Traveling Waves in a Wilson-Cowan Model of Cortex

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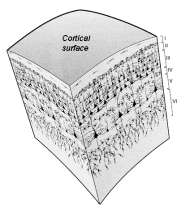
Abstract

Cortical slow oscillations play a significant role in activating subcortical structures and determining internal brain states. Recent investigations have characterized the spread of activity across and between the six layers of neocortex as a wave of neuronal activation, and have suggested that infragranular layer 5 is primarily responsible for initiating and maintaining widespread cortical activity while supragranular layers (layer 2/3) are subsidiary. We propose a model of interacting excitatory and inhibitory neural fields in layers 2/3 and 5 that illustrates the existence, stability, and properties of these waves. Our analysis demonstrates numerically and analytically that small amplitude traveling waves can be initiated in either cortical layer but require the contribution of layer 5. We consider the dynamics resulting from varying vertical and laminar connectivity parameters and find that the dominance of layer 5 can be attributed to increased local connectivity and stronger vertical projections originating in this layer.

Background

The cerebral cortex is organized in six layers



- L2/3 and L5 form a primary feedback loop
- Strong **laminar** projections characterize **L2/3**
- **L5** is primarily responsible for **vertical** projections
- Inhibitory modulation occurs locally [2].

Waves have been observed experimentally

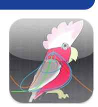
- L5 can initiate and propagate wave activity in the absence of L2/3 [1], [5], [6].
- L2/3 is insufficient to sustain wave activity in the absence of L5 [1], [5], [6].

Importance to cortical function:

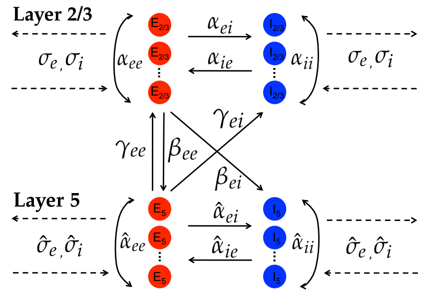
- **Background depolarization**: increased firing probability in that particular region
- A sensory-evoked wave propagating to a larger area would **increase sensitivity** to incoming stimulation.
- If a wave is associated with an oscillation, propagation can **organize spatial phase distributions** [7].

XPPAUT

Simulations were conducted using the XPPAUT software package, a tool for simulating, animating, and analyzing dynamical systems.



Wilson-Cowan Model



- Two-dimensional model of cortical layers 2/3 and 5
- Excitatory and inhibitory populations within each layer treated as neural fields
- Projections extend horizontally within both layers, between a series of connected columns
- Excitatory neurons project to both excitatory and inhibitory populations in other layer; inhibitory populations only project locally
- τ denotes the time constant; θ represents the firing threshold

Layer 2/3 Excitatory Activity: $\tau_e \frac{du_e}{dt} = -u_e + F(\alpha_{ee} w_e * u_e + \gamma_{ee}\hat{u}_e - \alpha_{ie} w_i * u_i - \theta_e)$

Layer 2/3 Inhibitory Activity: $\tau_i \frac{du_i}{dt} = -u_i + F(\alpha_{ei} w_e * u_e + \gamma_{ei}\hat{u}_e - \alpha_{ii} w_i * u_i - \theta_i)$

Layer 5 Excitatory Activity: $\hat{\tau}_e \frac{d\hat{u}_e}{dt} = -\hat{u}_e + F(\hat{\alpha}_{ee} \hat{w}_e * \hat{u}_e + \beta_{ee} u_e - \hat{\alpha}_{ie} \hat{w}_i * \hat{u}_i - \hat{\theta}_e)$

Layer 5 Inhibitory Activity: $\hat{\tau}_i \frac{d\hat{u}_i}{dt} = -\hat{u}_i + F(\hat{\alpha}_{ei} \hat{w}_e * \hat{u}_e + \beta_{ei} u_e - \hat{\alpha}_{ii} \hat{w}_i * \hat{u}_i - \hat{\theta}_i)$

$$F(x) = \frac{1}{1+e^{-x}}$$

$$w(x) * u(x) \equiv \int_\Omega w(x-x')u(x')\,dx'$$

Waves in Two Layers

Can waves be induced in a 2D EI network?

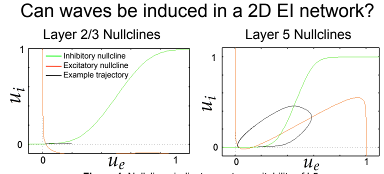


Figure 1: Nullclines indicate greater excitability of L5.

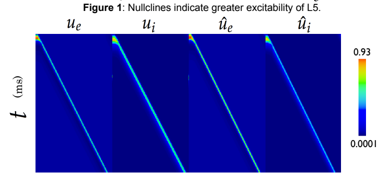


Figure 2: Waves resulting from stimulating 10 L5 neurons in a two-layer model with 400 neurons in each layer. Waves are also generated upon L2/3 stimulation, but velocity is reduced.

α_{ee}	5	$\hat{\alpha}_{ee}$	16	β_{ee}	2.69
α_{ei}	15	$\hat{\alpha}_{ei}$	25	β_{ei}	1
α_{ie}	15	$\hat{\alpha}_{ie}$	15	γ_{ee}	15
α_{ii}	3	$\hat{\alpha}_{ii}$	3	γ_{ei}	12.5
σ_e	6	$\hat{\sigma}_e$	2	τ_e	4
σ_i	2	$\hat{\sigma}_i$	1	τ_i	9
θ_e	4	$\hat{\theta}_e$	4		
θ_i	6	$\hat{\theta}_i$	10		

Table 1: connectivity parameter values that result in the waves generated for the two-layer model (Fig 1,2,3).

- Wave propagates with a **velocity** of **71 μm/ms**, using a space constant of 100μm (Space constants in cortex range from 50-100μm).
- When layers are disconnected, wave occurs and propagates in L5 but not in L2/3 upon stimulation.
- Amplitude and duration of excitatory activity greater in L5 than L2/3

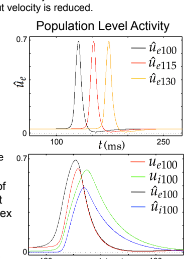


Figure 3: Activity of excitatory and inhibitory populations at individual locations within the network.

Incorporation of Delay

Adding a delay to the interaction between L2/3 and L5 accounts for the difference between lateral and vertical propagation of activity.

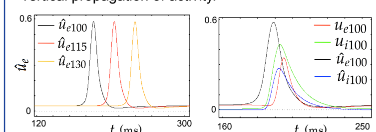
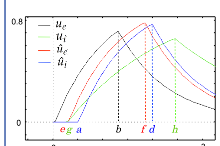


Figure 4: Population level activity after stimulating 10 L5 neurons in a two-layer model with a delay of 4 ms in conduction between layers. Connectivity parameters remain as stated in Table 1, excluding β_{ee}, which must be increased to 3 in order for waves to occur. The delay causes a decrease in the amplitude of the wave.

With the delay, velocity decreases to 57 μm/ms.

Piecewise Linear Model

Developing a piecewise linear model allows for properties of the waves such as their velocities to be computed analytically.



vel	**0.650**	→ ~65 μm/ms [space constant 100μm]
a	0.156	
b	0.588	
d	0.970	
e	0.122	
f	0.758	
g	0.523	
h	0.917	

Figure 5: Formulation of piecewise linear model. *e, g*, and *a* denote initiation of activity while *b, d, f,* and *h* represent peaks of activity in excitatory and inhibitory populations in L2/3 and L5.

Table 2: Analytically determined values for *a,b,d,e,f,g,h,* and wave propagation velocity. A velocity of 0.65 μm is within the range of values experimentally determined by Stroh et al. [5].

Conclusions

- Wave properties in the continuous model reflect recent experimental observations:
  - Velocity similar to that reported by Stroh et al. (48±7 μm/ms) [5].
  - In isolation, L5 is sufficient to initiate and propagate waves but L2/3 is not (Fig 6).
- These waves and their properties are attributable to the following connectivity parameters:
  - **L5** has stronger **local connections** and stronger vertical projections.
  - **Horizontal connectivity** is greater in **L2/3**.
- Adding a delay achieves a more biologically realistic value for wave velocity.
- Results obtained analytically from the piecewise linear model support the results from the continuous model.

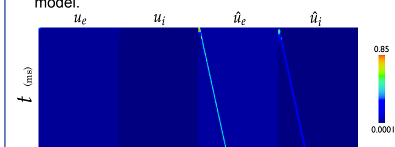


Figure 6: Activity resulting from stimulating 10 L2/3 neurons and 10 L5 neurons in a continuous two-layer model with no connections between layers. 400 neurons populate each layer.

Future Work

- Incorporate delay into piecewise linear model
- Determine wave stability in the piecewise linear model (eigenvalue problem)
- Account for spatial inhomogeneity
- Consider spike frequency adaptation

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