Dynamics of Coupled Thalamocortical Modules

Jonathan D. Drover, Nicholas D. Schiff, Jonathan D. Victor
Weill Medical College of Cornell Department of Neurology and Neuroscience

Weill Cornell Medical College

Motivation

The brain is a complex, hierachically organized system. Overall state (wakefulness, drowsiness, sleep) likely resides in the dynamics of large populations (10^7 or more) of neurons. The EEG is well suited to probing this level of organization: it has excellent temporal fidelity, and there is extensive empirical knowledge of how various normal and pathological brain states are correlated with EEG observables, chiefly spectra. However, the indirect nature of the relationship between surface recordings and the cellular processes that generate them hinders the understanding of the underlying mechanisms. Bridging this gap requires modeling at the appropriate level of detail, with the model developed in accordance with neuroanatomy, neurophysiology, and clinical evidence.

Therefore, we start with a building block of thalamocortical dynamics: a module consisting of a cortex, a thalamic relay nucleus, and a thalamic reticular nucleus. Models based on this structure account for EEG spectra during wakefulness, drowsiness, and sleep (Robinson, 2002), but do not account for interactions between cortical areas or spontaneous state changes. We add to this basic module a simple, biologically-inspired coupling via the reticular thalamus. As shown here, adding this coupling enables correlated activity among modules and switching between patterns of correlated activity. The model also suggests a mechanism for spontaneous changes in brain state.

Modules

- A thalamocortical module consists of a cortical region (e.g., primary visual cortex) and its associated thalamic nuclei.
- A cortical region is modeled by two reciprocally connected populations of neurons, excitatory (E) and inhibitory (I). The inhibitory neurons are all local, while the excitatory neurons project both within cortex and to the thalamus. Spread of excitatory activity within cortex is modeled by a wave propagation.
- A thalamic relay nucleus (e.g., the lateral geniculate nucleus) receives input from, and projects onto, its associated cortical region. It also projects onto the thalamic reticular nulceus. It is modeled as a single population (S), and the excitatory projection to cortex is associated with a conduction delay τ.
- A thalamic reticular nucleus inhibits a thalamic relay nucleus, and receives excitatory input from the cortex, also with a conduction delay τ. It is modeled as a single population (R).

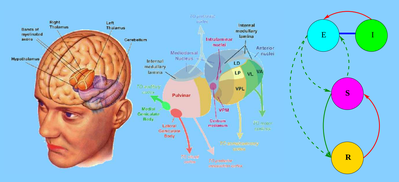

Figure 1: The left panel is a cartoon of the thalamus, and describes which cortical regions the various nuclei project onto. The panel on the right shows the connections used for the generic thalamocortical module. The dotted lines indicate connections with a delay, red lines denote inhibitory connections, and green lines indicate excitatory connections.

This thalamocortical module is repeated multiple times in each hemisphere. Examples include the visual system, the somatasensory system (ventral posterolateral/ posteromedial complex), and the motor system (ventral anterior/ lateral complex) Modeling at this level of detail can account for EEG spectra during a range of behavioral states (awake, drowsy, and the stages of sleep), as shown by Robinson et. al.

A distinctive feature of the reticular nuclei is that they connect to more than one relay nucleus. To model this, we construct a network consisting of two of the above modules (E_1, I_1, S_1, R_1 and E_2, I_2, S_2, R_2), to which we add a population of reticular neurons R that is shared between them. Since the number of shared and unshared neurons is not known, these correspond to the key parameters of the model (κ_s and κ_u).
The work of Crabtree, Isaac (2002) and Rigas, Castro-Alamancos (2007) suggests that subcortical inputs are more influential than input arriving from distant cortical areas. For now, we disregard distant cortical-cortical communication and use the strictly subcortical pathway.

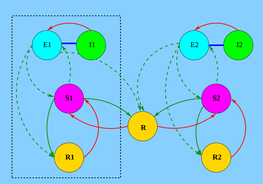

Figure 2: Two coupled modules, connected via a shared reticular population.

The Model

The model uses two variables for each population: the average potential (V_a) and the average firing rate (ϕ_a) for each of the populations, $a = E, S, R$ (The inhibitory cortical potential is slaved to the excitatory cortical potential). The inputs to each population are weighted depending on connection strength and summed.

$$DV_a = \sum_{i=E,I,S,R} \nu_{a,i}\phi_i(t - \tau_{a,i})$$

The differential operator is given by:

$$D = \frac{1}{\alpha\beta}\frac{d^2}{dt^2} + \left(\frac{1}{\alpha} + \frac{1}{\beta}\right)\frac{d}{dt} + 1$$

Wave propogation in excitatory cortex

$$\left(\frac{1}{\gamma^2}\frac{d^2}{dt^2} + \frac{2}{\gamma}\frac{d}{dt} + 1\right)\phi_E = Q(V_E)$$

All other populations (due to size):

$$\phi_a = Q(V_a)$$

where $Q(V_a) = Q_{max}\left[1 + \exp\left(-\frac{V_a - \theta}{\sigma}\right)\right]^{-1}$.

Parameters and effective coupling strengths

Population		Strength	Delay
Target (a)	Source (b)	$\nu_{a,b}$	$\tau_{a,b}$
E	E	1.7	0
E	I	−1.8	0
E	S	1.2	0.04
S	E	1.0	0.04
S	R	−1.0	0
R	E	0.4	0.04
R	S	0.2	0

α	$100.0\ s^{-1}$
β	$400.0\ s^{-1}$
Q_{max}	$250.0\ s^{-1}$
θ	$15\ mV$
σ	$3.3\ mV$
γ	$100.0\ s^{-1}$

Effective strengths

$$\nu^{Eff}_{R_{1,2},a} = \kappa_u \nu_{R,a}$$
$$\nu^{Eff}_{R,a} = \frac{1}{2}\kappa_s \nu_{R,a}$$
$$\nu^{Eff}_{S,R_{1,2}} = \kappa_u \nu_{S,R}$$
$$\nu^{Eff}_{S,R} = \kappa_s \nu_{S,R}$$

Results

We obtain a bifurcation diagram that delineates the possible behaviors as a function of the reticular coupling strengths.

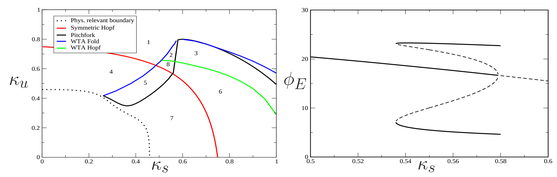

Figure 3: The left panel is the bifurcation diagram. The vertical axis is the parameter κ_u, the contribution from the unshared reticular populations. The horizontal axis is the parameter κ_s, the contribution from the shared reticular population. In regions 1 and 4 there is only one attractor, a fixed point for 1 and a periodic solution for region 4. In regions 2, 5, and 8 there are 3 attractors. In region 2, all three are fixed points - symmetric, and a pair of winner-take-all (WTA) solutions. In region 8, there is a symmetric fixed point and a pair of periodic WTA solutions. In region 5 all three attractors are periodic solutions. In regions 3, 6 and 7 there are two attractors. In region 3 there are a pair of WTA fixed point solutions. In regions 6 and 7 there are two periodic WTA solutions. The right panel shows the pitchfork bifurcation destabilizes the symmetric fixed point from left to right, and creates the unstable solutions that separate the attractors. For this diagram, $\kappa_u = 0.7$.

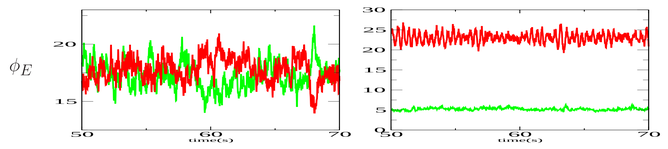

Figure 4: Time traces for the WTA region (region 2 in figure 3). The left panel is a noisy solution around the symmetric fixed point. The right panel is a noisy solution around one of the WTA fixed points.

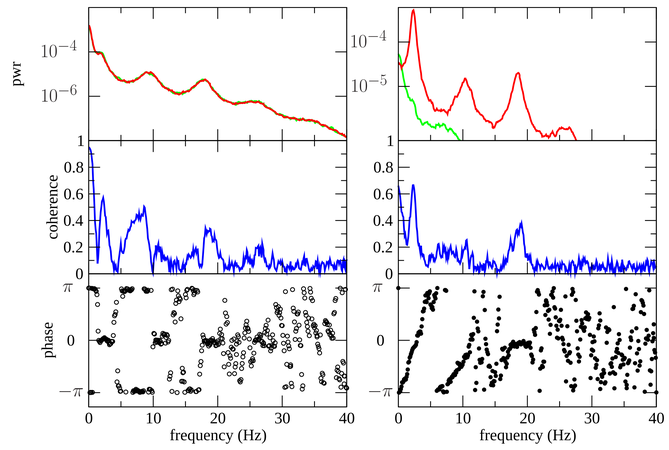

Figure 5: The left side shows the spectral information for the noisy solution shown in figure 4. The top panel is the power spectral density and the lower panels are the amplitude and phase of the coherence. Because we are using a symmetric network the power spectra for each of the solutions is identical. The coherence is strongest at the frequencies that are strongest for the individual modules. The right side shows the spectral information for the WTA solution. The *winner* shows clear peaks at certain frequencies, while the *loser* less so. The coherence, however, shows peaks according to the winner's peaks. The bottom figure shows the phase of the coherence. The slope of the phase, especially at low frequencies, along with the amplitude plot suggests that the winner is driving the loser.

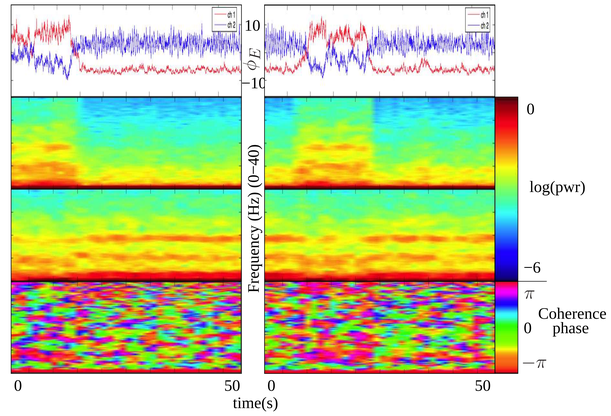

Figure 6: Two examples of spontaneous switching between winner take all behavior and symmetric behavior. When the noise is sufficiently large, it is possible for the trajectories to pass the separatix (the dashed lines in the right panel of figure 3) and change behaviors. This figure shows two time traces (top) and their corresponding spectrograms (2nd and 3rd, one for each channel), along with the phase of the coherograms. These figures make explicit the change in behavior and that the modes during the switching are consistent with the results shown in figure 5.

Summary

- Single module reproduces EEG across a variety of states, but lack the means for state change.
- Coupling two modules together via the reticular nucleus creates regions in parameter space that can produce multiple stable states, which suggests a role of the reticular thalamus in enabling correlated activity between distant modules.
- Bistability allows both symmetric and Winner-Take-All behaviors to exist simultaneously. Noisy inputs can cause jumps from one behavior to another, and vice versa. This suggests a mechanism for spontaneous behavioral state change.

This work was supported by the Swartz Foundation (JDD), and the James S. McDonnell Foundation (NDS,JDV)

References

Robinson et. al., Physical Review E 65 (2002), Crabtree, JW and Isaac, JT J Nuerosci. 22(19)(2002), Rigas, P., Castro-Alamancos, M.A., J. Neurosci 27 (2007)