subsequent return to a unique baseline rate?

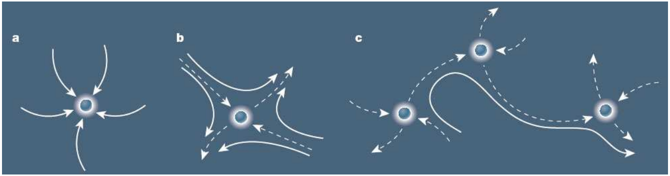
Phenomena of Interest

- The firing rate of the excitatory period is responsive to pheromone concentrations between 0.001 to 10 ng.

Question:

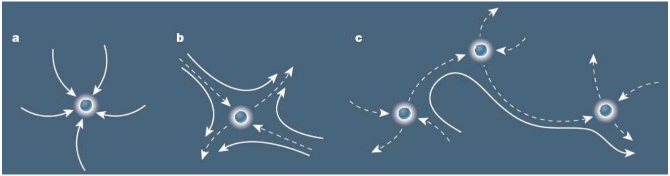
- What kind of rate dynamics could account for the *sensitivity* and *dynamic range scaling* of the MGC.

Heteroclinic Orbits



- The slow patterning dynamics are described by sequence of transitions between saddle equilibria (Rabinovich et. al. 2001).
- Odour *reparameterises* the orbit (rather than setting the initial conditions).
- The odour identity is described by the temporal dynamics of the system.

Heteroclinic Orbits



- The theory is done in the Lotka-Volterra model which was developed in ecology.
- Lotka-Volterra has weaknesses as a neural model.

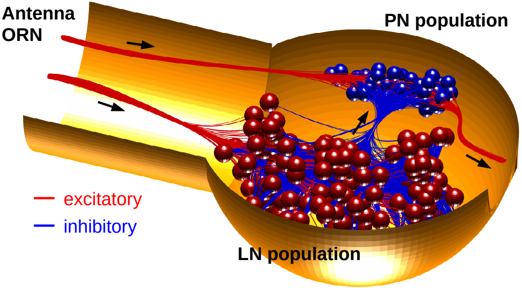
$$\dot{a}_i = a_i \cdot F(g_{ij}, a_j)$$

- Consequently it is not clear how to build a biologically plausible model of this.

Reservoir Dynamics

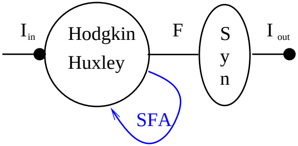
- *Liquid* and *echo* state paradigms (Maas, W. et. al. 2002 and Jaeger, H. 2002).
- Perturbations produce stimulus specific transient excursion that eventually fade back to baseline.
- Described by a *single* globally stable fixed point attractor.

The Network



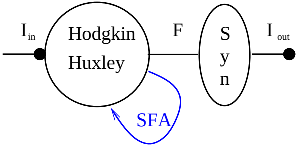
- ORN-LN (excitatory).
- A large random, recurrent network of LN-LN (slow inhibitory, $GABA_B$).
- LN-PN (inhibitory).

The Neurons



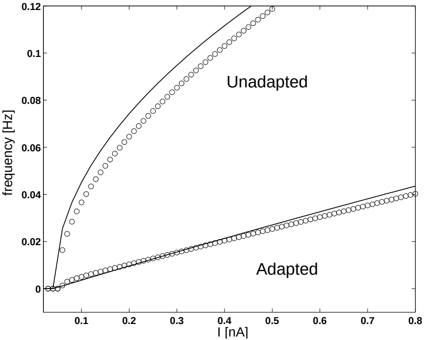
- Hodgkin–Huxley neuron model.
- Spike frequency adaptation via a calcium-dependent potassium current.
- Neurons coupled through a standard first order "$\alpha - \beta$" synapse (Destexhe et.al. 1994).

The Neurons



- GABA_B synapses are much slower than the membrane dynamics.
- Adiabatically eliminate the membrane dynamics.
- Represent the whole system in terms of the synapse variable which can be transformed to a rate.
- The goal is to produce a set of first order ODE that we can do some analysis with.

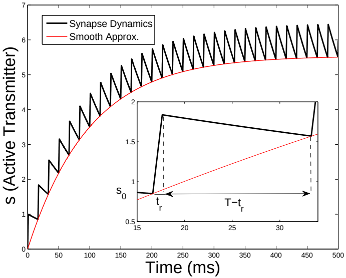
First step: Eliminating the Membrane Dynamics



The F-I curve of a Hodgkin–Huxley model with spike frequency adaptation is well approximated by

$$f_{adapt}(I - I_c) = \frac{-A^2 g\beta + \sqrt{[A^2 g\beta + 4A^2(I - I_c)]}}{2}$$

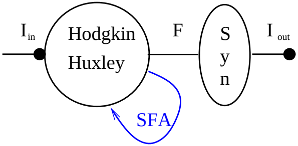
Second step: Approximating smooth synapse dynamics



- Construct a smooth system that has the same dynamics as the discontinuous "$\alpha - \beta$" synapse.

$$\mu(F) = \frac{\alpha e^{\beta t_r} - 1}{e^{\frac{\beta}{F}} - 1} \qquad \dot{s} = -\beta s + \mu(F)$$

Putting it all together

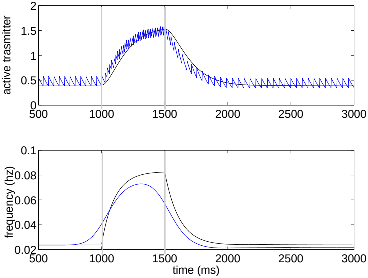


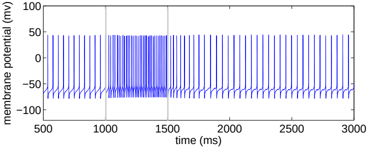
$$\dot{s_i} = -\beta s_i + \gamma \left[\sum_j g_{ij} s_j + I_c^i \right]$$

- The frequency of the i^{th} neuron is just

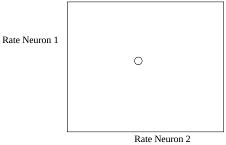
$$F_i = f_{adapt}(\sum_j g_{ij} s_j)$$

Example Dynamics



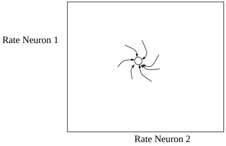


Developing Conditions for the Reservoir Property



1. Specify a baseline rate (point equilibrium) by adjusting the constant input current.

Developing Conditions for the Reservoir Property



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2. Ensure the system returns to baseline under small perturbations (local stability) by constraining the synaptic weights (condition the eigenvalues of the Jacobian).

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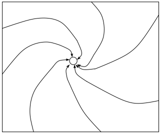
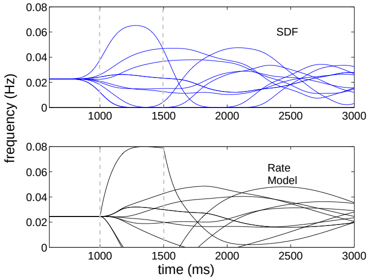
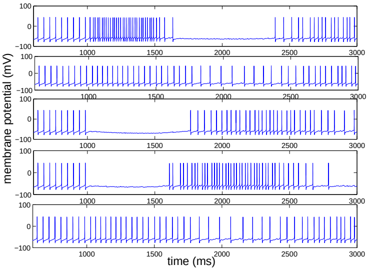


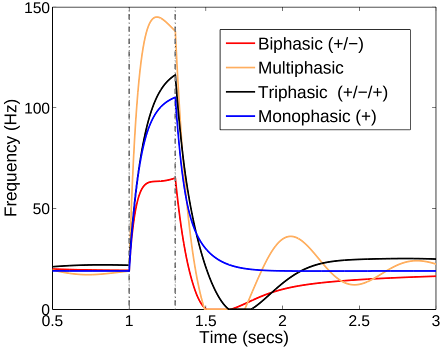
1. Specify a baseline rate (point equilibrium) by adjusting the constant input current.
2. Ensure the system returns to baseline under small perturbations (local stability) by constraining the synaptic weights (condition the eigenvalues of the Jacobian).
3. Proof that if the baseline state (point equilibrium) coincides with the most sensitive part in the rate dynamics then the system will return for all sizes of perturbations (global stability).

Example Dynamics



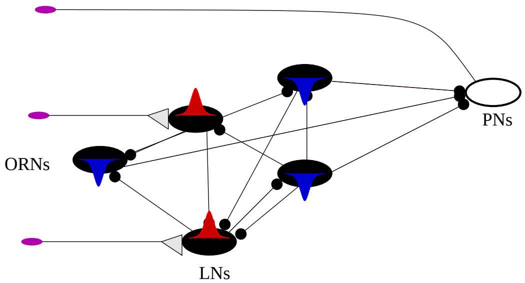


Explaining the The Dynamics



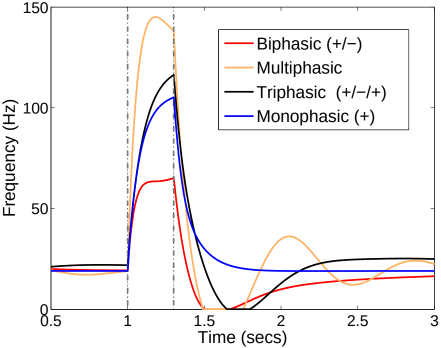
- Dynamics can be split into two regime: During and after stimulation with pheromone.

During Stimulation



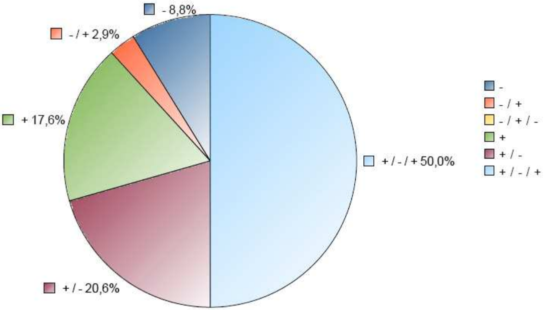
- During stimulation a minority subset of LNs become 'winners'.
- These inhibit the majority of LNs which become losers.
- PNs receive summed input from the LNs.
- The majority of losers result in the disinhibition of PNs.
- Provides disinhibition in addition to direct ORN connections.

After Stimulation



- Asymmetries in the synaptic weights mean they settle in a transient oscillatory manner.
- Could account for the phasic profile we see in the data.

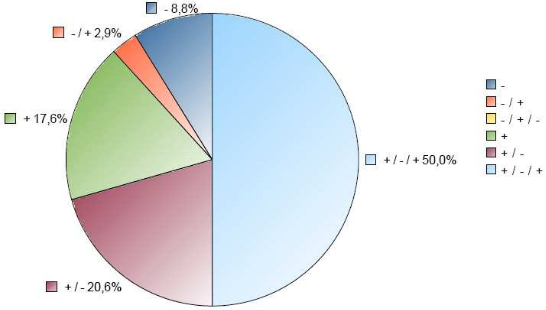
Predictions and Inference



Prediction:

- The number of phases of a given PN will depend on the concentration.
- Use this to determine whether the MGC dynamics are best described by a heteroclinic orbit or reservoir dynamics.

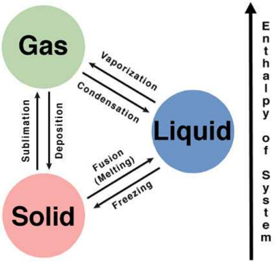
Predictions and Inference



Inference:

- At a given concentration the distribution phasic profile across the PN's depends on the degree of asymmetry.
- Maybe possible to use this to infer the connectivity of the LN network.

The Critical Brain Hypothesis



- Alan Turing speculated that the brain may exist in a "barely critical state".
- Brain dynamics are not completely ordered (inert) or completely disordered (wild oscillations).
- Inspired by the notion of a critical point of a phase transition in physics.
- Critical point in physical systems possess a suite of unique properties.

The Critical Brain Hypothesis

Similarly, the dynamics of neural networks at an analogous critical point has been shown to confer

- Signal transmission (Beggs, J. et al. 2003).
- Information storage (Haldeman, C. et. al. 2005).
- Sensitivity and dynamic range (Kinouchi et al. 2006).
- Computational properties (Legenstein, R. et. al. 2007).

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Experimental evidence

- Beggs et al. (2003) claimed that data from organotypic cultures and acute slices of rat cortex exhibit the hallmarks of criticality.
- As of yet there is no convincing *in vivo* evidence for criticality.

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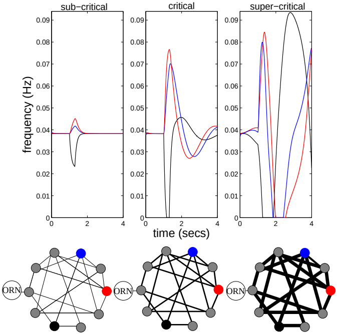
The Critical Brain Hypothesis

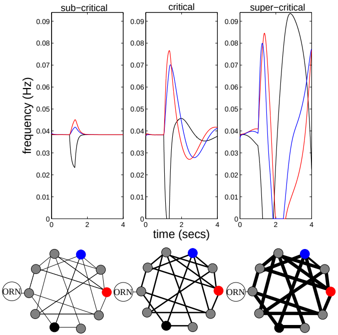
- The current theory and formalism draws heavily on physical models.
- Only works for excitatory networks of excitable neurons that have low rate.
- MGC is inhibitory and has a high baseline rate.
- Kinouchi et. al. (2007) tried to explain the dynamic range of the olfactory bulb by suggesting gap junctions underpin and excitable network.
- Gap junctions have not been observed in the MGC and the dynamics do not look like an excitable system.

Critical Dynamics in the MGC



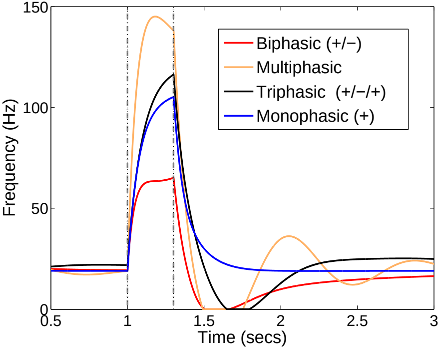
- Here we define the critical point where the baseline state (point equilibrium) is barely stable (just before the bifurcation).
- A related concept idea has been used to explain the sensitivity of hair bundles in the auditory system (Camalet 2000).

Critical Dynamics in the MGC



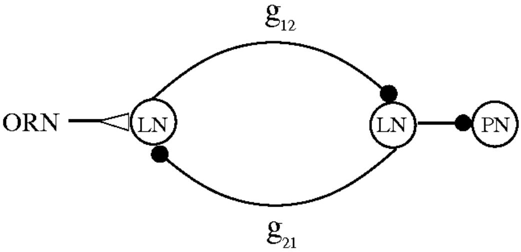
- Weak synaptic weights (subcritical) lead to dynamics that are of of low amplitude, short lived and monophasic.
- Strong synaptic weights (supercritical) lead to saturating, oscillatory, or even chaotic dynamics.

Dynamic Range and Sensitivity



- Want to understand how the initial rise scales with input current.

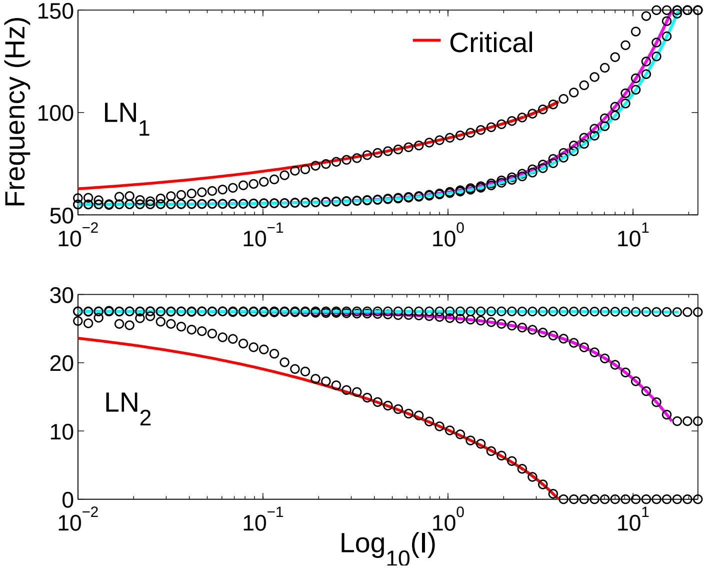
Dynamic Range and Sensitivity



An excitatory response in the projection neuron arises from disinhibition in the local neurons.

- LN1: Takes input from ORN.
- LN2: Outputs to a projection neuron.

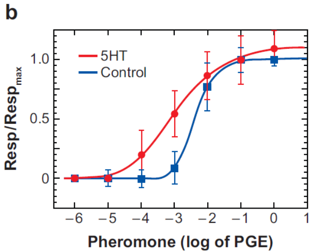
Dynamic Range and Sensitivity



Looking for Criticality

- With the help of Antoine we have begun looking for signature of criticality in the data.
- *Critical slowing down*: Some variables of critical system will take a very long time to return to baseline. Antoine's data shows 60 second transients.
- *Critical fluctuations*: The statistical distribution of the fluctuations around baseline will be senstive to the critical point. Initial results are promising but not enough data to show it categorically.

Looking for Criticality



- Perfusing MGC with 5HT when the moth is in an inactive phase increases the dynamic range (Kloppenburg 2008).
- Suggests the systems is closer to criticality when the moth is in a state of arousal.
- Look at how baseline fluctuations and the critical exponents change with arousal state and the application of 5HT.

Future Work

Experimental

- Look for the hallmarks of criticality in the experimental data. Could constitute the first evidence of criticality *in vivo*.
- Infer the LN connectivity from the distribution of phasic responses.

Theoretical

- Determine whether reservoir or heteroclinic dynamics are the most appropriate paradigm for the MGC.
- Extend the model to the general olfactory system. We can use the fact that it was inspired by reservoir computing ideas.

Thank you!