Sparse gamma rhythms arising through clustering in adapting neuronal networks: Supplementary information (S1)
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Singular perturbation theory and exact calculation of periodic solution to idealized spiking model with adaptation

The following text consists of two companion sections to the main manuscript, Sparse gamma rhythms arising through clustering in adapting neuronal networks. The first section details an approximation of the periodic solution of a theta model neuron with spike frequency adaptation. This makes use of the slow timescale of spike frequency adaptation to separate the system into a fast and a slow subsystem, which can be analyzed together using singular perturbation theory. These results are summarized in the main manuscript section entitled Approximating the periodic solution and cluster number with singular perturbation theory. The next section exactly calculates the periodic solution of a quadratic integrate-and-fire model neuron with spike frequency adaptation. This is used in the main manuscript section entitled Phase-resetting curve of an adapting neuron to compute the phase-resetting curve of the model.

Singular perturbative approximation of periodic solution

In this section, we proceed to compute a singular perturbative approximation to the periodic solution of

\[
\begin{align*}
\dot{\theta} &= 1 - \cos \theta + (1 + \cos \theta)(I - \beta z), \\
\dot{z} &= -z/\tau_a + \delta(\pi - \theta),
\end{align*}
\]

with period \(T\), such that \(\theta(0) = -\pi\) and \(\theta(T) = \pi\). With these assumptions, we can solve for

\[
z = z_0 e^{-t/\tau_a} = \frac{e^{-t/\tau_a}}{1 - e^{-T/\tau_a}}.
\]

Therefore the system (1) reduces to a single nonautonomous equation for the phase variable,

\[
\dot{\theta} = 1 - \cos \theta + (1 + \cos \theta)(I - \beta z_0 e^{-\epsilon t}),
\]

where we have defined \(\epsilon = 1/\tau_a \ll 1\), since we know the adaptation time constant is large, \(\tau_a \gg 1\). By ignoring dynamics that occur on the slow timescale \(s = \epsilon t\), we can consider a fast subsystem

\[
\dot{\theta} = 1 - \cos \theta + (1 + \cos \theta)(I - \beta z_0),
\]

which should describe initial dynamics within an initial boundary layer. It is straightforward to solve (4), along with the boundary condition \(\theta(0) = -\pi\) to find

\[
\theta(t) = 2 \tan^{-1} \left[ \sqrt{I - \beta z_0} \tan \left( \sqrt{I - \beta z_0 t - \frac{\pi}{2}} \right) \right]
\]

within the initial layer. Once the dynamics of the fast subsystem (5) have settled to their limiting value,

\[
\lim_{t \to \infty} 2 \tan^{-1} \left[ \sqrt{I - \beta z_0} \tan \left( \sqrt{I - \beta z_0 t - \frac{\pi}{2}} \right) \right] = -\frac{\pi}{2},
\]
they will evolve along a manifold determined by the slow subsystem
\[ 0 = 1 - \cos \theta + (1 + \cos \theta)(I - \beta z_0 e^{-s}), \]
where \( s = \epsilon t \) is a slow time variable. We can solve (6) for the outer layer’s dynamics
\[ \theta(s) = -\cos^{-1} \left[ \frac{I - \beta z_0 e^{-s} + 1}{\beta z_0 e^{-s} + 1 - I} \right]. \]
Notice that this solution will vanish when \( \beta z_0 e^{-\epsilon T_{SN}} = I \). This is related to the fact that as the total input to the neuron passes through zero, there is a saddle-node bifurcation in the equilibria structure of the associated fast subsystem \([1]\). This is a common mechanism for initiating the fast part of a relaxation oscillation \([2]\). The slow solution will therefore last about
\[ T_{SN} = \frac{1}{\epsilon} \ln \frac{\beta z_0}{I}. \]
When the system reaches the vicinity of the saddle-node (\( t \approx T_{SN} \)), it will begin to evolve according to fast dynamics. Therefore, we must calculate the terminal dynamics of the periodic solution within a boundary layer. To do this, we presume perturbative solutions and fast timescales with arbitrary scaling \( \theta = \epsilon^p \theta_1 \) and \( \tau = \epsilon^q (t - T_{SN}) \). Substituting these expressions into (3), we have
\[ \epsilon^{p+q} \frac{d\theta_1}{d\tau} = \frac{1}{2} \epsilon^{2p} \theta_1^2 + 2 \beta z_0 e^{-\epsilon T_{SN}} \epsilon^{-q} \tau. \]
Upon setting \( p = q = 1/3 \), we find the order of all terms is matched. Now, we apply the Riccati transformation \( \theta_1 = -2\dot{y}/y \), as well as a change of variables \( r = B\tau \), where
\[ B = \left( \frac{\beta z_0 e^{-\epsilon T_{SN}}}{2} \right)^{1/3} = \left( \frac{I}{2} \right)^{1/3}. \]
This yields Airy’s equation
\[ \frac{d^2 y}{dr^2} = ry, \]
which has general solutions
\[ y(r) = c_1 \text{Ai}(r) + c_2 \text{Bi}(r), \]
where \( \text{Ai}(r) \) and \( \text{Bi}(r) \) are the Airy functions of the first and second kind. We specify the solution \( \theta_1 \) by transforming back, changing variables back to \( \tau \), and applying the initial condition \( \theta_1(0) = 0 \) to find
\[ \theta_1(\tau) = 2B \frac{\sqrt{3} \text{Ai}'(-B\tau) + \text{Bi}'(-B\tau)}{\sqrt{3} \text{Ai}(-B\tau) + \text{Bi}(-B\tau)}. \]
We can predict the point where the inner layer solution will diverge to be the minimal \( \tau_b \) such that \( \tau_b > 0 \) and
\[ \sqrt{3} \text{Ai}(-B\tau_b) = -\text{Bi}(-B\tau_b). \]
The blow up of this inner solution roughly denotes the end of the solution period. Converting back to the time variable \( t \), we find the period will be
\[ T = T_{SN} + \frac{\tau_b}{\epsilon^{1/3}} \]
\[ = \frac{1}{\epsilon} \ln \frac{\beta z_0}{I} + \frac{\tau_b}{\epsilon^{1/3}}. \]
Substituting (9) into (2) and requiring self-consistency, we can solve for the initial condition
\[ z_0 = 1 + \frac{I}{\beta} e^{-\epsilon^2/3 \tau_b}. \]

Therefore, the time it takes to reach the saddle-node is
\[ T_{SN} = \frac{1}{\epsilon} \ln \left[ \frac{\beta I + e^{-\epsilon^2/3 \tau_b}}{I} \right] \]
\[ \approx \frac{1}{\epsilon} \left\{ \ln \left[ \frac{\beta}{I} + 1 \right] - \frac{\epsilon^2/3 \tau_b}{\beta I + 1} \right\}, \tag{10} \]
when we Taylor expand to first order. Plugging (10) into (9) and rewriting \( \tau_a = 1/\epsilon \), we have the approximation for the period of the solution
\[ T \approx \tau_a \ln \left[ \frac{\beta}{I} + 1 \right] + \frac{\beta \tau_a^{1/3} \tau_b}{\beta + I}, \]
where \( \tau_b \) is determined by (8).

Note that the outer solution (7) becomes undefined once the saddle-node of the fast subsystem is reached at \( t = T_{SN} \). Thus, we must construct the singular solution in a piecewise manner with two regions, where one region is the sum of the initial and outer layers and another region is the terminal layer. Using the timescale \( t \) and noting \( \epsilon = 1/\tau_a \), we can write
\[ \theta(t) = 2 \tan^{-1} \left[ \sqrt{I - \tilde{z}_0} \tan \left( \sqrt{I - \tilde{z}_0} t - \frac{\pi}{2} \right) \right] + \frac{\pi}{2} \]
\[ - \cos^{-1} \left[ \frac{I - \tilde{z}_0 e^{-t/\tau_a} + 1}{\tilde{z}_0 e^{-t/\tau_a} + 1 - I} \right], \quad t \in (0, T_{SN}), \]
and
\[ \theta(t) = \frac{2B}{\tau_a^{1/3}} \frac{\sqrt{3} Ai'(B(T_{SN} - t)/\tau_a^{1/3}) + Bi'(B(T_{SN} - t)/\tau_a^{1/3})}{\sqrt{3} Ai(B(T_{SN} - t)/\tau_a^{1/3}) + Bi(B(T_{SN} - t)/\tau_a^{1/3})}, \quad t \in (T_{SN}, T). \]

**Exact periodic solution for quadratic integrate-and-fire model with spike frequency adaptation**

In this section, we explicitly solve for a periodic solution to
\[ \dot{x} = x^2 + I - \beta z, \tag{11} \]
\[ \dot{z} = -z/\tau_a + \delta(1/x). \]

To do so, we require the boundary conditions \( x(0) = -\infty \) and \( x(T) = \infty \). We can immediately solve the equation for the adaptation variable
\[ z(t) = \frac{e^{-t/\tau_a}}{1 - e^{-T/\tau_a}}. \]

Assigning the parameters \( \epsilon = 1/\tau_a \) and \( \tilde{\beta} = \beta/(1 - e^{-T_0}) \), we can express the equation for \( x \) now as
\[ \frac{dx}{dt} = x^2 + I - \tilde{\beta} e^{-t}. \tag{12} \]
Note, we use $\epsilon$ here for comparison with our singular perturbation theory results. Our next step is to employ the transformation $x = -\dot{y}/y$ to convert the Riccati equation (12) to
\[
\frac{d^2 y}{dt^2} = [\beta e^{-\epsilon t} - I]y,
\]
a second order linear equation. Now, by making the change of variables $r = e^{-\epsilon t/2}$, we can in fact convert (13) to
\[
r^2 \frac{d^2 y}{dr^2} + r \frac{dy}{dr} = \frac{4}{\epsilon^2} [\beta r^2 - I]y.
\]
Upon employing a change to imaginary variables $\mu = 2\beta ir/\epsilon$ and $\nu = 2\sqrt{T}/\epsilon$, we find $y(\mu)$ is described by Bessel’s equation
\[
\mu^2 \frac{d^2 y}{d\mu^2} + \mu \frac{dy}{d\mu} + [\mu^2 - \nu^2] y = 0,
\]
whose general solutions are given
\[
y(\mu) = c_1 J_{\nu}(\mu) + c_2 Y_{\nu}(\mu),
\]
where $J_{\nu}(\mu)$ and $Y_{\nu}(\mu)$ are Bessel functions of the first and second kind, respectively. Changing the constant $\nu$ and variable $\mu$ back, we find $y$ is given as the sum of Bessel functions with imaginary order and argument
\[
y(t) = c_1 J_{2\sqrt{T}/\epsilon} \left( \frac{2\sqrt{\beta} i}{\epsilon} e^{-\epsilon t/2} \right) + c_2 Y_{2\sqrt{T}/\epsilon} \left( \frac{2\sqrt{\beta} i}{\epsilon} e^{-\epsilon t/2} \right).
\]
We find that, by requiring that the left boundary condition, $x(0) = -\infty \Rightarrow y(0) = 0$, be satisfied, the solution $y$ is restricted to be of the form
\[
y(t) = c_1 \text{Im} \left\{ J_{2\sqrt{T}/\epsilon} \left( \frac{2\sqrt{\beta} i}{\epsilon} e^{-\epsilon t/2} \right) \right\},
\]
so that the period $T$ can be specified by the right boundary condition, $x(T) = \infty \Rightarrow y(T) = 0$, so
\[
y(T) = \text{Im} \left\{ J_{2\sqrt{T}/\epsilon} \left( \frac{2i}{\epsilon} \sqrt{\beta e^{\epsilon T} - 1} \right) \right\} = 0.
\]
This fully characterizes the solution, since the remaining constant $c_1$ is eliminated by the form of $x(t) = -\dot{y}(t)/y(t)$. In addition, since we now have a formula for the periodic solution to the system (11), we can compute the associated adjoint, related to the phase resetting curve.

References
