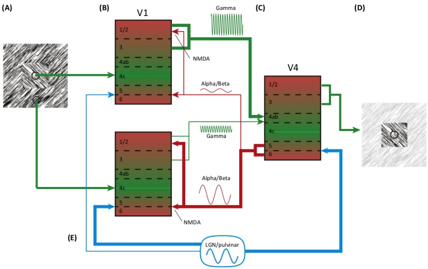
JÜLICH
FORSCHUNGSZENTRUM

Low-frequency oscillations for the multi-area model

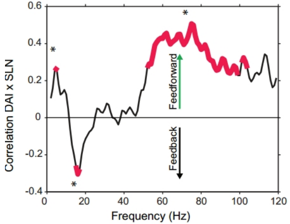
because having feedback is nice

July 31, 2016 | Daniel Mingers

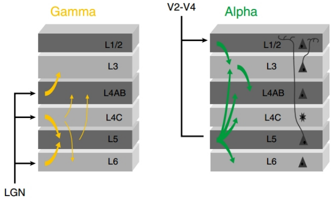
Why alpha range frequencies?
Recent experimental findings



[Jensen et al., 2015]: Feedforward and feedbackward information streams between visual areas.



[Bastos et al., 2014]: directionality in frequencies



[van Kerkoerle et al., 2014]: information streams propagate through layers

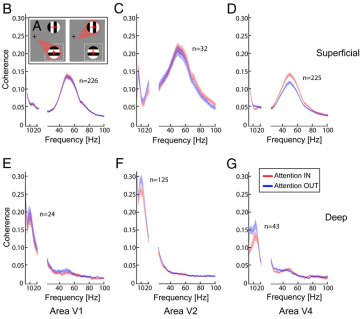
Questions:

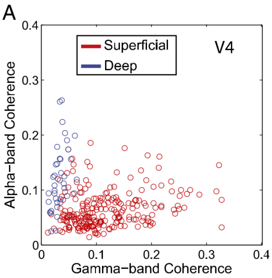
1. How do 7-10 Hz frequencies come to life?
2. What is necessary to have them propagate downstream?

Propagation of oscillations

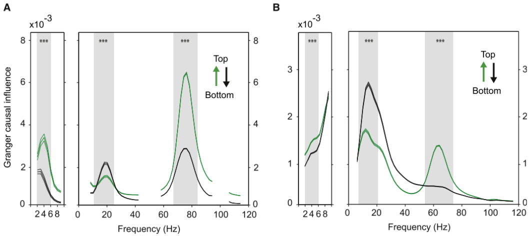
Here will be the graphic that I sketched during our meeting

What do we want? Coh, GC



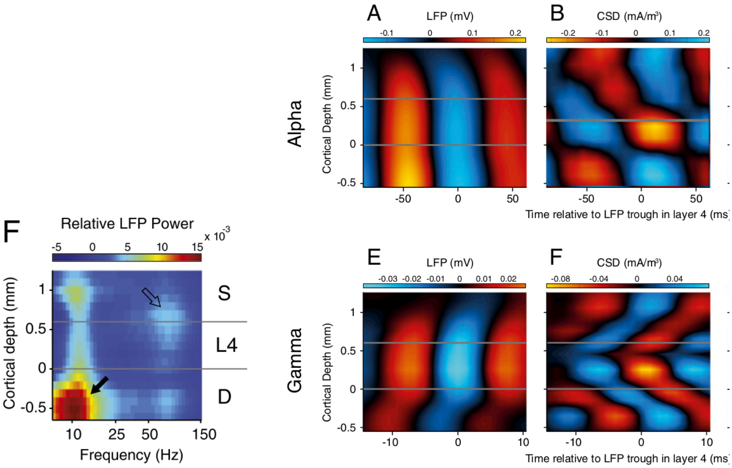


SFC results by Buffalo et al., 2011



Granger causal influence by Fries et al., 2015. We will extend this to spectral GC.

What do we want? LFP, MUA, CSD



CSDs adapted from Buffalo et al., 2011

Possible causes for alpha oscillations

1. How do 7-10 Hz frequencies come to life?
2. What is necessary to have them propagate downstream?

a) Additional drive: Thalamocortical feedback loops to L5
b) Single-neuron effect: Subthreshold resonance
c) Network effect: Eigenmode shift?
d) (Pacemaker effect: Phase delay between areas?)

Additional drive: Thalamocortical alpha

Here will be graphic of the spectrum and spectral GC, that we obtained with the Nitime package plus some explanation. It lies still on Blaustein, however, so I will only have it on Monday morning.

Single-neuron effect: Subthreshold resonance

- [Hutcheon et al., 1996a], [Hutcheon et al., 1996b]: $\exists$ subthreshold resonance $\Rightarrow$ (super-threshold) oscillatory responses occur with preferred frequencies
- Implementation we use: [Richardson, 2003]'s Generalised integrate-and-fire model with two variables (*GIF2*)

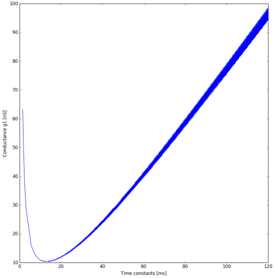
$$C_m \frac{\mathrm{d}V}{\mathrm{d}t} = -gv - g_1 w + I_{\mathrm{app}}(t) \tag{1}$$

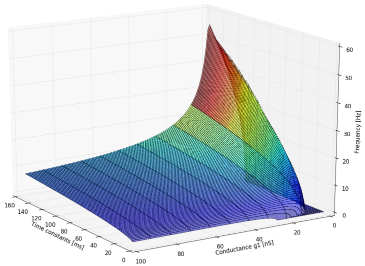
$$\tau_1 \frac{\mathrm{d}w}{\mathrm{d}t} = v - w \tag{2}$$

- GIF2 $\Leftrightarrow$ Resonating Neuron from [Izhikevich, 2000]
- [Brunel et al., 2003]: Theoretical framework for GIF2

A word on the accuracy of "10 Hz"

- Parameter ranges for 10 Hz narrow
- Different oscillation frequencies reported for different tasks/species
- Different resonance frequencies reported for: species/areas/neuron types/temperatures
- In vivo: model parameters change due to transmitter effects





GIF2-neurons: Properties & Testing

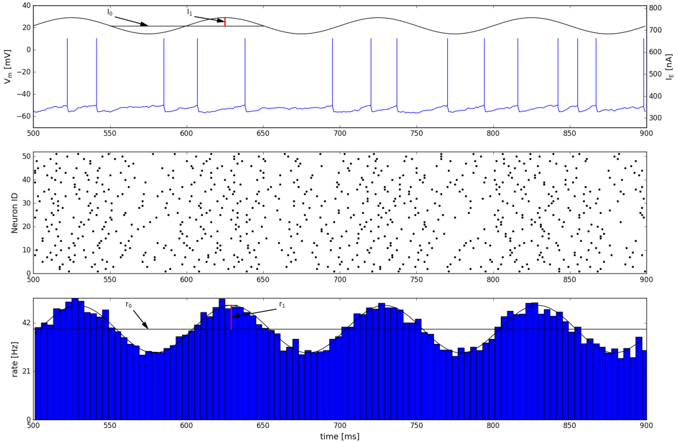
drive

$$I_{app} = I_0 + I_1 \sin(2\pi f t) + \xi(t)$$

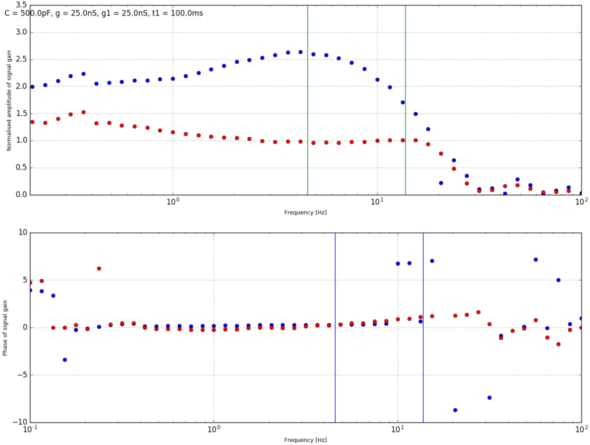
av. firing rate

$$r = r_0 + r_1 \sin(2\pi f t + \phi(t))$$

$$\Rightarrow |A(f)| := r_1(f)/I_1$$ gain [Gerstner, 2000]



GIF2: Noise-dependent frequency gain



- Phase not fitted correctly. Also: not documented in the paper.
- Peak for STR clearly visible in High-noise case.
- Exp-synapses acting as low-pass filter for poisson drive.

GIF2-neurons: Where, how many?

Problem: little evidence for macaque, none in-vivo

Intrinsic Oscillations of Neocortex Generated by Layer 5 Pyramidal Neurons

LAURIE R. SILVA, YAEL AMITAI,* BARRY W. CONNORS†

Rhythmic activity in the neocortex varies with different behavioral and pathological states and in some cases may encode sensory information. However, the neural mechanisms of these oscillations are largely unknown. Many pyramidal neurons in layer 5 of the neocortex showed prolonged, 5- to 12-hertz rhythmic firing patterns at threshold. Rhythmic firing was due to intrinsic membrane properties, sodium conductances were essential for rhythmicity, and calcium-dependent conductances strongly modified rhythmicity. Isolated slices of neocortex generated epochs of 4- to 10-hertz synchronized activity when *N*-methyl-D-aspartate receptor–mediated channels were facilitated. Layer 5 was both necessary and sufficient to produce these synchronized oscillations. Thus, synaptic networks of intrinsically rhythmic neurons in layer 5 may generate or promote certain synchronized oscillations of the neocortex.

SYNCHRONIZED OSCILLATIONS ARE pervasive in the cerebral cortex. Cortical rhythms, as revealed by the electroencephalogram (EEG), vary with behavioral state; their frequencies range from the 4- to 7-Hz theta waves of sleep to the 14- to 60-Hz waves dominant during alertness (*1*). Neuropathological conditions such as epilepsy and coma can elicit distinctive EEG rhythms. Cortical oscillations may encode sensory information (*2, 3*). Despite the prevalence of rhythmic neocortical activity, little is known about its mechanisms. Some cortical oscillations are clearly driven by periodic input from the thalamus (*4*); however, others may arise within the cortex itself, independent of the thalamus (*5, 6*).

Neurons generate rhythms in a variety of ways. Some have an intrinsic propensity to oscillate (*7*), and groups of these may interact synaptically to produce synchronous patterns (*4, 8*). Synchronized rhythms can also arise as an emergent property of a network of neurons that, as individuals, are nonrhythmic (*9*). Neurons in the middle layers of neocortex can initiate some nonrhythmic forms of synchronized activity (*10*). We show here that neurons of layer 5 alone have the intrinsic properties and synaptic connections necessary to generate synchronized oscillations.

Recordings were made from neurons in

Section of Neurobiology, Division of Biology and Medicine, Brown University, Providence, RI 02912.

*Present address: Department of Physiology, Ben-Gurion University of the Negev, Beer-Sheva, Israel.
†To whom correspondence should be addressed.

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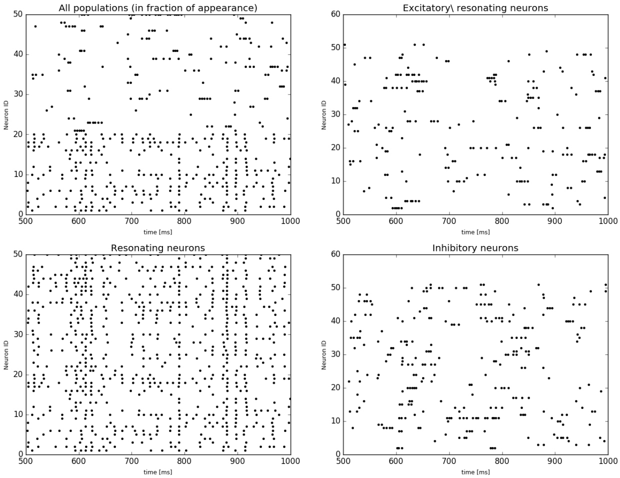
- Created NEST-implementation of GIF2: `gif2_psc_exp`
- rat somatosensory cortex: $\approx$ 50% of L5 pyramidals: resonating with $f_R \approx 7$ Hz
- Also: 60% of RS and IB neurons in rat somatosensory cortex L2-4? [Richardson, 2003]
- $\rightarrow$ more data on laminar distribution would be nice

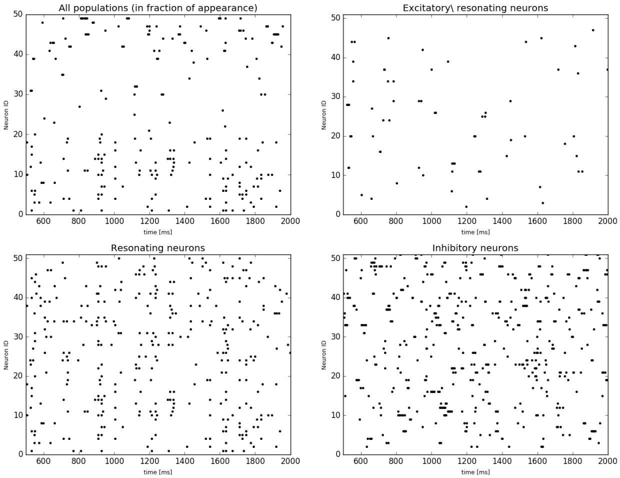
GIF2-neurons in networks: Brunel



$f_R = 10\,\text{Hz}$; Sinusoidal drive; Corrections:

Synpatic weight E $\rightarrow$ R reduced to 0.01, I $\rightarrow$ R reduced to 0.6.

GIF2-neurons in networks: L5 from microcircuit



Correction: Reduced inhibitory weight I→E/R.

Problem: Hard to estimate the relative noise level of the drive.

Bastos, A. M., Briggs, F., Alitto, H. J., Mangun, G. R., and Usrey, W. M. (2014).
Simultaneous recordings from the primary visual cortex and lateral geniculate nucleus reveal rhythmic interactions and a cortical source for gamma-band oscillations.
Journal of Neuroscience, 34(22):7639–44.

Brunel, N., Hakim, V., and Richardson, M. J. E. (2003).
Firing-rate resonance in a generalized integrate-and-fire neuron with subthreshold resonance.
Physical Review E, 67(5):051916.

Gerstner, W. (2000).
Population Dynamics of Spiking Neurons : Fast Transients, Ascynchronous Stats, and Locking.
Neural Computation, 12:43–89.

Hutcheon, B., Miura, R., and Puil, E. (1996a).
Subthreshold membrane resonance in neocortical neurons.
Journal of Neurophysiology.

Hutcheon, B., Miura, R. M., and Puil, E. (1996b).
Models of subthreshold membrane resonance in neocortical neurons.
Journal of neurophysiology, 76(2):698–714.

Izhikevich, E. M. (2000).
Neural excitability, spiking and bursting.
International Journal of Bifurcation and Chaos, 10(6):1171–1266.

Jensen, O., Bonnefond, M., Marshall, T. R., and Tiesinga, P. (2015).
Oscillatory mechanisms of feedforward and feedback visual processing.

Richardson, M. J. E. (2003).
From Subthreshold to Firing-Rate Resonance.
Journal of Neurophysiology, 89(5):2538–2554.

van Kerkoerle, T., Self, M. W., Dagnino, B., Gariel-Mathis M A, Poort, J., van der Togt, C., and Roelfsema, P. R. (2014).
Alpha and gamma oscillations characterize feedback and feed- forward processing in monkey visual cortex.
Proceedings of the National Academy of Sciences of the United States of America, 111(40):14332–14341.