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# THE SLOW PASSAGE THROUGH A HOPF BIFURCATION: DELAY, MEMORY EFFECTS, AND RESONANCE*

S. M. BAER†, T. ERNEUX‡, AND J. RINZEL†

**Abstract.** This paper explores analytically and numerically, in the context of the FitzHugh-Nagumo model of nerve membrane excitability, an interesting phenomenon that has been described as a delay or memory effect. It can occur when a parameter passes slowly through a Hopf bifurcation point and the system's response changes from a slowly varying steady state to slowly varying oscillations. On quantitative observation it is found that the transition is realized when the parameter is considerably beyond the value predicted from a straightforward bifurcation analysis which neglects the dynamic aspect of the parameter variation. This delay and its dependence on the speed of the parameter variation are described.

The model involves several parameters and particular singular limits are investigated. One in particular is the slow passage through a low frequency Hopf bifurcation where the system's response changes from a slowly varying steady state to slowly varying relaxation oscillations. We find in this case the onset of oscillations exhibits an advance rather than a delay.

This paper shows that in general delays in the onset of oscillations may be expected but that small amplitude noise and periodic environmental perturbations of near resonant frequency may decrease the delay and destroy the memory effect. This paper suggests that both deterministic and stochastic approaches will be important for comparing theoretical and experimental results in systems where slow passage through a Hopf bifurcation is the underlying mechanism for the onset of oscillations.

**Key words.** delayed Hopf bifurcation transition, memory effect, resonance, FitzHugh-Nagumo equations, nerve accommodation

**AMS(MOS) subject classifications.** C34, 92

**1. Introduction.** In mathematical studies of bifurcation, it is customary to assume that the bifurcation or control parameter is independent of time. However, in many experiments that are modeled mathematically as bifurcation problems, the bifurcation parameter varies naturally with time, or it is deliberately varied by the experimenter. Typically, this variation is slow or is forced to be slow.

The recent interest in the effects of slowly varying control parameters arises in physical, engineering, biological, and mathematical contexts. The physical interest arises from the fact that the results of long-time experiments may depend on parameters that are slowly varying. For example, catalytic activities in chemical reactors are slowly declining due to chemical erosion and are decreasing the reactor performance [1], [2]. The effects of slowly varying parameters are not always undesirable. They may also lead to smooth transitions at bifurcation points and mediate a gradual change in the system to a new mode of behavior beyond the bifurcation point. This idea has been studied for quite different problems such as thermal convection [3], [4], laser instabilities [5], [6], and developmental transitions in biology [7].

From a modeling point of view, we expect that a slow variation of the control parameter can be useful for the experimental or numerical determination of the bifurcation diagram of the stable solutions. Also, to understand certain complicated multi-scale dynamic phenomena [8], it is useful to study the bifurcation structure of the fast processes with the slow variables treated as slowly varying control parameters.

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† Mathematical Research Branch, NIDDK, National Institutes of Health, Bethesda, Maryland 20892.

‡ Department of Engineeering Sciences and Applied Mathematics, Northwestern University, Evanston, Illinois 60208. This work was supported by the Air Force of Scientific Research under grant AFOSR85-0150 and the National Science Foundation under Grant DMS-8701302.

In such cases, it is important that we have detailed knowledge of the transition near the bifurcation point where transients are very slow.

From a mathematical point of view, these problems are formulated by non-autonomous differential equations that are difficult to solve. The study of these problems has led to new and interesting mathematical issues [9]-[11]. References [9]-[11] investigate the slow passage through a steady bifurcation or a steady limit point. An interesting study of the effects of a slowly varying parameter on a Hopf bifurcation is given for the slow passage through resonance [26], [27].

In this paper, we concentrate on the slow passage through a Hopf bifurcation. As we shall demonstrate, this case is quite different from a steady bifurcation or limit point. Our results for the Hopf bifurcation raise a series of new questions on the control of bifurcation instabilities. We shall consider a specific model problem for the Hopf bifurcation because our goal is to explore the effects of a slowly varying parameter both analytically and numerically. For example, one interesting phenomenon has been described as a delay or memory effect. It can occur when a parameter passes slowly through a Hopf bifurcation point and the system's response changes from a slowly varying steady state to slowly varying oscillations. On quantitative observations (see Fig. 1(a), (b)) we find that the transition is realized when the parameter is considerably beyond the value predicted from a straightforward bifurcation analysis which neglects the dynamic aspect of the parameter variation. We describe this delay and its dependence on the speed of the parameter variation. Also, we show that the delay is sensitive to small amplitude noise and to periodic environmental perturbations of near resonant frequency. This sensitivity may be helpful in the accurate determination of bifurcation points. The model involves several parameters and particular (singular) limits are investigated. These limits reveal other interesting features on the slow passage through the bifurcation point.

We employ the specific problem of the FitzHugh-Nagumo equations as a model to describe the mathematical and qualitative features of the slow passage through a Hopf bifurcation. Many of these features occur for other models [25].

## 2. Formulation.

**2.1. The FitzHugh–Nagumo equations.** In the early 1950s, Hodgkin and Huxley [12] proposed a model that describes the generation and propagation of the nerve impulse along the giant axon of the squid. The model consists of a four-variable system of nonlinear partial differential equations. Subsequently, Nagumo et al. [13] and FitzHugh [14] developed a simpler two-variable system, which describes the main qualitative features of the original Hodgkin-Huxley equations and which is analytically more tractable. The so-called FitzHugh-Nagumo (FHN) equations for the space clamped (i.e., spatially uniform) segment of axon have the form

$$\frac{dv}{dt} = -f(v) - w + I(t), \tag{2.1a}$$

$$\frac{dw}{dt} = b(v - \gamma w), \tag{2.1b}$$

where $b$ and $\gamma$ are positive constants and $f(v)$ is a cubic-shaped function given by

$$f(v) = v(v-a)(v-1), \qquad 0 < a < \tfrac{1}{2}. \tag{2.1c}$$

Here $v(t)$ denotes the potential difference at time $t$ across the membrane of the axon and $w$ represents a recovery current which, according to the second equation (2.1b), responds slowly, when $b$ is small, to changes in $v$. The first equation (2.1a) expresses

Kirchhoff's current law as applied to the membrane; the capacitive, recovery, and instantaneous nonlinear currents sum to equal the applied current, $I(t)$. The applied current is our control or bifurcation parameter. In this section, we consider either constant intensities or slowly varying intensities of the form

$$I(\varepsilon t) = I_i + \varepsilon t, \qquad 0 < \varepsilon \ll 1. \tag{2.1d}$$

From biophysical considerations, it is reasonable to restrict $\gamma$ so that

$$\gamma < 3(1 - a + a^2)^{-1}. \tag{2.2}$$

This insures that (2.1) with $\varepsilon = 0$ have a unique steady state. The steady state $(v, w) = (v_s(I), w_s(I))$ satisfies the conditions

$$w_s = v_s/\gamma, \qquad I = f(v_s) + v_s/\gamma. \tag{2.3}$$

To analyze its stability, we consider small perturbations of the form $v = v_s + p\,e^{\lambda t}$ and $w = w_s + q\,e^{\lambda t}$ where $|p| \ll 1$ and $|q| \ll 1$. This leads to the following characteristic equation for $\lambda$

$$\lambda^2 + A\lambda + B = 0 \tag{2.4a}$$

where

$$A = f'(v_s(I)) + b\gamma, \tag{2.4b}$$

$$B = b[1 + \gamma f'(v_s(I))] \tag{2.4c}$$

The steady state is stable (unstable) if $A > 0$, $B > 0$ ($A < 0$ and/or $B < 0$). From the conditions $A = 0$, $B > 0$ we find two Hopf bifurcation points $I = I_\pm$. They satisfy the conditions

$$v_s(I_\pm) = v_\pm = \tfrac{1}{3}[a + 1 \pm (a^2 + 1 - a - 3b\gamma)^{1/2}] \tag{2.5}$$

$$\omega_0^2 = b(1 - b\gamma^2) > 0. \tag{2.6}$$

When $I < I_-$ or $I > I_+$ ($I_- < I < I_+$), the steady state is stable (unstable). To analyze the response of the system near $I_-$ or $I_+$, the approach of bifurcation theory is particularly useful. When $I > I_-$ or $I < I_+$, the transition to the oscillations can be smooth (supercritical bifurcation) or hard (subcritical bifurcation). Details of the bifurcation analysis are given in [15]-[17].

**2.2. Response to the slowly varying parameter.** We now consider the effect of a slowly varying parameter. We assume that the system is initially at a stable steady state i.e., $I_i < I_-$. Figure 1 illustrates the response to the slow, linearly rising current (2.1d); in Fig. 1(a), $v$ is plotted versus $t$ and in Fig. 1(b), $v$ is plotted versus $I$. For these parameter values, the Hopf bifurcation at $I_-$ is supercritical. From the bifurcation structure (Fig. 1(b)), one might expect that the response would approximately track the slowly varying steady state $(v, w) = (v_s(I), w_s(I))$, and then, as $I$ increases through $I_-$, the response would switch to the large amplitude oscillations. Such a switch is seen, but the value $I = I_j$ at which it occurs is considerably delayed beyond $I_-$. Moreover, the amount of delay increases with distance that $I_i$ is from $I_-$ (Fig. 1(c)). To understand this delay, we execute the following strategy: first, we determine a new (slowly varying) basic reference solution as a perturbation of the steady state $(v, w) = (v_s(I), w_s(I))$. Then, we analyze its stability with respect to the fast time of the oscillations. We show that loss in stability occurs well beyond $I_-$.

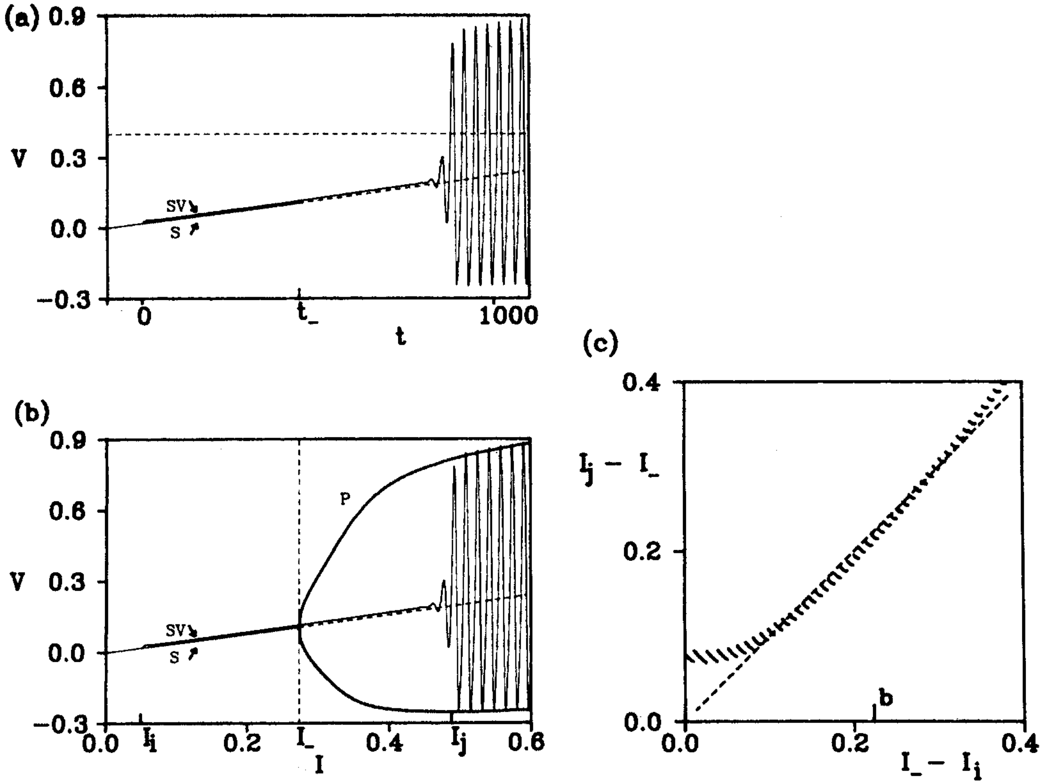


FIG. 1. *Delay or memory effect.* (a) *The transition to slowly varying oscillations is computed from the numerical integration of* (2.1) *for current* $I(\varepsilon t)=I_i+\varepsilon t$, *where* $I_i=0.05$. *Trajectory* (*SV*) *shows that the membrane potential varies slowly in response to a slowly rising current. The onset of oscillations is indicated when the trajectory first crosses the horizontal dashed line* $v=0.4$, *at* $t=880$. *Curve* (*S*) *is the steady state solution to* (2.1) *for increasing* (*time-independent*) *values of I. Solid denotes stable and dashed denotes unstable steady state solutions. A stability change occurs at the Hopf bifurcation point* $I_-=0.273$, *which corresponds to time* $t_-=(I_--I_i)/\varepsilon=446$. *Compared to the time of stability loss estimated from the Hopf bifurcation analysis, the onset of oscillations is considerably delayed.* (b) *The slowly varying response* (*SV*) *for slowly increasing I*; *and the steady state solution* (*S*) *and bifurcating branch of periodic solutions* (*P*) *for the parametric dependence on I. The onset of oscillations occurs at* $I_j=0.490$, *well past the value* $I_-=0.273$ *predicted from a Hopf bifurcation analysis, however, the amplitude of oscillations continue to track the bifurcation envelope computed using* AUTO [19]. (c) *Numerical determination of* $I_j$ *for many values of* $I_i$. *Label b refers to cases* (a) *and* (b) *above. The delay increases as* $(I_--I_i)$ *increases. Superimposed* (*dashed*) *are the predicted values of* $I_j$, *from the numerical integration of* (3.5), *at which the slowly varying solution loses stability with respect to the fast time. This illustrates the memory effect. Parameter values are* $a=0.2$, $b=0.05$, $\gamma=0.4$, *and* $\varepsilon=5\times10^{-4}$.

The "slowly varying steady state" is found by determining a solution of (2.1) of the form

$$\bar{v}(\tau,\varepsilon)=\sum_{j=0}^{\infty}\varepsilon^j v_j(\tau),\qquad \bar{w}(\tau,\varepsilon)=\sum_{j=0}^{\infty}\varepsilon^j w_j(\tau) \tag{2.7}$$

where $\tau$ is a slow time variable defined by

$$\tau=\varepsilon t. \tag{2.8}$$

The coefficients $v_j(\tau)$ and $w_j(\tau)$ are obtained by inserting (2.7) and (2.8) into (2.1) and equating to zero the coefficients of each power of $\varepsilon$. The analysis of the first two problems leads to the following results:

$$\bar{v}(\tau, \varepsilon) = v_s(I(\tau)) + \varepsilon \frac{\omega_0^2}{b\gamma B} v_s'(\tau) + O(\varepsilon^2) \tag{2.9}$$

and

$$\bar{w}(\tau, \varepsilon) = w_s(I(\tau)) - \varepsilon \frac{A}{B\gamma} v_s'(\tau) + O(\varepsilon^2) \tag{2.10}$$

where $v_s' = dv_s/d\tau$ and $A$, $B$ and $\omega_0^2$ are defined by (2.4b), (2.4c), and (2.6), respectively. From (2.9) and (2.10), we note that the expansion of the slowly varying solution does not become singular at the Hopf bifurcation point $I = I_-$. Indeed at $I = I_-$, $B = \omega_0^2 \neq 0$ and the functions in (2.9) and (2.10) remain $O(1)$ quantities. This contrasts with the case of a steady bifurcation or limit point where the expansion of the slowly varying solution becomes singular at and near the bifurcation or limit point [1], [10]. Note however from (2.9) and using the definitions (2.4) and (2.6) that the expansion is nonuniform if $b = O(\varepsilon)$ or $\gamma = O(\varepsilon)$. Both cases are of practical interest and we consider them in §§ 4 and 5, respectively.

Numerical computations were performed on a Vax 8600 using a classical fourth-order Runge–Kutta method with fixed step size ($DT = 0.1$). Results were also computed using a Gear method [18] for stiff differential equations. The two methods showed excellent agreement. To retain accuracy using Gear's method in problems with slow passage through bifurcation points, a tight control of relative error is imperative (we used $\text{TOL} = 10^{-12}$). Hence we found the RK4 method to be more efficient for these calculations. In addition, the simplicity of the method makes our results easily reproducible. When a control parameter varies slowly and/or when $I_- - I_i$ is large, numerical solutions to (2.1) are particularly sensitive to roundoff error. Thus we were careful to compare computations in single, double, and quadruple precision. The results for all figures (except as noted in Figs. 1(c) and 4) were computed in double precision. In numerical calculations the onset of oscillations was defined as the time $t_j$ when the $v$ versus $t$ trajectory first crossed the value $v = 0.4$. The bifurcation diagram in Fig. 1(b) was computed using AUTO [19].

**3. Stability of the slowly varying solution.** In this section, we analyze the stability of the slowly varying solution $(v, w) = (\bar{v}, \bar{w})$. After introducing the deviations

$$\begin{aligned} V(t, \varepsilon) &= v(t, \varepsilon) - \bar{v}(\tau, \varepsilon), \\ W(t, \varepsilon) &= w(t, \varepsilon) - \bar{w}(\tau, \varepsilon) \end{aligned} \tag{3.1}$$

into (2.1), we obtain the following linearized equations for $V$ and $W$:

$$\begin{aligned} \frac{dV}{dt} &= -f'(\bar{v}(\tau, \varepsilon))V - W \\ \frac{dW}{dt} &= b(V - \gamma W). \end{aligned} \tag{3.2}$$

Assuming now zero initial conditions for $V$ and $W$, we solve (3.2) by a WKB method [24]. Specifically, we seek a solution of (3.2) of the form

$$\begin{aligned} V(t, \varepsilon) &= V(\tau, \varepsilon) = \exp[\sigma(\tau)/\varepsilon] \sum_{j=0}^{\infty} \varepsilon^j V_j(\tau), \\ W(t, \varepsilon) &= W(\tau, \varepsilon) = \exp[\sigma(\tau)/\varepsilon] \sum_{j=0}^{\infty} \varepsilon^j W_j(\tau). \end{aligned} \tag{3.3}$$

Introducing (3.3) into (3.2) and equating to zero the coefficients of each power of $\varepsilon$, we obtain the following problem for $V_0$ and $W_0$:

$$\begin{aligned} \sigma'(\tau) V_0 &= -f'(v_s(\tau)) V_0 - W_0, \\ \sigma'(\tau) W_0 &= b(V_0 - \gamma W_0). \end{aligned} \tag{3.4}$$

A nontrivial solution is possible only if $\lambda = \sigma'(\tau)$ satisfies the characteristic equation (2.4a) where the coefficients $A$ and $B$ are now functions of $I(\tau)$. From (3.3) we conclude that at the time $\tau$, the slowly varying solution is stable with respect to the fast time $t$ if

$$\operatorname{Re}(\sigma) = \int_0^\tau \operatorname{Re}[\lambda(s)]\, ds < 0. \tag{3.5}$$

When the quantity $\operatorname{Re}(\sigma)$ becomes positive then the solution (3.3) exhibits rapid exponential growth and the slowly varying solution is therefore unstable on the fast time scale. From (3.5) we conclude that there is a memory effect. Destabilization of the slowly varying solution does not occur immediately when $\operatorname{Re}[\lambda(s)]$ changes sign (i.e., when $I$ increases through $I_-$), but only after the integrated effect of $\operatorname{Re}(\lambda) > 0$ overcomes the accumulated influence of $\operatorname{Re}(\lambda) < 0$. Moreover, (3.5) is independent of $\varepsilon$ so that the delay persists even if the control parameter is tuned infinitesimally slowly. The importance of this integral condition for predicting the delay was seen previously for steady bifurcation problems [5], [10] and for bursting oscillations [8].

We remark that the series (3.3) represents a valid approximation on the time interval $\tau$ if the discriminant of (2.4a) given by

$$D(\tau) = A^2(I(\tau)) - 4B(I(\tau)) \tag{3.6}$$

does not vanish. Points where $D(\tau)$ vanishes are where $(v_s, w_s)$ changes from a node to a focus. These points are called turning points (not to be confused with limit points). If $I_- - I_i$ is not sufficiently small, $D(\tau)$ may change sign on the interval of interest and the WKB solution (3.3) becomes invalid in the neighborhood of the turning points. Nevertheless, a global approximation to the solution of (3.2) can be obtained by the method of matched asymptotic expansions. In this study, we consider only the simplest case where there are no turning points, i.e., $D(\tau) < 0$ during the time interval of interest. The case with turning points will be presented elsewhere. Its analysis leads to a stability condition similar to (3.5).

We have obtained explicit expressions for the delay and for conditions which guarantee that $D(\tau)$ remains negative by exploiting algebraic simplifications which arise in the parameter range $O < a \ll 1$. In the limit $a \to 0$, we assume $I(\tau) = O(a)$, and find from (2.3) and then from (2.4(b), (c)) the following expressions for $v_s$, $A$, and $B$:

$$v_s(I) = \gamma I + O(a^2), \tag{3.7}$$

$$A = -2\gamma(I - I_-^0) + O(a^2), \tag{3.8}$$

$$B = b + O(a^2 b) \tag{3.9}$$

where $I_-^0 = a/2\gamma$ corresponds to the leading approximation of the first Hopf bifurcation point $I = I_-$ (from (2.5), $v_- = a/2 + O(a^2)$ and then using (2.3), $I_- = I_-^0 + O(a^2)$). Using the definition (3.6), we obtain an approximate expression for $D(\tau)$

$$D(\tau) \cong 4\gamma^2(I(\tau) - I_-^0)^2 - 4b \tag{3.10}$$

or, equivalently,

$$D(\tau) \cong 4\gamma^2(I - I_-^0 - b^{1/2}/\gamma)(I - I_-^0 + b^{1/2}/\gamma). \tag{3.11}$$

At $I = I_-^0$, $D(\tau) < 0$ and remains negative provided that

$$I_-^0 - b^{1/2}/\gamma < I(\tau) < I_-^0 + b^{1/2}/\gamma. \tag{3.12}$$

Thus, if $I_i > I_-^0 - b^{1/2}/\gamma$, then $D(\tau)$ is negative until $I = I_-^0 + b^{1/2}\gamma$ is reached. Because we assume that $D(\tau) < 0$ during the time interval of interest, the stability change of the slowly varying solution appears at $\tau = \tau_j$, which is defined by the condition

$$\int_0^{\tau_j} \mathrm{Re}\,[\lambda(s)]\, ds = 0 \tag{3.13a}$$

or, equivalently,

$$\int_0^{\tau_j} A(s)\, ds \cong -2\gamma \int_0^{\tau_j} (I(s) - I_-^0)\, ds = -\gamma\tau_j [(I(\tau_j) - I_-^0) - (I_-^0 - I_i)] = 0. \tag{3.13b}$$

Thus, since, $I_- = I_-^0 + O(a^2)$, we conclude from (3.13b) that

$$I(\tau_j) - I_- = I_- - I_i \tag{3.14}$$

to lowest order. Using (3.14) we easily verify that $D(\tau) < 0$ for $0 \leqq \tau \leqq \tau_j$. We call $I(\tau_j) - I_-$ the delay of the bifurcation transition. The expression (3.14) emphasizes two important features of the slow passage through the Hopf bifurcation: first, it is independent of $\varepsilon$, the rate of change of the control parameter $I$; second, the stability change of the slowly varying reference solution appears at a distance that is $O(1)$, with respect to $\varepsilon$, from the static bifurcation point $I_-$, as seen in Fig. 1. This distance can be controlled by changing $I_i$, the initial value of $I$. We thus observe a memory effect.

In Fig. 1(c), we illustrate the memory effect by integrating (2.1) numerically. Our calculations confirm that increasing $I_- - I_i$ increases the delay of the bifurcation transition. Moreover, (3.14) is in excellent agreement with the numerical results when $I_- - I_i > 0.2$. For $I_- - I_i < 0.2$ the numerics apparently deviate from our analytic prediction. This is due to the bifurcation being supercritical. The bifurcating branch of periodic solutions is locally stable, so when $I_i$ is near the static Hopf point there are several small oscillations whose amplitude remain below the prescribed "threshold." For larger delays there is usually only one or two such oscillations. Another feature observed in Fig. 1(c) is a sawtooth jump pattern that occurs because the final subthreshold oscillation before onset shifts in phase as $I_- - I_i$ increases. Eventually a value is reached that delays the onset for one more subthreshold oscillation. The size of the jump $\Delta I_j$ is estimated by multiplying the ramp speed $\varepsilon$ by the period of the oscillation $2\pi/\omega_0$, that is $\Delta I_j = \varepsilon(2\pi/\omega_0)$. When $I_- - I_i = 0$, six subthreshold oscillations occur before onset. Thus the jump magnitude in this case is about $6\varepsilon(2\pi/\omega_0)$.

**4. Slow passage through a low frequency Hopf bifurcation.** We now investigate the dynamics of the case $b$ small, which appeared as a singularity of the slowly varying reference solution (2.9) and (2.10). A detailed study of this singularity ($\varepsilon = O(b)$) leads to a rich discussion and will be presented elsewhere. In this section, we consider a particular relation between $\varepsilon$, $I_i - I_-$, and $b$ that is motivated by the parameter values used in our numerical study of the FHN equations ($\varepsilon = O(b^{3/2})$ and $I_i - I_- = O(b^{1/2})$). This special relation between the parameters does not correspond to the singularity of the slowly varying solution. However, it can be shown that the Hopf bifurcation is singular in this critical regime [20]. This motivates a careful analysis of this case. To lowest order, we find that the dynamical description is given by a nonlinear problem. Although we do not solve it analytically, we obtain useful insight showing that in this case the onset of oscillations exhibits an advance rather than a delay.

In order to analyze the slow passage through this low frequency Hopf bifurcation, we first introduce a new fast time and a slow time defined by

$$T = b^{1/2}t, \tag{4.1}$$

$$S = bt. \tag{4.2}$$

$T$ and $S$ correspond to the time scales of the oscillations and the control parameter, respectively. For mathematical simplicity, we shall restrict our analysis to the vicinity of the Hopf bifurcation point $(v, w, I) = (v_-, w_-, I_-)$ defined by (2.3) and (2.5), and assume that the deviation $I_- - I_i$ is small. Specifically, we seek a solution of the FHN equations (2.1) of the form

$$v(T, S, b^{1/2}) = v_- + b^{1/2}V_1(T, S) + bV_2(T, S) + \cdots, \tag{4.3}$$

$$w(T, S, b^{1/2}) = w_- + b^{1/2}W_1(T, S) + bW_2(T, S) + \cdots, \tag{4.4}$$

$$I(\varepsilon t) = I(S) = I_- + b^{1/2}I_1(S) + bI_2(S) + \cdots. \tag{4.5}$$

The expansion (4.5) for the slowly varying control parameter $I(S)$ and the requirement that $I$ is a function of the slow time $S$ imply

$$I_i - I_- = b^{1/2}P + bP_2 + \cdots \tag{4.6}$$

and

$$\varepsilon = b^{3/2}Q + b^2Q_2 + \cdots \tag{4.7}$$

where $P$ and $Q$ are prescribed $O(1)$ quantities. Consequently, we may write that

$$I_1(S) = P + QS. \tag{4.8}$$

Introducing (4.3)–(4.7) into (2.1) and equating to zero the coefficients of each power of $b^{1/2}$ leads to a sequence of problems for the coefficients $V_1, V_2, \cdots$ and $W_1, W_2, \cdots$. Applying the standard techniques of multi-scale analysis, we obtain that

$$W_1 = P + QS \tag{4.9}$$

and

$$\frac{\partial V_1}{\partial T} = -W_2 - f''(v_-)\frac{V_1^2}{2} + P_2 + Q_2S \tag{4.10}$$

$$\frac{\partial W_2}{\partial T} = V_1 - \gamma(P + QS) - Q \tag{4.11}$$

or, equivalently, if we eliminate $W_2$,

$$\frac{\partial^2 V_1}{\partial T^2} = -V_1 - f''(v_-)V_1\frac{\partial V_1}{\partial T} + \gamma(P + QS) + Q. \tag{4.12}$$

Defining $U(T, S) = f''(v_-)V_1(T, S)$ and using (4.8), (4.12) can be rewritten in a simpler form as

$$\frac{\partial^2 U}{\partial T^2} + U + U\frac{\partial U}{\partial T} = R(S) = f''(v_-)(\gamma I_1(S) + Q). \tag{4.13}$$

Equation (4.13) admits a slowly varying solution given by

$$\bar{U}(S) = f''(v_-)(\gamma I_1(S) + Q). \tag{4.14}$$

Using the expansions (4.3)–(4.7) it can be shown that

$$v = \bar{v}(S, b^{1/2}) = v_- + b^{1/2}\bar{U}(S)/f''(v_-) + O(b) \tag{4.15}$$

matches, as $b \to 0$, the outer expansion of the slowly varying reference solution, given by (2.9). To analyze the linear stability of (4.14) with respect to the fast time $T$, we must consider the following linearized problem

$$\frac{\partial^2 U}{\partial T^2} + f''(v_-)(\gamma I_1(S) + Q)\frac{\partial U}{\partial T} + U = 0. \tag{4.16}$$

The stability problem is similar to the problem studied in §3. If $I_1(S)$ is considered as a constant parameter, the critical point defined by

$$I_1(S_c) = -Q/\gamma \tag{4.17}$$

represents a Hopf bifurcation point of (4.16). However, since $I_1(S)$ is slowly varying, the change of stability of (4.14) will occur later. We analyze (4.16) by using the WKB method. If the discriminant $D(S) = [f''(v_-)(\gamma I_1(S) + Q)]^2 - 4 < 0$ during the interval of interest, we find that

$$I_1(S_j) - I_1(S_c) = I_1(S_c) - P \tag{4.18}$$

where $I_1(S_j)$ corresponds to the onset of the rapid oscillations. If $-2Q/\gamma - P < 0$, (i.e.,

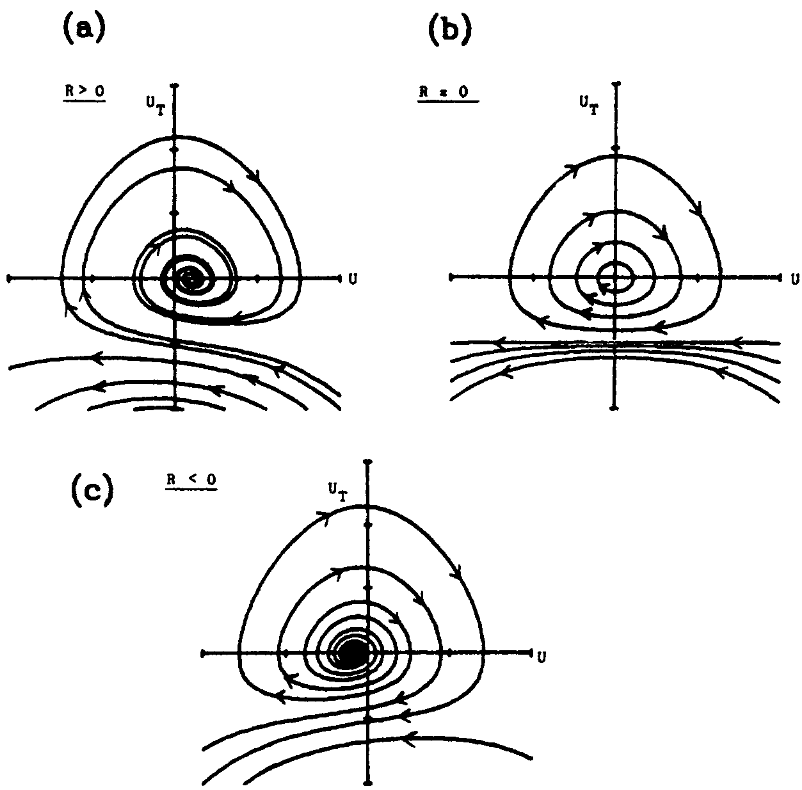


FIG. 2. *Approximation for slowly varying solution in the case of Hopf bifurcation with low frequency. Sequence of phase plane portraits of* (4.13) *for* $R > 0$, $R = 0$, *and* $R < 0$. (a) $R > 0$: *all initial points close to the singular point are attracted toward the singular point; this corresponds to a solution which tracks the slowly varying steady state.* (b) $R = 0$ *corresponds to the time at which I reaches a critical value,* $I(S_c)$. *The separatrix* $U_T = -1$ *divides a one-parameter family of periodic orbits from unbounded trajectories.* (c) $R < 0$ *corresponds to when the oscillations near the slowly varying steady state grow in amplitude. All initial points lead to unbounded trajectories.*

if $I_- - I_i < 2b^{1/2}Q/\gamma$) then $I_1(S_j)$ is negative. Consequently, the large amplitude oscillations that appear at

$$I_j = I_- + b^{1/2} I_1(S_j) + O(b) \tag{4.19}$$

occur before $I$ reaches the Hopf bifurcation point $I_-$. Then there is no delay, but rather an advance.

The preceding conclusion is based on the linearized equation (4.16). To analyze the full nonlinear problem (4.13) in which $R$ is a slowly varying function of $S$, we consider a slowly varying phase plane technique. Thus, in Fig. 2 we examine a sequence of phase planes for $R>0$, $R=0$, $R<0$. In Fig. 2(a), all initial points sufficiently close to the singular point lead to trajectories spiraling toward the singular point. This corresponds to the initiation of the slowly varying solution when the response tracks the slowly changing steady state. In Fig. 2(a) note that points located below a critical separatrix lead to unbounded trajectories. They correspond to the earlier stage of an excitable trajectory [20]. As $R(S)$ becomes zero, or, equivalently, $I_1(S) = I_1(S_c)$ (Fig. 2(b)), the separatrix is a straight line given by $U_T = -1$ and it separates the one-parameter family of periodic orbits surrounding the center $U = U_T = 0$ and the unbounded trajectories. Finally, Fig. 2(c) shows the phase plane portrait for $R<0$ that describes the slow growth of subthreshold oscillations just prior to the onset. The numerical results of Fig. 3 illustrate the phenomenon of an advance and confirm the above asymptotic treatment. For these parameter values (see figure legend), we have $I_- = 0.251$, $Q = 0.5$, and $P = -2.01$, which yield $I_1(S_c) = -1.25$ from (4.17) and $I_j = 0.202$, from (4.18), (4.19).

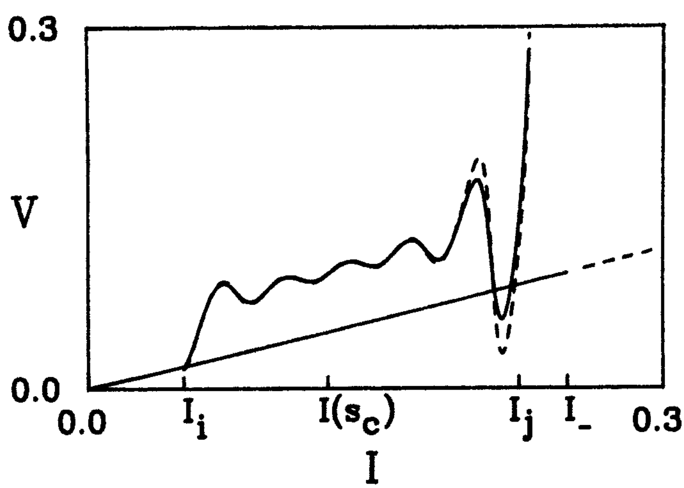


FIG. 3. *Advance rather than delay for low frequency oscillations (small $b$); comparison of numerical solutions to full problem* (2.1) *(dashed) and to the lowest order nonlinear approximation* (4.13) *(solid) for parameter values* $a = 0.2$, $\gamma = 0.4$, $b = 0.01$, *and* $\varepsilon = 5 \times 10^{-4}$. *The solution plotted versus I shows that the onset is advanced rather than delayed relative to the Hopf bifurcation point* $I_- = 0.25$. *For* $I_i = 0.05$, $I(S_c) = I_- - 0.125 = 0.125$ *and oscillations commence near* $I_j = 0.225 < I_-$, *thus indicating an advance. The numerical identification of* $I_j$ *differs from the prediction of* (4.19) *by approximately one subthreshold oscillation.*

**5. Effect of the rate of change of the control parameter.** In the previous sections, we have considered $\varepsilon$, the rate of change of the applied current, as a small parameter. Except when $b$ is small (low frequency Hopf bifurcation), the delayed bifurcation transition does not depend on $\varepsilon$ in first approximation. However, in a real experiment, we might study the dependence as $\varepsilon$ progressively increases from small to moderate values and determine if its increase has a stabilizing or destabilizing effect. In other words, we want to know if the onset of the large amplitude and rapid oscillations can be considerably delayed or, on the contrary, facilitated as a result of changing $\varepsilon$. Figure 4(a) shows numerical evidence of the delayed bifurcation transition $I_j - I_-$ as a function of $1/\varepsilon$. For now, we disregard the points labeled SP; these data will be discussed in

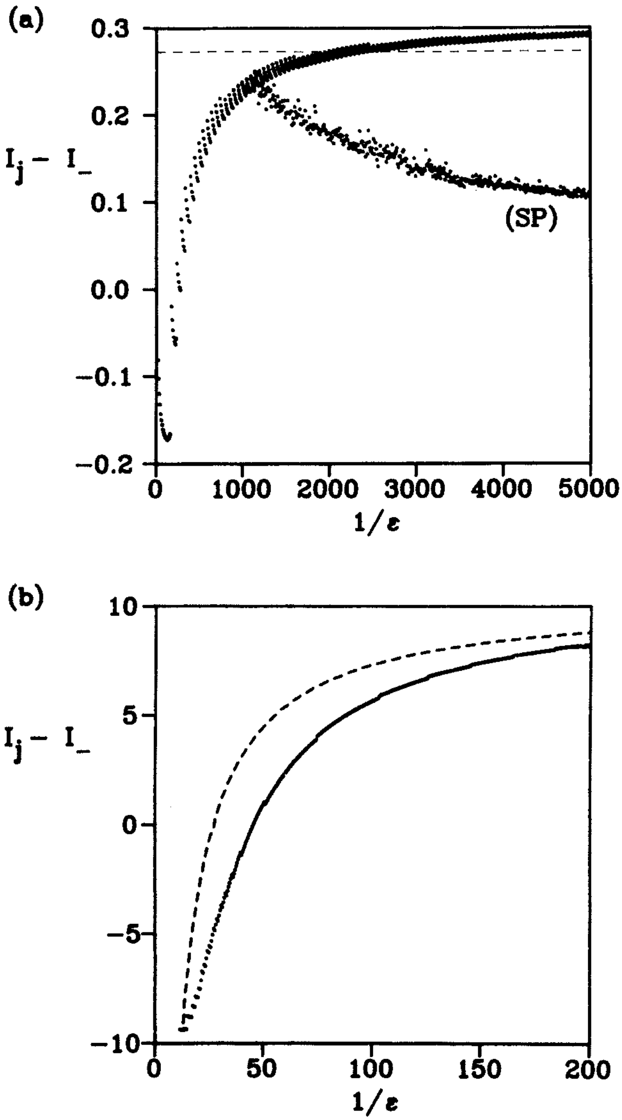


FIG. 4. *Increasing the ramp speed decreases the magnitude of the delay. Numerical solutions to* (2.1) *show the delayed bifurcation transition $I_j - I_-$ as a function of* $1/\varepsilon$. (a) *The parameter values as in Fig.* 1, *but with $I_i = 0$. Computed results asymptote to $I_j - I_- = 0.29$ as $\varepsilon \to 0$. The dashed curve represents the asymptotic approximation, as $\varepsilon \to 0$, determined from the direct integration of* (3.5). *Points labeled* (*SP*) *are discussed in* § 6. (b) *Delayed transition for low $\gamma$ case* (*note difference in scale in Figs.* 4(a) *and* 4(b)). *Parameter values are $a = 0.2$, $b = 0.4$, $\gamma = 0.01$, and $I_i = 0$. The dashed curve is a* WKB *approximation of the delayed transition, computed from* (5.7) *and* (5.8).

§ 6. Note that as $\varepsilon \to 0$ (or $1/\varepsilon \to \infty$) the curve asymptotes to a value consistent with the memory effect predicted by (3.5). Also, note that the magnitude of the jumps due to skipped oscillations decreases as $\varepsilon \to 0$, since $\Delta I_j = \varepsilon(2\pi/\omega_0) \to 0$ in this limit. Curves such as this one are useful in experimental and theoretical studies of nerve accomodation [21].

To better understand the effect of $\varepsilon$ we analyze the limit $\gamma \to 0$, with $\varepsilon$, $a$, and $b$ fixed in the FHN equations (2.1). At $\gamma = 0$, these equations admit an exact time dependent solution given by

$$\bar{v}(t) = \varepsilon/b, \qquad \bar{w}(t) = I(\varepsilon t) - f(\varepsilon/b) \tag{5.1}$$

where $I$ is given by (2.1d). We consider (5.1) as our new basic reference solution. Because $\bar{v}$ is constant, it is possible to study the linear stability of (5.1) by first reformulating the evolution equations (2.1) as a second-order equation for $v$ only and then by linearizing this equation about $\bar{v} = \varepsilon/b$. We find that the small deviation $V(t) = v(t) - \bar{v}$ satisfies the following equation:

$$\frac{d^2V}{dt^2} + f'(\varepsilon/b)\frac{dV}{dt} + bV = 0. \tag{5.2}$$

From (5.2) we easily obtain the characteristic equation, which is exactly (2.4) with $\gamma = 0$ and $v_s(I)$ replaced by $\bar{v} = \varepsilon/b$. Consequently, the reference solution (5.1) is stable (unstable) if $\bar{v} = \varepsilon/b < v_-$ or $\bar{v} = \varepsilon/b > v_+$ (if $v_- < \bar{v} = \varepsilon/b < v_+$) where $v_\pm(a)$ is defined by (2.5) with $\gamma = 0$. Thus for small or large values of $\varepsilon$, the reference solution is always stable. On the other hand for moderate values of $\varepsilon$, this solution is unstable and rapid oscillations will develop as soon as time increases.

We now consider the case of a reference solution, which is stable when $\gamma = 0$ ($\bar{v} < v_-$ or $\bar{v} > v_+$), and examine the limit $\gamma \to 0$. We first seek a slowly varying solution of (2.1) of the form

$$\begin{aligned} \bar{v}(\Theta, \gamma) &= v_0(\Theta) + \gamma v_1(\Theta) + \cdots, \\ \bar{w}(\Theta, \gamma) &= \gamma^{-1} w_0(\Theta) + w_1(\Theta) + \cdots \end{aligned} \tag{5.3}$$

where $\Theta$ is a new slow time defined by

$$\Theta = \gamma t. \tag{5.4}$$

We obtain the coefficients $v_0, v_1, w_0, w_1 \cdots$, by inserting (5.3) into the FHN equations (2.1) and by equating to zero the coefficients of each power of $\gamma$. We then obtain that $\bar{v}$ and $\bar{w}$ are given by

$$\bar{v}(\Theta, \gamma) = \varepsilon/b + \varepsilon\Theta + O(\gamma), \qquad \bar{w}(\Theta, \gamma) = \gamma^{-1}\varepsilon\Theta + O(1). \tag{5.5}$$

We now consider the linearized evolution equations and analyze the stability of (5.5). As $\gamma \to 0$, we obtain the following equation for the small deviation $V(t) = v(t) - \bar{v}(\Theta, \gamma)$

$$\frac{d^2V}{dt^2} + f'(\varepsilon/b + \varepsilon\Theta)\frac{dV}{dt} + bV = 0. \tag{5.6}$$

Note that this equation is similar to (5.2) except that the coefficient of $dV/dt$ is now a function $\Theta$. Since $I_i$ does not appear in (5.6), we do not expect, for fixed $\varepsilon$ and as $\gamma \to 0$, that the stability of the slowly varying reference solution depends on the initial position of $I$ (recall that the memory effect has been found for fixed $\gamma$ and as $\varepsilon \to 0$). However, we still have a delayed bifurcation transition. This delay can be found by a WKB analysis of (5.6) similar to the treatment in § 3. The analysis is tedious and we summarize the results.

The Hopf bifurcation point $I_-$ and the point $I_j$ where the jump transition occurs are given by (assuming $f'(\bar{v})^2-4b<0$):

$$I_- = \gamma^{-1}(\varepsilon_c - \varepsilon)/b + O(1), \tag{5.7}$$

$$I_j = \frac{\gamma^{-1}}{2}\{a+1-3\varepsilon/b-[(a+1-3\varepsilon/b)^2-4f'(\varepsilon/b)]^{1/2}\}+O(1) \tag{5.8}$$

where $\varepsilon_c$ is defined by the condition $f'(\varepsilon_c/b)=0$, i.e., $\varepsilon_c = bv_-$ and $v_-$ is defined by (2.5).

In conclusion, if $\varepsilon < \varepsilon_c$, the system approaches a slowly varying solution which remains stable until $I = I_j$ is reached ($I_j > I_-$), but if $\varepsilon > \varepsilon_c$, then the onset of oscillations occurs before $I = I_-$. We have analyzed these predictions numerically by considering the following values of the parameters $\gamma = 10^{-2}$, $a = 0.2$, and $b = 0.4$. We determine $\varepsilon_c = 0.038$. In Fig. 4(b) we compare the numerical results for (2.1) with the analytic approximation (dashed curve) given by (5.7) and (5.8) for different values of $\varepsilon$. For small values of $\varepsilon$, the instability of the slowly varying solution is considerably delayed; however, for larger values of $\varepsilon(\varepsilon > \varepsilon_c)$ oscillations quickly appear.

**6. Discussion.** In this paper we have considered the effect of a slow monotonic variation in a control parameter on the response of a system as it passes through a Hopf bifurcation. We have found that the onset of oscillations can be considerably delayed if the initial point is near the steady state in its stable regime (Fig. 1). That is, the system continues to track, for some measurable time, a "slowly varying steady state" even after it has lost stability (determined when the control variable is treated as a static parameter). Eventually the destabilizing influences accumulate and the response becomes oscillatory. The delay is greater if the initial point is further from the static bifurcation point (Fig. 1(c)). The integral condition (3.5), which expresses the new stability condition was derived analytically by perturbation methods for small $\varepsilon$, where $\varepsilon$ is the rate of the slow parameter variation. The condition applies over a robust parameter range in which the time scale of the characteristic frequency (associated with the Hopf bifurcation) is $O(1)$. The result does not depend on whether the bifurcation is sub- or supercritical. Although we applied our strategy to a particular model problem, the FitzHugh-Nagumo equation, our general result is applicable to a wide class of problems. For this, $\lambda$ in (3.5) is identified with the eigenvalue of largest real part.

In certain parameter ranges, we have gained additional insight to the model problem by considering limiting parameter values and using asymptotic methods. For example, if the Hopf bifurcation leads to a slow oscillation, e.g., as in the case of a relaxation oscillation [20], we find that the onset of oscillation may exhibit an advance instead of a delay.

We have also considered the dependence of the onset on the rate of variation of the control parameter. We have seen numerically (cf. Fig. 4) that the delayed instability point increases with $1/\varepsilon$. For fast ramps, the instability occurs earlier. We are uncertain as to how large a class of problems exhibit this behavior. However, numerical simulations of the Hodgkin-Huxley model (for which the FitzHugh-Nagumo equation is considered a simplification) reveal behavior similar to the curves in Fig. 4(a) [21], [23]. For the FitzHugh-Nagumo equation we have obtained an analytic description for the rate dependence in a special case, $\gamma \ll 1$, and we find using a WKB analysis that the onset point increases monotonically with $1/\varepsilon$.

We re-emphasize that numerical support for some of our analytic results requires careful error control. For example, when $\varepsilon$ is very small, we employ high precision numerics to reveal the predicted asymptotic value of the delayed $I_j$ (Fig. 4(a)). In this range, the numerical model is subject to sustained perturbing influences (i.e., roundoff errors) for a considerable duration as $I$ passes into the unstable regime beyond $I_-$ but before $I_j$ is reached; quadruple precision reduces the effect of roundoff. By analogy, we would anticipate similar sensitivities of delays and advances for an experimental system that is exposed to environmental or imposed fluctuations. These observations led us to explore specifically the effects of sustained perturbations (sinusoidal, as well as stochastic) on the delay phenomena. For this, we again considered a model problem of the FHN-type:

$$\frac{dv}{dt} = -f(v) - w + I(\varepsilon t) + \delta \sin(\omega t) \tag{6.1}$$

$$\frac{dw}{dt} = b(v - \gamma w) \tag{6.2}$$

in which both $\delta$ and $\varepsilon$ are small parameters. Note that the problem also depends on $\omega$, the frequency of the time periodic perturbation. As $\omega \to 0$, $\sin(\omega t) \sim 0$ if $t \ll 1/\omega$ and there is no effect of the perturbation (if $\delta \cos(\omega t)$ was considered instead of $\delta \sin(\omega t)$, then $\delta \cos(\sigma t) \sim \delta$ if $t \ll 1/\omega$; by redefining the initial value of $I$ as $I_i' = I_i + \delta$, we again find no effect of the time-dependent perturbations). On the other hand, as $\omega \to \infty$, the periodic forcing represents rapid oscillations and only its average value will contribute to the long time behavior of the solution. This can be shown by a multi-time analysis where $T = \omega t$ is now considered as the basic fast time. The average value of the periodic oscillation is zero and consequently, we do not expect an effect of the perturbation. We conclude that the delay and memory effects studied previously remain unchanged in the presence of small amplitude periodic forcing if the forcing frequency is either sufficiently small or sufficiently high.

As we expect, the delay is most sensitive to frequencies near $\omega_0$. Figure 5(a) illustrates that the delay is reduced considerably. The reduction is more dramatic for larger $\delta$, and we also see subharmonic and superharmonic resonance effects with delay reductions for $\omega$ near $\omega_0/3$, $\omega_0/2$, and $2\omega_0$.

If we now consider the perturbation amplitude $\delta$ as an adjustable parameter, then the sensitivity exhibits three regimes of behavior (solid curves of Fig. 5(b)). For $\delta$ sufficiently small, $\delta < \delta_c$, the delay is maximal and independent of $\delta$. If $\delta$ is sufficiently large, there is an advance with $I_j \sim I_i$. For intermediate $\delta$, $I_j - I_-$ decreases as $\delta$ increases with a sizable range of approximately linear dependence on $(-\ln \delta)^{1/2}$ for $\delta$ just below $\delta_c$.

Some features of the above numerical study of sensitivity are supported by preliminary analytic results from considering the linear stability of the slowly varying solution $(\bar{v}(\varepsilon t, \varepsilon), \bar{w}(\varepsilon t, \varepsilon))$ as $\delta \to 0$ when $\varepsilon$ is small but fixed. In particular, we find that $\delta_c = 0(e^{-1/\varepsilon})$, and that $I_j - I_-$ depends linearly on $(-\ln \delta)^{1/2}$ for $\delta$ just below $\delta_c$. A similar behavior has been found by an asymptotic analysis of a problem which exhibits a static bifurcation [22]. Our analysis also indicates the possibility of subharmonic resonance as seen in Fig. 5(b).

For our model problem we conclude that accurate identification of the small $\delta$ asymptote, in the presence of sustained perturbations, requires that perturbations with frequency components near $\omega_0$ be restricted to very small amplitudes, say less than about $10^{-7} - 10^{-8}$ relative to $I(\varepsilon t)$. Generally, a system is subject to fluctuations with many different frequency components and we should not assume that selected frequency ranges would be absent. To emphasize this we have simulated the effect of white noise superimposed upon the control parameter, i.e., we have replaced, in (6.1), (6.2), the

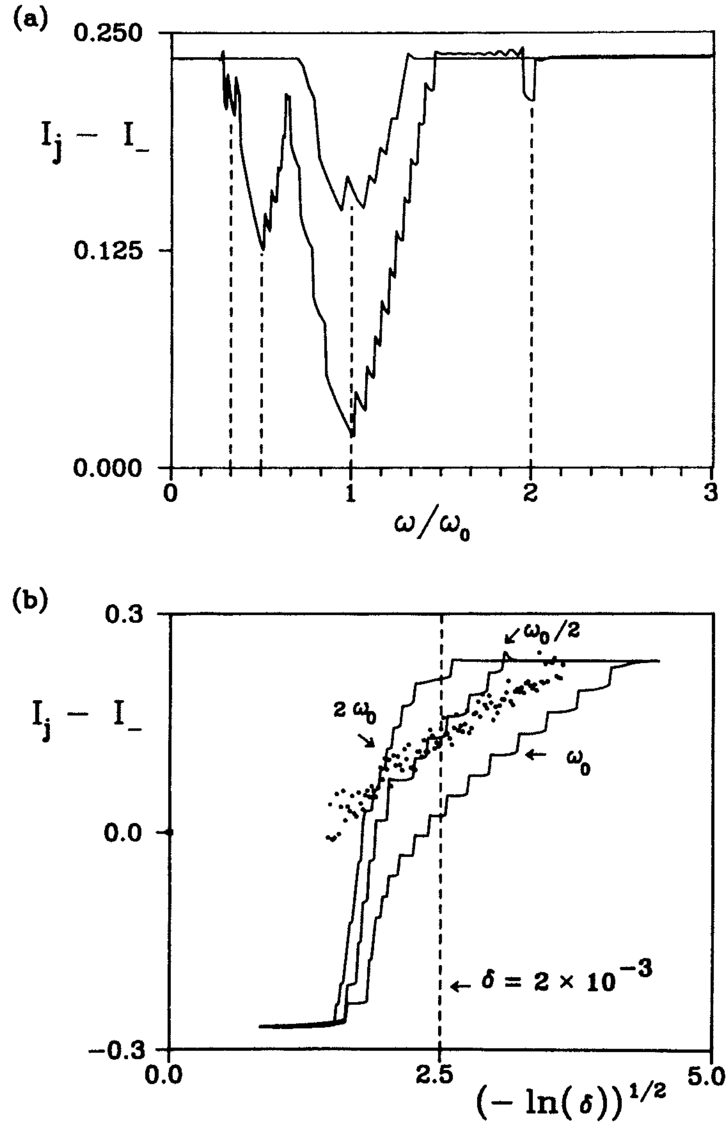


FIG. 5. *Delay is sensitive to small amplitude periodic and stochastic fluctuations (values of a, b, $\gamma$ as in Fig. 1, but with $\varepsilon = 10^{-3}$). (a) Numerical solutions to (6.1) and (6.2) show that the delay is most sensitive to small periodic fluctuations at frequencies near $\omega_0 = 0.223$, given by (2.6). Dashed lines indicate subharmonic and superharmonic resonance effects with delay reductions for $\omega$ near $\omega_0/3$, $\omega_0/2$, $\omega_0$, and $2\omega_0$. The two curves (lower for $\delta = 2 \times 10^{-3}$ and upper for $\delta = 5 \times 10^{-6}$) show that the delays are sensitive to the perturbation amplitude $\delta$. (b) Perturbation amplitude $\delta$ is treated as an adjustable parameter, and numerical solutions to (6.1) and (6.2) (solid curves) for near resonant frequencies $\omega_0/2$, $\omega_0$, and $2\omega_0$ are superimposed with numerical solutions to (2.1) for simulated white noise. The value of $I_j$ for each of 100 different values of $\delta$ is plotted as a discrete data point to represent the noise data. The delayed bifurcation transition $I_j - I_-$, for all cases, has an approximate linear dependence on $(-\ln \delta)^{1/2}$.*

sinusoidal forcing by the stochastic forcing term $\delta\sigma(t)$, where $\sigma(t)$ is a random number uniformly distributed in $[-0.5, 0.5]$. The value of $I_j$ for each of 100 different values of $\delta$ is plotted in Fig. 5(b) as a discrete data point. The trend is again that, even for small $\delta$, there is a deviation from the predicted delay for $\delta = 0$. We should also notice the sudden dropoff at a critical $\delta$ when the observed $I_j$ approximately equals $I_-$. If this feature is robust, then it could be used to estimate $I_-$.

The above calculations for the effects of periodic perturbations and small amplitude white noise help us to understand why numerical calculations involving slow passage through a Hopf bifurcation can be particularly sensitive to roundoff error. Random fluctuations, even as small as $10^{-8}$, can reduce the delay when $\varepsilon$ is small. This amplitude is approximately equal to that of single precision "machine noise" due to roundoff. To emphasize this point we compare, in Fig. 4(a), the dependence of $I_j$ on $1/\varepsilon$ computed with both quadruple and single precision; the latter results are distinguished by the label SP. Note how roundoff error seriously affects the single precision result as $\varepsilon$ decreases. The value of $\varepsilon$ below which the roundoff error first appears is dependent on the specific numerical algorithm. However, deviation from the deterministic prediction due to roundoff error is unavoidable if $\varepsilon$ is small.

Every biological or physical experiment is subject to noise. Noise can influence the outcome of an experiment if the system is particularly sensitive. In this paper, the parameter range for which most of our analytic results are applicable, $\varepsilon \ll 1$, is also the parameter range for which the FHN system seems to be quite sensitive to noise. We have shown that in general we may expect delays in the onset of oscillations but that small amplitude fluctuation may decrease the delay and diminish the memory effect. We suggest that both deterministic and stochastic approaches will be important for comparing theoretical and experimental results in systems where slow passage through a Hopf bifurcation is the underlying mechanism for the onset of oscillations.

**Acknowledgment.** We thank Shihab Shamma for helpful discussions and suggestions.

**Note added in proof.** It has recently come to our attention that a different approach can be used to analyze the delay due to the slow passage through the Hopf bifurcation point [A. I. Neishtadt, *Persistence of stability loss for dynamical bifurcations* I, Differential Equations, 23 (1987), pp. 1385–1391].

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