

Multistability as a mechanism for modulation of EEG coherences

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Introduction

Coordinated activity between multiple cortical areas is necessary for organized behavior and cognitive activity. It is speculated that deep brain structures, specifically the reticular thalamus, play an important role in coordinating this activity. We developed a mean field model of a thalamocortical network consisting of two thalamocortical modules (each module containing cortical, thalamic relay, and thalamic reticular populations) coupled via a shared population of reticular neurons. We showed that this network is capable of spontaneous transitions, distinguishable by changes in the coherence between the two cortical populations modeled. These transitions can occur when the parameters of the model are such that there are multiple stable attractors: symmetric solutions, where each module maintains a similar activity level; and winner-take-all solutions, where one of the modules suppresses the other. We show that this behavior is present for a range of parameters for the thalamocortical module, including parameter sets that reproduce the EEG spectrum in wakefulness (eyes open or eyes closed) and light sleep (S2), but not for parameters that correspond to deep sleep (S3).

We analyzed EEG/CCTV recordings from patients with severe brain injury and calculated time-localized EEG spectra and coherences during eyes-open rest. We then applied principal component analysis to the coherograms obtained from pairs of channels within each hemisphere, revealing bimodal behavior. Thus, these time varying patterns of coherence can also be identified in the EEG of human subjects.

The Model

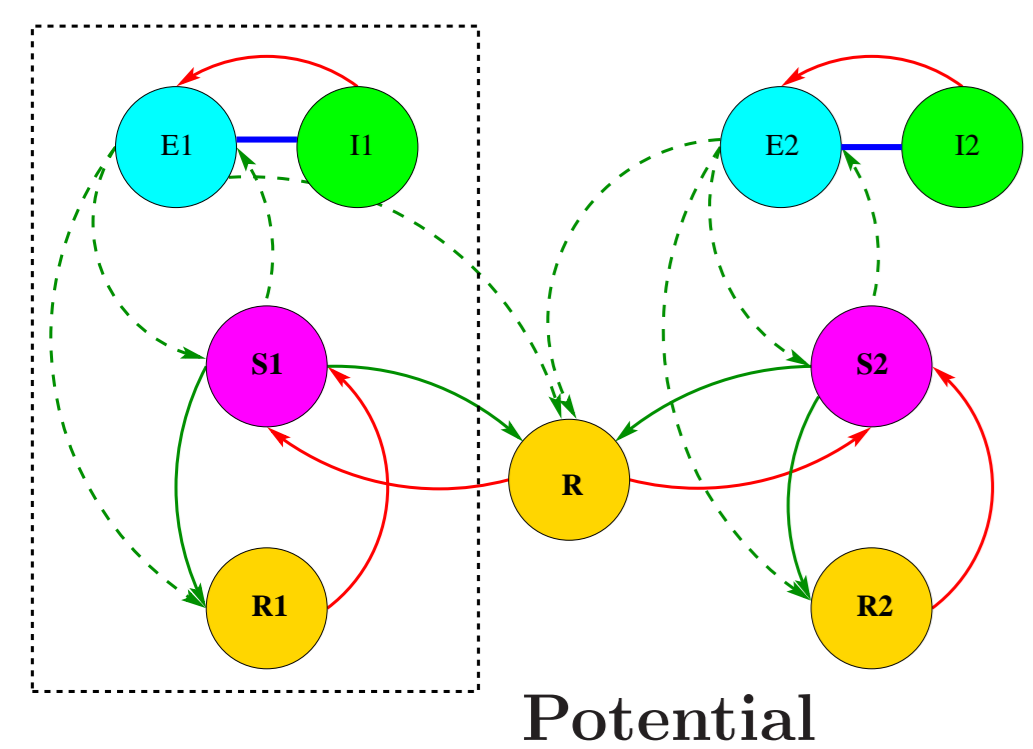


Figure 1: The network of populations consists of two thalamocortical modules. Each module consists of cortical populations (excitatory ($E_{1,2}$) and inhibitory ($I_{1,2}$)), a relay nucleus ($S_{1,2}$), and a populations of neurons in the reticular nucleus ($R_{1,2}$). The modules are connected together with a shared population in the reticular nucleus (R - no subscript). Populations quantified by average potential and activity of neurons in the population.

For all except inhibitory cortex:

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

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

For inhibitory cortex:

$$V_I = V_E$$

Activity

For excitatory cortex:

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

For other populations (a=I,S,R):

$$\phi_a = Q(V_a)$$

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

Parameters

	EO	EC	S2	S3	Table: connectivity for a single module that reproduce the EEG spectrum in behavioral states: eyes open (EO), eyes closed (EC), stage 2, 3 sleep (S2, S3). We use two bifurcation parameters: κ_s scales all of the connections to and from the shared reticular populations, R and κ_u scales all connections to and from the specific reticular populations (R_1 and R_2).	
α	100.0 s^{-1}	ν_{EE} 1.7	1.3	1.8	1.8	
β	400.0 s^{-1}	ν_{ES} 1.2	1.2	1.7	1.7	
Q_{max}	250.0 s^{-1}	ν_{SE} 1.0	1.0	0.7	0.4	
θ	15 mV	ν_{SR} -1.0	-1.0	-0.8	-0.6	
σ	3.3 mV	ν_{RS} 0.2	0.2	0.4	0.4	
γ	100.0 s^{-1}	ν_{RE} 0.4	0.2	0.2	0.5	
		α	100.0	60.0	60.0	40.0
		ν_{EI}	-1.8	-1.8	-1.8	-1.8

Multistability

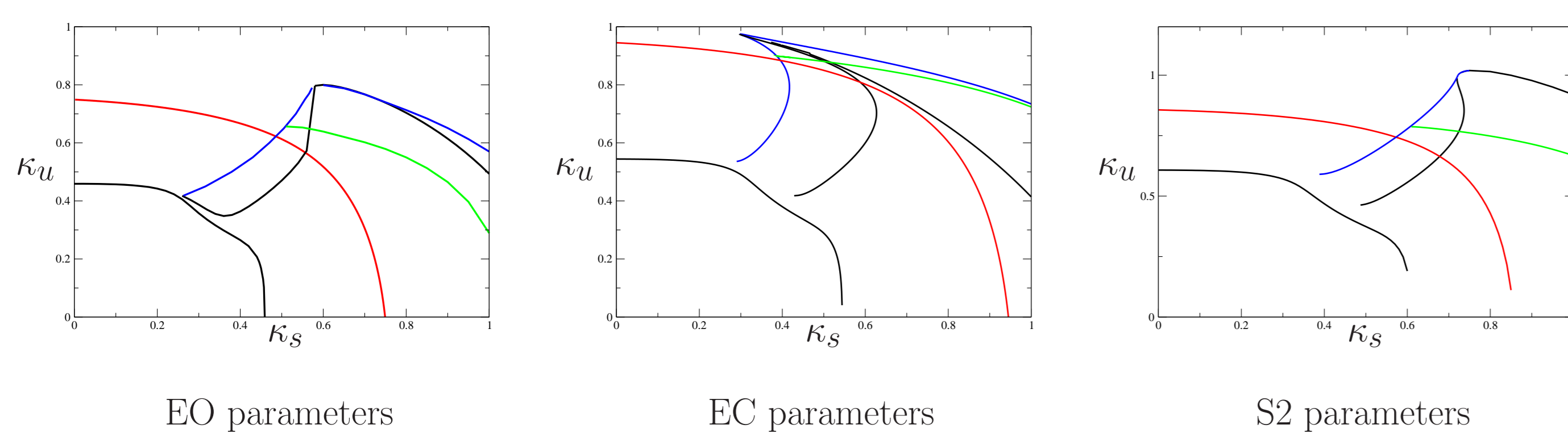


Figure 2: Bifurcation diagrams for three of the parameter sets. The red curve indicates that the symmetric solution undergoes a Hopf bifurcation, the blue curve indicates a winner-take-all generating fold bifurcation, the solid black curve indicates a pitchfork bifurcation for the symmetric solution, and the green curve indicates a winner-take-all Hopf bifurcation. For the parameter sets EO, EC, and S2 the fold bifurcation and (subcritical) pitchfork bifurcation bookend a region where both the WTA and symmetric solution exist and are stable. This region of multistability is a mechanism for spontaneous state changes in the model.

Spontaneous Switching

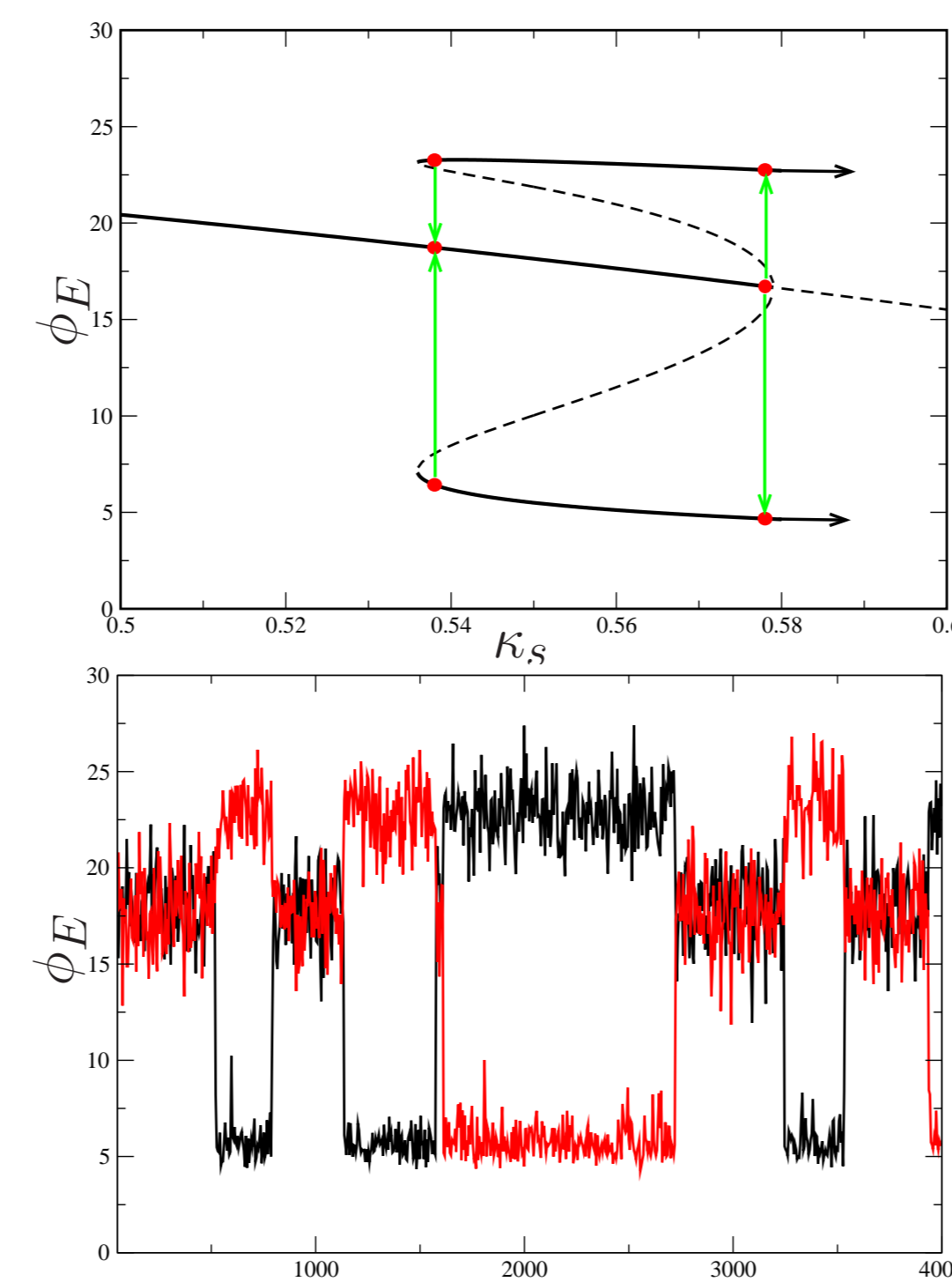


Figure 3: The top panel is a $\kappa_u = 0.7$ slice of the bifurcation diagram for the EO parameter set. The unstable fixed points (dashed lines) act as a separatrix between the symmetric fixed point and the WTA fixed points. Noisy input can cause the orbit to escape the basin of attraction of these fixed points and switch. An example time series is shown in the lower panel, for $\kappa_s = 0.558$. The green arrows indicate the area of the most likely transition. One cannot determine DC activity levels directly from EEG, but if the different activity patterns manifest themselves in the spectra or the coherence, these could be used to determine whether or not these changes are taking place. Thus, the next step is to determine whether these changes in activity level demonstrate marked changes in the second order statistics.

Spectra and Coherence

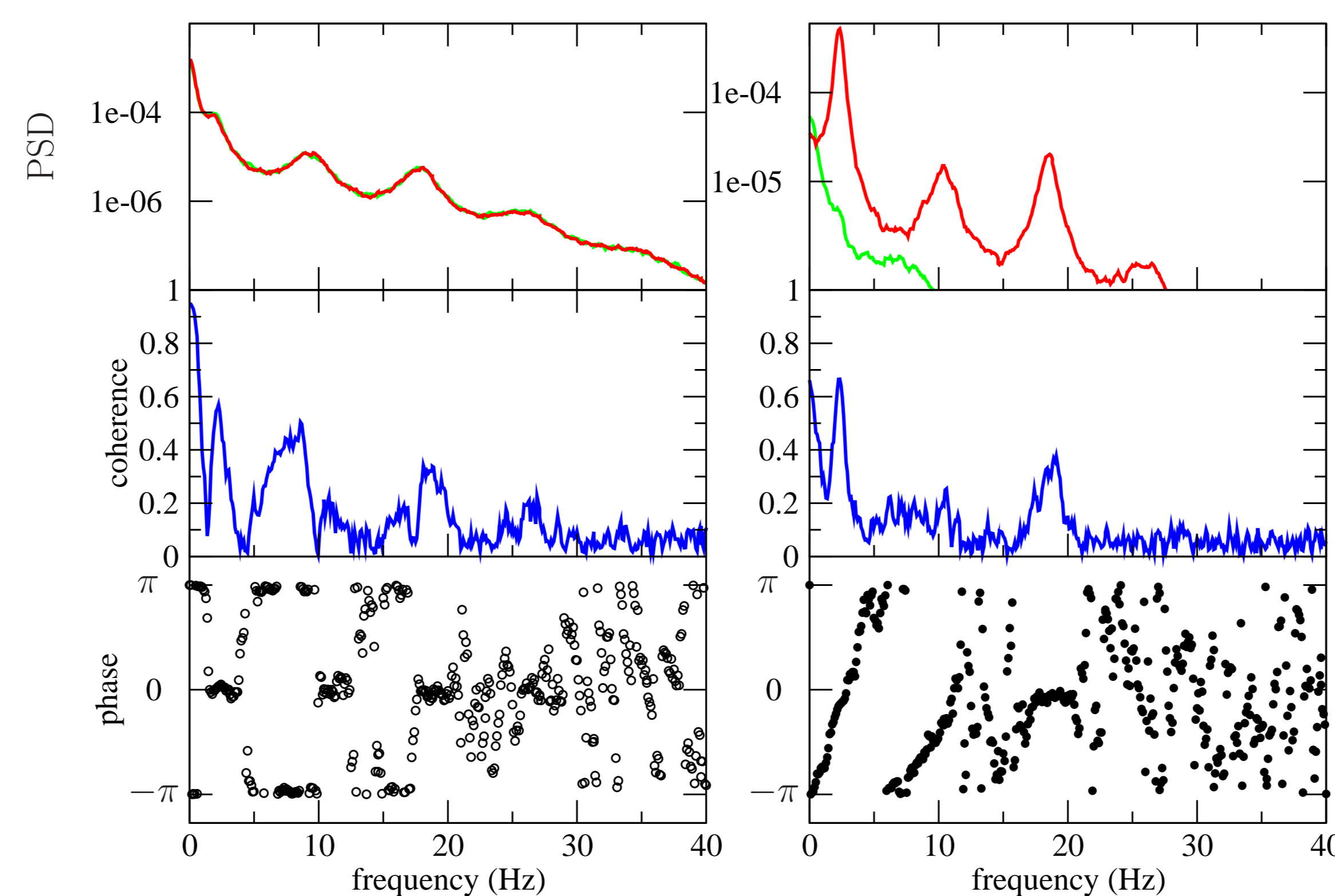


Figure 4: The left (right) panels are the power spectral density (PSD), coherence amplitude, and coherence phase for the symmetric (WTA) solutions. The important point is that the coherence amplitude is very different between the two types of solutions in the 5-12 Hz. range. Thus, for the model, the switches can be detected by changes in the patterns of power and coherence. We look for these changes in EEG from patients with severe brain injury, looking for temporally multimodal behaviors.

Multistability in EEG data

Figure 5: Spectrograms and cohereograms from the left hemisphere of a patient with severe brain injury:

- 40 year old man.
- Emergent minimally conscious state (EMCS)
- Traumatic brain injury at age 19, motor vehicle accident.
- Evaluated 21 years later.
- Behavior: coma for 6 weeks, then in MCS for 19 years, then spontaneous recovery of language indicating relative preservation of left hemisphere function.

The top two panels are spectrograms, the third panel from the top is the cohereogram. The red curve is the first principal component of the cohereogram, and the purple curve is the first principle component of the joint spectrogram. The histograms on the right show that there is indeed multimodal behavior. Multimodality was seen in three pairs of left-hemisphere channels (one example is shown here), but only one pair of right-hemisphere channels.

Loss of Multistability

The multistability is not ubiquitous. For parameter sets that produce spectra corresponding to deep sleep (S3), these spontaneous phase transitions are not present. Here we demonstrate the mechanism by which the region of multistability shrinks and eventually vanishes.

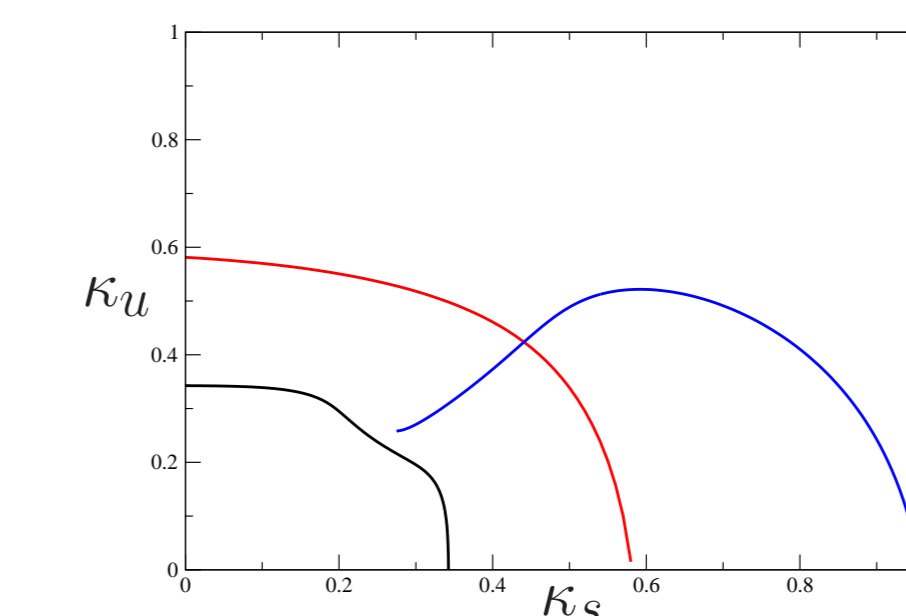


Figure 6: The bifurcation diagram for the parameter set S3. The color coding is identical to figure 2, though the pitchfork is super-critical in for this set of parameters.

Multistability is destroyed when the fold bifurcation and the pitchfork bifurcation coalesce, changing the pitchfork bifurcation from sub-critical to super-critical. The changes in the two-parameter bifurcation diagram along the transition from $t^* = 0$ to $t^* = 1$ give the appearance of a zipper, where the multistable region closes from top to bottom as t^* is increased.

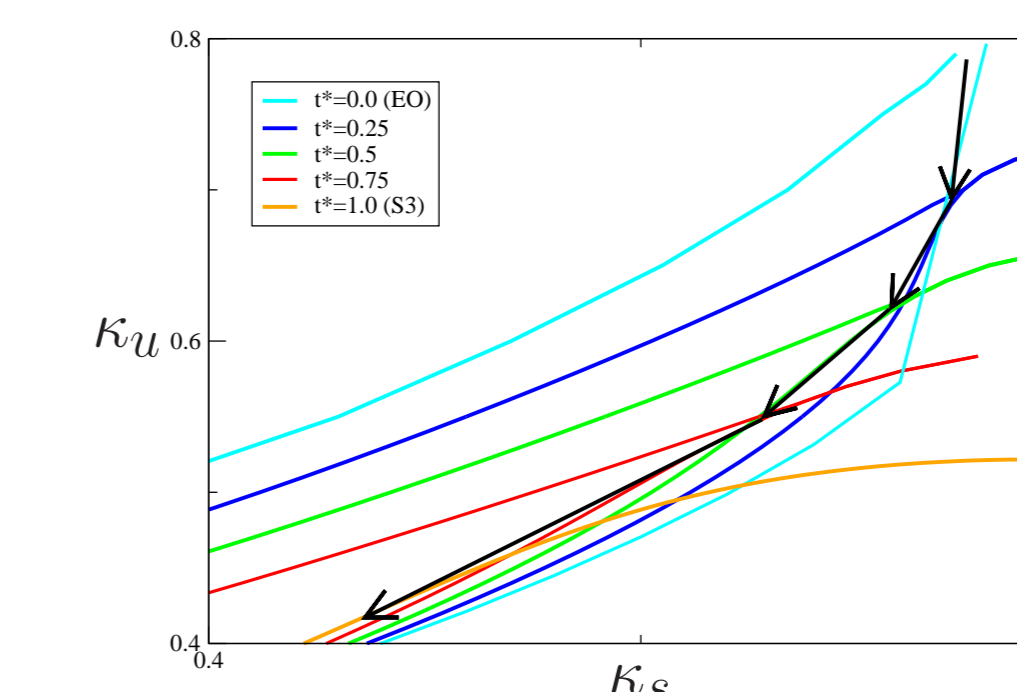


Figure 7: The "zipper". The curves in this figure represent the fold-pitchfork pair for five different values of t^* . Each value of t^* generates two bifurcation loci - fold and pitchfork (left and right). As in figure 2, the multistable region lies between these curves. As the value of t^* increases the parameters are shifted toward the S3 parameter set and the multistable region "zips" shut. The black arrows indicate the direction of the closing as t^* increases. For the case $t^* = 1$, there is only a single curve, indicating a super-critical pitchfork bifurcation.

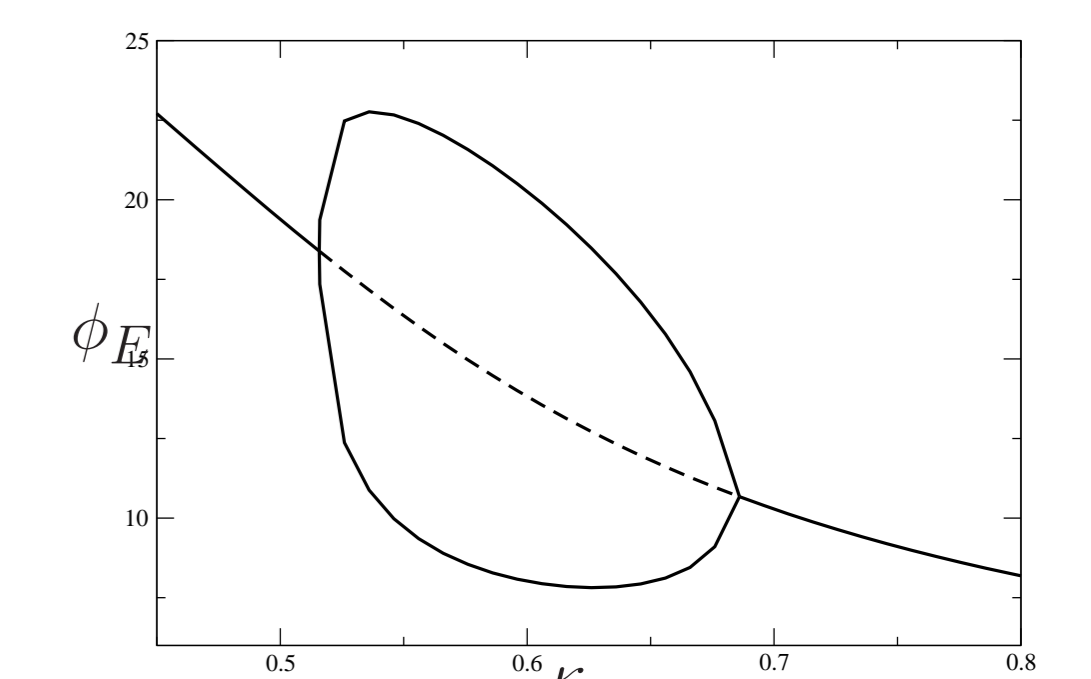
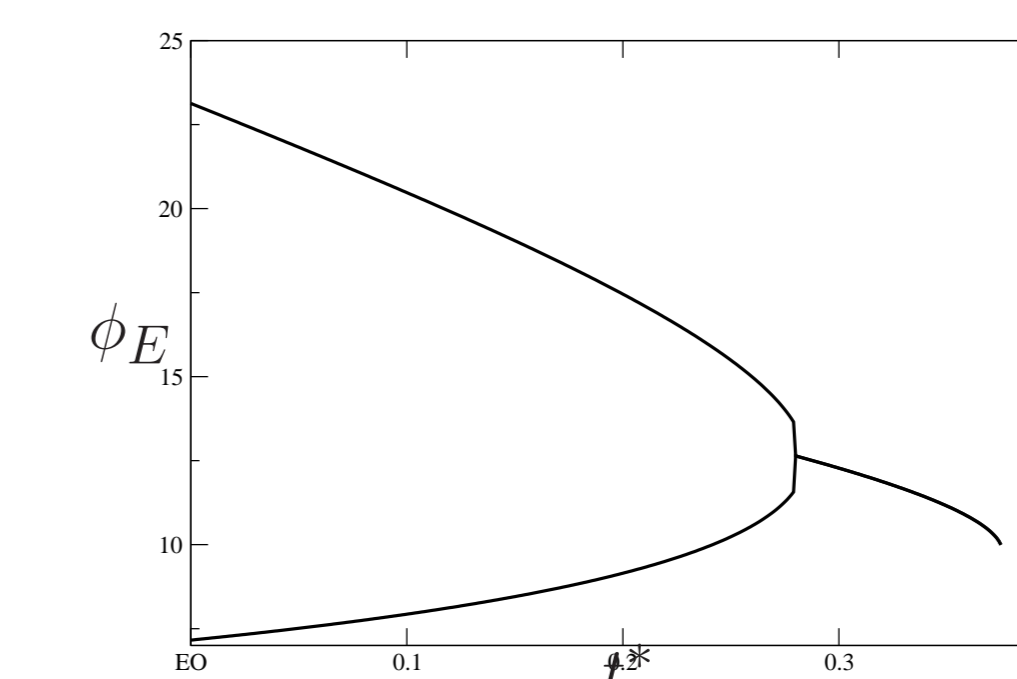


Figure 8: The left panel shows the location of the elbows of the fold bifurcations (see the upper panel of figure 3) as a function of t^* . As t^* increases, these elbows (and hence the WTA solutions) collapse onto the symmetric solution where the pitchfork occurs. The right panel shows the analogue to figure 3, after the criticality of the pitchfork has been reversed. This figure is along the $\kappa_u = 0.5$ slice in figure 6 (both the entrance and exit pitchforks are visible).

Summary

- Thalamocortical modules coupled together via a population of neurons in the reticular nucleus (non topographic GABAergic) allows for multistable behavior over a wide range of intra-module connection strengths.
- The different stable elements in the multistable regime are manifest in different patterns in the spectra and the coherence between cortical regions.
- Multimodal behavior can be seen in the EEG.
- The process by which the multistability is destroyed is a smooth process, thus ensuring that multistability is robust to intra-module connectivity changes.

References

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Acknowledgements

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