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Resonating to Musical Rhythm: Theory and Experiment

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1. Introduction

> *Music is a temporal art ... in the banal sense that its tones are given in temporal succession. ... Music is a temporal art in the more exact sense that, for its ends, it enlists time as force. ... Music is a temporal art in the special sense that in it time reveals itself to experience (Victor Zuckerkandl, 1956, pp. 199-200).*

Music is an interactive activity in which dancing, singing, toe tapping, playing an instrument, or even simply listening, is temporally coordinated with complex, rhythmically structured acoustic stimulation. Analyses of scores and recordings reveal musical sounds to be intricate dynamic patterns, in which elegant serial structures unfold in elaborate temporal organizations. Thus, when humans "synchronize" musical interactions, we enter into a form of temporal coordination that is among the most elaborate observed in nature. For example, temporal interaction in music contrasts with observations of simple synchronous chorusing in other species. In insects and amphibians, coordination of rhythmic visual or auditory communication signals appears to be limited to synchronization or anti-synchronization of periodic events (Buck, 1988; Greenfield, 1994; Klump & Gerhardt, 1992). Moreover, synchronous chorusing has rarely been reported among non-human primates (Merker, 2000). It has been argued that the ability to temporally coordinate dynamic patterns with complex auditory stimuli was an important adaptation in the development of human communication (Merker, 2000).

This chapter considers the complexity of human musical rhythm and discusses its implications for the coordination of perception, attention, and behavior. Following this introduction, Section 2 begins with music analytic perspectives, which address musical complexity and the phenomenology of pulse and meter. With few exceptions, even the most complex rhythmic interactions are organized around a fundamental frequency called pulse. Pulse is endogenously generated, and it is experienced as varying in strength such that some pulses are felt as strong and others as weak, suggesting a metrical property. When humans organize complex temporal interactions, we synchronize – or more generally, entrain – pulse frequencies. However, investigation of rhythm and rhythmic interactions in humans has, to a large extent, been confined to periodic behavior and synchronization/antisynchronization, and it is from these studies that we have gleaned most of our current knowledge of human rhythmic perception and behavior. Therefore, Section 3 offers a brief, historically oriented outline of studies of periodic rhythmic behavior. The goal will be to interpret these results within the context of musical rhythm perception, setting the stage for the remainder of the discussion.

Sections 4 and 5 constitute the core of the chapter. Section 4 introduces a resonance theory of musical rhythm, beginning with a brief tutorial on neural resonance, and moving on to review linear and nonlinear oscillator models of pulse and meter that have been proposed over the past several years. The goal is to show how this approach predicts the main psychological attributes of pulse and meter. Section 5 will review the empirical literature on musical pulse and meter, focusing on studies that use music and/or complex rhythms and have explored the theoretical predictions of neural resonance. The chapter closes with a discussion of some of the significant open issues in this area.

2. Rhythm, Pulse and Meter

The sounds that humans use for communication may be conceived as complex, temporally structured sequences of nearly discrete events, such as musical notes and speech syllables. In common musical parlance, meter refers to canonical patterns of timing and accentuation that serve as conventional frameworks for performing music. Similarly, in linguistics, meter refers to the temporal organization of stress patterns in a speech utterance. In music perception and cognition, however, *pulse* and *meter* refer to percepts. They are responses to patterns of timing and (depending on the theorist) stress in the acoustic rhythm. Although responsive to stimulus properties, pulse and meter are not themselves stimulus properties. These terms refer to endogenous dynamic temporal referents that shape experiences of musical rhythms. The rhythms of music, which are temporally complex and richly articulated, are heard in relation to a relatively stable percept of pulse and meter. In this section I focus on the phenomenology of this experience, as related by music theorists.

Musical Rhythm

To illustrate the nature of rhythmic pattern in music, Figure 1A shows the sound pressure wave for the beginning of a musical sequence, the first four bars of the Aria from J. S. Bach's *Goldberg Variations*, as performed on piano. The subtlety of the temporal organization can be appreciated, in part, by examining the amplitude modulation of the acoustic time series. Each event has a relatively well-defined onset, followed by a gradual decay of amplitude, and often the next event begins before the previous sound has ended. The complexity of the relationships between serial and temporal structures can be further apprehended by observing how the frequency components of individual musical events delineate a potentially endless variety of temporal intervals (see Figure 1 B).

Figure 1 about here

When I refer to the rhythm of the sequence, I refer to the organization of events in time[1], and specifically to patterns of onset timing and event stress. Figure 1C illustrates these concepts by attempting to isolate the *rhythmic pattern* from other aspects of the musical pattern. It shows impulses marking the onset times of the various events, with differing amounts of stress represented as impulse amplitude.[2] The key observation is this: Although we casually discuss musical rhythms as though they were periodic, they almost never are. The onset times of musical events mark a wide variety of temporal intervals. It is likely that we tend to think of musical rhythms as periodic because we tend to feel them as periodic. At the bottom of Figure 1C, I have illustrated a hypothetical pulse for this musical performance, with dots drawn near the times at which one might tap along with this rhythm. Pulses correspond to some events, but not to others. Sometimes the event coinciding with a pulse has more stress than its immediate neighbors, often it does not. In general, the relationship between timing, stress and pulse is quite subtle.

Pulse and meter

Pulse, as described by music theorists, is a kind of *endogenous periodicity*, explained by Cooper and Meyer (1960) as “a series of regularly recurring, precisely equivalent” psychological events that arise in response to a musical rhythm. There is wide agreement that pulse, although responsive to a rhythmic stimulus, is not itself a stimulus property (Epstein, 1995; Lerdahl & Jackendoff, 1983; London, 2004; Yeston, 1976; Zuckerkandl, 1956). Rather, pulse provides a stable, dynamic referent with respect to which a complex musical rhythm is experienced.

Stability is emphasized by Cooper and Meyer (1960), who observe that pulse, “once established, tends to be continued in the mind and musculature of the listener” even after a rhythmic stimulus ceases. *Periodicity* is assumed by most theorists, especially those who are concerned primarily with musicological analysis (for example, Figure 2) (Cooper & Meyer, 1960; Lerdahl & Jackendoff, 1983; Yeston, 1976; Zuckerkandl, 1956). Others highlight the significance of tempo change, or rubato in music performance. Epstein (1995), for example, emphasized that pulse, as experienced in actual music, is not purely periodic, but responds to tempo change in a way that is important in the conveyance of motion and emotion in music. The pulses in Figure 1C, for example, are not purely periodic.

Pulse exhibits a *generalized synchrony* with musical rhythm. The term synchrony alone does not suffice, because the complexity of musical rhythm means that not every event onset can coincide with a periodic pulse (Figure 1C), and pulses may occur in the absence of event onsets, even in analysis of notated rhythms (Figure 2) cf. (Lerdahl & Jackendoff, 1983). Yet there is a tendency for pulses to gravitate towards event onsets in a way that produces (approximate) synchrony when a stimulus rhythm is purely periodic. To complicate matters even further, some musical rhythms are syncopated, such that event onsets may regularly fall between experienced pulses, for example. Cooper & Meyer (1960) argue that pulse continues even if musical events “fail for a time to coincide with the previously established pulse”, in effect arguing that pulse has a special kind of temporal stability – that pulses need not always gravitate toward event onsets. However, “(syncopated) passages point to the re-establishment of pulse coincidence” so that synchrony is somehow more stable than syncopation. Thus, the term generalized synchrony is more accurate, and will be operationalized in subsequent sections.

Figure 2 about here

Individual pulses are usually perceived to possess differing degrees of *metrical accent*. The terms *meter* and *metrical structure* refer to patterns of regularly recurring stronger and weaker pulses (Cooper & Meyer, 1960; Lerdahl & Jackendoff, 1983). Theorists sometimes transcribe metrical structures as in Figure 2, using arrangements of dots, called beats, that can be aligned with a musical score (Lerdahl & Jackendoff, 1983; London, 2004; Yeston, 1976). For example, in Lerdahl & Jackendoff's (1983) system, the fundamental pulse periodicity (the rate at which one might spontaneously tap with a musical rhythm) would be notated as a single row of beats, and the pattern of strong and weak pulses as additional rows of beats at related frequencies. The time points at which the beats of more levels coincide denote stronger pulses. This notational convention facilitates the discussion of structural constraints for metrical accent. Lerdahl and Jackendoff (1983) propose two kinds of constraints, one on the relative frequencies, and the other on the relative phases, of adjacent beat levels. Western tonal music, they argue, adheres to restrictive constraints. With respect to a particular referent level (e.g., the pulse level in Figure 2), the next higher frequency must be either the second or third harmonic (a 2:1 or 3:1 frequency relationship); the next lower frequency must be either the second or third sub-harmonic (a 1:2 or 1:3 frequency relationship). The relative phases of adjacent levels must be such that the discrete beats come into temporal alignment on each cycle of the slower frequency. Figure 2 illustrates three structural levels, the fundamental pulse frequency, its second harmonic (2:1) and its third subharmonic (1:3). More comprehensive structural descriptions, encompassing non-Western musical cultures including those of the Balkans, South Asia, Africa, and Latin America, additionally allow simple integer frequency ratios, such as 3:2, 4:3, 5:2 and so forth (London, 2004; cf. Yeston, 1976).

The process by which pulse and meter emerge is referred to as *induction*. The key questions involve the complex relationship between a stimulus rhythm and an experienced pulse and meter. Onset timing is widely agreed to be critical in the perception of pulse and meter. Somewhat more controversial is the role of stress at the musical surface (Cooper & Meyer, 1960; Lerdahl & Jackendoff, 1983; Zuckerkandl, 1956). Stress arises through complex interactions of loudness, duration, pitch and harmony (Huron & Royal, 1996; Jones, 2008; Jones & Yee, 1993; Lerdahl & Jackendoff, 1983), and there is no simple calculation to arrive at its quantification. Theorists disagree on the role of stress in determining perceptions of pulse and meter (Jones, 2008). For example, Lerdahl & Jackendoff (1983) describe pulse and meter as perceptual inferences from timing and stress patterns in an acoustic stimulus, while Zuckerkandl (1956) argues that pulse and meter arise solely from the demarcation of time intervals.

As a pattern of metrical accent emerges in response to a rhythmic pattern, it stabilizes, becoming resistant to change (Epstein, 1995; Lerdahl & Jackendoff, 1983; London, 2004; Yeston, 1976; Zuckerkandl, 1956). Once stabilized, a single stressed event at the musical surface cannot change an unaccented pulse into an accented pulse; the pattern can be de-stabilized only in the face of strongly contradictory evidence (Cooper & Meyer, 1960; Lerdahl & Jackendoff, 1983; Zuckerkandl, 1956). The stability of metrical accent patterns is key to explaining syncopation, a fundamental concept in musical rhythm. "Syncopation takes place where cues are strongly contradictory yet not strong enough or regular enough to override the inferred pattern" (Lerdahl & Jackendoff, 1983), pp. 17-18). Thus, the stability of pulse and meter, and in particular, the response to syncopated rhythms, is of significant interest in the study of rhythm perception. Some theorists highlight the potential multistability of metric structures, the possibility that more than one accent pattern could be perceived (at different times, or by different individuals) for a given rhythm (Lerdahl & Jackendoff, 1983; London, 2004).

Not all theorists conceive of meter as a structure of discrete time points. For Zuckerkandl (1956), meter is a series of waves that carry the listener continuously from one downbeat to the next. Time is not considered an "empty vessel, which contains the tones," time is an active force, experienced as waves of intensification (Zuckerkandl, 1956). A tone acquires its special rhythmic quality from its place in the cycle of the wave, from "the direction of its kinetic impulse." Metric waves are described as a natural consequence of the passage of time, made perceivable by the rhythmic organization of music. Section 4 will link concepts of pulse and meter to neural oscillation, and continuous time formalisms will be prominent in that discussion.

Summary

In summary, musical rhythms comprise complex patterns of stress and timing, and are not periodic. Pulse is a nearly periodic experience, while meter corresponds to the percept of alternating strong and weak pulses. Pulse and meter are influenced by patterns of timing, and perhaps stress, in the stimulus. Yet pulse and meter are not stimulus properties, they are endogenous dynamic structures with reference to which musical patterns are experienced. Pulse is a stable, endogenous periodicity that exhibits a generalized form of synchrony with complex rhythmic patterns. Strong and weak pulses alternate forming stereotypical patterns called metrical structures, that can be described in terms of phase and frequency relationships among multiple frequency components. Frequency relationships among components appear restricted to harmonics (e.g., 1:2, 1:3), subharmonics (e.g., 2:1 and 3:1), and, in general other simple integer ratios (e.g., 3:2, 4:3). The notion of stability is important here, and applies to multiple aspects of pulse and meter. Pulse is stable in the sense that it can continue in the absence of a stimulus, and it possesses a form of temporal, or phase stability such that it normally synchronizes with events, but can persist in the face of rhythmic conflict, or syncopation. Finally, metrical structures are stable in the sense that, once induced, they tend not to change to reflect stimulus accentuation, but provide a temporal referent against which rhythm is experienced.

3. Periodic Rhythms

Most of our current knowledge of human rhythmic behavior comes from studies of the perception of periodic acoustic stimuli, the production of periodic behavior, and synchronization or anti-synchronization of periodic behavior with periodic stimuli. Because this work has formed the basis for studies that involve complex musical rhythms, I briefly review some of the basic results in this area to set the stage for our discussion of musical pulse and meter.

Stevens (Stevens, 1886) introduced the *synchronize-continue paradigm*, in which participants listened to a periodic sequence, synchronized taps to the sequence, and continued tapping after the stimulus sequence was discontinued. He used a metronome to produce stimulus sequences of various rates, and recorded Morse-key taps on moving paper. He reported that listeners were able to internalize and reproduce, with some variability, the periodicity of the stimulus. The inter-tap intervals (ITIs) observed in such experiments have often been used to test the ability to estimate, remember, and reproduce time (Bartlett & Bartlett, 1959; Wing & Kristofferson, 1973b). However, from a musical perspective, continuation tapping may be considered the simplest demonstration of endogenous periodicity: Pulse is induced in response to a periodic rhythm, it stabilizes, and when the stimulus rhythm ceases it persists, in the form of rhythmic motor behavior.

As measured by continuation tapping, pulse is pseudo-periodic. It includes both short-term fluctuations, which Stevens described as a "constant zigzag" and longer-term fluctuations, described as "larger and more primary waves." Two-level timing models (Daffertshofer, 1998; Wing & Kristofferson, 1973a) have been proposed to predict short term fluctuations as a negative lag one autocorrelation of the ITI sequence, which are often reported in experiments that collect short sequences (tens of taps). Studies that collect hundreds of successive intervals, and apply a spectral analysis to the resultant time series, typically find that the spectrum is characterized by a linear negative slope in of log power versus log frequency (Delignières *et al.*, 2004; Gilden *et al.*, 1995; Lemoine *et al.*, 2006; Madison, 2004; Yamada, 1996). Thus, longer term temporal fluctuations exhibit a *1/f* structure, a ubiquitous feature in biological systems (West & Shlesinger, 1989, 1990), that has recently been observed in other psychological time series (Gilden, 2001; Van Orden *et al.*, 2003).

Pulse also has a characteristic time scale. Fraisse (1978) reported pulse tempi of around 600 ms (1.67 Hz, or 100 bpm), based on data from both spontaneous tapping and preferred tempo tasks. The notion of a universal preferred tempo has since given way to the notion of a tempo region that elicits good performance on tasks such as tempo discrimination and perception-action coordination (Drake *et al.*, 2000a; London, 2004; McAuley *et al.*, 2006). Drake & Botte (1993) measured tempo discrimination at various rates, reporting adherence to Weber's law (JND ~ 2%) within a limited range from about 200 ms (5 Hz; 300 bpm) to about 1 second (1 Hz, or 60 bpm). Repp measured the upper limit of pulse perception using subharmonic synchronization, and while individual differences were large, 100 ms (10 Hz; 600 bpm) represents an extreme limit (Repp, 2003b). A lower limit of pulse perception had been putatively indexed by transition from anticipation to reaction tapping at about 2.4 s (.43 Hz; 25.6 bpm) (Mates *et al.*, 1994), however, a more comprehensive study has found no such clear transition up to inter-onset times of 3.5 sec (Repp & Doggett, 2007). Moreover, the notion of fixed limits has been seriously called into question (Drake, 1993; Drake et al., 2000a; Drake & Palmer, 1993; McAuley et al., 2006). In the most comprehensive set of studies to date participants, aged 4 to 95, performed both synchronize-continue and tempo judgment tasks. In these studies preferred tempo was found to slow with age, and the width of the entrainment region to widen up to about age 65, when it narrows again.

Research on coordination of motor behavior with periodic auditory stimuli has a long history (Dunlap, 1910; Fraisse, 1978; Michon, 1967; Stevens, 1886; Woodrow, 1932), and over the past several years numerous studies have probed the coordination of periodic behavior with periodic auditory sequences (for a recent review, see Repp, 2005). One commonly observes a tendency of taps to precede auditory events, known as the anticipation tendency.[3] Although at one time thought to result from differential delays for auditory stimuli and proprioceptive feedback, this hypothesis has not held up (Aschersleben, 2002; Aschersleben *et al.*, 2001) and the results to date suggest multiple determinants of this tendency (Repp, 2005). Additionally, fractal, or 1/*f* structure has also been reported in coordination with periodic sequences (Chen *et al.*, 1997; Pressing & Jolley-Rogers, 1997).

A major issue has been the maintenance of synchrony with temporally fluctuating stimuli, studied using phase and/or tempo perturbations of periodic sequences. Overall, people can track temporally fluctuating sequences, and it has been suggested that phase coupling and tempo adaptation depend upon different mechanisms (Repp, 2001b; Thaut *et al.*, 1998a). People respond quickly and automatically to phase perturbations of periodic sequences (Large *et al.*, 2002; Repp, 2001a, 2002a, 2003a; Thaut *et al.*, 1998b) and phase correction response profiles are nonlinear (Repp, 2002b). People are also able to adapt to tempo perturbations (Large et al., 2002), however tempo tracking appears to be a controlled process, requiring active attending (Repp, 2001b; Repp & Keller, 2004). A related area is that of anti-synchronization, a simple form of syncopation in which listeners are instructed to maintain a 1:1 frequency relationship between repeated motor movements and a series of periodically delivered tones, in an anti-phase fashion (see Repp, 2005). Such behavior is stable for lower frequencies, however increases in stimulus presentation rate induce a spontaneous switch in behavior from syncopation to synchronization (Kelso *et al.*, 1990; Mayville et al., 1999) at about 400 ms (2.5 Hz; 150 bpm).

Interestingly, people report percepts of metrical accent even in unaccented, periodic event sequences. Bolton (1894) asked subjects to listen to an isochronous series of tones of identical frequency and intensity. He found that such sequences are actually heard as accented, such that strong pulses alternate with weak pulses, usually in 1:2 patterns, but sometimes in 1:3 or other patterns. He called this phenomenon subjective rhythmization, although using the current terminology it would be more appropriate to name it *subjective meter*. Notice that according to this astonishing observation, people spontaneously hear subharmonics of the rhythmic frequency that is presented. Vos (1973) investigated this phenomenon in greater detail. He presented isochronous tone sequences at various tempi, and after each presentation listeners reported the size of the groups in which they heard the sequence. The number of responses in each category was found to depend on both the tempo and the group size. Vos found a clear tendency to prefer group sizes 2, 4 and 8, with subharmonics 3, 5, 6 and 7 more rarely reported. Spontaneous perception of structure has also been observed in synchronization tasks. Parncutt (1994) presented isochronous tone sequences with various tempi to participants and asked them to tap along with the sequences in a regular way. He found that for faster sequences, people tended to tap subharmonics of the event frequency that was presented, similar to the reported groupings in perceptual experiments (Vos, 1973). Thus, people perceive and produce metric relationships such as 1:2 and 1:3 spontaneously, in the absence of stressed stimulus events.

Summary

Studies with periodic, unaccented event sequences have confirmed and extended basic predictions of music theorists. In response to periodic sequences, an endogenous periodicity stabilizes, and can then persist after cessation of the stimulus. Pulse is not strictly periodic, however; it has both short term and longer time scale (*1/f*) structure. Pulse has a characteristic time scale, which changes with age. People can synchronize motor actions with periodic stimuli, and they tend to anticipate stimulus events in periodic sequences. Synchrony is a stable state, resistant to perturbations in phase and tempo. Anti-synchrony (syncopation) is also stable at lower frequencies, but reverts to synchrony as it loses stability. Finally, people spontaneously perceive metrical accent patterns even in periodic stimuli, in the form of subharmonics of the rhythmic frequency of the stimulus. In the next section, I consider the kinds of neural processes that might exhibit these basic characteristics.

4. A Theoretical Framework

To briefly summarize the discussion so far, pulse and meter refer to the experience of a regular temporal structure in a rhythm whose actual temporal structure may be quite complex. Nevertheless, the percept depends upon the multiple periodicities of the stimulus sequence. Therefore it is not surprising that one of the main frameworks that has emerged for theorizing about musical meter involves resonance (e.g., Large & Kolen, 1994; van Noorden, 1999). *Resonance* refers to the response of an oscillation, exposed to a periodic stimulus, whose frequency stands in some particular relationship to the oscillator's natural frequency. In general, both linear and nonlinear oscillators resonate, and both linear and nonlinear resonance models have been proposed to account for perceptions of pulse and meter. However, these exhibit different properties, and therefore make different predictions, as we shall see.

In this section I describe a theory that links the phenomenology of pulse and meter with concepts of neural oscillation, which is a nonlinear phenomenon. The basic idea is that when a network of neural oscillators, spanning a range of natural frequencies, is stimulated with a musical rhythm, a multi-frequency pattern of oscillations is established. Endogenous pulse is linked with the concept of spontaneous oscillation, generalized synchrony with entrainment, and metric accent structure with higher order resonances, found in nonlinear oscillators at simple integer ratios. The stability properties of pulse and meter will be thought of as dynamical stability within this framework: amplitude stability in a limit cycle, phase stability in entrainment, and pattern stability in a network of neural oscillators.

Neural Oscillation

Interaction of excitatory and inhibitory neural populations can give rise to neural oscillation. This arrangement is illustrated schematically in Figure 3A, showing the necessary synaptic connections between excitatory and inhibitory populations (Aronson *et al.*, 1990; Hoppensteadt & Izhikevich, 1996; Izhikevich, 2007; Wilson & Cowan, 1973). There are many different mathematical models available that can be used to describe nonlinear oscillations, and the principle concern is to choose a level of mathematical abstraction that is appropriate for the type of data that are available and the type of predictions that are desired. Figure 3B shows the main possibilities: 1) the biophysical level, where each neuron is modeled by its own set of Hodgkin-Huxley equations (Hodgkin & Huxley, 1952), 2) the oscillator level, where various mathematical simplifications of more detailed models are available, or 3) the canonical level, which results from mathematical analysis of oscillator-level models, given certain assumptions about parameter values (cf. Hoppensteadt & Izhikevich, 1997). Discrete time models have also been studied, enabling analysis of oscillator behavior under slightly different assumptions than canonical models. Importantly, such analysis has shown that, under certain assumptions, all nonlinear oscillator models share a set of universal properties, independent of many details (Wiggins, 1990). This makes such models especially attractive from the point of view of modeling human behavior.

Figure 3 about here

A detailed discussion of neural oscillation is beyond the scope of this chapter, however I present some of the main ideas and results from this literature to demonstrate the basic predictions of neural resonance, as well as to enable deeper understanding of specific models that have been proposed for pulse and meter. In this section, the reader will encounter a few equations, which should be treated as guideposts, to enable connection of these ideas with the theoretical neuroscience literature. Less mathematically inclined readers can ignore these details, but should read the sections on universal properties of nonlinear oscillation and oscillator models of pulse and meter. The reader who chooses to embrace the details will find a rich research area that has only begun to be explored by theorists. Excellent general introductions to nonlinear dynamics are the books by Strogatz (1994) and Scheinerman (1996); a thorough and readable treatment of nonlinear oscillation with a strong focus on experimentation is the book by Pikovsky et al. (2001). Two excellent and rigorous, but readable, discussions of neural oscillation are the books by Hoppenstadt & Izhikevich (1997) and Izhikevich (2007).

Biophysical Models. At the biophysical level, one can construct realistic models of neural oscillation in which each neuron is described by a set of Hodgkin-Huxley equations (Hodgkin & Huxley, 1952). In animals, this approach has enabled understanding of neural pattern generation (Marder, 2000) and neural responses to external sound stimuli (e.g.,Large & Crawford, 2002). However, no one has yet ventured a model of human rhythm perception at this level, for two main reasons. First, biophysical models are stated in terms of voltage and conductance, making predictions about variables that are best observed in neurophysiological experiments. Second, the large systems of equations necessary to predict human behavior would be rather intractable, both from the point of view of mathematical analysis and computer simulation (but see Izhikevich & Edelman, 2008).

Oscillator Models. Beginning in the 1960's, theorists such as FitzHugh (1961), Nagumo (1962), Wilson & Cowan (1973), and others applied various simplifying assumptions to produce more tractable mathematical models of neural oscillation. FitzHugh and Nagumo, for example, created a two-dimensional simplification of the four-dimensional Hodgkin-Huxley neuron. The Wilson-Cowan model of neural oscillation (Wilson & Cowan, 1973) can be thought of as describing two neural populations, one excitatory and one inhibitory, as illustrated schematically in Figure 3A. Each population is modeled by a single differential equation (Hoppensteadt & Izhikevich, 1996).

$$\begin{aligned} \frac{dx}{dt} &= -x + S(\rho_x + ax - by + s(t)) \\ \frac{dy}{dt} &= -y + S(\rho_y + cx - dy) \end{aligned} \qquad (1)$$

Here *x* describes the activity of the excitatory population and *y* describes the activity of the inhibitory population. The parameters *a* and *d* capture properties of the excitatory and inhibitory populations, respectively, while *b* and *c* capture the interaction of the two populations. The function S is sigmoidal, and ρ_x and ρ_y are parameters that control whether the system oscillates spontaneously or comes to rest. The sigmoid function is a nonlinearity that limits the maximum amplitude of the oscillation, so *x* and *y* vary between zero and one. The time-varying input, *s(t)*, represents an input rhythm. It also appears inside the sigmoid function, meaning that coupling to the external input is also nonlinear. In principle input can affect both populations, but for simplicity I consider only input to the excitatory population. Figure 4A shows the time series generated by Equation 1, for a stimulus with a frequency (ω_0) that approximates the natural frequency of the oscillator (ω). Figure 4B plots *x* and *y* against one another, revealing the oscillation as a cycle in the state space trajectory.

Figure 4 about here

Oscillator-level models such as Wilson-Cowan (Hoppensteadt & Izhikevich, 1996; Wilson & Cowan, 1973) are two-dimensional and in the absence of stimuli they exhibit two stable behaviors: They can oscillate spontaneously (limit-cycle) or they relax toward a stable state (fixed point)[3]. Below, I will associate the spontaneous oscillation of a stable limit-cycle with the endogenous periodicity of musical pulse. The details of oscillator behavior can be diverse, however, making it difficult to compare the predictions of different models at this level of description. Therefore, we employ normal-form analysis (Wiggins, 1990), which involves a coordinate transformation, followed by a Taylor expansion of the nonlinearities, truncating at some point ignoring the *higher order terms* of the expansion (abbreviated as h.o.t). Effectively, this transforms the oscillation of Figure 4A&B to the oscillation in Figure 4C&D, regularizing the limit cycle and approximating the nonlinearities, producing what is called a canonical model. A canonical model is usually the simplest (in analytical terms) of a class of equivalent dynamical models. More importantly, this transformation works for virtually any model of neural oscillation, under certain assumptions that are generally reasonable for neural systems (Hoppensteadt & Izhikevich, 1997).

The Canonical Model. The canonical model is useful because it reveals significant similarities among the behavior of all neural oscillators, despite potentially important physiological differences. The surprising result is that virtually all neural oscillator models share the same canonical model (Hoppensteadt & Izhikevich, 1996). Thus, the canonical model uncovers universal properties, making predictions that hold under a rather general set of assumptions (Hoppensteadt & Izhikevich, 1997). The following is the canonical model for neural oscillation as derived from the Wilson Cowan model of Equation 1 (Aronson et al., 1990; Hoppensteadt & Izhikevich, 1996).

$$\frac{dz}{dt} = z(\alpha + i\omega + (\beta + i\delta)|z|^2) + c\, s(t) + \text{h.o.t.} \tag{2}$$

This differential equation is two-dimensional, because z is a complex variable, having real (*Re(z)*) and imaginary (*Im(z)*) parts. It has both real (α, β) and imaginary (ω, δ) parameters as well, whose meanings will be disclosed momentarily. For simplicity, the connection strength, *c*, of the time-varying rhythmic stimulus, *s(t)*, is taken to be a real number. This model can be readily analyzed. For example, Equation 2 may be rewritten in polar coordinates, by setting $z = re^{i\phi}$, and using Euler's formula $e^{i\phi} = \cos\phi + i\sin\phi$. This transformation reveals the dynamics of amplitude, r, and phase, ϕ, separately and clearly.

$$\begin{aligned}\frac{dr}{dt} &= r(\alpha + \beta r^2) + c\,s(t)\cos\phi + \text{h.o.t.}\\ \frac{\mathrm{d}\phi}{\mathrm{dt}} &= \omega + \delta r^2 - c\frac{s(t)}{r}\sin\phi + \text{h.o.t.}\end{aligned} \qquad (3)$$

The polar formulation makes no assumptions about the canonical equation, and it is not an approximation. It shows how the parameters relate directly to the behavior of the oscillator in terms of changes in amplitude and phase. The parameters are α, the bifurcation parameter, β, the nonlinear saturation parameter, ω, the eigenfrequency (natural frequency; $\omega = 2\pi f$, f in Hz), and δ, the frequency detuning parameter. The connection strength, c, represents influences of the stimulus on the oscillator. The canonical model allows one to manipulate properties of the oscillation separately. For example, the bifurcation parameter (α), which determines whether or not the system oscillates spontaneously, can be manipulated independently of frequency (ω). We can also see that when $\delta \neq 0$, the instantaneous frequency of the oscillator depends not only on its natural frequency (ω), but also on its amplitude ($\omega + \delta r^2$). The main properties revealed by this analysis are described next.

Universal properties of neural oscillators

Universal properties of neural oscillation are revealed in the canonical form (Equations 2 & 3). These properties are generic, and thus expected to be observed in all neural oscillators, despite differences in neurophysiology or network organization. I focus on those predictions that relate to the main phenomenological properties of pulse and meter: endogenous periodicity, generalized synchrony, and metrical accent.

Spontaneous oscillation. Consider a nonlinear oscillator in the absence of a stimulus (e.g., Equation 3, with $s(t) = 0$). In this case the oscillator can display two behaviors depending upon the bifurcation parameter, α. As illustrated in Figure 5A, when $\alpha < 0$ the system behaves as a damped oscillator, but when $\alpha > 0$ (negative damping) the system generates a spontaneous oscillation. In the latter case, the amplitude of the oscillation stabilizes at $r = \sqrt{\alpha/\beta}$. $\alpha = 0$ is the bifurcation point, the critical value of the parameter at which the behavior changes from damped oscillation to spontaneous oscillation. The bifurcation is called the Andronov-Hopf bifurcation. If one continues the expansion of higher order terms one finds other bifurcations, such as the Bautin bifurcation (Guckenheimer & Kuznetsov, 2007) that also lead to spontaneous oscillation. The capacity for spontaneous oscillation may explain the experience of endogenous periodicity. It predicts the capacity of pulse to continue after a stimulus ceases ($s(t) = 0$), as observed in some experiments.

Figure 5 about here

Entrainment. When a stimulus is present spontaneous oscillation continues, however stimulus coupling affects the oscillation's phase. Figure 5B plots coupling as a function of relative phase for two different stimulus frequencies. The two curves depict two different amounts of frequency (mis)match between the stimulus and the oscillation. The point at which each function crosses the horizontal axis with negative slope is a stable state, the relative phase at which the system settles in the long run. The phase coupling described above (Equations 2 & 3), and depicted in Figure 5B, generates 1:1 synchrony, and additionally provides a means of predicting systematic deviations from precise synchrony, such as the anticipation tendency observed in some synchronization experiments. If the frequency of a stimulus (ω_o) is equal to that of the oscillator (ω) the two enter into a state of precise synchrony. If oscillator frequency is greater than that of the stimulus, relative phase will be negative, anticipating the stimulus. The capacity for 1:1 synchrony is observed in both linear and nonlinear models. Entrainment of nonlinear oscillators also predicts a more general form of synchrony (e.g., 1:2, 3:2, 3:1). The terms that describe this behavior, however, are hidden in the higher order terms of Equations 2 and 3. Higher order terms describe the capacity for anti-phase and multi-frequency modes of coordination with rhythmic stimuli, described in more detail next.

Higher order resonance. Figure 5C presents the results of three simulations of an array of nonlinear oscillators, based on Equation 2. The frequencies of the oscillators in the array vary from 0.5 – 8.0 Hz, along a logarithmic frequency gradient, and the stimulus is a sinusoid with a frequency of 2 Hz (period 500 ms). In these simulations, I included higher order terms (abbreviated h.o.t. in Equation 2) to illustrate the some of the coordination modes possible for neural oscillations. These simulations illustrate a number of important properties of nonlinear resonance. First, nonlinear oscillators have a sort of filtering behavior, responding maximally to stimuli near their own frequency. At low levels, high frequency selectivity is achieved. As stimulus amplitude increases, frequency selectivity deteriorates due to nonlinear compression ($\beta < 0$). Frequency detuning ($\delta \neq 0$) predicts that the peaks in the resonance curve begin to bend as the strength of the stimulus increases. Most importantly, oscillations arise at frequencies that are not present in the stimulus, due to nonlinear stimulus coupling, described in the higher order terms. The strongest response is found at the stimulus frequency, but oscillations are also observed at harmonics (e.g., 2:1 and 3:1), subharmonics (e.g., 1:2 and 1:3) and more complex integer ratios (e.g., 3:2) of the stimulus frequency. At low stimulus intensities, higher order resonances are small; they increase with increasing stimulus intensity. Nonlinear resonance predicts that metrical accent may arise even when no corresponding frequency is present in the stimulus. This could explain the subharmonic accent patterns that have been observed in perception and coordination with periodic sequences (e.g., Parncutt, 1994; Vos, 1973). Moreover, coupling between oscillators in such a network would also exhibit nonlinear resonances, giving rise to stable patterns of metrical accent, and favored frequency ratios including harmonics, subharmonics, and integer ratios (cf. Large 2000). Coupling between oscillators in a multi-frequency network (e.g., Large & Palmer, 2002) may also explain the subdivision effects that have been observed in synchronization experiments (Large et al., 2002; Repp, 2008b) described in the next section.

A discrete time model

Before moving on to review particular resonance models of pulse and meter, I briefly describe a related mathematical abstraction that has proven useful for capturing pulse and meter, the discrete time circle map. If we consider an oscillator spontaneously generating an oscillation with a stable limit cycle amplitude, and we further assume that the stimulus is not too strong (Pikovsky, 2001) then we can ignore amplitude and work entirely in the phase dimension. Thus we consider the phase equation of the system above (Equation 3, assume $r(t) = 1$) and to further simplify matters, we also ignore frequency detuning ($\delta = 0$) and higher order terms.

$$\frac{\mathrm{d}\phi}{\mathrm{dt}} = \omega - c\,x(t)\sin\phi \tag{4}$$

Next, assume the stimulus to be a periodic series of discrete impulses (arguably a reasonable assumption for rhythmic stimuli), with fixed period, T_0 ($T_0\ (sec) = 1/f_0\ (Hz)$; note also, $\omega_0 = 2\pi f_0$).

Then the above phase equation can be integrated to create the discrete time (stroboscopic) mapping,

$$\phi_{n+1} = \phi_n + \omega T_0 - c\sin(\phi_n) \tag{5}$$

known as a circle map. Formally, one should also apply the operation modulo 2π to the right hand side, but it is omitted it here for simplicity of presentation. Once this transformation has been accomplished, the phase variable, ϕ, represents relative phase, the phase of the oscillator when an input event occurs. Importantly, although Equation 5 is derived here from the canonical model (cf. Pikovsky et al., 2001), circle maps can be arrived at in several different ways, and are used in the study of relaxation oscillations as well. In this case, Equation 5 has been derived using the truncated normal form, thus this coupling term takes on the simplest possible form (a sine function). In the general case the coupling term would be a more complex periodic function[4]. The discrete time model is simple, but powerful. Although it ignores the dynamics of amplitude, it exhibits entrainment and higher order resonance properties that make it useful for describing important aspects of pulse and meter, discussed below.

To sum up, the hypothesis of neural resonance to rhythmic stimuli makes certain generic predictions about responses to rhythms. It predicts endogenous periodicity as spontaneous oscillation in the neural system. It predicts the generalized synchrony of pulse and meter as entrainment of nonlinear oscillations to an external stimulus. It predicts the perception of metrical accent as higher order resonances in nonlinear oscillators. It is crucial to realize that neural resonance is not a computational model that adds mechanisms for entrainment and multi-frequency resonance to an underlying clock mechanism. The predictions arise from the intrinsic physics of neural oscillation, as revealed by mathematical analysis. The next section reviews how mathematical models, at various levels of abstraction, have been used to create specific computational simulations of pulse and meter.

Models of Pulse and Meter

Historically, the study of neural oscillation has followed the path from most detailed to most abstract, from Hodgkin-Huxley (1952) through the oscillator-level models of FitzHugh (1961), Nagumo, et al., (1962), Wilson & Cowan (1973), and others, to canonical models of Aronson et al. 1990 (1990) and Hoppenstadt & Izhikevich (1996). Resonance models of pulse and meter perception have so far followed the opposite course, from most abstract to least abstract, beginning with discrete time models (Large & Kolen, 1994; McAuley, 1995) through linear resonance models (Scheirer, 1998; Todd, 1999) and the canonical nonlinear model of Large (2000a), to the oscillator-level model of Eck (2002).

Discrete time Models. The first nonlinear resonance models of pulse and meter were the discrete time models of Large & Kolen (1994) and McAuley (1995), which were soon followed by the more refined approaches of Toivianen (1998), Large & Jones (1999) and Large & Palmer (2002) and others. All adopted the most abstract mathematical model of nonlinear oscillation, the circle map, and therefore make quite general predictions. Furthermore, all share the basic goal of modeling perception and attention in a temporally flexible way that could deal with the naturally variable tempi of music performance (see Palmer, 1997).

To create a model of phase entrainment to musical rhythm, it is first assumed that a musical rhythm (Figure 6A) may be adequately described as temporally discrete impulses (Figure 6B). Such data is readily collected in the laboratory in the form of MIDI recordings of musical performances, and retains the most basic information about event timing. The key insight is to replace the fixed period, T_0 of a discrete map with the succession of IOIs recorded in a music performance.[6]

$$\phi_{n+1} = \phi_n + \omega(t_{n+1} - t_n) - cF(\phi_n) \qquad (6)$$

This formulation was conceived as a model of temporal expectation by Large & Kolen (1994), who linked this approach to Meyer's theory of musical emotion. The idea is that a specific point in the limit cycle, $\phi = 0$, corresponds to the times at which musical events are expected, illustrated in Figure 6B. According to McAuley (1995), the basic theoretical insight is to model of the perception of time as phase. The models implicitly assume a stable limit cycle, or endogenous oscillation, although they are silent on the issue of how such an oscillation might arise.

Figure 6 about here

One of the most interesting aspects of the behavior of a simple discrete time model is the nonlinear resonances that arise in the system. These were studied through analysis as well as numerical simulation of the basic phase equation (Large & Kolen, 1994; McAuley, 1995). Figure 6C shows the results of one such analysis, illustrating that a neural oscillator responds both to its own frequency and to frequencies that approximate integer ratios of its frequency. In the figure, only a few of the largest regions are shown. The resonance regions of Figure 6C are generic. In biophysical and oscillator-level models the same resonances are observed, however the regions they occupy in parameter space may appear transformed.

In early models, generally one or a few oscillators were considered, and the focus was on tracking changes in performance tempo. It was noted at the time that phase entrainment alone would not provide sufficient flexibility to follow large tempo changes (Large & Kolen, 1994; McAuley, 1995). Thus, a model of tempo adaptation was added as a parameter dynamics, and such models became known as adaptive oscillator models (McAuley, 1995). Finally, all that is required of the phase coupling function, *F,* is that it be periodic. *F = sin* is the simplest choice; however, for tracking very complex rhythms, a modification can be used. The modification was to limit the extent of phase adaptation to a critical region, or temporal receptive field, within which the oscillator will adapt to tempo change (Large & Kolen, 1994; Large & Palmer, 2002). Outside of this region, events will have little phase-resetting effect. As pointed out by Eck (2002), the effect of this choice of *F* was for the model to behave more like a relaxation oscillator. Large & Jones (1999) conceptualized this window as an expectancy region, termed an attentional pulse, within which events were expected. We discuss a conceptualization of oscillator dynamics as attentional dynamics in the next section.

Canonical Models. Due to the special relationship between linear resonance models and the canonical form of Equation 2, I consider linear models as a special case of canonical models[6]. In linear models of rhythm perception, band-pass or comb filters (Oppenheim & Schafer, 1975) are arranged in an array by center frequency, from lowest to highest, and stimulated with a continuous time representation of a rhythmic stimulus (e.g., Figure 1C). Scheirer (1998) constructed a gradient-frequency bank of comb filters, similar to pitch tracking models, but presented a continuous time rhythmic signal, creating a continuous time model for pulse and meter (see also Klapuri *et al.*, 2006). Todd, et al., (1999) proposed a similar model, using bandpass filters. In such a model, a linear filterbank extracts the amplitude and phase of the frequency components of a rhythmic stimulus, and the output with the highest amplitude can be used to drive a motor output, providing a model of synchronization behavior (Todd et al., 1999) . Bandpass filter models predict 1:1 phase synchrony of resonators with stimulus frequencies, and capture metrical accent to the extent that a metrical stress pattern is physically present in the stimulus time series. Simple linear resonators do not exhibit spontaneous oscillations or higher order resonances. Interestingly, comb filters are sensitive to multiple frequencies (comparable to higher order resonances), but at the expense of temporal delays on a rhythmic time-scale (100 ms to several seconds). However, even comb filters do not possess stability properties that enable resistance to change in the face of syncopation (cf., Large, 2000a). Nevertheless, various linear models have had success in identifying tempo, beat and meter in digital audio recordings, especially for certain musical styles (Eck, 2006; Klapuri et al., 2006; e.g. Scheirer, 1998).

Large (2000) used a canonical model of nonlinear resonance to model meter perception. The model was a network of nonlinear oscillators, arranged along a frequency gradient, quite similar in concept to an array of linear filters (cf. Scheirer, 1998; Todd et al., 1999). Large's model was essentially the truncated normal form of Equation 2, and ignored higher order terms, and thus did not include higher order resonances. Instead, the focus of this model was to show how network interactions could give rise to stable oscillations and multi-frequency patterns of oscillation. Rhythmic input drove the system through bifurcations, giving rise to rise to self-sustained oscillations at several frequencies. The resulting patterns dynamically embodied beat and meter; they were stable and persistent in the face of rhythmic conflict. The performance of the model was compared with the results of a pulse induction study (Snyder & Krumhansl, 2001, described in further detail below) in which musicians tapped along with musical rhythms. The network matched human performance for natural musical signals and showed a similar pattern of breakdowns as the input degraded.

Oscillator Level Models. Eck (2002) used the FitzHugh-Nagumo model (FitzHugh, 1961; Nagumo et al., 1962), to simulate neural synchronization to music-like rhythms. FitzHugh-Nagumo is a two-variable simplification of the Hodgkin-Huxley model, and Eck chose the parameters of his model such that the oscillators operated in relaxation mode, meaning that the pair of differential equations exhibited both a fast and a slow time scale, which provided certain advantages in modeling responses to musical rhythms. First, the model displays a sort of phase dependent input filter, responding strongly to events that happen near phase zero (where the oscillator "expects" events to occur) and relatively less to events at other points in the cycle. Second, the model exhibits stable synchronization in large groups, enabling potentially large networks of oscillators to contribute to an emergent percept of meter. Finally, such oscillators display asymmetrical responses to early versus late events, as humans sometimes do (e.g.,Jones *et al.*, 2002; Zanto *et al.*, 2005). Eck tested the ability of the oscillator model to determine downbeats in the patterns of Essens & Povel (1985), and the model simulated human responses well.

Summary

The neural resonance theory of pulse and meter holds that listeners experience dynamic temporal patterns, and hear musical events in relation to these patterns, because they are intrinsic to the physics of the neural systems involved in perceiving, attending and responding to auditory stimuli. Nonlinear oscillations are ubiquitous in brain dynamics, and the theory merely asserts that some neural oscillations – perhaps in distributed cortical and subcortical areas – entrain to the rhythms of auditory sequences. The generic predictions of the theory arise from mathematical analysis of neural oscillation. This not a computational theory in the sense that pulse and meter are computed by special purpose mechanisms. However, computer models of pulse and meter can be created based on the general theory. These should be treated as simulations of a physical phenomenon based on mathematical models that make necessary simplifying assumptions about neural oscillations. As such, not every model makes predictions about every aspect of pulse and meter. Models formulated at different levels of abstraction may make qualitatively different kinds of predictions. Moreover, models may be constructed to isolate certain aspects while ignoring others. Thus, different models should be evaluated in their respective contexts. The computational models that have been proposed to date have explored a relatively small area of the space of possibilities afforded by neural oscillation. Additional possibilities are suggested by the empirical findings discussed next.

5. Nonperiodic Rhythms and Musical Stimuli

One point that arises from the preceding theoretical discussion is that it is important to distinguish between the type of physical system hypothesized by resonance theory, and individual computational models, which may simulate the system at different levels of abstraction. Experiments address different levels of abstraction as well. Some address canonical predictions – spontaneous oscillation, entrainment and higher order resonance. Some reveal details of the phenomena, such as asymmetries in attending or synchronizing, or the relative prominence of higher order resonances. Others address implicit predictions such as neural correlates or development. Exploration of different tasks and constraints has uncovered resonance-like effects in perception, attention and motor coordination. In this section, I consider how various empirical studies, conducted with musical stimuli and other nonperiodic rhythms, bear upon the predictions of neural resonance. The discussion is organized according to the theoretical issues, although the fit is rarely neat and tidy, because individual studies may addresses multiple concerns.

Spontaneous oscillation

The first prediction of neural resonance is spontaneous oscillation, i.e. that pulse is an endogenous periodicity that can exist outside the influence of a rhythmic stimulus. Palmer and Krumhansl (1990) demonstrated endogenous pulse in a perceptual task by using goodness-of-fit judgments for events presented in *imagined* metrical contexts. Low-pitched sounds represented the first event in a measure, and listeners were instructed to think of these as the first of 2, 3, 4, or 6 intervening pulses. After several beats, a probe tone was presented at one of the imagined pulse times. The results implied that participants successfully imagined a pulse, and their ratings further revealed differential accent strengths that conformed to metrical patterns. The authors interpreted this to imply abstract knowledge of metrical structure internalized through musical experience. But this result can also be considered from the point of view of neural resonance. On this interpretation, not only did they find support for a stable endogenous pulse, but also the complex response pattern observed was consistent with higher order resonance. In principle, this technique could be used to ask more specific questions about pulse stability.

The next question that arises is that of periodicity versus pseudo-periodicity. Empirical research on music performance has clearly demonstrated that pulse in musical performance is not periodic, and has revealed important relationships between musical structure and patterns of temporal fluctuation (for a review, see Palmer, 1997). For example, rubato is used to mark group boundaries, especially phrases, with decreases in tempo and dynamics, and amount of slowing at a boundary reflecting the depth of embedding (Henderson, 1936; Shaffer & Todd, 1987; Todd, 1985). Patterns of temporal fluctuation have further been shown to reflect the metrical structure of the music (Henderson, 1936; Palmer & Kelly, 1992; Sloboda, 1985). Thus, as Epstein (1995) emphasizes, pulse in music is not rigidly periodic, and in musical interactions, pulse must coordinate in a temporally flexible way. It has not yet been established whether pulse in music performance exhibits 1/f structure, nor have any studies used musical patterns as stimuli for continuation tapping of sufficient length to gauge long-term structure. Given the structure observed in continuation from simple periodic sequences, such studies might provide valuable insight into the nature of musical pulse.

Resonance theory implies that biologically preferred periods should exist (McAuley, 1995), and studies with periodic stimuli and behavior support this prediction (Fraisse, 1978; McAuley et al., 2006; Parncutt, 1994; Vos, 1973). van Noorden & Moelants (1999) extended such studies to musical stimuli, by asking listeners to tap along with a wide variety of musical excerpts. They determined the distribution of perceived pulse tempi for musical pieces heard on radio and in recordings of several styles, and fit the distributions with linear resonance curves, showing that over a wide variety of musical rhythms, resonance peaks varied from about 300 ms (3.3 Hz or 200 bpm) to about 600 ms (1.7 Hz or 100 bpm), and depended on musical style. Thus, pulse in music and can vary over a wide tempo range that depends on many factors. They used the same technique to fit tempi of perceived pulse in the subjective meter study of Vos (1973), the pulse tapping study of Parncutt (1994), and a study in which listeners tapped the pulse of polyrhythms (Handel & Oshinsky, 1981). They were able to characterize the latter three datasets (Handel & Oshinsky, 1981; Parncutt, 1994; Vos, 1973) with a resonance period of 500-550 ms (about 2 Hz or 120 bpm) and a width at half height of about 400 – 800 ms (2.5 Hz or 150 bpm to 1.25 Hz or 75 bpm). It is critical to remember, however, that in the experiments of Vos and Parncutt people responded at pulse frequencies that were not present in the stimuli, but at subharmonics of stimulus frequencies[8]. Thus, although linear resonance curves can fit the tempo distributions, they cannot *explain* subharmonic synchronization behavior (cf. McKinney &

Moelants, 2006). On the other hand, nonlinear resonance curves as shown in Figure 5C, with peaks at a preferred frequency and also at harmonics and subharmonics, can explain such behavior.

Other studies have considered the process of pulse induction in mechanical performances of composed music (e.g. Snyder & Krumhansl, 2001; Toiviainen & Snyder, 2003). These measured the number of beats required for participants to start tapping, which can be taken as an index of the amount of time to reach a stable limit cycle (the so-called relaxation time; Large, 2000a). They varied the amount of musical information (i.e. pitch), level of syncopation, and level of musical training. Both amount of musical information and level of syncopation affected relaxation time, which varied between about 3 and 12 beats on average over different conditions. Moreover, timing information was more important than pitch information in determining the number of beats required to hear a pulse. For highly syncopated sequences, a greater instance of unsuccessful synchronization was also observed, and this has been replicated for more carefully controlled rhythmic patterns (Patel *et al.*, 2005). In addition to synchronization at the frequency of the notated beat (about 600 ms, or 100 bpm), participants also often synchronized at harmonics and subharmonics of this frequency, frequencies that were also usually present in the rhythms, and so were not necessarily indicative of higher order resonance. One resonance model of pulse and meter has replicated these results in some detail (Large, 2000a).

Entrainment

Many studies have also examined ongoing entrainment with complex and musical rhythms. One recurrent finding is that the anticipation tendency is generally not observed in synchronization with musical stimuli (Snyder & Krumhansl, 2001; Toiviainen & Snyder, 2003). This may be significant, because the anticipation tendency is reliably observed in synchronization with in periodic stimuli[8], and it has been suggested to imply the ability to predict upcoming events, and thus is sometimes considered the signature of an endogenous rhythmic process (Engstrom *et al.*, 1996; Mates et al., 1994). Importantly, however, even randomly timed "raindrops" interspersed amongst periodic events appear to defeat the anticipation tendency (Wohlschlager & Koch, 2000), indicating that spectro-temporal complexity itself somehow is responsible for the elimination of this effect. From the point of view of resonance, early tapping indicates a rhythmic process whose period is shorter than that of the stimulus sequence, leading Wolschlager and Koch (2000) to suggest that empty time intervals are perceptually underestimated. However, direct tests of this hypothesis have not yielded strong support (Flach, 2005; Repp, 2008a). One possibility is that this is a dynamical effect arising from the frequency detuning that occurs in nonlinear resonance (i.e. the bend in the resonance curve of Figure 5C).

A few studies have quantified stability in the face of rhythmic conflict, by comparing phase entrainment to periodic versus metrically structured versus more syncopated rhythms (Patel et al., 2005; Snyder & Krumhansl, 2001; Toiviainen & Snyder, 2003). Compared with synchronization to periodic rhythms of the same pulse frequency, metrical structuring does not improve overall synchronization accuracy (Patel et al., 2005). Listeners are generally able to synchronize with syncopated patterns as well, however level of syncopation is a good predictor of pulse-finding difficulty (Patel et al., 2005; Snyder & Krumhansl, 2001). Moreover, metrical position of the first note of excerpts biases participants to tap with the corresponding phase (Snyder & Krumhansl, 2001; Toiviainen & Snyder, 2003). Syncopation causes more off-beat taps, more switches between on-beat and off -beat tapping, higher variability of the inter-tap interval, and larger deviations from the beat, findings that are predicted by Large's (2000a) nonlinear resonance model. Thus, stability in the face of rhythmic conflict is not absolute, both humans and nonlinear oscillators tend to fare more poorly as rhythms become more complex.

Using a rhythm reproduction task, Povel & Essens (1985) provided evidence that metric rhythms are easier to remember and reproduce than nonmetric rhythms. They explained this as a memory effect, although Large & Jones (1999) argued that maintenance of attentional coordination was the primary difficulty, an argument that is supported in a general way by findings of motor coordination difficulty. However, Fitch and Rosenfeld (2007) used a recognition memory task to assess the immediate and longer-term perceptual salience and memorability of rhythm patterns as a function of amount of syncopation. They found that for highly syncopated rhythms, listeners tended to reset the phase of the pulse (in memory), often pursuing a strategy of reinterpreting the rhythm as more standard or canonical. Thus, rhythmic complexities such as syncopation have implications for real time coordination as well as for memory.

Only a few studies have addressed responses to phase perturbations in complex rhythms, and because these have specific relevance to higher order resonance, I discuss these in the next section. Here I focus on the issue of following tempo fluctuations in musical sequences, an issue that has been of primary concern in the development of resonance-based approaches (Large & Jones, 1999; Large & Kolen, 1994; Large & Palmer, 2002; McAuley, 1995). Drake *et al.* (2000b) asked listeners' to tap the pulse of musical excerpts in varied Western tonal styles, each presented mechanically synthesized, mechanically accented, or expressively performed by a concert pianist. Results confirmed that musicians and nonmusicians are readily able to coordinate with temporally fluctuating musical performances. Entrainment with expressive versions occurred at slower frequencies, within a narrower range of synchronization levels, and corresponded more frequently to the theoretically correct metrical hierarchy. Repp (2002c) showed that synchronization with expressively timed music was better than synchronization with a sequence of identical tones that mimicked the expressive timing pattern, or with music that followed a structurally inappropriate (phase-shifted) expressive timing pattern, emphasizing the importance of musical information beyond onset timing.

Dixon, et al., (2006) asked listeners to rate the correspondence of click tracks to musical excerpts and, on different trials, to tap along with the excerpts. Their data suggested that in rubato performances, perceived pulses did not coincide precisely with sounded events, instead listeners heard smooth tempo changes, such that some events were early and others late with respect to perceived pulse. This observation is consistent with tempo tracking dynamics that have been proposed for nonlinear oscillators (e.g., Large & Kolen, 1994). Honing (2005, 2006) has provided an analysis that suggests that perceptual limitations on tracking ability may be taken into account as performers shape temporal fluctuations. Large & Palmer (2002) showed that nonlinear oscillators can track tempo changes successfully, and they showed how deviations from temporal expectancies (embodied in the oscillations) could be successfully used to discern the structural interpretations (phrase and melody) intended by the performers. Overall, the available evidence suggests that listeners smoothly track tempo fluctuations, nonlinear oscillators can track tempo fluctuations of complex rhythms, and deviations from temporal expectancies may provide a means of perceiving structural intentions of performers. Interestingly, the study of musical entrainment has almost exclusively focused on tapping with recorded music; the issue of real time musical interactions between people has so far received far less attention (Repp, 2005).

Higher order resonance

Resonance theory predicts spontaneous harmonic and subharmonic resonance (see Figure 5C), and experiments with periodic stimuli have borne out some of these predictions (Vos, 1973;

Parncutt, 1994). A further hypothesis suggests that multiple endogenous frequencies would couple internally to instantiate dynamic metrical patterns (Large & Jones, 1999; Large, 2000a; Jones, 2008). Moreover, Large & Palmer (2002) demonstrated that, when stimulated with temporally fluctuating rhythms, internally coupled oscillations (with metrically related frequencies) are more resilient than individual oscillators in tracking temporal fluctuations, such as rubato. Such predictions have recently been evaluated with musical stimuli and more complex rhythms.

Repp (Repp, 1999, 2002c) considered both perception of timing and synchronization of taps with a mechanical excerpt of Chopin's *Etude in E major, Op.10, No.3.*, sequenced on a computer with precise note durations and a steady tempo, creating an isochronous excerpt. In perception experiments, accuracy of time change detection exhibited a consistent pattern when averaged across trials and participants, even though the music was in strict time. In synchronization experiments, accuracy also exhibited a consistent pattern across trials and participants; moreover, synchronization accuracy profiles correlated strongly with detection accuracy profiles. Listeners' endogenous temporal fluctuations reflected mainly the metrical structure of the music (Repp, 2005). Musical structure, and/or spontaneous higher order resonance may have influenced both perception of sequence timing and timing of coordinated movement. This finding is consistent with the hypothesis of a network of oscillators of different frequencies, coupled together in the perception of a complex rhythm (Large & Jones, 1999; Large, 2000a; Large & Palmer, 2002).

Two recent studies (Large *et al.*, 2002; Repp, 2008b) have implicated higher order resonances and internal coupling of endogenous oscillations in coordination of motor behavior with complex rhythms. Large et al. (2002) explicitly instructed participants at to synchronize at different metrical levels on different trials, with complex rhythms that contained embedded phase and tempo perturbations. They observed that adaptation to perturbations at each tapping frequency reflected information from other metrical levels. In Repp's (2008) study, participants tapped on target tones (''beats'') of isochronous tone sequences consisting of beats and subdivisions (1:n tapping). Phase perturbations at subdivisions perturbed tapping responses, despite the fact both task instructions and stimulus design encouraged listeners to ignore the perturbations. Moreover, responses were observed both when subdivisions were present throughout the sequence, and when they were introduced only in the cycle containing the perturbation. These results show that synchronization to complex rhythms is not merely a process of error correction; rather listeners covertly monitor multiple levels of temporal structure. This provides evidence for spontaneous resonance at harmonics (subdivisions), and internal coupling among multiple endogenous frequencies. To date such observations have been limited to complex rhythms, and it will be important to extend these experiments to musical excerpts.

A number of studies have shown perceptual categorization of time intervals, and demonstrated that metric context modulates categorization (Clarke, 1987; Desain & Honing, 2003; Essens, 1986; Large, 2000b; Povel, 1981; Schulze, 1989). With brief rhythms, Nakajima and colleagues report an intriguing phenomenon, called time shrinking (ten Hoopen et al., 2006). When a short time interval is followed by a long one, listeners underestimate the latter, revealing gravitation to a preferred interval ratio of 1:1. Using three-element rhythmic figures, expressed as serial interval ratios, Desain & Honing (2003) notated patterns along the perimeter of an equilateral triangle to assess combined weights of different ratios, finding systematic distortions of rhythms favoring simple temporal ratios. Moreover, listeners perceive both rhythmic categories and temporal deviations from categorical durations, where duration categories appear determined by metrical context (Clarke, 1987; Desain & Honing, 2003; Large, 2000b). Further support for the preferential stability of integer-ratio frequency relationships in meter comes from studies of North American adults asked to synchronize and then continue tapping to complex (additive) meter patterns (Snyder *et al.*, 2006) (serial interval ratios of 2+2+3 or 3+2+2). During synchronization participants produced long:short serial ratios that were between the target ratio of 3:2 and a simple-meter ratio of 2:1, and during continuation the ratios were stretched even more toward 2:1. Thus, people raised in North America (at least) find it difficult to produce additive accent patterns.

Dynamic Attending

Dynamic attending theory (DAT) addresses 'in-the-moment' expectancies that occur during listening (Jones, 1976; Jones & Boltz, 1989) Large and Jones (1999) theorized that active *attending rhythms* synchronize with temporally structured sequences, generating temporal expectancies for future events, thus linking dynamic attention with the concepts of nonlinear resonance (Large, 2000a; Large & Kolen, 1994; McAuley & Jones, 2003). Large & Jones (1999) proposed that endogenous oscillations focus pulses of attending energy toward expected points in time, enabling attentional tracking of complex rhythmic sequences, and online temporal anticipation of individual events. This notion of attentional energy goes beyond the mere existence of neural resonance, to address the issue of how resonance may be exploited by an organism to enable attentional coordination with the dynamic external world (for a review, see Jones, 2008). By virtue of the close link between DAT and neural resonance, much of the empirical research presented in the general context of resonance is directly relevant to DAT.

Here I point out the empirical findings that relate specifically to the issue of focusing attentional energy toward individual events as rhythmic sequences unfold in time.

Evidence for the temporal targeting of attentional energy comes from time discrimination, pitch discrimination and phoneme monitoring tasks, using both sensitivity (*percent correct* or *d'*) and reaction time measures (Barnes & Jones, 2000; Jones & McAuley, 2005b; Jones et al., 2002; Jones & Yee, 1997; Large & Jones, 1999; McAuley & Kidd, 1995; Quene & Port, 2005). For example, time and pitch discrimination judgments are thwarted when made in the context of metrically irregular sequences. Jones and Yee (1997) found that when musicians and non-musicians had to determine 'when' a slightly asynchronous tone occurred in metrically regular versus irregular patterns, metrically regular sequences supported time-change detection, while irregular sequences did not, even when metrically regular and irregular sequences were controlled for statistical regularity. Moreover, global context effects of timing and tempo change disrupted time change detection as predicted by resonance models of meter perception (Large & Jones, 1999, Jones & McAuley, 2005a). Temporal regularity has also been found to affect the accuracy and speed of pitch judgments in rhythmic sequences. In one recent study, participants listened for a target's pitch change within recurrent nine-tone patterns having largely isochronous rhythms. Sensitivity to pitch changes (*d'*) was enhanced for probes that occurred at expected, versus unexpected times. Moreover, attentional focus was temporally asymmetric (cf. Eck, 2002), such that disruption of pitch change was greater for tones that occurred early versus those that occurred late (Jones *et al.*, 2006). In a phoneme monitoring experiment, regular versus irregular timing of stressed vowels facilitated reaction times (Quene & Port, 2005), providing support for a domain-general dynamic attentional mechanism. Theoretically, Large & Jones (1999) linked the notion of entrainment via phase coupling to attentional capture in the time domain; faster reaction times and higher false alarm rates for temporally unexpected events support the notion of attentional capture (Penel & Jones, 2005).

Development

In part because coordination with music is observed in all known cultures, and because neural resonance provides a potentially universal explanatory mechanism, pulse and meter have been hypothesized to constitute a universal aspect of musical perception and behavior (Trehub & Hannon, 2006). Thus it is logical to ask whether infants perceive meter. In one study, (Bergeson & Trehub, 2006) found that 9-month-old infants' detected a change in the context of strongly metric sequences but not in the context of sequences that induce a metric framework only weakly or not at all. This observation is consistent with adult findings (e.g. Yee *et al.*, 1994), thus supporting dynamic attending in infants. Two additional experiments by (Bergeson & Trehub, 2006) found that infants were able to detect changes in duple meter, but not triple meter patterns. Another study, found that 7-month old infants discriminated both duple and triple classes of rhythm on the basis of implied meter, despite occasional ambiguities and conflicting grouping structure (Hannon & Johnson, 2005). Additionally, infants categorized melodies on the basis of contingencies between metrical position and tonal prominence.

The above findings are consistent with predispositions for auditory sequences that induce a metric percept, and provide evidence for a preference for 1:2 over 1:3 temporal organization, as predicted by higher order resonance in nonlinear systems (see Figure 5C). However, 6-month-old infants were able to perceive rhythmic distinctions within the context of additive stress patterns (a.k.a. complex meters), but 12-month-old infants were not (Hannon & Trehub, 2005). Brief exposure to foreign music enabled 12-month-olds, but not adults, to perceive rhythmic distinctions in this foreign musical context. This finding raises some questions related to the universality of structural relationships in meter, a question to which I return below.

Finally, a fundamental sound-movement interaction in the perception of rhythm has been demonstrated in infants. Phillips-Silver & Trainor (2005) showed that bouncing 7-month-old infants on every second versus every third beat of an ambiguous pattern influences whether that auditory rhythm pattern is perceived in duple (1:2) or in triple (1:3) form. Moreover, visual information was not necessary for this effect, indicating a strong, early-developing interaction between auditory and vestibular information in the human nervous system. This early cross-modal interaction between body movement and perception of musical rhythm persists into adulthood as well (Phillips-Silver & Trainor, 2007). Parallel results from adults and infants suggest that the movement-sound interaction develops early and is fundamental to music processing throughout life.

Neural Correlates

Resonance theory predicts that listeners experience temporally patterned metrical structures, and hear musical events in relation to these patterns, because they would be intrinsic to the physics of oscillatory neural systems driven by rhythmic stimuli. The generic predictions of the theory–spontaneous oscillation, entrainment and higher order resonance–arise from mathematical analysis of neural oscillation. To close the loop, then, it makes sense to attempt to identify neural activity that anticipates events within a sequence, persists in the absence of acoustic events, demonstrates phase stability and is sensitive to metrical structures. Electroencephalography (EEG) and magnetoencephalography (MEG) are the two main techniques for studying the temporal dynamics of auditory processing in the human brain and this section will concentrate on this literature. Studies of music utilizing functional imaging techniques and brain lesion data have been ably reviewed elsewhere (Peretz & Zatorre, 2005), although at the end of the section, we will touch upon the results of a few recent studies that are of the greatest relevance to issues that have been raised in the current review.

Long-latency auditory event related potentials (ERPs) have been studied extensively but typically with stimulus repetition rates slower than rhythmic tempos, in part because the responses diminish in amplitude at fast tempos and because responses from adjacent tone onsets begin to overlap at IOIs around 500 ms (Carver *et al.*, 2002). However, using rhythmic stimuli, a number of authors have observed emitted potentials (or omitted stimulus potentials), which display an early modality-specific negative component (Simson *et al.*, 1976) with topography and latency similar to the N100, a negative deflection 100 ms after tone onset (Janata, 2001). This earlier component of the emitted potential may reflect mental imagery, rather than a violation of expectation (Janata, 1995, 2001), as with later components. Emitted potentials are also observed as a positive peak around 300 ms after the omitted event and have been equated with the P300, which occurs following an oddball event (see, e.g., Besson *et al.*, 1997). Brochard et al. (Brochard *et al.*, 2003) (2003) utilized an oddball methodology to study subjective meter (Bolton, 1894; Vos, 1973). Tones were decremented in intensity at odd (hypothetically strong) or even (hypothetically weak) metrical positions, and P300 responses to omitted tones were observed. Differences in the P300 to odd and even tones provided evidence of subharmonic neural responses indicative of subjective metrical accent. Another study using probe beats in different metrical patterns observed that the P300 plays a role in metrical processing for musicians (Jongsma *et al.*, 2004).

Snyder and Large (2005) observed that peaks in the power of induced beta- and gamma-band activity (GBA) anticipated tone onset (average ~0 ms latency), were sensitive to intensity accents, and persisted when expected tones were omitted, as if an event actually appeared. By contrast, evoked activity occurred in response to tone onsets (~50 ms latency) and was strongly diminished during tone omissions. Thus, the features of induced and evoked activity matched the main predictions for pulse and meter. Zanto et al. (2005) tested the synchrony of GBA, using phase perturbations of a periodic stimulus. Sequence periodicity was violated every 6-10 tones with an early or late tone onset. After both types of perturbation, the latency of the induced activity relaxed to baseline in a fashion similar to what has been observed in motor synchronization studies (e.g. Large et al., 2002; Repp, 2002a). Additionally, asymmetric responses were observed to early versus late tones (cf. Eck, 2002; Jones et al., 2002). A recent MEG study found subharmonic rhythmic responses in the beta-band when subjects were instructed to impose a subjective meter on a periodic stimulus (Iverson *et al.*, 2006), and Fujioka et al. (2008), reported anticipatory beta-band responses for periodic sequences, and metrical sequences, but not randomly timed sequences. Thus beta and gamma band responses to auditory rhythms in EEG and MEG correlates with predictions of neural resonance.

Finally, functional imaging studies strongly support the notion that rhythmic information is represented across broad cortical and subcortical networks, in a manner that is dependent upon task and level of syncopation (Chen *et al.*, 2008; Grahn & Brett, 2007; Jantzen *et al.*, 2007; Sakai *et al.*, 1999). It is known that metrical rhythms are easier to remember and reproduce than more syncopated rhythms (Essens & Povel, 1985; Fitch & Rosenfeld, 2007), and recently it has been observed that metrical rhythms result in characteristic patterns of functional brain activation (Sakai et al., 1999). Grahn & Brett (2007) observed improved reproductions for metric rhythms, and observed that these rhythms also elicited higher activity in the basal ganglia and SMA, suggesting that these motor areas play a role in mediating pulse and meter perception. Musicians show additional activation unrelated to rhythm type in premotor cortex, cerebellum, pre-SMA and SMA. Chen et al. (2008) investigated how performance and neural activity were modulated as musicians and nonmusicians tapped in synchrony with progressively more syncopated auditory rhythms. A functionally connected network was implicated, with secondary motor regions recruited in musicians and non-musicians, while musicians recruited the prefrontal cortex to a greater degree than nonmusicians. The dorsal premotor cortex appeared to mediate auditory–motor interactions. Finally, when subjects *continued* synchronized versus anti-synchronized rhythmic movements, different patterns of functional brain activation were observed, despite the fact that the rhythmic stimulus had ceased and the movement itself was identical under the two different conditions (Jantzen et al., 2007).

Summary

Experiments with musical rhythms and other nonperiodic laboratory rhythms have turned up findings that are broadly consistent with fundamental predictions of neural resonance: spontaneous oscillation, entrainment and higher order resonance. The relevant time scales of the phenomena have been identified, and a number of important details of temporal engagements with music have been cataloged. Signatures of nonlinear oscillation have been reported across a range of tasks involving perception, attention, categorization, memory and performance. Infants as young as 7 months show effects of higher order resonance in discrimination and categorization. Potential physiological correlates of neural resonance have been identified. Engagement in rhythmic tasks has been shown to activate broad cortical and subcortical networks. An increasing number of studies are directly evaluating the predictions of nonlinear resonance, yet a surprising number of areas remain largely untouched.

6. The Future

Neural theories of pulse and meter perception

The careful reader will have noticed that, to date, computational simulations of pulse and meter have been derived from mathematical models of single neuron action potentials or from models of alternating excitatory and inhibitory activity. As observed by Eck (2002), the timescale of such neural processes may not provide a good match to the time scale of musical pulse and meter (Vos, 1973; Parncutt, 1994; van Noorden & Moelants, 1999). Therefore, it is fair to ask whether neural resonance really is a plausible theory of pulse and meter. A clue to the answer may come from the experiment of Snyder & Large (2005), who observed bursts of cortical beta- and gamma-band activity to have properties associated with pulse and meter. Bursting is a dynamic state where a neuron repeatedly fires discrete groups, or *bursts* of action potentials, and each burst is followed by a period of quiescence before the next occurs. Interburst periods, the time interval between one burst and the next, would be generally consistent with timescales of musical pulse and meter.

Burst oscillation is not yet as well understood as simpler forms of neural oscillation. For example, a complete classification of electrophysiological types of bursters is not currently available. Nevertheless, burst oscillation is currently receiving a great deal of attention in the computational neuroscience literature, and mathematical analyses (Coombes & Bressloff, 2005; Izhikevich, 2007) have shown that bursters display key properties we have relied upon to predict pulse and meter. Moreover, burst oscillation displays both fast and slow time-scales (Izhikevich, 2007) as do relaxation oscillations. Figure 7 shows a computational simulation of burst oscillation (Izhikevich, 2000) responding to a simple rhythm, displaying both entrainment to the sequence and persistence in the absence of a stimulus event. Neuronal bursting is thought to play an important role in communication between neurons, and neural bursting figures prominently in motor pattern generation and neural synchronization. The picture that emerges is one of rhythmic communication, via neural bursting, between different neural areas as they resonate to musical rhythms. Bursting may also provide additional properties and degrees of freedom that would expand the explanatory potential of neural oscillation in regards to musical rhythm and in relation to other musical dimensions.

Meter or Rhythm?

An interesting issue that is sometimes posed as a challenge to nonlinear resonance is that of the complex meters found in some musical cultures of the Balkans, South Asia, Africa, and Latin America (London, 1995). Complex meters typically contain three beat levels: a slow isochronous level corresponding to the measure, a fast isochronous level that subdivides the measure (into 5, 7, 11, or 13 beats for example), and an intermediate beat level that groups the faster beats in an uneven fashion, thus creating a nonisochronous pulse. The nonisochronous pulse falls within the typical pulse timescale (van Noorden, 1999), and serves as the framework for drumming and dancing that accompanies the music.

In contemplating this issue, there are several questions to consider. First, it is imperative to ask whether “complex meters”–accentuation patterns used as conventional frameworks for making music–are meters in the sense that has been discussed here. An alternative would be that complex stress patterns are compelling specifically because they thwart an intrinsic expectation of periodicity. This begs the hefty theoretical question of how can we establish whether any given pattern of stress qualifies as a pulse or a meter. Unfortunately, the field currently lacks an empirical, operational definition. If it turns out that complex meters meet whatever definition the field can muster, then we must ask whether the spontaneous generation of these particular nonisochonous patterns can be explained within the framework of neural oscillation. Moreover, irrespective of how these questions are answered, the larger question–spontaneous generation of musical rhythm, in all its temporally fluctuating, syncopated and nonperiodic complexity–remains. As far as I can tell, this is a question that has been almost completely ignored. Here I merely observe that significant theoretical possibilities, such as chaotic oscillation and burst oscillation, remain unexplored. Thus, in terms of music making, the relationship between complex (nonperiodic) musical rhythms, pulse and meter remains a mystery.

Pitch and rhythm

In the above discussion, we said next to nothing about the musical content of the stimulus, beyond its temporal structure. At the surface, it is rather surprising that resonance models of pulse and meter have been as successful as they have, while almost totally ignoring intensity, pitch, harmony and other important musical dimensions. However, in many cases, rhythmic information seems to be significantly more important than melodic accents in predicting listeners' perception of meter (Hannon *et al.*, 2004; Snyder & Krumhansl, 2001). Huron & Royal (1996) have questioned the effectiveness of melodic accents for marking meter, suggesting that melody and meter are perceptually independent. However, is it really appropriate to ignore other kinds of musical salience, such as *pitch accents* (Jones, 2008)? Jones' joint accent structure hypothesis suggests that temporal, melodic, harmonic and other factors interact to provide periodicity information. Indeed, it appears that melodic patterns can contribute to a listener's sense of meter and that listeners also respond differentially to various combinations of melodic and temporal accents (Hannon et al., 2004; Jones & Pfordresher, 1997) especially if the relative salience of different accent types are well calibrated (Ellis & Jones, in press; Windsor, 1993).

If we accept that melodic and other musical accents can affect meter, then the significant theoretical question arises of how such information couples into a resonant system. Is it sufficient to consider accents arising from different features (for example, intensity, duration, pitch, harmony, and timbre) as combining into a single scalar value that determines the strength of each stimulus event? Probably not. The flip side of this coin is the effect of pulse and meter on the perception of individual musical events. Recall Zuckerkandl's (1956) view of meter as a series of waves, away from one downbeat and towards the next. As such, meter is an active force; each tone is imbued with a special rhythmic quality from its place in the cycle of the wave, from "the direction of its kinetic impulse." It is, perhaps, a start to show that attention is differently allocated in time; however, it seems clear that future work must consider these issues. Perhaps, if high frequency neural oscillations are important in binding acoustic features (Wang & Chang, 2008), and if bursts of high frequency oscillation are operative in resonance to rhythm, this will provide a theoretical vehicle for a future understanding of the relationship between rhythm and melody.

Emotional Responses

According to Meyer, composers and performers set up expectancies in listeners, which they skillfully manipulate, fulfilling some and thwarting others, and it is through expectancy violations that listeners come to experience affective responses to music. Meyer's theory is wonderfully dynamic and seems to explain a great deal about human responses to music (Huron, 2006; Juslin & Sloboda, 2001; Meyer, 1956). However, Meyer dealt mainly with melody and harmony; rhythm is scarcely mentioned. Large & Kolen (1994) explicitly linked resonance to temporal expectancy and to Meyer's theory of musical affect, arguing that the expectancy theory should also extend into the temporal domain; dynamic attending theory is also deeply concerned with temporal expectancy (Jones, 1976). Such considerations imply that violations of temporal expectancies should give rise to affective responses. After all, global rhythm characteristics, such as tempo and articulation, have already been linked to communication of basic emotions through music. Do temporal expectancy violations, such as syncopations or tempo fluctuations, give rise to affective responses? In one study, in which listeners rated the moment-to-moment level of perceived emotionality while listening to musical performances, a systematic relationship between emotionality ratings, timing and loudness was observed (Sloboda & Lehmann, 2001). This type of study has the potential to link violations of temporal expectancy, which can be measured and modeled in great detail for specific pieces of music, with dynamical musical affect, which is still not well understood. Thus, this area also seems a promising one for future research.

Concluding Remarks

I have argued that universal properties of nonlinear resonance predict the fundamental features of pulse and meter. The approach derives its predictions from a simple physical hypothesis, that pulse and meter arise when nonlinear neural oscillations are driven by musical rhythms. The predictions themselves derive from analyses of neural oscillation. Thus, pulse and meter are seen not as computational “problems” to be solved by the brain; they are simply what happens when nonlinear resonators, operating at the proper time scale, are stimulated by music. To suggest that pulse and meter are therefore “innate” does not really hit the mark; it would be more apt to claim that they are intrinsic to the physics of neural oscillation. All that is then required is coupling to a rhythmic stimulus. A great deal of evidence now supports these predictions, and numerous questions remain open for future investigation.

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Footnotes

1. The term *rhythm* is commonly used to refer both to the stimulus and to aspects of its perception (e.g., its perceived grouping, see Lerdahl & Jackendoff, 1983). Throughout this review I use the term to I refer to the stimulus structure.
2. Impulse amplitude is a common representation of stress. However, pitch, duration and other aspects of the acoustic wave–which play significant roles in the perception of stress–are problematic for this simple approach.
3. An important methodological concern is the amount of delay is present in tap time measurements relative to the arrival of sound at the ear. This is not frequently reported in such studies.
4. Another influential model for human rhythmic behavior is a van der Pol–Rayliegh hybrid model (Haken *et al.*, 1985; Jirsa *et al.*, 2000), which includes nonlinear coupling and exhibits similar properties to neural models.
5. In the continuous time canonical model (Equations 2 & 3), this coupling term captures only 1:1 coupling, higher order terms are required to produce the higher order resonances. However, owing to the differences between the continuous time and discrete time formulations, in this map, the coupling term produces the full variety of higher order resonances pictured in Figure 6C.
6. It should also be noted that phase varied from 0 to 1, whereas the equations here work in radians, and $\omega = 2\pi / T$ because of the way they have been derived.
7. Equation 2 can be used to create a linear resonance model that is directly comparable to the nonlinear model. To do this, one chooses the coefficients of

the nonlinear terms (β and δ) to be zero, and one also ignores higher order terms (because there are none).

8. In Handel & Oshinsky's experiment listeners generally tapped at frequencies that were present in the polyrhythms, and the same would likely be true for most of the musical rhythms.

Figure Captions

1. The first four bars of the Aria from by J. S. Bach's *Goldberg Variations*, as performed by a student pianist. A) Acoustic sound pressure; B) Spectrogram; C) Event onsets and hypothetical pulses.
2. Notation and music theoretic metrical structure for the first four bars of the *Goldberg Variations* Aria.
3. Neural oscillation. A) A neural oscillation can arise from the interaction between excitatory and inhibitory neural populations. (Adapted from Hoppenstadt & Izhikevich, 1996a). B) Multiple levels of mathematical abstraction for describing neural oscillation.
4. Transforming an oscillator-level model to a canonical model. A) Time series generated by a driven Wilson-Cowan system (Equation 1). B) The time series of (A) projected onto state space (x, y). C) Time series generated by the equivalent canonical model (Equation 2). D) The time series of (C) projected onto state space ((Re(z), Im(z)), in Cartesian coordinates, or (r, ϕ) in polar coordinates).
5. Three universal properties of nonlinear oscillation: spontaneous oscillation, entrainment and higher order resonance. A) Spontaneous oscillation. When the bifurcation parameter crosses zero, a spontaneous oscillation is generated, as energy is added into the system. B) Entrainment. Entrainment of phase is brought about by stimulus coupling (see Equation 3). C) Higher order resonance. The amplitude response of a nonlinear oscillator bank (Equation 2) stimulated with a sinusoid at 2 Hz, at three different amplitudes.

6. Discrete time models of pulse. A) Continuous time series of event onsets from the *Goldberg Variations*. B) Discrete time representations of the same onsets. Onsets coinciding with the basic pulse are shown as heavy lines. Time is transformed into relative phase via Equation 6. C) Resonance regions in a discrete time model (adapted from Large & Kolen, 1994).
7. Response of a burst oscillator (Izhikevich, 2000) to a rhythmic pattern. A) Continuous time series representation of event onsets. B) Bursts of activity entrain to the stimulus and are observed in the absence of a stimulus event.

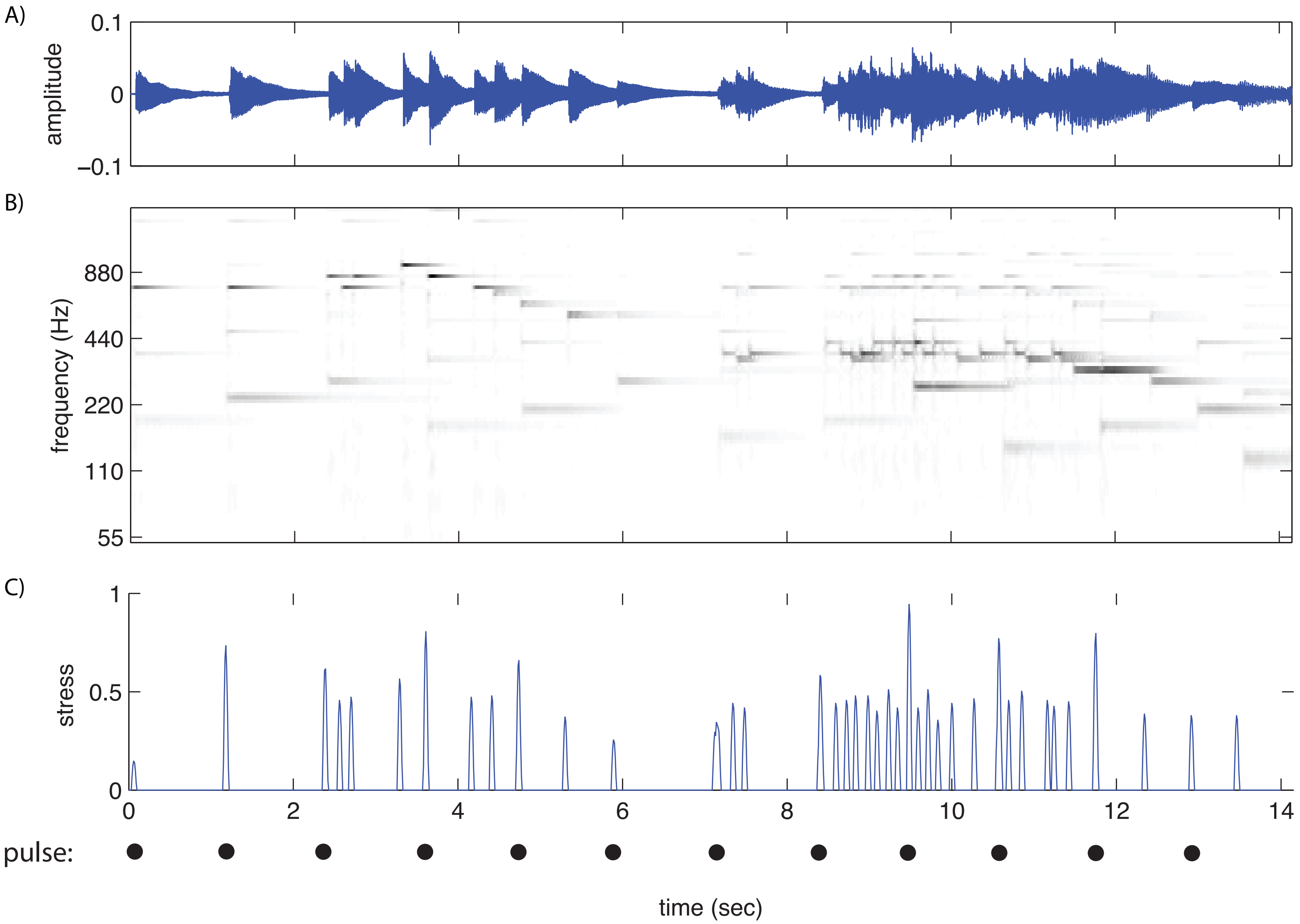

A)
0.1
0
–0.1
amplitude
B)
880
440
220
110
55
frequency (Hz)
C)
1
0.5
0
stress
0
2
4
6
8
10
12
14
pulse:
time (sec)

Figure 1

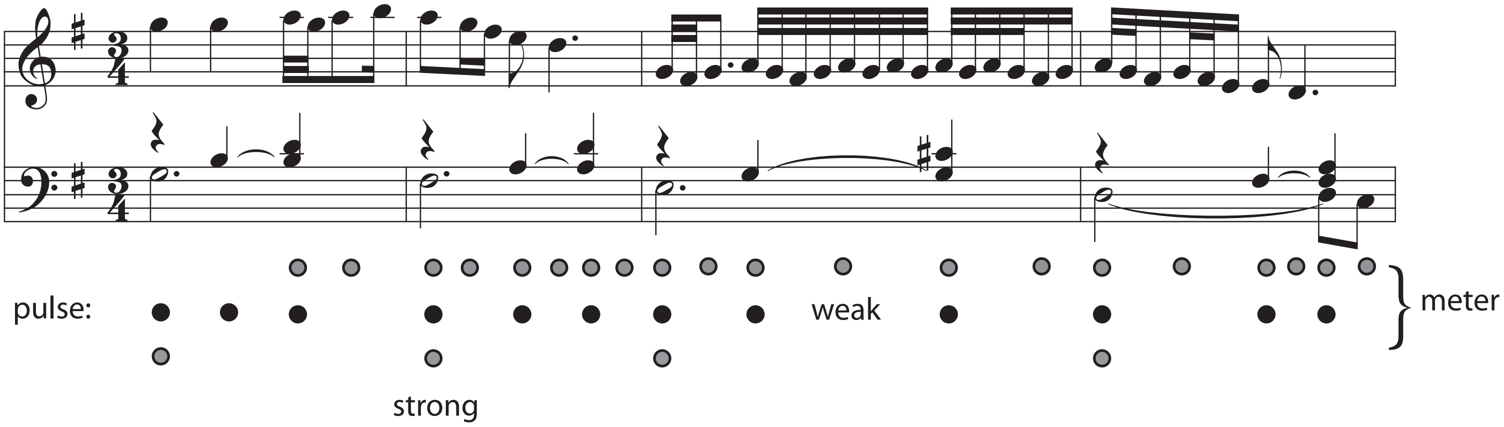


Figure 2

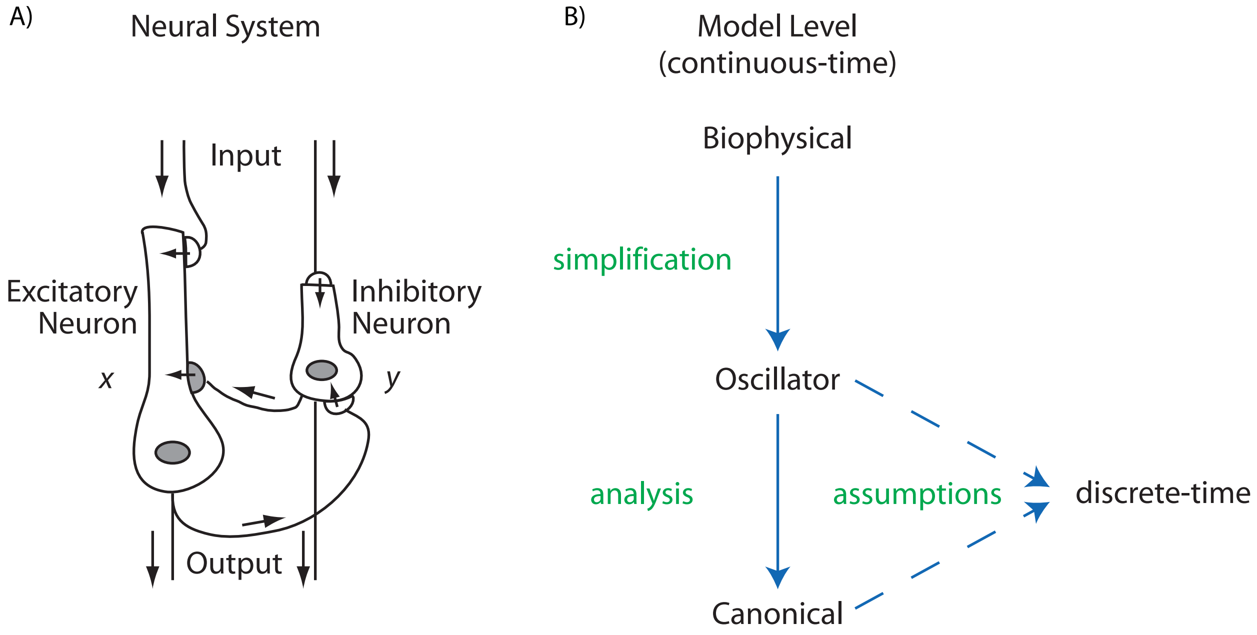
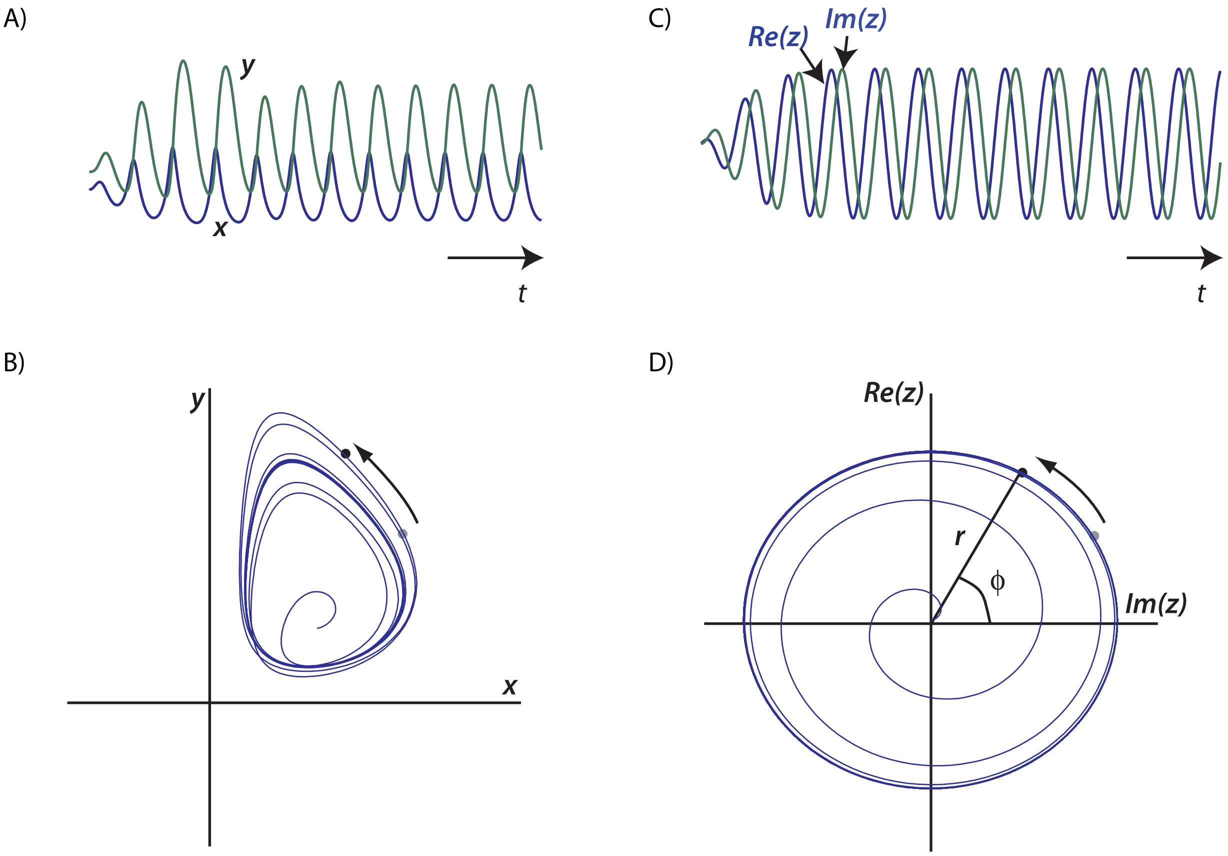

A)
Neural System
Input
Excitatory Neuron
Inhibitory Neuron
x
y
Output
B)
Model Level (continuous-time)
Biophysical
simplification
Oscillator
analysis
assumptions
discrete-time
Canonical

Figure 3



Oscillator Model

Canonical Model

Figure 4

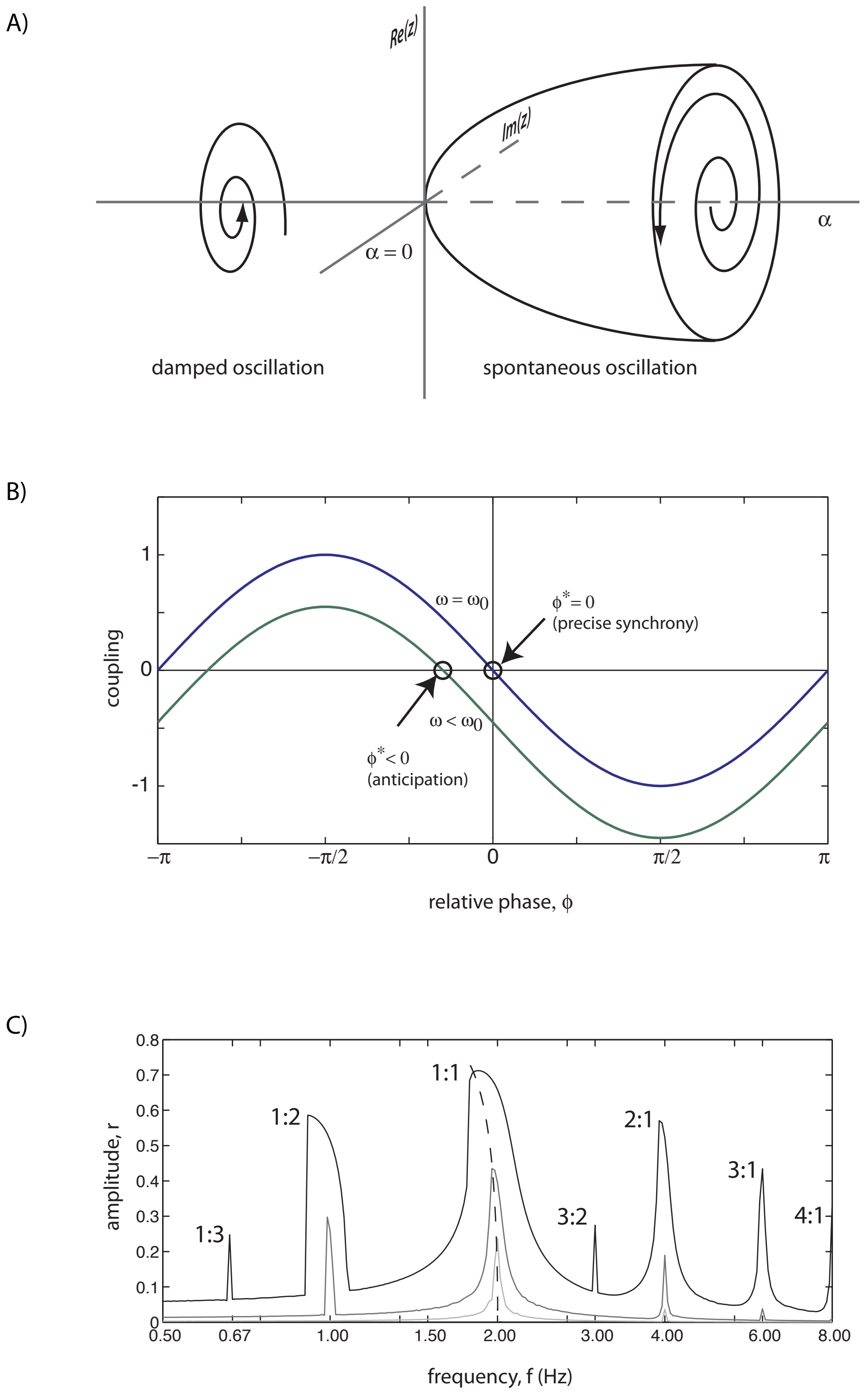

A)
Re(z)
Im(z)
α = 0
α
damped oscillation
spontaneous oscillation
B)
coupling
1
0
-1
ω = ω0
ϕ* = 0
(precise synchrony)
ω < ω0
ϕ* < 0
(anticipation)
−π
−π/2
0
π/2
π
relative phase, ϕ
C)
amplitude, r
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1:3
1:2
1:1
3:2
2:1
3:1
4:1
0.50
0.67
1.00
1.50
2.00
3.00
4.00
6.00
8.00
frequency, f (Hz)

Figure 5

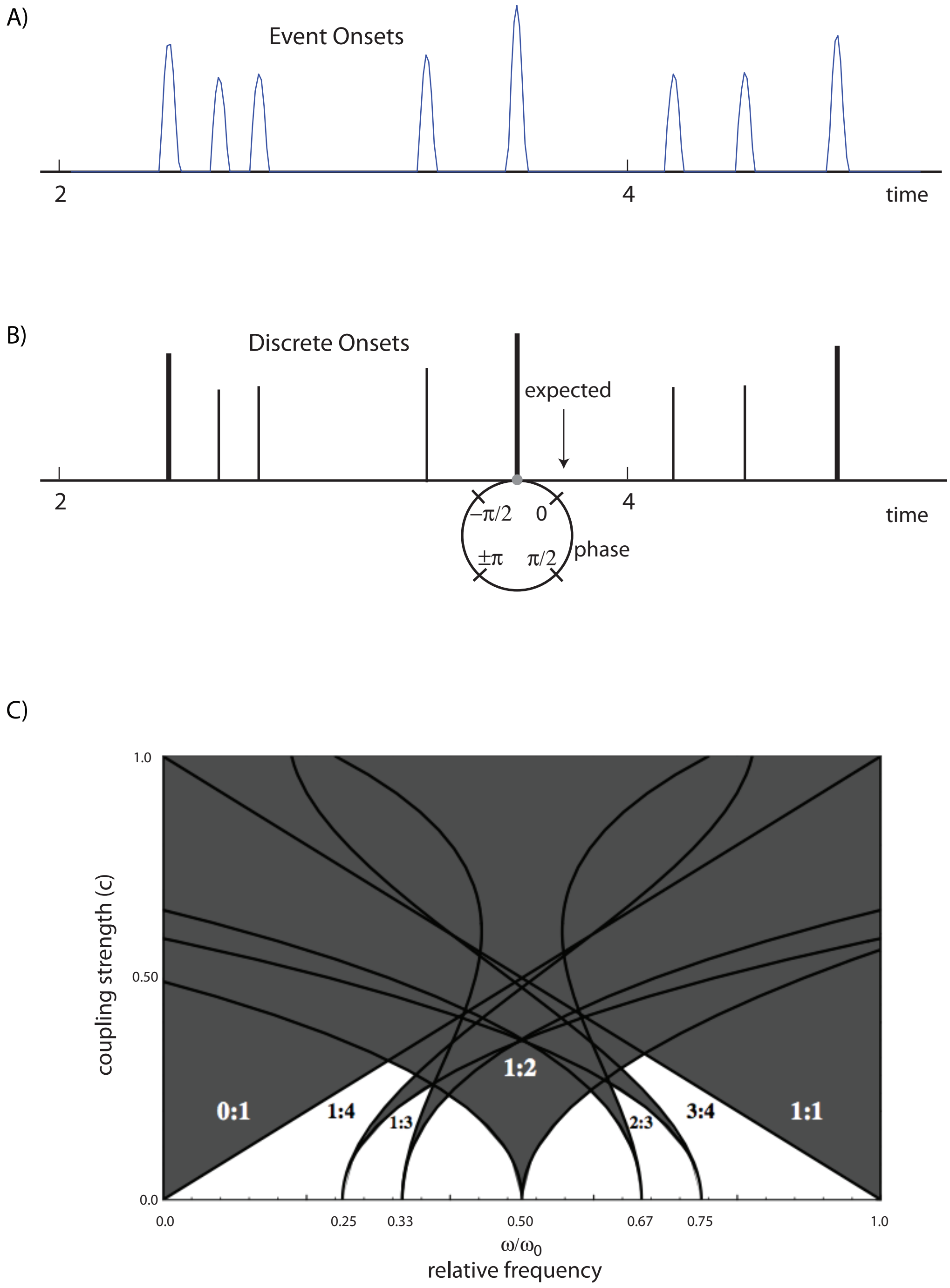

A)
Event Onsets
2
4
time
B)
Discrete Onsets
expected
2
4
time
−π/2
0
±π
π/2
phase
C)
1.0
0.50
0.0
coupling strength (c)
0:1
1:4
1:3
1:2
2:3
3:4
1:1
0.0
0.25
0.33
0.50
0.67
0.75
1.0
ω/ω0
relative frequency

Figure 6

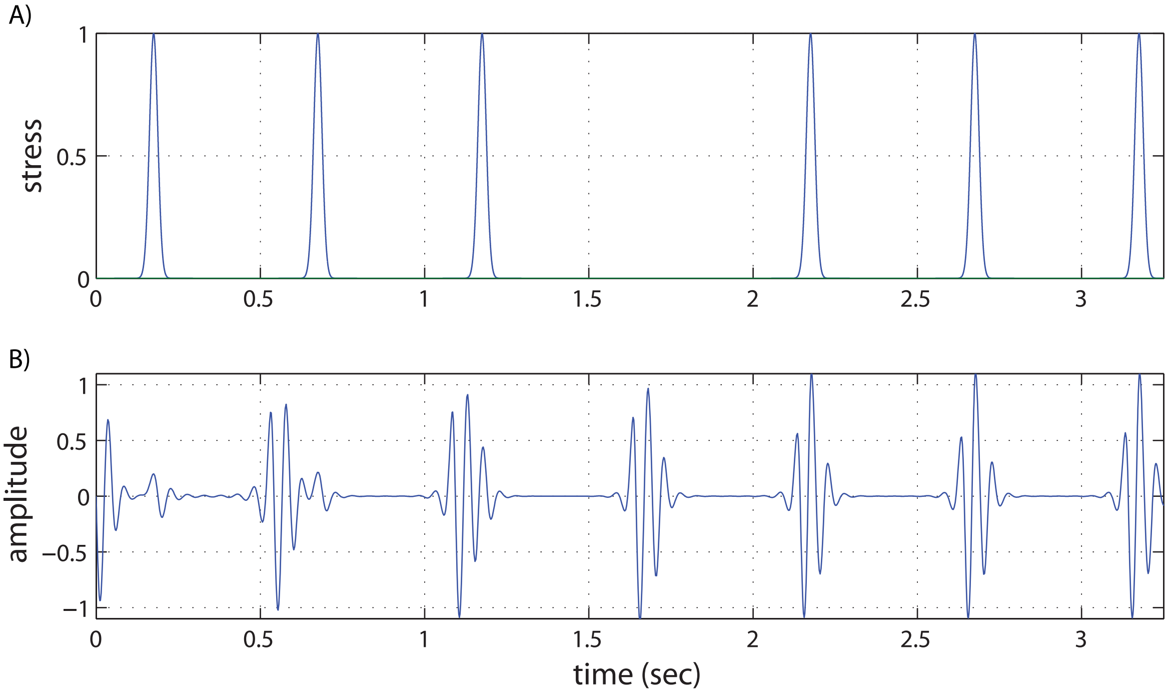

A)
1
0.5
0
stress
0
0.5
1
1.5
2
2.5
3
B)
1
0.5
0
−0.5
−1
amplitude
0
0.5
1
1.5
2
2.5
3
time (sec)

Figure 7