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Effects of quasiactive membrane on multiply periodic traveling waves in integrate-and-fire systems

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We consider the dynamics of a one-dimensional continuum of synaptically interacting integrate-and-fire neurons with realistic forms of axodendritic interaction. The speed and stability of traveling waves are investigated as a function of discrete communication delays, distributed synaptic delays, and axodendritic delays arising from the spatially extended nature of the model neuron. In particular, dispersion curves for periodic traveling waves are constructed. Nonlinear ionic channels in the dendrite responsible for a so-called *quasiactive* bandpass response are shown to significantly influence the shape of dispersion curves. Moreover, a kinematic theory of spike train propagation suggests that period-doubling bifurcations of a singly periodic wave can occur in dendritic systems with a quasiactive membrane. The explicit construction of period-doubled solutions is used to confirm this prediction.

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I. INTRODUCTION

Traveling waves of activity have been experimentally observed in many neural systems. Examples include thalamocortical regions of humans [1], the retina of developing rabbits [2] and mice [3], the visual cortex of the turtle [4], and the olfactory system of the mollusc [5]. The functional significance of waves in these systems is not always clear. Elucidating the mechanisms of wave initiation, propagation, and bifurcation is therefore directly relevant to determining the functional roles that waves may take. Indeed, the propagation of synchronous spikes has been proposed by Abeles as a mechanism for generating the precisely timed spike events observed in multielectrode recordings of cortical circuits [6].

To capture the essence of a wave of spiking activity it is natural to work with perhaps the most simple spiking neuron model, namely, the integrate-and-fire (IF) model. At the network level, analytical and numerical studies have already shown wave behavior consistent with more detailed biophysical models (see Ref. [7] for a recent review). In particular, we refer to the work of Golomb and Ermentrout [8–10] and Bressloff [11,12]. Importantly, these authors have developed a mathematical framework that can provide an exhaustive analysis of the speed and stability for solitary traveling pulses. It has been shown by Bressloff that, away from the long-wavelength limit, the determination of wave stability is a highly nontrivial mathematical problem, involving the solution of a linear map of infinite order. Hence, almost nothing is known about the stability of periodic waves nor of the actual mechanisms by which periodic waves can lose stability.

In this paper we address these problems within a kinematic framework for spike train dynamics. Here the spatial evolution of spiking events is considered to be completely determined in terms of the dispersion curve (speed as a function of period) for a periodic wave. The existing mathematical framework for constructing dispersion curves in IF networks is therefore ideally suited to building a kinematic theory. The kinematic stability of waves in a synaptically coupled IF network, and indeed many other spatially extended excitable systems, can be determined by the sign of the gradient of the dispersion curve. The identification of parameters that underlie the generation of stationary points in the dispersion curve can therefore be used to highlight the neurophysiological features responsible for wave instability and bifurcation. A major result is that synaptic responses with a bandpass nature can lead to the creation of multiple stationary points in the dispersion curve. Such bandpass characteristics of neuronal response arise naturally in spatially extended models of neurons with dendritic trees possessing the so-called quasiactive membrane. The theory of the quasiactive membrane has been proposed by Koch [13] as a model for the small signal voltage response of an excitable neuron arising from nonlinear ionic channels embedded in the dendritic membrane. It is obtained by linearizing the Hodgkin-Huxley equations about a steady state and may be regarded as a linear resistor-capacitor (LRC) model of nerve tissue with an inductive element, i.e., an electrical LRC circuit. The analysis of dendrites with LRC resonant frequencies has been developed by Bressloff [14], and feeds naturally into the formalism developed for the study of dispersion curves in IF systems.

The structure of the paper is as follows. In Sec. II, we present the model and the mathematical framework appropriate for the construction of dispersion curves. The work by Bressloff on periodic traveling waves is extended in a straightforward manner to cover the important case of multiply periodic waves (which will be shown later to bifurcate from singly periodic waves). Also presented are the kinematic theory of spike train propagation and the conditions for the stability of a multiply periodic spike train. Illustrations of the theory are given in Sec. III for delayed synaptic interactions in a point IF model and in Sec. IV for a spatially extended dendritic model. In the latter case, the inclusion of a quasiactive (as opposed to purely passive) membrane is shown to produce an oscillation in the upper branch of the dispersion curve leading to alternating regions of stability. An explicit construction of period-doubled solutions shows that they branch from local maxima of the dispersion curve of the singly periodic orbit. Finally, in Sec. V, we summarize the major points of this paper and suggest natural extensions of our work.

II. ONE-DIMENSIONAL INTEGRATE-AND-FIRE CONTINUUM

Consider a one-dimensional continuum of integrate-and-fire neurons. The dynamic equation for the membrane potential $V(x,t)$ is given by

$$\frac{\partial V(x,t)}{\partial t} = -\frac{V(x,t)}{\tau} + S(x,t), \quad x\in\mathbb{R}, t\geqslant 0, \tag{1}$$

where τ is the membrane time constant (hereafter set to unity without loss of generality) and $S(x,t)$ is the synaptic input at position x and time t. Equation (1) is supplemented by the reset condition such that, whenever $V(x,t)=1$, $V(x,t^+)=0$. As it stands, the IF model allows for an arbitrarily high, and therefore unphysical, firing rate. There are several ways in which to introduce some level of refractoriness into the IF model such as via a large negative reset or a time-varying threshold [15]. For simplicity, we shall adopt a simple absolute refractory mechanism whereby a neuron is held at the reset level for a time τ_R after a spiking event. The synaptic input to each neuron has the form

$$S(x,t) = \epsilon \int_{-\infty}^{\infty}\int_{0}^{\infty} W(x-y) J(s) \Psi(y,t-s)\, ds\, dy, \tag{2}$$

where $\epsilon>0$ is the global coupling strength and $W(x)=W(|x|)$ is the synaptic weight kernel (or footprint) between neurons separated by a distance $|x|$. The temporal delay kernel $J(t)$ determines the shape of the postsynaptic potential and can model axonal delays, dendritic delays, and synaptic processing as discussed in previous papers (see, for example Ref. [16]). Neglecting the shape of an individual pulse, the output spike train of each neuron is represented as a sequence of Dirac delta functions $\Psi(x,t)=\Sigma_{m\in\mathbb{Z}}\delta(t-T^m(x))$, where $T^m(x)$ is the mth firing time of the neuron at position x.

For a Δ_1 periodic traveling wave, the firing time ansatz is $T^m(x)=(m+kx)\Delta_1$ for some wave number k [12]. This defines a wave of speed $c=1/(k\Delta_1)$. Integrating Eq. (1) between successive firing events gives

$$1 = \epsilon \int_{-\infty}^{\infty} W(x) K(kx)\, dx, \tag{3}$$

where

$$K(x) = \int_{\tau_R}^{\Delta_1} e^{-\Delta_1} e^{s} \sum_{m\in\mathbb{Z}} J(s+(m+x)\Delta_1)\, ds. \tag{4}$$

Equation (3) implicitly defines a dispersion relationship $c=c(\Delta_1)$ giving the wave speed c as a function of the period Δ_1. Since $K(x)$ is a real periodic function of x, Fourier transforms are a natural way in which to evaluate the dispersion relation. Using this approach, Eq. (3) may be written in the computationally useful form

$$1 = \epsilon \sum_{m\in\mathbb{Z}} A\left(\Delta_1, \frac{2\pi m}{\Delta_1}, \Delta_1\right) \hat{W}(2\pi m k), \tag{5}$$

where

$$A(P,\omega,\Delta) = \frac{e^{-P}}{\Delta}\{[e_c(P,\omega)-e_c(\tau_R,\omega)]a(\omega) - [e_s(P,\omega) - e_s(\tau_R,\omega)]b(\omega)\}. \tag{6}$$

Here, $e_c(x,y)=e^x\cos(xy)$, $e_s(x,y)=e^x\sin(xy)$, $a(\omega)=\mathrm{Re}[\hat{J}(\omega)/(1+i\omega)]$, $b(\omega)=\mathrm{Im}[\hat{J}(\omega)/(1+i\omega)]$, and the caret indicates Fourier transforms such that

$$\hat{F}(k) = \int_{-\infty}^{\infty} e^{-ikx} F(x)\, dx. \tag{7}$$

Multiply periodic waves may be constructed in an analogous fashion to singly periodic ones with an appropriate choice of firing times. Instead of a wave train with a single period, consider a wave train with periods (interspike intervals) Δ_j, $j=1,\ldots,n$. Let $d_{j-1}=\Sigma_{m=1}^{j}\Delta_m$, and then the period of oscillation is given by $\Delta=d_{n-1}$. The set of n firing times are defined by $T^m(x)=([m/n]+kx)\Delta+d_{m(n)}$, where $m(n)=m \bmod n$, and $[\cdots]$ takes the integer part. The speed of this wave is given by $c=1/(k\Delta)$. For later convenience, we shall denote a traveling wave with n distinct periods by P_n. A generalization of the previous analysis leads to a system of n equations

$$1 = \epsilon \sum_{m\in\mathbb{Z}} A_j\left(\frac{2\pi m}{\Delta}, \Delta\right) \hat{W}(2\pi m k), \quad j=1,\ldots,n, \tag{8}$$

where

$$A_j(\omega,\Delta) = \sum_{l=0}^{n-1} \cos(\omega[d_{j-1}-d_l]) A(\Delta_j,\omega,\Delta) - \sum_{l=0}^{n-1} \sin(\omega[d_{j-1}-d_l]) B(\Delta_j,\omega,\Delta), \tag{9}$$

and

$$B(P,\omega,\Delta)=\frac{e^{-P}}{\Delta}\{[e_{\mathrm{s}}(P,\omega)-e_{\mathrm{s}}(\tau_R,\omega)]a(\omega)+[e_{\mathrm{c}}(P,\omega)-e_{\mathrm{c}}(\tau_R,\omega)]b(\omega)\}. \tag{10}$$

A general theory for the stability of periodic waves is developed in Ref. [11], but requires substantial mathematical analysis to gain any real insight. By considering perturbations of the firing times, and linearizing the resulting firing time map, Bressloff characterizes the stability of traveling waves with the use of an integro-difference equation of infinite order. Finding the solutions of this characteristic equation is a nontrivial mathematical problem. Another approach to provide insight into the stability of traveling waves involves the use of direct numerical simulations. However, this will only determine stable waves and, for a fixed wave speed, finite-spike waves, periodic waves, and other infinite-spike waves may all occur. The desire for a practical treatment of stability leads us to a kinematic theory of spike train propagation.

The kinematic formalism allows one to follow the evolution of the spike train without recourse to studying the full nonlinear IF firing map. Miller and Rinzel [17] considered impulse propagation along the Hodgkin-Huxley cable equations using numerical experiments and deduced that the kinematic approximation provides a reasonable estimate for the variation in interspike intervals and the influence of dispersion during propagation. They derived the kinematic approximation as follows. The quantity dT^{n+1}/dx is the reciprocal of instantaneous velocity of the pulse upstroke and is assumed to be determined by the time spent in the recovery wake of the preceding pulse. This time differs from the interspike interval by approximately a constant so that we can express pulse velocity in terms of the interspike time. Thus, we have

$$\frac{dT^n}{dx}=\frac{1}{c[T^n(x)-T^{n-1}(x)]}, \tag{11}$$

where $c[\cdots]$ is the velocity as a function of interspike interval as given by the dispersion relation for periodic wave trains. This reduces to our firing time ansatz for singly periodic waves when the interspike interval $T^n(x)-T^{n-1}(x)$ is constant. Moreover, this framework is ideally suited for the analysis of irregular spike trains and is easily extended to the multiply periodic case. Linear stability analysis of the kinematic ordinary differential equations (given in the Appendix) shows that any P_1 solution of system (11) is unstable if $c'(\Delta_1)<0$ and stable if $c'(\Delta_1)>0$. The stability of more general P_n orbits requires that $c'(\Delta_j)>0$ for all $j=0,\ldots,n-1$.

In the following sections, we illustrate the usefulness of the above theoretical framework in determining the effects of realistic forms of synaptic and dendritic responses on the speed and stability of periodic traveling waves in spiking neural systems. The normalized exponential $[W(x)=\exp(-|x|/\sigma)/(2\sigma)]$ and square $[W(x)=\Theta(\sigma-|x|)/(2\sigma)]$ synaptic weight kernels are considered.

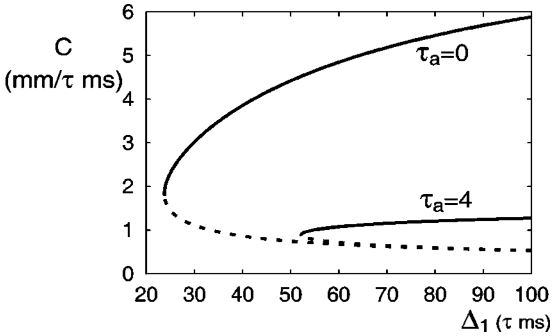

FIG. 1. Dispersion curves for the square synaptic footprint and α-function distributed delay kernel. Parameter values are $\alpha=0.5$, $\epsilon=60$, $\sigma=10$, and $\tau_R=0$. Solid (dashed) lines correspond to linearly stable (unstable) traveling waves according to the kinematic theory. In this and subsequent figures, the temporal units are given in terms of τ milliseconds, since we set $\tau=1$, and the spatial units are in millimeters.

III. SYNAPTIC PROCESSING IN A POINT NEURON MODEL

The evolution of a postsynaptic potential (PSP) can often be accurately described with a functional form such as a difference of exponentials or a so-called α function. For simplicity, we restrict our attention to this common form and write $J(t)=\alpha^2(t-\tau_a)e^{-\alpha(t-\tau_a)}\Theta(t-\tau_a)$, where an additional discrete delay has been included. In this section, we will regard the neuron as a point processor that generates a PSP a time τ_a after the arrival of a presynaptic spike. It is also possible to include a space-dependent axonal communication delay by letting $J(t)\rightarrow J(t-|x|/c_s)$, where $|x|$ is the separation of the neurons and c_s the speed of an action potential. However, this merely leads to a shift $1/c\rightarrow 1/c-1/c_s$, so it will not be considered further. The theory of the preceding section can be applied in a straightforward manner once the Fourier transform of $J(t)$ is calculated. For our choice of a delayed α function, this is given by

$$\hat{J}(\omega)=\frac{\alpha^2 e^{-i\omega\tau_a}}{(\alpha+i\omega)^2}, \tag{12}$$

which has a double pole at $\omega=i\alpha$.

Figure 1 shows dispersion curves for the case of a square synaptic footprint [with $\hat{W}(\omega)=\sin(\sigma\omega)/(\sigma\omega)$]. For nonzero communication delays, the basic shape of the dispersion curve is the same as that for zero delays, but shifted to the right. Hence, the presence of discrete communication delays acts to suppress waves of small period. Kinematic theory indicates that the upper (faster) branch is stable since it has a positive gradient (see the Appendix).

It is also possible for dispersion curves to develop *bumps* of supernormal speed. An example using an exponential synaptic footprint is presented in Fig. 2 [with $\hat{W}(\omega)=1/(1+\sigma^2\omega^2)$], where the stationary point in the dispersion curve clearly has a greater speed than the long-wavelength (solitary wave) solution. Since the kinematic theory flags an instability at precisely this point the question arises as to

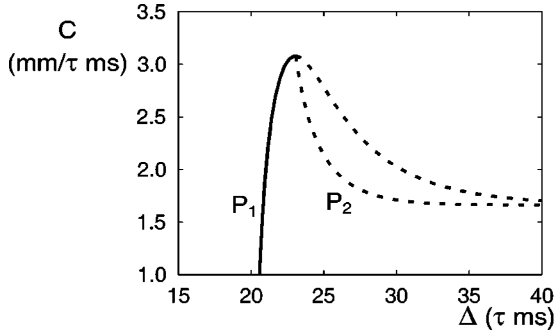

FIG. 2. Dispersion curves for P_1 and P_2 orbits (periodic traveling waves with one $[\Delta=\Delta_1+\Delta_1]$ and two $[\Delta=\Delta_1+\Delta_2]$ periods, respectively) in a synaptically coupled network with an exponential footprint with $\alpha=0.5$, $\epsilon=60$, $\tau_R=10$, and $\sigma=1$. Solid (dashed) lines correspond to linearly stable (unstable) traveling waves according to the kinematic theory, i.e., stable (unstable) for positive (negative) gradients. Both P_1 and P_2 upper branches become flat for large Δ.

whether other solutions may branch from this instability. Explicit construction of the P_2 solution using Eqs. (8)–(10) shows that this is true. However, for typical parameter choices we find that the emerging wave is unstable. Moreover, for a sufficiently large choice of absolute refractory period, the supernormal bump and the emerging unstable P_2 can be lost, suggesting that a robust mechanism for stable P_2 generation is not possible for this form of synaptic interaction. In the following section, we shall see that the inclusion of active membrane in a spatially extended neuron model can lead to dispersion curves with a much richer structure where bifurcations of P_1 waves lead to stable P_2 waves.

IV. DENDRITIC PROCESSING

The passive membrane properties of a neuron's dendritic tree are known to result in a diffusive spread of current through the system. Such a diffusive process is commonly described with the well known cable equation [18]. The Green's function of the cable equation provides a spatiotemporal delay distribution that may be used to model axodendritic interactions within the framework of this paper. Recent experiments, however, suggest that the representation of dendrites in terms of purely passive membranes is an oversimplification, and that more realistic models should incorporate some notion of active, voltage-dependent ionic channels (see Ref. [14] for a discussion). In general, the active channel conductances depend nonlinearly on voltage and time. However, for relatively small deviations of the membrane potential from rest, Koch [13] has suggested that a linearization of the channel kinetics is appropriate. The resulting *quasiactive* continuum cable model of the dendrites has a membrane impedance that displays resonantlike behavior due to the additional presence of inductances. Hence, for a purely passive dendrite, the membrane impedance acts as a low-pass filter and for an active dendrite as a bandpass filter.

For simplicity, we consider an unbranched model of a dendritic tree and consider only a single synapse on the tree located at a distance ξ from the cell body (soma). The soma itself will again be a simple IF unit. In this case, the synaptic input current is given by Eq. (2), with $J(t)=G(\xi,t)$, and $G(\xi,t)$ is the Green's function of the cable equation describing the dendrite. An extensive review of the form of this Green's function can be found in Ref. [14,19], where the Fourier transform is given in the form

$$\hat{J}(\omega)=\frac{1}{D\gamma(\omega)}e^{-\gamma(\omega)\xi}. \tag{13}$$

The diffusion coefficient of the cable is D, while the form factor $\gamma(\omega)$ depends upon whether the dendrite is passive or quasiactive. For a purely passive cable $\gamma^2(\omega)=(1+i\omega\tau_D)/(D\tau_D)$ with τ_D the dendritic membrane time constant. For a quasiactive cable [13]

$$\gamma^2(\omega)=\frac{r_a[r_D+r_l-\omega^2 l\tau_D+i\omega(l+r_l\tau_D)]}{r_D(r_l+i\omega l)}. \tag{14}$$

Here, the membrane leakage resistance and capacitance for a cable of unit surface area are r_D and c, respectively, with $\tau_D=r_Dc$. The longitudinal resistance of a unit length of cable is given by r_a. Compared to the passive form factor, the quasiactive one also incorporates the effects of a resistance r_l in series with an inductance l. In contrast to the Green's function of the passive dendrite, that of the quasiactive one possesses an oscillatory tail. In the limit $r_l\to\infty$, the passive dendritic case is recovered with $D\tau_D=r_D/r_a$. Resonantlike behavior in which the impedance $|\gamma(\omega)^2/r_a|$ has a maximum value for some nonzero frequency $\omega_{\max}$ is apparent in this system. The resonant frequency $\omega_{\max}$ is given by

$$\omega_{\max}=\{-(r_l/l)^2+[(r_l/l)^4-E]^{1/2}\}^{1/2}, \tag{15}$$

provided $E\equiv(Br_l^2-l^2C)/(Al^2)<0$, where $A=(\tau_d l)^2$, $B=l^2+(\tau_d r_l)^2-2\tau_d rl$, and $C=(r+r_l)^2$ [13].

The calculation of the dispersion curve for a passive dendrite also shows a correspondence with the behavior found in Sec. III with a fast stable branch coexisting with a slow unstable branch. However, with the inclusion of a quasiactive membrane, a far more interesting dispersion curve can be obtained. In Fig. 3, we present such an example for the case of an exponential synaptic footprint. There is an additional oscillatory behavior in the upper branch of the dispersion curve for quasiactive dendrites, which arises from the bandpass nature of the membrane. This behavior becomes more pronounced as $r_l\to 0$ (i.e., as the membrane switches from passive to quasiactive). A similar effect can be produced by decreasing τ_R or l, or by increasing τ_d. In the long-wavelength limit, the speed is increased for an increase in the resonant frequency.

The stability of the periodic wave train is determined by the gradient of the dispersion curve, in accordance with the kinematic theory. The oscillatory nature of the upper branch leads to alternating regions of stable (positive gradient) and unstable (negative gradient) periodic traveling waves. Hence, it is possible that a quasiactive membrane can act to tune

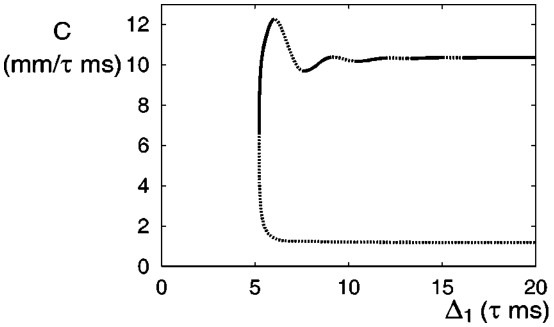

FIG. 3. Dispersion curve for the exponential footprint in a system with quasiactive membrane. Parameter values: $D=\tau_D=r_D=r_a=\sigma=1$, $\epsilon=15$, $\xi=0.2$, $l=0.2$, $r_l=0.01$, and $\tau_R=5$. Solid (dotted) lines correspond to linearly stable (unstable) traveling waves according to the kinematic theory, i.e., stable (unstable) for positive (negative) gradients.

traveling waves to specific frequency windows. These stable regions can be made larger by increasing τ_d or decreasing l. As in Sec. III, extra P_2 curves appear from the local maxima in the P_1 curve. However, in this case and for generic choices of parameter values, the emerging P_2 orbits are found to be stable over certain regions. Some examples of P_2 orbits emerging from local maxima of the P_1 dispersion curve are shown in Fig. 4. The oscillatory nature of the upper branch is also apparent in the P_2 branches, thus leading to alternating bands of stable and unstable P_2 traveling waves.

V. DISCUSSION

In this paper we have extended recent work on traveling waves in IF systems in two ways. First, we have shown how to analyze waves possessing more than one period, and second, how to use a kinematic theory to determine wave stability. This framework has been used to investigate the effects of realistic forms of synaptic and dendritic processing on the propagation of waves in a one-dimensional model with nonlocal coupling. Importantly, neurons with a bandpass response have been shown to have dispersion curves with a richer structure than those without it. Resonant properties of neurons have been modeled using an effective inductance, which itself can be attributed to the behavior of voltage- and time-dependent conductances in membranes near rest. It is already known that resonant behavior can subserve a specific neuronal function. For example, hair cells of a vertebrate cochlear exhibit their maximal sensitivity at some nonzero frequency, which depends on their location along the cochlear [20]. Moreover, rod photoreceptors of lower vertebrates have a receptive field that increases with the temporal frequency of the stimulus [21]. The analysis presented in this paper further suggests that a quasiactive membrane can have an important role to play in shaping the firing patterns of traveling waves.

A natural extension of this work is to consider two-dimensional sheets where it is likely that nontrivial geometric structures such as spirals and target patterns are to be found. The case of plane waves has been discussed in Ref. [12], but the generalization of a firing time ansatz to cover other solutions has yet to be performed. Another important question that has not been addressed in this paper is the nature of wave initiation, where some recent progress has been made [22]. Also, spike train C in Fig. 4 suggests that a propagating doublet is a (kinematically) stable waveform in the long-wavelength limit. More generally, the $\Delta_{n-1}\to\infty$ limit of our work produces a traveling packet of n spikes. Using a combination of analysis and numerics, investigations into the existence of this interesting class of solutions have been performed by Osan *et al.* [23].

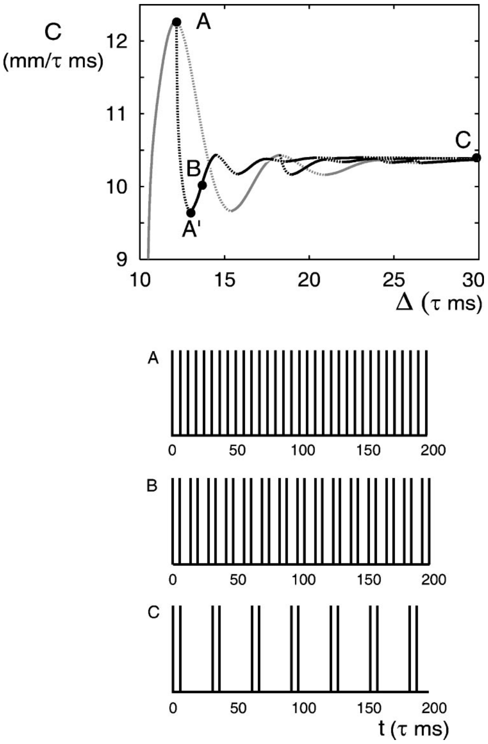

FIG. 4. The dispersion curve for P_1 (gray) and P_2 (black) traveling waves in the case of quasiactive membrane and exponential synaptic footprint. Parameter values as given for Fig. 3. Solid (dotted) lines correspond to linearly stable (unstable) traveling waves according to the kinematic theory, i.e., stable (unstable) for positive (negative) gradients. P_2 branches of solution terminate at local maxima of the P_1 dispersion curve. The spike trains underneath show the trains produced at the points indicated.

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APPENDIX: KINEMATIC THEORY—LINEAR STABILITY

A steadily propagating wave train is stable if under the perturbation $T^n(x)\to T^n(x)+u^n(x)$ the system converges to the unperturbed solution during propagation, or $u^n(x)\to 0$ as $x\to\infty$. For the case of uniformly propagating traveling waves of period Δ, we insert the perturbed solution in Eq. (11), so that to first order in u^n,

$$\frac{du^n}{dx} = -\frac{c'(\Delta)}{c^2(\Delta)}[u^n - u^{n-1}]. \tag{A1}$$

Thus, a uniformly spaced, infinite wave train with period Δ is stable (within the kinematic approximation) if and only if $c'(\Delta) > 0$. Hence, for the dispersion curves presented here, it would seem, to a first approximation, that it is always the faster of the two periodic branches which is stable. Note that where there are oscillations in the upper branch (including the bumps of supernormal speed) then it is only the wave of smaller period which is stable.

We now consider the stability of finite nonuniform trains, rather than the more involved case of general trains of infinite extent. This allows us to make the realistic assumption that the speed of the leading pulse is c_0 (the speed of a solitary pulse), so that we may write $T^n(x) = x/c_0 + \Sigma_{k=1}^{n} \Delta_n$, $n = 1, \ldots, N$ [24]. Proceeding as before we find the linear equations

$$\frac{du^1}{dx} = 0, \quad \frac{du^n}{dx} = -\frac{c'(\Delta_n)}{c^2(\Delta_n)}[u^n - u^{n-1}], \quad n = 2, \ldots, N. \tag{A2}$$

Thus, a nonuniform train is stable if and only if $c'(\Delta_n) > 0$ for each n (ignoring the zero eigenvalue associated with translations of the leading pulse).

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