

Traveling Waves in Stochastic Neural Field Equations

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A Spiking Neuron

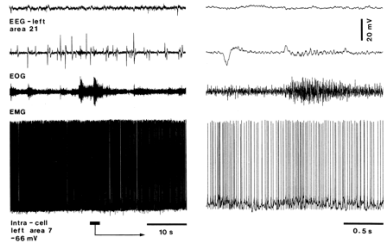
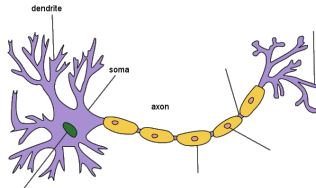


Figure: (a) Neuron ³(b) Membrane potential activity recording in an awake cat ⁴

- ▶ neuron receives input from other neurons on the dendrites charging the membrane
- ▶ when the membrane potential crosses a certain threshold → action potential
- ▶ transmitted to other neurons via synapses

⁴from Quasar Jarosz at en.wikipedia

⁴from Steriade, Timofeev, Grenier, 2001

Traveling Waves in Brain Slices

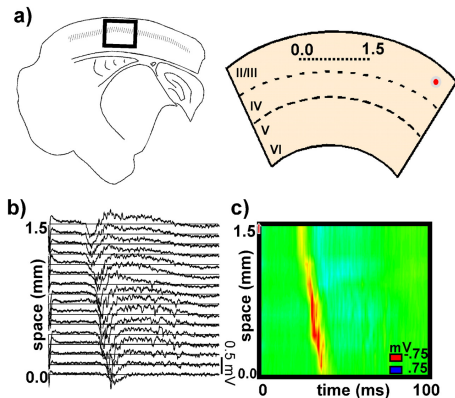


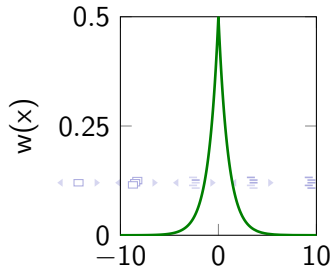
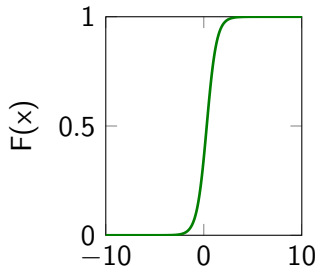
Figure: Propagating activity in a brain slice ⁵

⁵From D.Pinto, S. Patrick, W. Huang, B. Connors: Initiation, Propagation, and Termination of Epileptiform Activity in Rodent Neocortex In Vitro Involve Distinct Mechanisms; The Journal of Neuroscience, 2005

The Neural Field Equation

$$\frac{\partial}{\partial t} u(x, t) = -u(x, t) + \int_{-\infty}^{\infty} w(x - y) F(u(y, t)) dy$$

- ▶ $u(x, t)$: average membrane potential in the population of neurons at position $x \in \mathbb{R}$ at time t
- ▶ $F : \mathbb{R} \rightarrow [0, 1]$: gain function; proportion of firing neurons in the population
- ▶ $w : \mathbb{R} \rightarrow [0, \infty)$: strength of synaptic connections between neurons at x and neurons at y



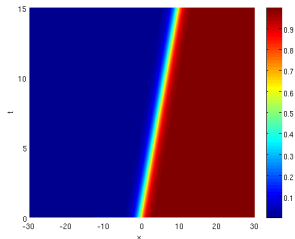
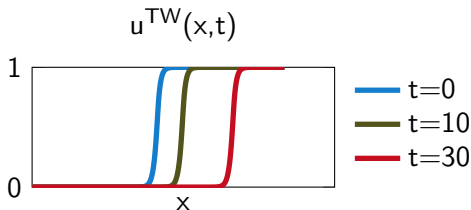
Traveling Waves

Theorem (Ermentrout, McLeod '93)

Assume that the equation has two stable fixed points separated by an unstable fixed point. Then there exists a unique (up to translations) monotone increasing wave profile $\hat{u} : \mathbb{R} \rightarrow \mathbb{R}$ and a unique wave speed $c \in \mathbb{R}$ such that

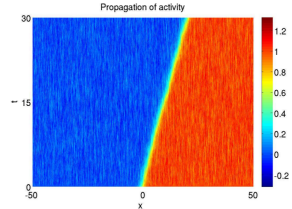
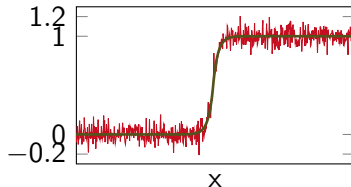
$$u^{TW}(x, t) := \hat{u}(x - ct)$$

is a traveling wave solution connecting the two stable states



Goals

- ▶ determine the influence of noise on the dynamics
- ▶ stochastic stability
- ▶ stochastic differential equation for the wave speed
- ▶ attempts in this direction: P. Bressloff, M. Webber 2012 ⁶(not rigorous)



⁶ P. C. Bressloff, M. A. Webber: Front Propagation in Stochastic Neural Fields; SIAM J. Applied Dynamical Systems, 2012

The Stochastic Neural Field Equation

- ▶ want to realise the neural field equation as a stochastic evolution equation

$$du(x, t) = (-u(x, t) + w * F(u_t)(x)) dt + \sigma dW(x, t)$$

- ▶ one possibility: work in weighted \mathcal{L}^2 space (Faugeras, Inglis 2013)⁷
- ▶ consider the difference $v(x, t) = u(x, t) - u^{TW}(x, t)$ leading to the equation

$$dv_t = \left(-v_t + w * (F(v_t + u_t^{TW}) - F(u_t^{TW})) \right) dt + \sigma dW_t$$

- ▶ (W_t) Q -Wiener process on \mathcal{L}^2 with $tr(Q) < \infty$
- ▶ for any initial condition $v^0 \in \mathcal{L}^2$, $\exists!$ strong solution admitting a continuous modification

⁷O. Faugeras, J. Inglis: Stochastic Neural Field Equations: A Rigorous Footing; arXiv:1311.5446, 2013

Stability

- ▶ is the wave solution stable under small perturbations?
- ▶ in the deterministic case: if $\|v^0\|$ is small, does $\|v_t\| \rightarrow 0$?
- ▶ in the stochastic case: $u_t = \text{traveling wave} + \text{fluctuations}$ around wave profile

Linearisation

- ▶ Ansatz: linearise the equation around the traveling wave

$$\begin{aligned} dv_t &= \left(-v_t + w * (F(v_t + u_t^{TW}) - F(u_t^{TW})) \right) dt + \sigma dW_t \\ &= \left(-v_t + w * (F'(u_t^{TW})v_t) \right) dt + R(t, v_t)dt + \sigma dW_t \end{aligned}$$

where

$$\|R(t, v_t)\| = O(\|v_t\|^2)$$

- ▶ then, in the deterministic case,

$$\frac{1}{2} \frac{d}{dt} \|v_t\|^2 \approx \langle Lv_t, v_t \rangle$$

where

$$Lu = -u + w * (F'(u^{TW})u)$$

- ▶ cannot expect L to be strictly dissipative (i.e. $\langle Lu, u \rangle \leq -\kappa \|u\|^2$)

Adaptation of the Wave Speed

- ▶ need to adapt to the right phase of the wave
- ▶ idea: minimise the \mathcal{L}^2 -distance, i.e. find y^* such that

$$\|u_t - u_t^{TW}(\cdot - y^*)\| = \min_y \|u_t - u_t^{TW}(\cdot - y)\|$$

- ▶ note that

$$\begin{aligned} & \frac{1}{2} \frac{d}{ds} \|u_t - u_t^{TW}(\cdot - y(s))\|^2 \\ & = y'(s) \langle u_t - u_t^{TW}(\cdot - y(s)), \partial_x u_t^{TW}(\cdot - y(s)) \rangle \leq 0 \end{aligned}$$

for $y'(s) = -m \langle u_t - u_t^{TW}(\cdot - y(s)), \partial_x u_t^{TW}(\cdot - y(s)) \rangle$ for any $m > 0$

- ▶ define the phase adaptation as the unique solution to the ode

$$C'(t) = c - m \langle u_t - \hat{u}(\cdot - C(t)), \hat{u}_x(\cdot - C(t)) \rangle$$

(P-a.s. in the stochastic case)

The Case $c = 0$

- ▶ $L(\hat{u}_x) = 0$ and (under some assumptions)

$$\langle Lu, u \rangle \leq -\kappa \|u\|^2 + K \langle u, \hat{u}_x \rangle^2$$

(L., Stannat 2013)

- ▶ $\tilde{v}_t := u_t - \hat{u}(\cdot - C(t))$ satisfies

in the deterministic case:

$$\frac{1}{2} \frac{d}{dt} \|\tilde{v}_t\|^2 \lesssim -\kappa \|\tilde{v}_t\|^2 + (K - m) \langle \hat{u}_x(\cdot - C(t)), \tilde{v}_t \rangle^2 \leq -\kappa \|\tilde{v}_t\|^2$$

in the stochastic case:

$u_t \approx \hat{u}(\cdot - C(t)) +$ Ornstein-Uhlenbeck process

The Case $c = 0$

- ▶ noise influences the speed of the wave
- ▶ for large relaxation constants m ,

$$C(t) \approx -\frac{1}{\|\hat{u}_x\|^2} \left(\langle \tilde{v}_0, \hat{u}_x \rangle + \sigma \int_0^t \langle \hat{u}_x(\cdot - C(s)), dW_s \rangle \right)$$

- ▶
$$\left[\sigma \int_0^\cdot \langle \hat{u}(x - C(t)), dW_s \rangle \right]_t \approx \sigma^2 \langle u^{TW}, Qu^{TW} \rangle_t$$
- ▶ $\rightarrow \approx$ Brownian motion

The Case $c > 0$

- ▶ for sufficiently small c

$$\langle -v + w * (F'(\hat{u})v), v \rangle \leq -\kappa_c \|v\|^2 + K_c \langle v, \hat{u}_x \rangle^2$$

(L., 2013)

- ▶ $c = \frac{\int_0^1 u - F(u) du}{\int \hat{u}_x^2(x) F'(\hat{u}(x)) dx}$ is generally not known

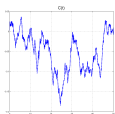
- ▶ control over c in terms of F : for $w(x) = \frac{1}{2\alpha} e^{-\frac{|x|}{\alpha}}$

$$\frac{\alpha}{\sqrt{2}} \frac{\int_0^1 u - F(u) du}{\sqrt{\int_0^a u - F(u) du}} \leq c \leq \frac{\alpha}{4} \frac{\int_0^1 u - F(u) du}{\int_a^1 F(u) - u du}$$

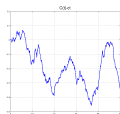
where $F(a) = a$

Numerical Simulations: $c = 0$

$c = 0$:



$c > 0$:



green: reference wave profile

red: wave profile moving at adapted speed

blue: solution to the stochastic neural field equation

The Noise

$$\frac{d}{dt}u^i(t) = \left(-u^i(t) + \sum_j w_{i,j}F(u^j(t)) \right) + \text{"noise"}$$

- ▶ source of the noise?
- ▶ source of intrinsic noise: finite size effects
- ▶ idea: set up a continuous time Markov chain describing the evolution of the activity a (= fraction of 'active' neurons) of M coupled populations of finite size N that yields the NFE for $u = F^{-1}(a)$ in the limit
 - ▶ Buice, Cowan '07; Bressloff '09; Buckwar, Riedler '13

The Noise

- ▶ Markov chain: M populations à N neurons
- ▶ activity in population i jumps from a^i to $a^i \pm \frac{1}{N}$ at rate $N F'(F^{-1}(a^i)) \left(-F^{-1}(a^i) + \sum_j w_{i,j} a^j \right)_{\pm}$
- ▶ $da_t^i = F'(F^{-1}(a^i(t))) \left(-F^{-1}(a_t^i) + \sum_j w_{i,j} a^j(t) \right) + dM_t^i$
- ▶ $\sqrt{N}[M^i]_t \xrightarrow{N \rightarrow \infty} \int_0^t F'(F^{-1}(a_s^i)) \left| -F^{-1}(a_s^i) + \sum_j w_{i,j} a_s^j \right| ds$
- ▶ suggests the diffusion approximation

$$du_t^i = -u_t^i + \sum_j w_{i,j} F(u_t^j) + \frac{1}{\sqrt{N}} \sqrt{\frac{\left| -u_t^i + \sum_j w_{i,j} F(u_t^j) \right|}{F'(u_t^i)}} dB_t^i$$

- ▶ yields a stochastic NFE in the continuum limit