Network Activity: Oscillations, Patterns, Waves

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Game Plan

• Organised in time: Oscillations
  – Central Pattern Generator
  – Gamma Oscillations: inhibitory control of synchrony

• Organised in Space
  – Patterns in disinhibited cortex
  – Funky waves

• Presentation and Refs List:
  www.gnt.ens.fr
Take Home Message

- Organised network behavior can appear without organised inputs.
- Synaptic mechanisms organise network behavior into oscillations: fast excitation/slow inhibition.
- Inhibition is crucial to synchrony.
- Patterned connections give rise to organised network behavior without patterned inputs.
Oscillations is not a new thing

Hans Berger first published EEG (1929).

Olfactory bulb (Adrian, 1930s)

Theta (5-10Hz) oscillations in the hippocampus

Up- states in neocortex in vivo and in vitro

Sanchez-Vives and McCormick, Nat. Neurosci. 3, 1027

Synchronization of up states between the neocortex and the hippocampus

LFP: neocortical field potential; MP: hippocampal interneuron memb. pot.

Hahn, Sakmann and Mehta, Nat. Neurosci. 9, 1359 (2006)
Measuring Rhythms In Vivo

Rhythms can be seen in

EEG/MEG recordings

Excellent temporal resolution

Bad spatial resolution

Field recordings

Single-cell recordings
Power and Synchrony Change Dynamically, In Task-Oriented Manner

Tallon-Baudry et al., J. Neurosci 2001
Gamma Frequency Oscillations
Some rhythms in the nervous system:

- delta (1-4 Hz)
- theta (4-12)
- alpha (9-11) Hz
- beta (12-30)
- gamma (30-90)
- spindling (11-15)
- ripples (100-200)
- slow ( <1 Hz)

- These are associated with a variety of cognitive states.
- Frequency ranges are somewhat arbitrary and overlapping.
- Needed: classification by mechanisms, not (just) by frequency.
How to organise these oscillations?

1. Central pattern generator gives inputs to the whole cortex, bulb, hippocampus and organises the activity
2. Oscillations and synchrony is self-organised

Central Pattern Generators: plenty in subcortical structures:
- circadian rhythms: supra-chastrmatic nucleus
- brain-stem: control of motion
- isolated spinal chord
  Locus Coeruleus can be one at times.

How do you build a CPG (Oscillator)?
CPG/Wilson-Cowan Oscillator

Populations of neurons described with firing rates sigmoid input/output coupling is analog

Self-excitation is strong enough
Feedback inhibition is strong enough
Inhibition is slow enough
External input is just right
Input controls existence of oscillations

Speed of inhibition amplitude existence of oscillations and their frequency

Strength of excitatory to inhibitory coupling controls amplitude
Synchrony in a network of CPGs

Key: fast (recurrent) excitation, slow inhibition
Sustained synchronous oscillations in slices! (no CPG)

Tetanic stimulation of CA1 slice activates metabotropic Glu transmission:

- Slow excitation
- GABA-A relatively fast inhibition

Bartos, Vida, Jonas 2006
Cholinergic induction of 40 Hz oscillations in rat hippocampal slices

The Hippocampal network: The hippocampus forms a principally unidirectional network, with input from the Basolateral (BL) and corniculate (CN) complexes with the Dentate Gyrus (DG) and CA3 pyramidal neurons via the Schaffer Collateral Pathway (SC), via the entorhinal cortex (EC) and CA3 pyramidal cells via the Extracellular Pathway (EC), as well as to CA1 pyramidal cells via the Schaffer Collateral Pathway (SC), as well as to CA1 cells in the entorhinal cortex (EC) and to the dentate gyrus (DG). CA3 neurons receive input directly from the perforant Path and send axons to CA1 pyramidal cells. CA1 pyramidal cells send the main hippocampal output back to the EC, forming a loop.

The figure shows the power spectrum of CA3 activity under control conditions, with +20 μM Carbamol and -10 μM Pirenzepine, indicating the induction of 40 Hz oscillations by cholinergic stimulation.
Them Gammas are not the same Gamma!
Gamma Oscillations: inhibition vs excitation?

How can we understand these results?
Math/Models to the rescue!

Consider that neurons are tonically firing even if disconnected
Neurons = Oscillators
Consider that synaptic coupling is relatively weak
Develop a theory that allows to understand what are the important players:

• Excitation
• Inhibition
• Intrinsic properties
• Frequency dependence of synchrony
Synchrony with inhibition

- Math analysis of a pair of weakly coupled oscillators shows that synchrony is stable with:
  - Excitation if synapses are instantaneous
  - Inhibition if synapses have a finite time course
- Van Wreeswijk et al. 1995
- This depends on the intrinsic properties of the cell as defined by its

  Phase Response Curve
Phase Response Curves: effect of input on spike time

Define Phase:
Natural position for \( x_0 \) -- the top of the spike, or the time of the spike

Define PRC

\[ t \text{ or } \theta \quad T' \quad T \text{ or } 2\pi \]

\[ \% \text{ change } T \]
Experimental PRC Construction

Reyes and Fetz, 1993
Two classes of PRC

Class 1
PRC - positive

Class 2
PRC - bi-modal

Entrainment with inhibition

Entrainment with excitation
Potassium currents control the shape of the PRC

Spike-dependent AHP

Voltage-dependent AHP
Spike to spike synchrony: 2 cell analysis

- Consider two coupled oscillating neurons
- Find phase configurations where neither neuron changes its neighbor phase: fixed phase difference solutions (phase-locked)
- By symmetry: in-phase and out of phase solutions are always possible
- Which is stable?

Van Vreeswijk et al (1995) analysis:

Phase difference vs. Synaptic speed
Synchrony with inhibition or excitation depending on intrinsic properties

Fast excitation, inhibition

Fast inhibition, excitation
Neurons with adaptation (I-M) synchronize with excitation.

PRC shape controls mechanisms of synchrony.
Synchronization depends on firing frequency

- Speed of synapse is relative to the firing frequency
- PRC shape changes with firing frequency
ING (Interneuronal Network Gamma)

- Important currents: spiking and inhibition
- PRCs is of type II (fast inhibition)
- Cells track inhibitory conductance
- Decay time of inhibition determines period
- Interneurons fire on every gamma cycle
- Pyramidal neurons fire intermittently (coupling is weak)

(Whittington, Traub; White, Chow, Ritt, NK; Wang, Buzsaki)
Pyramidal Interneuron Network Gamma (PING)

Whittington et al., J. Physiol. 1997

- E-cells (type I) are synchronized by I cells, I cells (type II) are synch’d by E-cells
- Pyramidals fire at every cycle
- Synchrony of both pops. depend on number of inputs to each cell
- Change of parameters can destroy PING synchrony but create ING synchrony: weaker, slower excitation, slower inhibition
Summary of synchrony

• Inhibition is needed for spike-to-spike synchrony
• Oscillations can be induced and synchronised by a number of mechanisms:
  • fast excitation + slow inhibition
  • slow excitation + fast inhibition
• Synchrony does not necessarily depend on pyramidal neurons
• Intrinsic properties determine the synaptic mechanisms

• Shape of the PRC depends on the firing frequency: implies changes in synchrony at different bands:
  • Kopell et al 1999: Gamma and Beta have different synchrony properties.
Shunting inhibition + gap junctions - robustness of spike to spike synchrony to noise

• PING is coherent with heterogeneity, sparse coupling
• ING is very sensitive to noise and heterogeneity

Vida, Bartos, Jonas 2006
Coherent Oscillations in a single cell: dendritic mechanisms

Shunting inhibition on trunk

soma
Fast excitation synchrony in WM network: excitable cells

Slow excitation: NMDA

+AMPA

Compte et al 2000
Spatial Patterns in cortical models

• Let us consider a network of neurons (populations) with spatially structured connections:
  • mexican hat
  • fast local excitation
  • slower wider inhibition

• Connectivity scales determine stable states with homogeneous input:
  • Inhibition dominated: “linear homogeneous state”
  • Excitation Dominated: “All active epileptic state”

• Slightly disinhibited state:
  • Symmetry breaking, Turing instability
  • math predicts patterns!
Neural Field Models: Spatially structured connectivity

Describe neurons with firing rates

Spatially disorganised input

Spatially organised output
Example of pattern forms in cortical networks

Cortex activity

Retinotopic transform

What you would perceive

LSD

Kluver's hallucination

form constants

Gutkin et al. 2003
Pattern formation and orientation preference

Ernst et al 2001

Average activity

Model

Model stimulated with bars

VSD data V1

From Bonhoeffer
Experimental Evidence for Spontaneous Patterns in V1

• Average patterns have a specific order of “appearance”
  • Stripes
  • Blobs
• Math predicts a hierarchy of patterns
• In time blobs should change spatial phase randomly, blobs and stripes should alternate
• Found in V1 (Kenet et al. 2003)
Spiral waves in slices!

Theory predicts that when the inhibition is blocked and cells adapt, standing patterns should destabilise into waves.
Coffee time