Existence of Traveling Pulses in some Neural Models

Stuart Hastings

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Stuart Hastings (University of Pittsburgh) Existence of Traveling Pulses in some Neural

Travelling pulses instead of traveling fronts for FitzHugh-Nagumo: Add a slowly changing "recovery" variable w.

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 $w_t = \varepsilon (u - \gamma w).$

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The speed increases, until some w_2 such that $c = c_0^*$ again. The symmetry of f(u) = u(1-u)(u-a) around its inflection point implies that such a w_2 exists.

Three models of neural behavior:

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Pinto-Ermentrout model of a neural network:

$$\frac{\partial u(x,t)}{\partial t} = -u(x,t) - v(x,t) + \int_{-\infty}^{\infty} J(x-y) S(u(y,t)) dy$$
$$\frac{1}{\varepsilon} \frac{\partial v(x,t)}{\partial t} = u(x,t) - \beta v(x,t)$$

where S is the firing rate and J gives strength of connectivity within a population of cells along the x axis.

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G. Faye (like Bressloff, Kilpatrick; includes synaptic depression)

$$\frac{\partial u(x,t)}{\partial t} = \int_{-\infty}^{\infty} J(x-y) q(y,t) S(u(y,t)) dy - u(x,t)$$
$$\frac{1}{\varepsilon} \frac{\partial q(x,t)}{\partial t} = 1 - q(x,t) - \beta q(x,t) S(u(x,t))$$

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Fourier transform or differentiation converts the integral equations to PDEs

$$\zeta=x+ct$$
 converts the PDEs to systems of ODEs, $'=rac{d}{d\zeta}$

$$u' = v$$

$$v' = cv - f(u) + w$$

$$w' = \frac{\varepsilon}{c} (u - \gamma w)$$
(FHN)

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$$u' = \frac{w - u - v}{c}$$

$$w' = z$$

$$z' = b^{2} (w - S(u))$$

$$v' = \frac{\varepsilon}{c} (u - \beta v)$$

(PE)

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$$u' = \frac{v-u}{c}$$

$$v' = w$$

$$w' = b^{2} (v - qS(u))$$

$$q' = \frac{\varepsilon}{c} (1 - q - \beta qS(u))$$
(FAYE)

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$$\lim_{\zeta\to-\infty}p\left(\zeta\right)=\lim_{\zeta\to\infty}p\left(\zeta\right)=p_{0},$$

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- Show why existence for (PE) is apparently harder than for (FAYE)

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- Outline the proof of a non-trivial extension of the results of Faye about existence of pulses for his model
- Show why existence for (PE) is apparently harder than for (FAYE)
- Discuss the extension of results on (FHN) to more general functions f.

FitzHugh-Nagumo:

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It has been shown that if f is in the cubic form above and ε is sufficiently small, then homoclinic orbits exist for at least two positive values of c. See Hastings and McLeod, 2012, for a recent exposition.

Recall that for FitzHugh-Nagumo we have considered the existence of travelling fronts, which exist if $\varepsilon = 0$.

$$\frac{\partial U(x,t)}{\partial t} = \int_{-\infty}^{\infty} J(x-y) S(U(y,t)) dy - U(x,t).$$

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However, no existence proofs for pulses has been obtained for (PE).

For most of this lecture we will outline such a proof for the model of Faye.
Results of Faye:

$$u' = \frac{v-u}{c}$$

$$v' = w$$

$$w' = b^{2} (v - qS(u))$$

$$q' = \frac{\varepsilon}{c} (1 - q - \beta qS(u))$$

$$S(u) = \frac{1}{1 + e^{\lambda(\kappa - u)}}$$
(FAYE)

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Equilibrium points:

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Fast system ($\varepsilon = 0$):

$$U' = \frac{V - U}{c}$$
$$V' = W$$
$$W' = b^{2} (V - qS(U))$$

where q is constant.

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$$U' = \frac{V - U}{c}$$

$$V' = W$$

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$$(FF)$$

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Consider values of $q \in (q_{\min}, q_0]$.

Three equilibria for the fast system:



Theorem (Ermentrout and McLeod): The system (FF) has a traveling wave solution (U, V, W) with c > 0 connecting $(u_{q,0}, u_{q,0}, 0)$ to $(u_{q,+}, u_{q,+}, 0)$ for each $q \in (q_{\min}, q_0]$.

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(ode proof straightforward)





 $q_1 \in (q_{\min}, q_0)$, close to q_{\min} .

Theorem (Ermentrout and McLeod, Faye) Let U_q be the traveling front or back solution for some $q \in (q_{\min}, q_0]$. Then the speed c(q) of this solution is

$$c\left(q
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With $S(u) = \frac{1}{1+e^{\lambda(\kappa-u)}}$ there is a unique \bar{q} in (q_{\min}, q_0) such that $c(\bar{q}) = 0$. For higher q, the connecting wave is a front, while for $q \in (q_{\min}, \bar{q})$ the connecting wave is a back.

Faye proves the existence of a pulse using the method of geometric perturbation.

The first piece is the front with speed $c(q_0)$.

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The second part is a slow trajectory moving along the right branch of the nullcline u = qS(u).

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The third part of the singular solution is a "downjump", or "back", from a point $q = q_1$ determined by where $c(q_1) = c(q_0)$.

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Nullclines: Red, Blue Singular solution: Green.

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Nullclines: Red, Blue Singular solution: Green.

The fourth part of the singular solution is a slow return along the left branch of the nullcline.

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(i) The system (FAYE) has a unique equilibrium point $(u_0, u_0, 0, q_0)$.

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$$g\left(u
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has exactly three solutions, $u_0 < u_m < u_+$, with $g'(u_0) > 0$, $g'(u_m) < 0$, and $g'(u_+) > 0$.

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It follows that the back of the singular solution is required to be at the knee. This condition can only be verified by numerical integration of the fast system.


The orbit of the singular solution is the green curve.

(Hypotheses (iv) is that the downjump (back) is "at the knee".)

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Our result is

Theorem: Under hypotheses (i), (ii), and (iii), if ε is sufficiently small then the system (FAYE) has a homoclinic orbit for at least two positive values of c.

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(Demo)

BREAK

Outline of proof:

Assume:

- (i) unique equilibrium point, $(u_0, u_0, 0, q_0)$
- (ii) $\frac{u}{S(u)}$ is S shaped, and equals q_0 when $u = u_0 < u_m < u_+$.
- (iii) $\int_{u_0}^{u^+} (q_0 S(u) u) du > 0$

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Then for c > 0 and $\varepsilon > 0$ there is a one dimensional unstable manifold \mathcal{U} at $p_0 = (u_0, u_0, 0, q_0)$.



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Then for c > 0 and $\varepsilon > 0$ there is a one dimensional unstable manifold \mathcal{U} at $p_0 = (u_0, u_0, 0, q_0)$.



Specify a unique solution $p_c = (u_c, v_c, w_c, q_c)$ on \mathcal{U} by requiring that $u_c(0) = u_m$.

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Let c_0^* be the speed of the front solution of the fast system which connects $(u_0, u_0, 0)$ to $(u_+, u_+, 0)$ and let $c_1 = \frac{1}{2}c_0^*$.

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solutions on ${\mathcal U}$ for $c=c_0^*$ and c_1

Then set

$$\begin{split} &\Lambda = \{ c \geq c_1 \mid \text{There exist } t_1, \ t_2, \text{ and } t_3 \text{ such that } 0 < t_1 < t_2 < t_3 \text{ and} \\ &(\text{a}) \quad u_c' > 0 \text{ on } [0, t_1), \ u_c'(t_1) = 0, \ u_c(t_2) = u_0, \\ &(\text{b}) \text{ either } u_c(t_3) = 0 \text{ or } q_c(t_3) = q_0, \\ &(\text{c}) \ u_c''(t_1) < 0, \ u_c' < 0 \text{ on } (t_1, t_2] \text{ and } u_c < u_0 \text{ on } (t_2, t_3] \}. \end{split}$$



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$$\begin{split} \Lambda &= \{ c \geq c_1 \mid \text{There exist } t_1, \ t_2, \text{ and } t_3 \text{ such that } 0 < t_1 < t_2 < t_3 \text{ and} \\ \text{(a)} \quad u'_c > 0 \text{ on } [0, t_1), \ u'_c (t_1) = 0, \ u_c (t_2) = u_0, \\ \text{(b)} \quad \text{either } u_c (t_3) = 0 \text{ or } q_c (t_3) = q_0, \\ \text{(c)} \ u''_c (t_1) < 0, \ u'_c < 0 \text{ on } (t_1, t_2] \text{ and } u_c < u_0 \text{ on } (t_2, t_3] \}. \end{split}$$



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Each figure shows one solution with $c \in \Lambda$ and one solution with $c \notin \Lambda$

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Lemma 1: $c_1 \in \Lambda$, and for some $\delta > 0$ Λ is a relatively open subset of $[c_1, c_0^* - \delta)$.

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Image: A mathematical states of the state



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The proof uses the fact that c^* is on the boundary of Λ .



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The proof uses the fact that c^* is on the boundary of Λ .

Neither solution shown above is for *c* on this boundary, but possibly other solutions, with different behavior, are.

For example, behaviors like the following must be eliminated. A solution like one of these would be on the boundary of Λ and yet not homoclinic.



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Most interesting: Eliminate this:

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Let
$$p_* = (u_*, v_*, w_*, q_*) = p_{c^*}$$
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Most interesting: Eliminate this:



Let
$$p_* = (u_*, v_*, w_*, q_*) = p_{c^*}$$
.
Then

$$\begin{split} u_{*}'(\tau) &= w_{*}'(\tau) = q_{*}'(\tau) = 0\\ v_{*}'(\tau) &< 0. \end{split}$$

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We trace the solution backwards, by letting

$$P\left(s
ight)=\left(\mathit{U},\mathit{V},\mathit{W},\mathit{Q}
ight)\left(s
ight)=p_{st}\left(au-s
ight).$$

Then

$$U' = \frac{U-V}{c}$$
$$-V' = W$$
$$W' = b^2 (QS(U) - V)$$
$$Q' = \frac{\varepsilon}{c} (Q + \beta QS(U) - 1)$$

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(1)

Then

$$\begin{array}{l} U' = \frac{U-V}{c} \\ -V' = W \\ W' = b^2 \left(QS \left(U \right) - V \right) \\ Q' = \frac{\varepsilon}{c} \left(Q + \beta QS \left(U \right) - 1 \right) \end{array} .$$

Also,

$$\begin{array}{l} U\left(0\right) = u_{0}, \ V\left(0\right) = u_{0}, \ Q\left(0\right) = q_{0}, \\ U'\left(0\right) = W'\left(0\right) = Q'\left(0\right) = 0, \ -V'\left(0\right) < 0, \end{array}$$

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Then

$$U' = \frac{U-V}{c} - V' = W$$

$$W' = b^2 (QS(U) - V)$$

$$Q' = \frac{\varepsilon}{c} (Q + \beta QS(U) - 1)$$
(1)

Also,

$$U(0) = u_0, V(0) = u_0, Q(0) = q_0, U'(0) = W'(0) = Q'(0) = 0, -V'(0) < 0,$$

Because the terms on the right of (1) are increasing in U, -V, W, and Q, these variables decrease as long as the solution exists.

We show that this must happen instead:



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Hence, $u_*(-\infty) \neq u_0$, a contradiction because the solution was chosen on the unstable manifold \mathcal{U} .


But in this region, q' > 0.



But in this region, q' > 0. Hence $\lim_{t\to\infty} q_{c^*}(t)$ exists and it follows that $\lim_{t\to\infty} p_{c^*}(t) = (u_0, u_0, 0, q_0)$.



But in this region, q' > 0. Hence $\lim_{t\to\infty} q_{c^*}(t)$ exists and it follows that $\lim_{t\to\infty} p_{c^*}(t) = (u_0, u_0, 0, q_0)$. This method values are used to first nuclear values on the first nuclear values.

This method relies on results for the fast system when $q = q_0$, but pays no attention to whether the recovery is "below the knee" or not.

Ideally we would like to extend Λ to the left of c_1 and show that if $c_* = \inf \Lambda$ then p_{c_*} is also homoclinic.

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Unfortunately, proving existence of a slow wave requires different sets on the c axis.

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Unfortunately, proving existence of a slow wave requires different sets on the c axis.

Reason: If $\frac{\varepsilon}{c}$ is large then the concept of fast and slow waves breaks down.



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Why is it harder to prove that (PE) has a homoclinic orbit?

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The eigenvalues of the linearization around equilibrium can have complex roots if ε is not too small. The geometry above does not work, since even if ε is too small to allow complex eigenvalues, the solution may oscillate around $u = u_0$ a few times.



Why is it harder to prove that (PE) has a homoclinic orbit?

The eigenvalues of the linearization around equilibrium can have complex roots if ε is not too small. The geometry above does not work, since even if ε is too small to allow complex eigenvalues, the solution may oscillate around $u = u_0$ a few times.



Complex roots have interesting consequences.

What more is to be said about the FitzHugh-Nagumo equations?

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What more is to be said about the FitzHugh-Nagumo equations? Does the issue of "below the knee" come up there? Yes, except it is "above the knee": For the standard cubic,

$$f(u) = u(1-u)(u-a)$$
 ,

there is symmetry which implies that the downjump of the singular solution is always below the knee.



The graph is symmetric around the inflection point of f. Hence the downjump occurs at a w value where the ratio of positive area to negative area under f - w is inverted from that of the upjump.

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However, consider another function f:



Note that

Area A < Area B.

Question: What is the relation between area and speed?

Question: What is the relation between area and speed?

$$|c| = \frac{\left|\int_{0}^{1} f(\sigma) \, d\sigma\right|}{\int_{-\infty}^{\infty} u'(t)^{2} \, dt}$$

This only seems useful when $\int_0^1 f(\sigma) d\sigma = 0$. For example, is |c| a monotone function of $\int_0^1 f$ in intervals where $c \neq 0$?