

A mathematical criterion based on phase response curves for stability in a ring of coupled oscillators

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Abstract. Canavier et al. (1997) used phase response curves (PRCs) of individual oscillators to characterize the possible modes of phase-locked entrainment of an N -oscillator ring network. We extend this work by developing a mathematical criterion to determine the local stability of such a mode based on the PRCs. Our method does not assume symmetry; neither the oscillators nor their connections need be identical. To use these techniques for predicting modes and determining their stability, one need only determine the PRC of each oscillator in the ring either experimentally or from a computational model. We show that network stability cannot be determined by simply testing the ability of each oscillator to entrain the next. Stability depends on the number of neurons in the ring, the type of mode, and the slope of each PRC at the point of entrainment of the respective neuron. We also describe simple criteria which are either necessary or sufficient for stability and examine the implications of these results.

1 Introduction

Rings of coupled oscillators play an important role in a variety of physiological systems. Rings of two neuronal oscillators have been studied in systems ranging from the reciprocal inhibition network controlling swimming in the pteropod mollusk *Clione* (Satterlie 1989) to the mixed

inhibitory and excitatory circuit coordinating the motion of locust wings during flight (Robertson and Pearson 1985). Recurrent cyclic inhibition circuits, composed of three unidirectionally coupled oscillators, may coordinate segmental undulations in the leech (Friesen 1989). Rings with more complex connections coordinate the escape swimming motor program in *Tritonia* (Getting 1989) and respiratory activity of *Lymnaea* (Bulloch and Syed 1992). Linkens et al. (1976) used rings of coupled oscillators to model colorectal muscular activity. Recently, coupled oscillators have received a great deal of attention in connection with the spinal central pattern generators (CPGs) that coordinate the muscular activity of locomotion in all vertebrates (Grillner et al. 1995). In quadrupedal mammals, the four oscillators controlling the limbs may be coupled in some form of ring (Collins and Richmond 1994; McClellan 1996). The wing oscillators of a bird appear to be reciprocally coupled by excitatory connections, forming a ring of two oscillators (McClellan 1996). Collins and Stewart (1993) also employed a dihedrally symmetric six-neuron ring to model hexapodal gait generation in insects.

In this paper, we concentrate on unidirectionally coupled ring networks of endogenous oscillators with either excitatory or inhibitory connections, such as those illustrated in Fig. 1. Neither the oscillators nor their connections need be identical. In some cases, such as reciprocal inhibition and recurrent cyclic inhibition networks, a ring network with unidirectional coupling provides an accurate model for a physiological system. In cases where the coupling is more complex, it represents a minimal model which may capture the essential behavior of the system. For example, Collins and Stewart (1994), Canavier et al. (1997), and DeFranceschi (1995) demonstrated that a network of four unidirectionally coupled oscillators can generate patterns corresponding to the various gaits of a quadruped. Rings of two or more oscillators may also serve as components of larger CPGs (Collins and Stewart 1994).

Despite their apparent simplicity, unidirectionally coupled ring circuits of oscillators exhibit complex dynamics. The oscillators tend to entrain or phase-lock one

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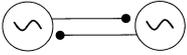
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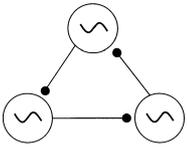
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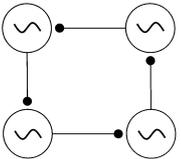


Fig. 1A–C. Ring networks in which each oscillator receives an input from one other oscillator and delivers an input to one other oscillator. These include the bidirectionally coupled two-neuron ring shown in **A** and larger rings with unidirectional coupling, such as those shown in **B** and **C**. Coupling may be excitatory, or inhibitory, or a mixture of the two. Neither the oscillators in the ring nor the synapses coupling them need be identical. Although most of the examples presented in this paper are for rings of 2, 3, and 4 neurons, the stability criterion that is developed applies to arbitrarily large rings

another such that the circuit settles into an oscillatory mode where the various oscillators fire at fixed frequencies and with fixed phasic relationships (Collins and

Richmond 1994; Ermentrout 1985; Baxter et al. 1999). We refer to such a limit cycle as a steady-state mode, in the sense that the phasic relationships between the various oscillators repeat from cycle to cycle. A single ring circuit may support several different stable modes under fixed physiological conditions. A transient synaptic input to such a multistable circuit may induce a parameter-independent shift from one stable pattern of behavior to another, which the circuit will maintain until receiving additional input. For example, Fig. 2 (modified from Baxter et al. 1999) shows intracellular recordings from an experimentally constructed ring network of three R15 neurons from *Aplysia*. Each neuron in the ring received inhibitory input from one neuron and produced inhibition in another neuron. This network oscillated initially in a stable steady-state mode labeled **A**. A brief current pulse applied to neuron N2 switched the firing pattern to a second stable mode, labeled **B**, in which the neurons fire in different order. If this circuit were a central pattern generator, the steady-state modes could correspond to the different patterns produced by such a CPG. Analogously, in the CPG for quadrupedal gait, which may consist of a ring of four oscillators, such a change in the phasic relationships and firing order of the limb oscillators may correspond to a transition from one gait to another.

Several approaches have been used to predict the steady-state modes supported by a ring network of oscillators. Kling and Székely (1968), Ádám (1968), and Kling (1971) predicted oscillations due to recurrent inhibition in ring networks whose components do not oscillate in isolation. While these authors did not consider networks of endogenous oscillators, their work and

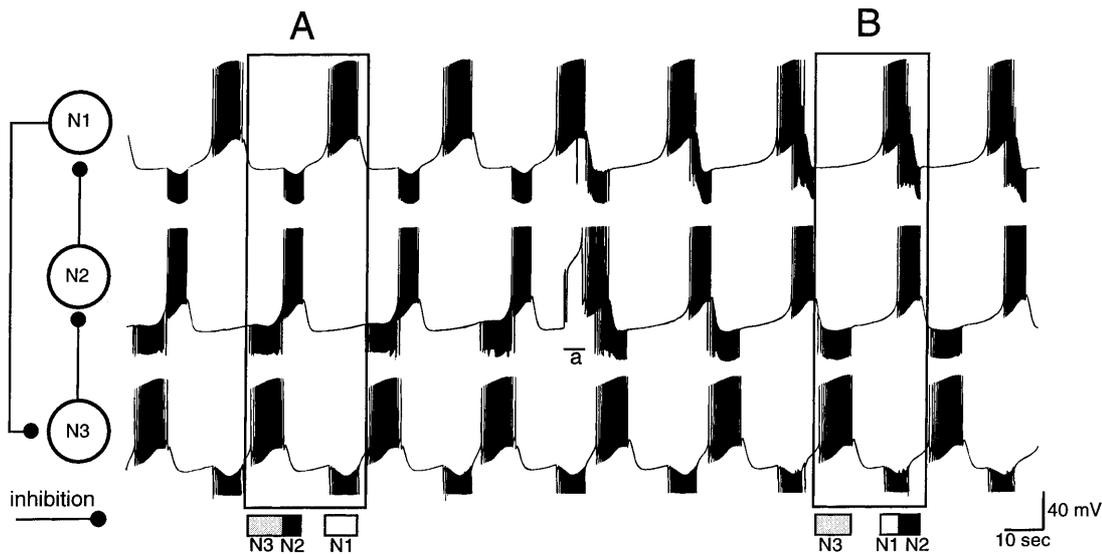


Fig. 2. Membrane potential recordings from an experimentally constructed ring network of three R15 neurons from *Aplysia* with inhibitory coupling. R15 is an endogenous burster found in the abdominal ganglion of *Aplysia*. Three separate abdominal ganglia were placed in a single recording chamber. Each was penetrated with a microelectrode used to record membrane potential and to inject current. The neurons were interconnected with simulated synapses. A spike in each neuron triggered a pulse generator that produced a brief hyperpolarization in the following neuron. The network oscillated initially in a steady-state mode labeled **A**. A depolarizing current pulse applied to neuron N2 for several seconds (see *bar* labeled *a*) switched the circuit to a second steady-state mode, labeled **B**, in which the neurons fire in a different order. This mode of activity persisted for several minutes until a second pulse perturbation was applied to return the network to mode **A**. (modified from Baxter et al. 1999)

ours exhibit a number of mathematical parallels. Ermentrout (1985) and others have analytically solved systems composed of identical single-variable phase oscillators, generally with weak coupling. Kopell (1988) as well as Ermentrout and Kopell (1991) developed a theory of average phase differences to analyze systems of oscillators with relatively weak coupling and applied it specifically to pairs of coupled oscillators such as those shown in Fig. 1A. Collins and Stewart (1994) used a group-theoretic approach to identify general properties of symmetric ring networks of identical oscillators. Recently, Canavier et al. (1997) and DeFranceschi (1995) applied phase-sensitivity analysis to unidirectional ring networks. These two studies employed phase response curves (PRCs), which have been used extensively to study phase-locked entrainment of biological oscillators, including neurons, cardiac cells, and circadian oscillators (Clay et al. 1990; Demir et al. 1997; Glass and Mackey 1988; Guevara et al. 1981; Moore et al. 1963; Pavlidis 1973; Perkel et al. 1964; Shrier et al. 1990; Shumaker et al. 1991; Wessel 1995; Winfree 1980). A unidirectional ring network operating in a steady-state mode may be viewed as an example of entrainment, wherein each neuron entrains the following one. By generalizing conventional entrainment analysis (Perkel et al. 1964), Canavier et al. (1997) established simple criteria to predict all steady-state modes of a unidirectional ring network, given the PRC of each component neuron. This method applies to rings consisting of an arbitrary number of neurons, and does not assume that the oscillators in the ring are identical or that coupling between the oscillators is weak. These criteria are easily applied to specific physical systems, given that the PRCs can be determined experimentally.

Some of the limit cycles predicted by the criteria of Canavier et al. (1997) are not observed because they are unstable. Since every physical system exhibits some level of noise, the only relevant steady-state modes are the stable ones, i.e., those to which the network will return if slightly disturbed. Entrainment analysis using PRCs has made extensive use of a stability criterion derived by Moore et al. (1963) and Perkel et al. (1964). To use PRC methods as an effective tool for the analysis or design of ring circuits, an analogous stability criterion is needed for ring networks.

The present work extends the analysis of Canavier et al. (1997) by establishing a criterion for determining the local stability of a steady-state mode of a ring network based on PRCs. In order to apply this stability criterion to a generic unidirectional ring network of oscillators, one need only determine a PRC for each oscillator, either experimentally or computationally. The results indicate that the analysis of Moore et al. (1963) and Perkel et al. (1964) for the case of phase-locked entrainment by a free-running pacemaker neuron cannot be directly applied to a ring network. Specifically, we show that the stability of a mode of a ring network is affected by feedback effects operating on the ring as a whole. This feedback can: (a) destabilize modes in which the entrainment of each individual neuron appears stable by the criterion of Perkel et al. (1964) or (b) stabilize

modes involving entrainment phenomena that would be unstable in isolation.

We begin by describing the conventions used to present PRCs and reviewing the criteria of Canavier et al. (1997) for determining steady-state modes of a ring network. Next, we consider the case of simple entrainment and derive local stability results closely related to those of Moore et al. (1963) and Perkel et al. (1964). We then build on these methods to analyze ring networks. Specifically, we reduce the stability analysis problem locally to a discrete-time linear system which can be analyzed using classical tools from control theory. Finally, we examine several special cases, simplifications, and the implications of these results. Although the analysis in this paper applies to rings composed of any type of oscillator, for simplicity we will refer to each oscillator as a neuron and to the connections between them as synapses.

2 Methods of PRC analysis

2.1 Simple entrainment

Entrainment analysis using PRCs is based on a single underlying assumption: the primary effect of synaptic input on the postsynaptic oscillator is to advance or delay the time at which that oscillator will fire next. This approximation ignores the possibilities that: (a) a stimulus to a given neuron will have some effect on the waveform with which that neuron fires and (b) a stimulus may have a longer-lasting effect, such as lengthening or shortening periods other than the one during which it is applied. These effects are typically minor, however, compared with the modification of the length of the current cycle of the postsynaptic neuron (Perkel et al. 1964; Shumaker et al. 1991). For example, in a study employing a computational model of the endogenously bursting neuron R15 of the abdominal ganglion of *Aplysia*, Demir et al. (1997) showed that a neuron stimulated during the first 3/4 of its period will return to its limit cycle by the beginning of the next burst; a neuron stimulated in the last quarter of its period will experience only a slight modification in the waveform of the following burst and in the duration of the following period.

PRCs have been widely used to analyze entrainment for two reasons. First, they are easy to construct in both experimental and computational settings using perturbations with single pulses. Second, the reduction of a system to one characterized entirely by PRCs (via the aforementioned assumption) enables precise and tractable mathematical analysis of relatively complex situations. Moore et al. (1963) analyzed the case in which a free-running pacemaker neuron entrains a second periodic oscillator. They established two criteria: one for determining when entrainment is possible based on PRCs, and the second for determining whether an entrained mode is stable. These criteria have been supported experimentally by a variety of studies (Moore et al. 1963; Perkel et al. 1964; Guevara et al. 1981; Shumaker et al. 1991; Wessel 1995).

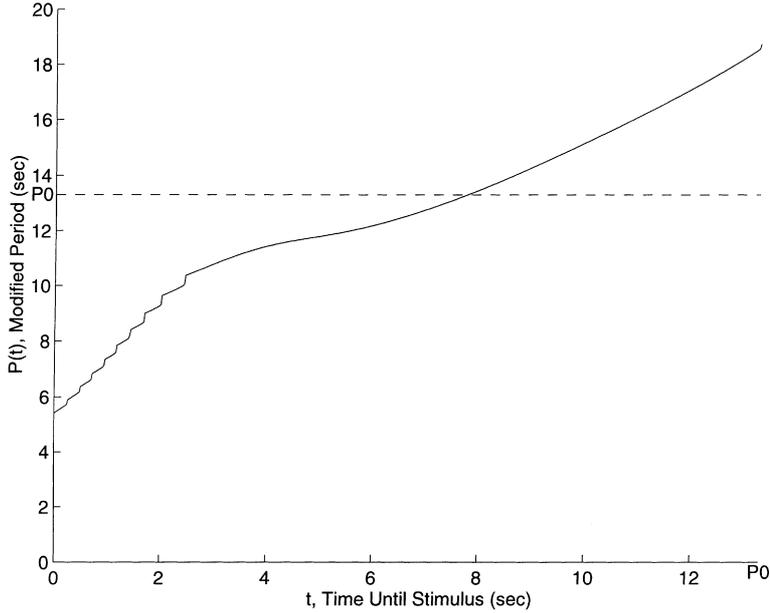


Fig. 3. Phase response curve (PRC) of the R15 neuron modeled in DeFranceschi (1995) in response to inhibitory stimuli. *Dotted horizontal line* represents P_0 , the period of the neuron in the absence of stimuli. A stimulus delivered in the 8 s after the neuron begins its burst shortens the interburst interval, advancing the time at which the neuron will burst again. A stimulus delivered later in the cycle, on the other hand, delays the time at which the neuron will burst again

A PRC for a given oscillator represents the phase advance or delay resulting from stimuli applied at different points in the cycle of the oscillator. We choose the instant at which the neuron fires as a reference point, and assume the neuron stimulates the next neuron in the ring at that time. The PRC¹ is presented as a graph of $P(t)$ vs t (Fig. 3), where t represents the interval between initial neuron discharge and the time at which the neuron receives a synaptic stimulus. Time (t) ranges from 0 to P_0 , the intrinsic free-running period of the given neuron in isolation. $P(t)$ represents the modified period of the neuron, measured as the time interval between the firing times before and after application of the stimulus. Periodic stimuli may entrain the neuron such that its entrained period P_e differs from P_0 . For the purpose of analysis, we assume ideal behavior. That is, after receiving a stimulus, an oscillator will always return to a point on its limit cycle by the time it fires again.

2.2 Ring networks

Suppose that N neurons are coupled in a ring, and that the neurons are phase-locked in a steady-state oscillatory mode. We are particularly interested in the case in which all neurons are firing at the same frequency (i.e., each oscillator entrains the following one in a 1:1 manner). The output of one neuron becomes the input for the next neuron in the ring, and thus the assumption that the characteristic waveform of the output is not significantly affected by the input is necessary in order to apply PRCs constructed with inputs consisting of fixed waveforms to the analysis of a ring circuit. A steady-state mode in the ring network is characterized by the

delays $t_i[\infty]$ ($1 \leq i \leq N$), which represent the differences in firing times of adjacent neurons in the ring. Specifically, $t_i[\infty]$ is the steady-state time interval between the firing time of the i th neuron and the firing time of the neuron which next drives it (the ∞ index represents the fact that this is a steady-state value which remains constant from cycle to cycle). Thus, if P_i is the PRC of the i th neuron, $P_i(t_i[\infty])$ represents its entrained period. Since all neurons are entrained at the same frequency,

$$P_1(t_1[\infty]) = P_2(t_2[\infty]) = \dots = P_N(t_N[\infty]) = P_e \quad (1)$$

where P_e represents the common entrained period of all the neurons in the ring. Since any neuron is in phase with itself, the sum of all the phase differences around the ring must be an integer multiple of the common entrained period:

$$t_1[\infty] + t_2[\infty] + \dots + t_N[\infty] = j * P_e, \quad (2)$$

where j is an integer. Since $0 \leq t_i[\infty] < P_e$, j must be in the range $[0, N - 1]$.

A specific value of j characterizes each steady-state mode of a ring circuit. For example, a mode in which all oscillators fire simultaneously has $j = 0$. Mode B of Fig. 2 has $j = 1$, because the sum of the phase differences between adjacent oscillators, as defined above, is equal to a single entrained period. On the other hand, mode A of Fig. 2 has $j = 2$ since the sum of phase differences between adjacent oscillators is double the entrained period. While j equals 0 only in a mode where all oscillators fire simultaneously, several distinct modes may share a common nonzero value of j . The value of j plays an important role in the stability analysis of Sect. 3.2 because it determines the feedback rate, the speed with which small perturbations from the steady state can propagate around the ring.

Canavier et al. (1997) derived these two equations used them to determine all steady-state modes of a ring

¹ Notation used to represent PRCs in this paper differs from that used in Canavier et al. (1997). In this paper, t replaces ϕ , $P(t)$ represents the PRC function, and neither t nor $P(t)$ are normalized.

network. Some of the predicted modes are never observed, however, because they are locally unstable.

3 Results: stability analysis using PRCs

If the time at which a given neuron fires and the time at which it next receives a stimulus are known, then the neuron's PRC determines its next firing time. This firing time also corresponds to the time at which the postsynaptic neuron, which the given neuron drives, receives a stimulus. The next time at which the postsynaptic neuron will fire can therefore be predicted using its own PRC. At any given cycle, the distance of the system from steady state can be quantified by measuring the difference between the intervals t_i and their steady-state values $t_i[\infty]$. The component PRCs determine a discrete-time map that defines the values of these differences in the following cycle in terms of their values in the present cycle.

Suppose the firing times of the neurons in the ring are slightly perturbed from a steady-state mode. That mode is considered stable if any such small perturbation will die away with time, with the system decaying back to the original limit cycle (orbital stability). More precisely, a steady-state mode is stable if whenever the original differences of the values $t_i[\infty]$ from steady state are chosen sufficiently close to 0, they will approach 0 as the recursive map defined by the PRCs is repeatedly applied to predict their values in subsequent cycles (Guckenheimer and Holmes 1983).

Since the PRCs are typically nonlinear, the discrete-time map in question is nonlinear. The Stable Manifold Theorem for a Fixed Point (Guckenheimer and Holmes 1983) relates the stability of the nonlinear map to that of its local linear approximation. The stability of the linear approximation depends on the eigenvalues of the Jacobian matrix (which becomes the state transition matrix of the linearized system). If the eigenvalues all have a magnitude less than 1, the linearized system will be stable, and so will the original system. If any of the eigenvalues have magnitude greater than 1, the linearized system will be unstable, as will the original system. In the special case where the largest eigenvalue has a magnitude of exactly 1, the linearized system will be critically stable, and the original system may be either stable or unstable (Guckenheimer and Holmes 1983). Determination of stability by linear approximation of the discrete-time system defined by the PRCs underlies both the classical stability analysis of entrainment and the stability analysis of ring networks presented in this paper.

3.1 Entrainment

In the classical entrainment problem considered by Moore et al. (1963) and Perkel et al. (1964), neuron 2, which is periodic, entrains neuron 1, with the firing of neuron 2 following that of neuron 1 by a delay $t_1[n]$ in the n th cycle. Figure 4 illustrates the firing times of

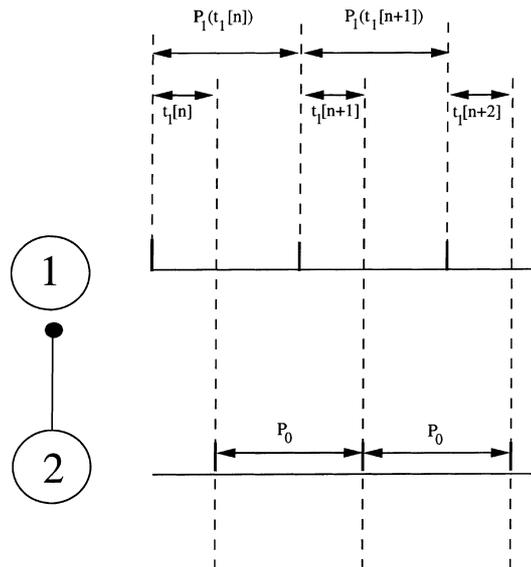


Fig. 4. Stability analysis for simple entrainment. Neuron 2, whose intrinsic period is P_0 , entrains neuron 1. At steady state, $P_1(t_1[n]) = P_0$ for all n . Solid vertical line segments indicate firing times of the neuron to their left

neurons 1 and 2 in this and the following two cycles, together with time delays between these firing times. Denote by P_1 the function whose graph is the PRC of neuron 1. The system is in a steady state if $t_1[n+1] = t_1[n]$. This is true if and only if the entrained period of neuron 1 is equal to the intrinsic period of neuron 2, that is, if $P_1(t_1[n]) = P_0$. We denote such a steady-state value of $t_1[n]$ by $t_1[\infty]$.

Suppose the system is perturbed from steady state such that $t_1[n] = t_1[\infty] + \Delta t_1[n]$, where $\Delta t_1[n]$ represents the perturbation in firing time of neuron 1. We wish to express $\Delta t_1[n+1]$, defined as $t_1[n+1] - t_1[\infty]$, as a function of $\Delta t_1[n]$. From Fig. 4,

$$t_1[n+1] = t_1[n] - P_1(t_1[n]) + P_0 \quad (3)$$

Using the facts that $P_0 = P_1(t_1[\infty])$, $t_1[n] = t_1[\infty] + \Delta t_1[n]$, and $t_1[n+1] = t_1[\infty] + \Delta t_1[n+1]$, and then subtracting $t_1[\infty]$ from both sides of (3) gives:

$$\Delta t_1[n+1] = \Delta t_1[n] - P_1(t_1[\infty] + \Delta t_1[n]) + P_1(t_1[\infty]) \quad (4)$$

This system may be linearized about its steady-state entrainment pattern by making the approximation:

$$P_1(t_1[\infty] + \Delta t_1[n]) - P_1(t_1[\infty]) \cong P_1'(t_1[\infty])\Delta t_1[n] \quad (5)$$

where the derivative $P_1'(t_1[\infty])$ represents the slope of the function $P_1(t)$ at $t = t_1[\infty]$. Thus, (4) becomes

$$\Delta t_1[n+1] = \Delta t_1[n] - P_1'(t_1[\infty])\Delta t_1[n] = (1 - P_1'(t_1[\infty]))\Delta t_1[n] \quad (6)$$

Let $m_1 \equiv P_1'(t_1[\infty])$, the slope of the PRC of neuron 1 at the point corresponding to steady-state entrainment. Equation 6 states that $\Delta t_1[n+1] = (1 - m_1)\Delta t_1[n]$, so as $n \rightarrow \infty$, $\Delta t_1 \rightarrow 0$ if $|1 - m_1| < 1$. The original orbital

solution of the nonlinear system is stable if $0 < m_1 < 2$ and unstable if $m_1 < 0$ or $m_1 > 2$. Indeed, the Jacobian matrix for this system is simply $[1 - m_1]$, with the single eigenvalue $1 - m_1$. If m_1 is exactly equal to 0 or 2, then $|1 - m_1| = 1$, so the linearized system is critically stable, and the stability of the original system depends on the second derivative of the PRC at the point of entrainment. This stability criterion agrees with the global stability criterion derived by Moore et al. (1963) and restated by Perkel et al. (1964). We derived the result as a local stability criterion depending on the slope of the PRC only at the point of entrainment so that the criterion applies even to multistable systems. We now generalize this criterion to ring networks, including those which may support several stable modes of oscillation.

3.2 Ring networks

The preceding stability criterion applies equally well to chains of coupled oscillators, where neuron 2 drives neuron 1, neuron 3 drives neuron 2, and so on. A steady-state mode of the chain will be stable if the slope of the PRC of each entrained neuron is between 0 and 2 at its point of entrainment. The addition of a connection between the first and last neuron of the chain to form a closed ring significantly alters the situation. Now, if the firing time of a given neuron is perturbed, the perturbation will propagate around the ring, eventually affecting the firing times of the neuron which drives the originally perturbed neuron.

Given the differences in firing times of the component neurons, as well as the slopes of their PRCs at the points of entrainment, one can determine the stability of the linearized mapping, which in turn indicates the stability of the nonlinear discrete-time system defined by the PRCs. The analysis must be generalized, however, to account for the effect of feedback. For rings consisting of three or more neurons, multiple state variables are necessary to relate the difference of a system from steady state in one cycle to the difference from steady state in the next. We first consider a ring consisting of only two neurons, and then the more general N -neuron ring. The following derivations apply to steady-state modes in which adjacent oscillators do not fire exactly simultaneously; in particular, this rules out the potential mode with $j = 0$ [see (2)] in which all oscillators in the ring fire at once (see Discussion, however).

3.2.1 Two-neuron ring

In the ring circuit shown in Fig. 5, neuron 1 and neuron 2 form a two-neuron ring due to reciprocal (but not necessarily identical) connections. The firing time of neuron 2 follows that of neuron 1 by a time delay $t_1[n]$; neuron 1 follows neuron 2 by a time delay $t_2[n]$. P_1 and P_2 denote the PRCs of neuron 1 and neuron 2, respectively. At steady state, both neurons are entrained at a common period P_e , with phase differences $t_1[n] = t_1[\infty]$ and $t_2[n] = t_2[\infty]$. In general,

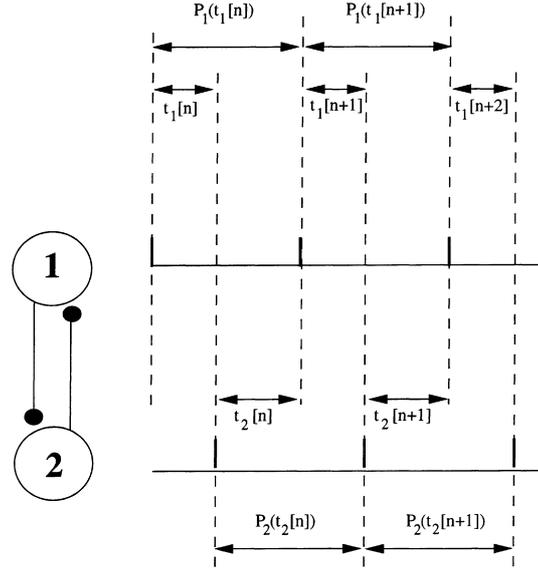


Fig. 5. Stability analysis for a two-neuron ring. *Solid vertical line segments* indicate firing times of the neuron to their left

$$t_i[n] = t_i[\infty] + \Delta t_i[n] \quad (7)$$

The slope of the PRC of the i th neuron at its point of entrainment is given by $m_i \equiv P'_i(t_i[\infty])$. For the system linearized about the steady-state solution,

$$P_i(t_i[n]) = P_e + m_i \Delta t_i[n] \quad (8)$$

The relationship between $t_1[n]$ and $t_1[n+1]$ differs from (3) only in that the periods of both neurons are now dependent on past states:

$$t_1[n+1] = t_1[n] - P_1(t_1[n]) + P_2(t_2[n]) \quad (9)$$

Substituting (7) and (8) into (9), we have for the linearized system:

$$\Delta t_1[n+1] = \Delta t_1[n] - m_1 \Delta t_1[n] + m_2 \Delta t_2[n] \quad (10)$$

We wish to eliminate $\Delta t_2[n]$ from the above equation. Figure 5 illustrates that $t_1[n]$ and $t_2[n]$ are related by:

$$t_2[n] = P_1(t_1[n]) - t_1[n] \quad (11)$$

For the linearized system, substituting (7) and (8) into (11) and simplifying with (2) for $j = 1$ yields:

$$\Delta t_2[n] = m_1 \Delta t_1[n] - \Delta t_1[n] \quad (12)$$

Substituting (12) into (10) and grouping terms algebraically, we have:

$$\Delta t_1[n+1] = (m_1 - 1)(m_2 - 1) \Delta t_1[n] \quad (13)$$

The Jacobian matrix relating $\Delta t_1[n+1]$ and $\Delta t_1[n]$ for the linearized system is $[(m_1 - 1)(m_2 - 1)]$, with eigenvalue $(m_1 - 1)(m_2 - 1)$. The original system is stable when $|(m_1 - 1)(m_2 - 1)| < 1$ and unstable when $|(m_1 - 1)(m_2 - 1)| > 1$. If both slopes are between 0 and 2, the entrained mode in question is stable. The system may also be stable when one of the slopes is far outside the range (0, 2), as long as the other slope is

sufficiently close to 1. In such cases, the feedback effect serves to stabilize the system.

3.2.2 N -neuron ring

We now consider the generalized ring of N neurons coupled in a ring circuit as shown in Fig. 6. Again $t_i[n]$ denotes the time delay from the firing time of the i th neuron to the firing time of the neuron that drives it. At steady state, $t_i[n] = t_i[\infty]$. P_e again denotes the common entrained period of the N neurons, P_i is the PRC of the i th neuron, and the m_i are as previously defined. Equations (7) and (8) hold for all i .

Although we approach this general case much as we approached the two-neuron ring, several factors complicate the analysis. One state variable no longer suffices to describe the system. For example, $\Delta t_1[n]$ does not uniquely determine the future behavior of the system, since knowledge of $\Delta t_1[n]$ is not sufficient to determine the value of $\Delta t_1[n+1]$. The system is fully described by $\Delta t_1[n], \Delta t_2[n], \dots, \Delta t_{N-1}[n]$. $N-1$ state variables suffice since the relationship of t_1, t_2, \dots, t_N expressed in (2) allows us to write $t_N[n]$ as a function of $t_1[n], t_2[n], \dots, t_{N-1}[n]$. Instead of expressing $t_1[n+1]$ as a scalar multiple of $\Delta t_1[n]$, we express the vector

$\Delta \mathbf{t}[n+1] = (\Delta t_1[n+1], \Delta t_2[n+1], \dots, \Delta t_{N-1}[n+1])$ as a linear function (matrix multiple) of $\Delta \mathbf{t}[n] = (\Delta t_1[n], \Delta t_2[n], \dots, \Delta t_{N-1}[n])$. That is, $\Delta \mathbf{t}[n+1] = A \Delta \mathbf{t}[n]$, where A is a Jacobian matrix of the discrete-time system determined by the PRCs. The eigenvalues of A determine the stability of the linearized system, which in turn determines the stability of the original system. An exception to this rule is that if the linearized system is critically stable, the stability of the original system cannot be determined by this method.

The analogs of (9) and therefore also of (10) hold in general for the i th neuron in the ring of Fig. 6, where $1 \leq i \leq N-1$:

$$t_i[n+1] = t_i[n] - P_i(t_i[n]) + P_{i+1}(t_{i+1}[n]) \quad (14)$$

$$\begin{aligned} \Delta t_i[n+1] &= \Delta t_i[n] - m_i \Delta t_i[n] + m_{i+1} \Delta t_{i+1}[n] \\ &= (1 - m_i) \Delta t_i[n] + m_{i+1} \Delta t_{i+1}[n] \end{aligned} \quad (15)$$

When $i = N-1$, the right-hand side of (15) depends on $\Delta t_N[n]$. In order to complete the construction of the Jacobian matrix A , $\Delta t_N[n]$ must be expressed in terms of the $N-1$ independent state variables $\Delta t_1[n], \Delta t_2[n], \dots, \Delta t_{N-1}[n]$. This relationship depends on

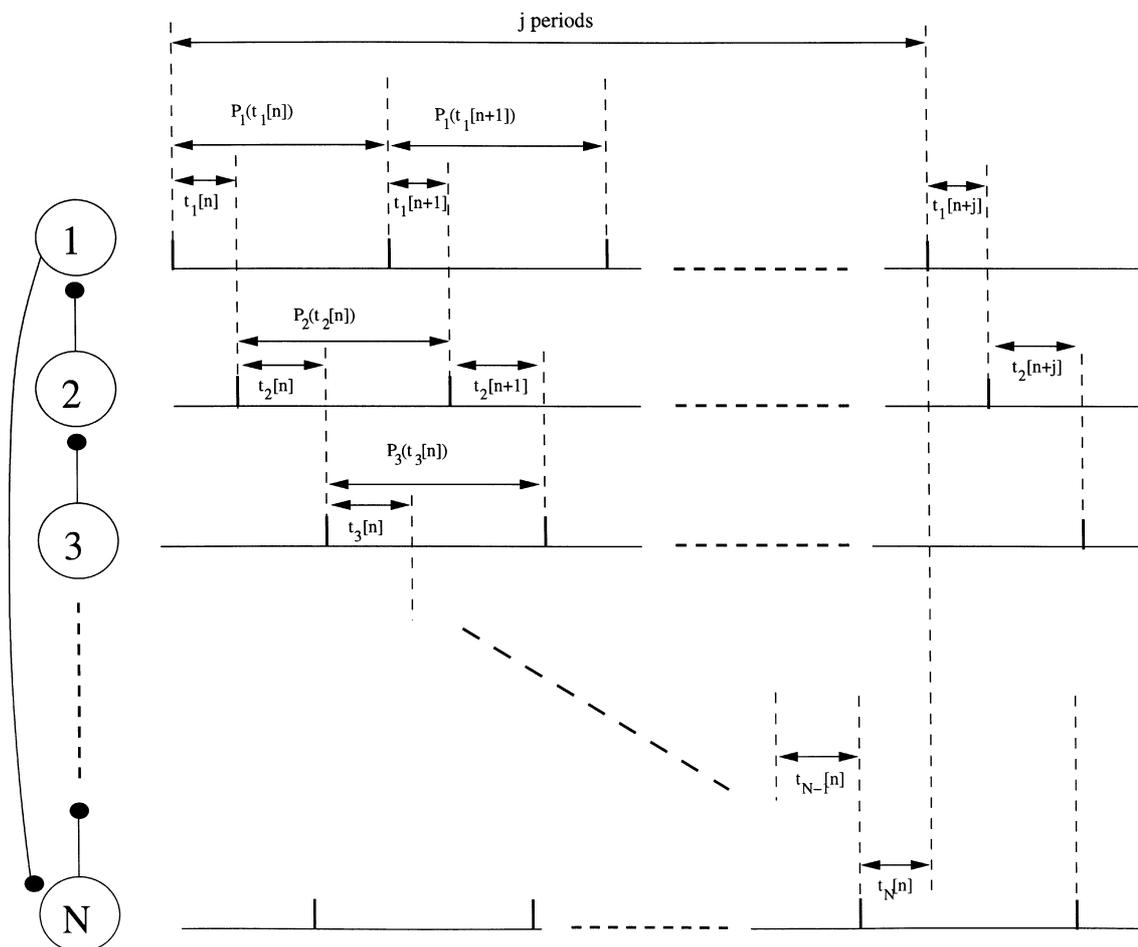


Fig. 6. Stability analysis in the general case for an N -neuron ring. Only selected neurons are shown. The analysis depends on j because the time intervals $t_1[n], t_2[n], \dots, t_N[n]$ sum to jP_e at steady state. If the firing time of neuron 1 is perturbed slightly from steady state, the effects of this perturbation will propagate all the way around the ring in j periods

j , the integer parameter in (2), which is characteristic of a given mode. By determining the number of full periods a perturbation will take to propagate around the ring, the integer j effectively characterizes the feedback interval of the system as a multiple of the entrained period P_e . Figure 7 illustrates the difference between modes with $j = 1$ and $j = 2$ in a three-neuron ring.

When the system is perturbed from a steady-state mode, (2) generalizes to:

$$t_1[n] + t_2[n] + \dots + t_N[n] = P_1(t_1[n]) + P_1(t_1[n+1]) + \dots + P_1(t_1[n+j-1]) \quad (16)$$

Substituting (7) and (8) into (16), the following relationships hold for the linearized system:

$$\begin{aligned} \Delta t_1[n] + \Delta t_2[n] + \dots + \Delta t_N[n] &= m_1 \Delta t_1[n] \\ &+ m_1 \Delta t_1[n+1] + \dots \\ &+ m_1 \Delta t_1[n+j-1] \end{aligned} \quad (17)$$

$$\begin{aligned} \Delta t_N[n] &= m_1 (\Delta t_1[n] + \Delta t_1[n+1] + \dots + \Delta t_1[n+j-1]) \\ &- (\Delta t_1[n] + \Delta t_2[n] + \dots + \Delta t_{N-1}[n]) \end{aligned} \quad (18)$$

We express $\Delta t_1[n+1], \Delta t_1[n+2], \dots, \Delta t_1[n+j-1]$ in terms of $\Delta t_1[n], \Delta t_2[n], \dots, \Delta t_{N-1}[n]$ by repeated application of (15). Note that $t_1[n+k]$ depends on $\Delta t_1[n], \Delta t_2[n], \dots, \Delta t_{k+1}[n]$. Therefore, $\Delta t_1[n+j-1]$ depends on $\Delta t_1[n], \Delta t_2[n], \dots, \Delta t_j[n]$; since $j < N$, the right-hand side of (18) can be written entirely in terms of $\Delta t_1[n], \Delta t_2[n], \dots, \Delta t_{N-1}[n]$.

The above equations provide a systematic method to compute the Jacobian matrix A , in terms of the slopes m_1, m_2, \dots, m_N , for a mode with given nonzero j in a ring circuit of N neurons. Table 1 shows the resulting matrices for all values of j for $N = 2, 3$, and 4. When $N = 2$, the matrix shown agrees with that derived explicitly in Sect. 3.2.1 for the two-neuron ring.

Substituting values of the slopes m_1, m_2, \dots, m_N into one of these matrices gives a numerical Jacobian (state transition) matrix whose eigenvalues determine the stability of the mode. The magnitude of the largest eigenvalue determines the maximum rate at which a perturbation from the steady state can grow. If λ_{\max} , the eigenvalue of maximum magnitude, has multiplicity k , the growth rate is bounded above by $n^{k-1} |\lambda_{\max}|^n$. If $|\lambda_{\max}| > 1$, some perturbations to the system will grow exponentially, so the system is unstable. If $|\lambda_{\max}| < 1$, all small perturbations will decay exponentially. The smaller $|\lambda_{\max}|$, the faster the rate of decay, the quicker the convergence to steady state, and the more stable the system. Thus, the magnitude of the largest eigenvalue of matrix A not only determines whether a mode will be stable, but also provides a measure of its relative stability.

The method outlined above allows determination of the stability of any given steady-state mode in a ring network, subject to the limitations noted in Sect. 4.2. This process may be automated. We implemented a function which produces a symbolic Jacobian matrix, such as those shown in Table 1, for any N and j . We also implemented a function which computes a numerical

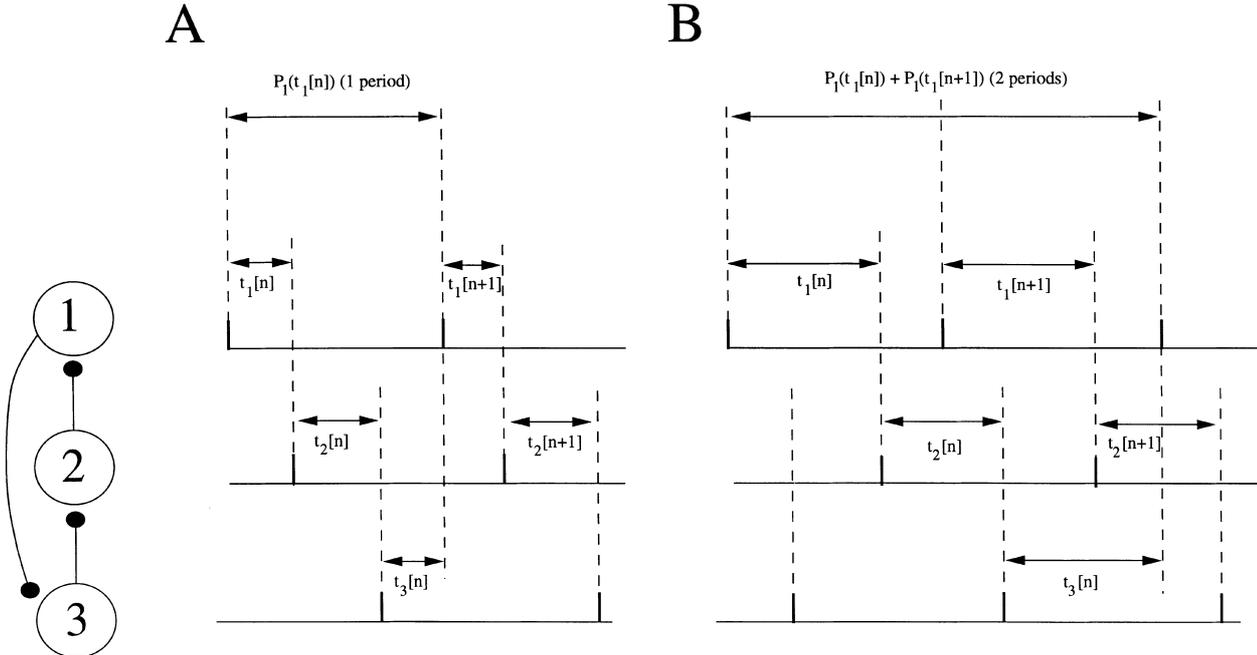


Fig. 7A,B. Two different steady-state modes in a three-neuron ring. The modes differ in the firing order of the neurons. The mode in **A** has $j = 1$, because the sum of the phase differences between adjacent oscillators is equal to a single entrained period. The mode in **B** has $j = 2$, since the sum of phase differences between two adjacent oscillators is double the entrained period. Phase difference between two adjacent oscillators is measured as the time interval elapsing between the firing time of an oscillator and the next time at which that oscillator receives a stimulus. If one oscillator in the mode of **A** is slightly perturbed, the effects of the perturbation will spread all the way around the ring in a single entrained period. In the mode of **B**, however, this will take two entrained periods

Table 1. Jacobian matrices of the discrete-time systems describing propagation of perturbations from steady state through ring networks of 2, 3, and 4 neurons. A mode is stable if all eigenvalues of the corresponding Jacobian matrix (transition matrix) have magnitude less than 1. N represents the number of neurons in the ring. Matrices are listed for each permissible nonzero value of the integer j [see (2)]. The matrices are parameterized by the slopes m_1, m_2, \dots, m_N of the PRCs at the respective points of entrainment. For a given value of N , only the bottom row of the Jacobian matrix depends on j

N	j	Jacobian matrix
2	1	$[(1 - m_1) \quad (1 - m_2)]$
3	1	$\begin{bmatrix} 1 - m_1 & m_2 \\ m_3(m_1 - 1) & 1 - m_2 m_3 \end{bmatrix}$
3	2	$\begin{bmatrix} 1 - m_1 & m_2 \\ -m_3(m_1 - 1)^2 & 1 - m_2 + m_1 m_2 m_3 - m_3 \end{bmatrix}$
4	1	$\begin{bmatrix} 1 - m_1 & m_2 & 0 \\ 0 & 1 - m_2 & m_3 \\ m_4(m_1 - 1) & -m_4 & 1 - m_3 - m_4 \end{bmatrix}$
4	2	$\begin{bmatrix} 1 - m_1 & m_2 & 0 \\ 0 & 1 - m_2 & m_3 \\ -m_4(m_1 - 1)^2 & m_4(m_1 m_2 - 1) & 1 - m_3 - m_4 \end{bmatrix}$
4	3	$\begin{bmatrix} 1 - m_1 & m_2 & 0 & 0 \\ 0 & 1 - m_2 & m_3 & 0 \\ m_4(m_1 - 1)^3 & m_4(3m_1 m_2 - m_1^2 m_2 - m_1 m_2^2 - 1) & 1 - m_3 + m_1 m_2 m_3 m_4 - m_4 & 0 \end{bmatrix}$

measure of the stability of a mode (the magnitude of the largest eigenvalue of the Jacobian matrix) given the number of neurons N in the ring, the integer j , and slopes m_1, m_2, \dots, m_N which characterize the mode. These functions, available by ftp, are described in the Appendix.

Combined with (1) and (2) for locating steady-state modes of a ring network, this stability analysis provides an algorithm to determine stable steady-state modes of a ring network given only the PRC of each oscillator. We have written a computer program, also described in the Appendix, which automates the entire process, finding all steady-state modes and testing the stability of each. This method allows characterization of the steady states of any unidirectional ring network of oscillators.

3.2.3 Example using four-neuron ring

In this section, we illustrate the use of the method described in the previous section by applying it to the quadrupedal gait generation model of Canavier et al. (1997). While this particular model happens to be symmetric, our method does not depend on symmetry; each PRC can be different. Also, while Canavier et al. determined PRCs computationally from a mathematical model, our method applies equally to experimental PRCs.

The model of Canavier et al. (1997) consists of four identical neurons unidirectionally coupled by synaptic connections. Each neuron is a bursting neuron, represented by the model of Butera et al. (1996) for neuron R15 of *Aplysia*. By applying constant bias currents to all the neurons in the network, one can modify their intrinsic properties. Canavier et al. (1997) considered the network at three different values of this constant bias current. In each case, they performed 256 numerical simulations with randomly chosen initial conditions to locate stable steady-state modes of the system. They also

simulated single-pulse experiments to compute the PRCs of the individual neurons at each bias current.

We first predicted all steady-state modes at each bias current, regardless of stability, using (1) and (2) and the PRCs at that bias current. We replicated the results of Canavier et al. (1997) using the computer program described in the Appendix. Table 1 of Canavier et al. (1997) lists the steady-state modes predicted from the PRCs, giving the entrained period P_e and the steady-state phase differences $t_1[\infty], \dots, t_4[\infty]$ for each.² These values define a value of j for each mode [$j = (t_1[\infty] + t_2[\infty] + \dots + t_N[\infty])/P_e$]. Between 6 and 15 different modes were located at each bias current. While all modes observed in simulations were accurately predicted by this method, at most three modes were observed in the numerical simulations at any given bias current. The other modes were not stable. The analysis described in the previous section provides a method to predict the stability of each mode. In order to predict the stability for a given mode, we need only the value of j and the slopes of each PRC at the point of entrainment of the respective neuron. As defined earlier, we denote the slope $P'_i(t_i[\infty])$ by m_i . Canavier et al. (1997) computed the values of these four slopes from the PRCs for each steady-state mode identified; the slopes are also listed in Table 1 of that paper. To test stability for a mode, we substituted the values m_1, m_2, m_3 , and m_4 into the matrix listed in Table 1 for $N = 4$ and the appropriate value of j . We then found the eigenvalues of the resulting numerical matrix. If any eigenvalue has a magnitude greater than unity, we expect instability; otherwise, we expect stability.

² Canavier et al. (1997) use different notation, listing P_e as $1 + F(\phi)$ and $t_i[\infty]$ as ϕ_i .

Table 2. Values of $|\lambda_{\max}|$ for various modes of a four-neuron ring network. The first four columns indicate the various slopes; the last three columns indicate $|\lambda_{\max}|$ for various values of j . The mode is stable if $|\lambda_{\max}| < 1$

m_1	m_2	m_3	m_4	$ \lambda_{\max} (j=1)$	$ \lambda_{\max} (j=2)$	$ \lambda_{\max} (j=3)$
0	0	0	0	1	1	1
0.5	0.5	0.5	0.5	0.69	0.5	0.46
1.6	1.6	1.6	1.6	2.37	3.66	3.45
1	1	1	1	1	1	0
0.1	0.9	0.3	0.7	0.47	0.55	0.61
1.5	1.5	0.9	0.9	1.36	1.78	0.2
2.9	2.9	0.9	0.8	2.65	4.28	0.90
-2.0	1.2	2.8	0.8	2.49	0.83	5.22

Predictions by this method agree with the results of numerical simulation for all modes at all three bias currents in the model of Canavier et al. (1997). Observed modes were predicted stable, while others were predicted unstable.³ Since the coupling between neurons in this model is weak, the slopes of the PRCs tend to be small. This leads to eigenvalues relatively close to 1 for stable modes, suggesting that these modes will converge only slowly to exact steady state from approximate initial conditions. This phenomenon was in fact observed in simulations. Moreover, the closer the maximum eigenvalue from the preceding stability analysis to 1, the slower the system converged to the steady-state mode.

4 Discussion

4.1 Special cases and simplified stability criteria

The stability of a steady-state mode in a ring network, measured by the magnitude of the largest eigenvalue of the Jacobian matrix, is a complicated function of the slopes m_i and the integer j . In the case of the two-neuron ring with nonsynchronous oscillators, the matrix has only one eigenvalue, $(1 - m_1)(1 - m_2)$. For rings with more than two neurons, such simple expressions for the eigenvalues do not exist, although the eigenvalues are easily computed numerically. Table 2 shows the magnitude of the largest eigenvalue for several different combinations of slopes m_i and mode number j for a four-neuron ring. A mode is stable if this magnitude is less than 1. Some modes with all slopes in the range (0,2) are unstable, whereas other modes with some slopes outside this range are stable. Large positive or negative slopes usually decrease stability, while slopes in the range (0,1) usually increase stability. This generalization has notable exceptions, however. As illustrated in Table 2, stability depends not only on the slopes m_i , but on the type of mode as characterized by j . For certain combinations of slopes, modes with one value of j are stable, but those with another value of j are unstable. Typically, higher values of j lead to greater stability, but this trend also has exceptions.

In addition to analyzing the stability of experimentally observed biological networks, one might wish to

design a synthetic network of oscillators for use in an artificial control system (Yuasa and Ito 1990). In analyzing a preexisting ring circuit, one can easily determine the stability of a given mode by computing the magnitude of the largest eigenvalue of the corresponding Jacobian matrix. The process of designing a ring circuit, however, would be expedited by simple guidelines which allow the designer to gauge the stability of various steady-state modes supported by the circuit without computation. In a few cases, the stability criterion can be stated in a simpler form. For example, in a two-neuron ring, a steady-state mode in which the two oscillators are not coherent is stable when $|(1 - m_1)(1 - m_2)| < 1$ and unstable when $|(1 - m_1)(1 - m_2)| > 1$. The stability criterion also simplifies in the special case where all the slopes m_i are equal to one another. Such modes are common in circuits composed of identical neurons (Canavier et al. 1997; DeFranceschi 1995). In such cases, the Jacobian matrix for fixed N and j has only one parameter, and for small numbers of neurons, we were able to determine the ranges of this parameter in which the system would be stable using a Routh-Hurwitz criterion (Kuo 1995). These ranges are presented for various values of N and j in Table 3.

In the general case, determination of stability requires finding the eigenvalues of a matrix, as discussed above. However, we have established a few criteria for stability which are either necessary or sufficient and which may be useful as guidelines to give some intuitive prediction of stability during the design process. Although we believe these are true in general, we state them as conjectures because we have proved them only for small N . Denote by $A(N, j)$ a transition matrix parametrized by m_i , $1 \leq i \leq N$, for given values of N and j .

$$\text{Conjecture 1: } \det(A) = (1 - m_1)(1 - m_2) \cdots (1 - m_N)$$

We have proved this for all values of j for $N \leq 10$. Since $\det(A)$ is the product of the eigenvalues of A , a necessary

Table 3. Ranges of m which lead to stability in ring networks where all slopes are equal to m . For the cases described in this table, the stability range is (0,1) if $j < N - 1$ and $(0, N/(N - 1))$ if $j = N - 1$. We conjecture that this holds for all N ; we have checked it numerically for $N = 5$ and 6

	$N = 2$	$N = 3$	$N = 4$
$j = 1$	(0, 2)	(0, 1)	(0, 1)
$j = 2$		(0, 3/2)	(0, 1)
$j = 3$			(0, 4/3)

³ Rigorous stability analysis for the pronk modes in which all oscillators fire simultaneously is more complicated, as explained in Sect. 4.2.

but not sufficient criterion for stability is that $|\det(A)| < 1$; in other words, $|(1 - m_1)(1 - m_2) \dots (1 - m_N)| < 1$. This implies that in order for a mode to be stable, at least one of the m_i must lie in the range (0,2).

Conjecture 2: If all the m_i lie in the range (0,1), then the mode is stable for any N and j .

We have proved this conjecture for a few specific values of N and j , and have checked it by fine numerical searches for all values of j for $N \leq 5$. This provides a sufficient but not necessary criterion for stability.

The following theorem implies that for a given N and j , any two modes with the same set of slopes will be equally stable, regardless of which slopes correspond to which neurons. For example, consider a four-neuron ring in which two neurons have corresponding slopes 0 and the other two have slopes 1. The stability of the mode does not depend on whether neurons with equal slopes are adjacent or opposite one another in the ring.

Theorem 1: The characteristic polynomial of $A(N, j)$ is symmetric with respect to m_1, m_2, \dots, m_N . In other words, exchanging any two of these slopes does not change the polynomial.

Our proof of this theorem is based on the fact that a rotation (N -cycle) and a transposition generate the group of all permutations of a set of N elements (Herstein 1975). Since any neuron in the ring could have been denoted neuron 1, the characteristic polynomial of $A(N, j)$ is invariant under a rotational reassignment of the N slopes. Thus, one need only show that the characteristic polynomial will remain unchanged under a single transposition, such as when slopes m_1 and m_2 are interchanged. This can be proven by analyzing the propagation of small perturbations through a system of two coupled neurons and showing that the input-output relationship remains the same when the slopes are interchanged.

4.2 Limitations

In addition to the basic assumption justifying PRC analysis (after being perturbed, an oscillator will return to a point on its limit cycle before it fires again, Sect. 2.1), our analysis of stability in the ring network assumed that a small change from steady state in the firing times of the neurons would not alter the parameter j . This additional assumption is valid as long as two adjacent neurons do not fire at exactly the same time at steady state. Suppose, for example, that in Fig. 7A, neurons 1 and 2 fire simultaneously ($t_1[n] = 0$). If an external perturbation slightly advances the firing time of neuron 1, j will remain 1, but if it slightly delays the firing time, j will become 2. This is because j is determined by successive firing time intervals in a particular order around the ring, as illustrated in Fig. 6. Hence, infinitesimal changes in the firing times actually change the value of j for the mode, and therefore the nature of the feedback. Stated in another way, if neuron 1 fires slightly before neuron 2, it will receive an input at a time delay $t_1[n]$ slightly greater than

zero, but if neuron 1 fires slightly after neuron 2, it will receive its next input at a time delay $t_1[n]$ of nearly P_e . Even if the slopes of the PRC at 0 and P_e are the same, the derivatives necessary to construct a linear approximation to the system about such a steady state do not exist. Instead, one must construct a piecewise linear approximation whose analysis, though possible through the general techniques used previously, is much more complicated. In the case of modes with $j = 0$, where all the neurons fire simultaneously, slight perturbations can change j to any value between 1 and $N - 1$, so the local approximation is composed of multiple linear pieces. If the matrix corresponding to each of these is stable, then the mode in question will also be stable. The converse is not true, although stability still correlates with small positive slopes.

Another limitation of our stability analysis is the assumption of 1:1 entrainment for all neurons in the ring. Although the aforementioned analysis techniques apply to more general forms of entrainment, PRCs do not predict the recovery time of a neuron which receives two or more stimuli in the same period, and therefore do not provide the necessary information for analysis in this case. Many applications, such as gait generation, are exclusively concerned with 1:1 entrainment, however. For similar reasons, conventional PRCs are not sufficient to predict the behavior of a bidirectionally coupled ring circuit, where even in the case of 1:1 entrainment, each neuron will receive two stimuli per period.

4.3 Physiological implications

The results obtained in the example given in Sect. 3.2.3 illustrate some of the interesting implications of the stability criterion. In general, a mode can be stable even if some of the slopes at points of entrainment are less than 0 or greater than 2. For example, the ‘‘gallop’’ at a bias current of -0.15 nA in the model of Canavier et al. (1997) is predicted and found stable, even though the slope m_1 is slightly negative, implying that if any connection in the ring were cut, neuron 2 would fail to entrain neuron 1. In fact, with $|\lambda_{\max}| = .931$, the gallop is predicted to be the most stable of the four stable modes at this bias current. More striking examples of the same stabilization phenomenon are illustrated by the last two lines of Table 2. Such stabilization is even more likely in a two-neuron ring, where a mode is stable if $|(1 - m_1)(1 - m_2)| < 1$. If one of these two slopes is sufficiently close to 1, the other may become very large without violating the stability condition. Thus, the addition of a feedback path can stabilize entrainment. In other cases, feedback can have the opposite effect. In rings with three or more neurons, a mode with all slopes between 0 and 2 may be unstable. The third and sixth lines of Table 2 provide examples of this phenomenon. Conjecture 1, if true, implies that this will occur only when one or more of the slopes is greater than one.

The stability criterion, together with the method of Canavier et al. (1997) for predicting steady-state modes, implies that even ring circuits with simple PRCs may

exhibit surprisingly rich behavior. A ring of N identical neurons with linear PRCs may support N distinct modes of oscillation, one for each value of j . These may all be stable, or all unstable. Changing the slope of the entire PRC may stabilize some modes while destabilizing others, because stability depends on the value of j . Theorem 1 implies that in a unidirectional ring circuit with identical neurons, such as that of Canavier et al. (1997), the existence and stability of one mode guarantees the existence and stability of all modes which are identical except that the phase differences between various neurons have been permuted. For example, in a four-neuron ring, the existence and stability of a mode where two pairs of adjacent oscillators fire nearly synchronously imply the existence and stability of a mode where diagonal pairs of oscillators fire nearly synchronously. This need not be true in a ring of non-identical oscillators.

Neuronal oscillators are often highly nonlinear systems with complex dynamic behavior. Although PRC theory simplifies the analysis of ring networks, it captures some of the essential nonlinear aspects of their behavior. It may serve as a valuable theoretical tool to analyze ring networks mathematically and an experimental tool to predict their behavior from easily measured data.

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Appendix

In order to determine the stability of a steady-state mode in a ring network using the methods described in Sect. 3.2.2, one must construct the appropriate Jacobian matrix and find the magnitude of its largest eigenvalue. Given values for N and j , one may construct a symbolic Jacobian matrix with the slopes m_1, m_2, \dots, m_N as parameters. Alternatively, given numerical values for all parameters, one may construct a numerical matrix and compute its eigenvalues.

We automated the process of constructing symbolic matrices using Maple, a symbolic mathematics language. Given N and j , the function ‘construct_matrix’⁴ returns the Jacobian matrix A such that $\Delta \mathbf{t}[n+1] = A \Delta \mathbf{t}[n]$. This code produces matrices such as those shown in Table 1. These matrices have a unique form which becomes particularly noticeable for large values of N . Due to (15), each row except the last contains only two entries, one on the matrix diagonal and one just to the right of the diagonal. Only the entries in the last row depend on j . In order to compute the entries in the last row, however, we must express $\Delta t_N[n]$ in terms of $\Delta t_1[n], \Delta t_2[n], \dots, \Delta t_{N-1}[n]$ using (18). This in turn requires us to express $\Delta t_1[n+1], \Delta t_1[n+2], \dots, \Delta t_1[n+j-1]$ in terms of $\Delta t_1[n], \Delta t_2[n], \dots, \Delta t_{N-1}[n]$ by repeated application of (15). The entries in the last row become complicated functions of m_1, m_2, \dots, m_N . For large N and j , these entries are computationally expensive to compute either symbolically or numerically.

The amount of computation required to construct the Jacobian matrix A may be decreased significantly through a different choice of state variables. Our choice in Sect. 3.2.2 of

$\Delta t_1[n], \Delta t_2[n], \dots, \Delta t_{N-1}[n]$ as state variables to describe the system at cycle n is not unique. Any $N-1$ independent linear combinations of these quantities could serve as the state variables, leading to a different but equivalent description of the system. Changing the states variable changes the transition matrix, but only by a similarity transformation; the matrix maintains the same eigenvalues and therefore the same implications for system stability. By using a proper choice of state variables, which depends on j , we can eliminate the recursive computation of $\Delta t_1[n+1], \Delta t_1[n+2], \dots, \Delta t_1[n+j-1]$ necessary in ‘construct_matrix.’ While such a choice of state variables may seem less intuitive, it will produce a matrix with the same eigenvalues as ‘construct_matrix’ and will therefore give identical results in a stability analysis. The following pseudo-code expresses the values of a certain set of state variables in the next cycle ($s_i[n+1]$) in terms of their values in the present cycle ($s_i[n]$). The operations are symbolic. Both the temporary variables P_i and the outputs $s_i[n+1]$ represent linear combinations of $s_1[n], s_2[n], \dots, s_{N-1}[n]$. The coefficients of these linear combinations are the entries in the state transition matrix A .

```

P0 = m1s_{N-1}[n]
for i = 1 to N - 1
  begin
    if i ≤ j
      then p_i = (1 - m_{i+1})s_i[n] + m_{i+1}p_{i-1}
      else p_i = (1 - m_{i+1})s_i[n] + m_{i+1}s_{i-1}[n]
    s_i[n + 1] = p_i - p_0
  end

```

This algorithm, implemented symbolically in Maple as ‘construct_matrix_2,’ is of a lower computational complexity than that necessary to implement ‘construct_matrix.’

We also implemented a numerical stability analysis function in C. The function ‘testmode’ takes as inputs the numerical values of N , j , and the slopes m_1, m_2, \dots, m_N . It constructs a numerical Jacobian matrix, finds its eigenvalues, and outputs a single value, the magnitude of the largest eigenvalue. This final numerical output indicates the stability of the given mode. This output value is independent of the choice of state variables used to construct the matrix, so we used the faster algorithm of ‘construct_matrix_2’ in implementing this function.

The program ‘findmode,’ written in C, automates the process of finding steady-state modes and determining their stability. It reads in N data files, each containing a set of values of t and $P(t)$ which describe the PRC of one neuron in the ring. The program uses (1) and (2) to locate all steady-state modes for the network described. It searches through potential values of P_e , the entrained period. For each, it uses (1) and the PRCs to locate all possible values of $t_1[\infty], t_2[\infty], \dots, t_N[\infty]$. It then tests whether any combination of these possible values satisfies (2). Whenever it locates such a steady-state mode, it calls ‘testmode’ to determine the mode’s stability. The program outputs a list of steady-state modes, described by the time intervals $t_1[\infty], t_2[\infty], \dots, t_N[\infty]$, and a measure of the stability of each mode.

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⁴ All functions and programs described in this appendix are available from <ftp://nba19.med.uth.tmc.edu/publish/jbyrne>.

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