Pulse and Meter as Neural Resonance

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The experience of musical rhythm is a remarkable psychophysical phenomenon, in part because the perception of periodicities, namely pulse and meter, arise from stimuli that are not periodic. One possible function of such a transformation is to enable synchronization between individuals through perception of a common abstract temporal structure (e.g., during music performance). Thus, understanding the brain processes that underlie rhythm perception is fundamental to explaining musical behavior. Here, we propose that neural resonance provides an excellent account of many aspects of human rhythm perception. Our framework is consistent with recent brain-imaging studies showing neural correlates of rhythm perception in high-frequency oscillatory activity, and leads to the hypothesis that perception of pulse and meter result from rhythmic bursts of high-frequency neural activity in response to musical rhythms. High-frequency bursts of activity may enable communication between neural areas, such as auditory and motor cortices, during rhythm perception and production.

Key words: **rhythm; pulse; meter; neural rhythms; beta; gamma; auditory; attention; bursting**

Introduction

Rhythm perception is fundamental to our experience of music in general and plays a particularly important role in our ability to coordinate music making and dance among individuals. Rhythm perception has been studied for many years[1,2] and the range of perceptual phenomena identified provides a rich set of constraints for theories of rhythmic behavior. A number of different theoretical approaches have been proposed to explain rhythm.[3] One approach that has proven useful in explaining a number of aspects of rhythm perception relies upon neural oscillations that resonate with rhythmic stimuli. Here, we describe a particular type of resonance model that appears to be especially well suited to providing an explanation of neural correlates of rhythm perception in high-frequency brain activity. First, we describe what is known about perception of pulse and meter, in particular those features of behavior that are most desirable to capture in a theoretical model of rhythm perception.

Pulse and Meter

The rhythms of music are not periodic; they are complex, temporally structured sequences of acoustic events. Nevertheless, in most musical rhythms people perceive periodicity, called *pulse* or *beat,* and structured patterns of accentuation among pulses, called *meter.*[4] Pulse may be defined as an *endogenous periodicity*, "a series of regularly recurring, precisely equivalent"[5] psychological events that arise in response to a musical rhythm. Periodicity is emphasized by theorists who are concerned primarily with musicological analysis because of its formal simplicity and its similarity to perceptual experience.[5–8] However, others highlight the significance of tempo change, or

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The Neurosciences and Music III—Disorders and Plasticity: Ann. N.Y. Acad. Sci. 1169: 46–57 (2009).
doi: 10.1111/j.1749-6632.2009.04550.x © 2009 New York Academy of Sciences.

rubato, in music performance.[9] In complex musical rhythms not every event onset coincides with a pulse, and pulses may occur in the absence of event onsets on account of syncopation and other intricacies of rhythmic patterning.[8] Yet there is a tendency for pulses to gravitate toward event onsets in a way that produces (approximate) synchrony when a stimulus rhythm is purely periodic. Thus, we can say that pulse exhibits a *generalized synchrony* with musical rhythm.[10] Finally, strong and weak pulses alternate, forming stereotypical patterns called *metrical structures*, which can be described in terms of phase and frequency relationships among multiple frequency components. Frequency relationships among components are theoretically restricted to harmonics (e.g., 2:1, 3:1), subharmonics (e.g., 1:2, 1:3,),[8] and other simple integer ratios (e.g., 3:2, 4:3).[4]

Palmer and Krumhansl[11] 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. Their results implied that participants successfully recruited an endogenous pulse, and furthermore that pulses possessed differential accent strengths conforming to metrical patterns. Pulse also has a characteristic time scale, a tempo region that elicits optimal performance on tasks, such as tempo discrimination and perception–action coordination, which changes with age.[4,12–16] For adults, variability in interval perception and production increases with interval duration, following Weber's law between about 250 ms and 2000 ms[17–19]; outside this range variability increases disproportionately. One hundred milliseconds (10 Hz; 600 bpm) represents an extreme upper limit for pulse perception[20]; however, a recent study has found no clear lower limit.[21] For musical rhythms, tapped pulse can vary over this entire range, depending on many factors including musical style.[22] Finally, pulse is not strictly periodic. In musical performance, patterns of temporal fluctuation exhibit important relationships to musical structure,[23] and a recent analysis of inter-beat interval time series from expressive piano performances has revealed long-range ($1/f$ type) serial correlations and fractal scaling,[24] as is common in continuation tapping[25,26] and other biological and psychological time series.[27–30]

People spontaneously coordinate periodic motor activity with complex musical rhythms, a phenomenon defined earlier as generalized synchrony. For periodic sequences, synchrony is a stable state.[18] Antisynchrony is stable for lower movement rates; however, increases in rate induce a spontaneous switch to synchrony.[31] Listeners are generally able to coordinate periodic tapping with complex rhythmic patterns. However, level of syncopation is a good predictor of pulse-finding difficulty.[32–34] Syncopation causes more off-beat taps, more switches between on-beat and off-beat tapping, and higher inter-tap interval variability.[32,33] People are also able to adapt to phase and tempo perturbations of simple and complex rhythmic patterns. People respond quickly and automatically to phase perturbations of periodic sequences,[35–39] and while people are also able to adapt to tempo perturbations,[39] tempo tracking appears to be a controlled process, requiring active attending.[40,41] People are readily able to coordinate with temporally fluctuating musical performances,[42] and listeners may hear smoothed tempo maps,[43] an observation that is consistent with the hypothesis of tempo tracking.[44,45] However, it appears likely that listeners are also able to predict tempo changes in performed musical rhythms to a great extent.[24,46]

People report perceiving metrical accent even in unaccented periodic sequences. An isochronous series of tones of identical frequency and intensity is often heard as accented, such that strong pulses alternate with weak pulses, usually in 1:2 patterns, but sometimes in 1:3 or other patterns.[1,47,48] In other words, people spontaneously hear subharmonics of the rhythmic frequency that is presented. Vos[47] found a tendency to prefer 1:2, 1:4, and 1:8,

with subharmonics 1:3, 1:5, 1: 6, and 1:7 more rarely reported. Spontaneous structure has also been observed in synchronization tasks. Parncutt[49] presented isochronous tone sequences with various tempi to participants and asked them to tap along with the sequences in a regular way. For faster sequences, people tended to tap subharmonics of the event frequency that was presented, similar to the reported groupings in perceptual experiments.[47] Barnes and Jones reported a similar result in attentional facilitation, such that a 300-ms induction sequence primed time discrimination performance for a subharmonic interval (600 ms), whereas nonharmonically related induction sequences resulted in poorer performance.[50] Thus, people perceive, attend to, and produce subharmonic (metric) relationships, such as 1:2 and 1:3 spontaneously, in the absence of stressed stimulus events.

Metrical perception has also been implicated in coordination of behavior with complex rhythms.[39,51] When participants tapped the pulse of complex rhythms containing embedded phase and tempo perturbations—at different metrical levels on different trials—adaptation to perturbations at each tapping frequency reflected information from other metrical levels.[39] Moreover, phase perturbations at subdivisions (harmonics) perturb tapping responses, even when task instructions and stimulus design encourage listeners to ignore perturbations.[51] Such responses are observed even when subdivisions are introduced only in the cycle containing the perturbation. In addition, time and pitch discrimination judgments are thwarted when made in the context of metrically irregular sequences, providing evidence for the temporal targeting of attentional energy.[45,50,52–55] Thus, synchronization to complex rhythms is not merely a process of error correction, nor is it the exclusive purview of the motor system; rather, listeners attend to multiple levels of temporal structure under a wide variety of task conditions.

Finally, Bergeson and Trehub[56] 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 findings in adults,[57] thus supporting dynamic attending in infants. In two additional experiments Bergeson and Trehub[56] found that infants were able to detect changes in duple-meter, but not in 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.[58] Additionally, infants categorized melodies on the basis of contingencies between metrical position and tonal prominence. These findings could be explained by innate predispositions or rapidly learned preferences for auditory sequences that induce metric percepts, and for 1:2 over 1:3 temporal organization, as predicted by higher-order resonance in nonlinear systems (see Fig. 2C, below).

A Theoretical Framework

One possible explanation that accounts for the empirical observations is that pulse and meter arise as a result of neural oscillations resonating to rhythmic stimulation.[10] Interaction of excitatory and inhibitory neural populations can give rise to neural oscillation, illustrated schematically in Figure 1, showing the necessary synaptic connections between excitatory and inhibitory populations.[59–61] Many different mathematical models are available that can be used to describe neural oscillations, and the principal concern is to choose a level of mathematical abstraction that is appropriate for the type of data that are available. The following canonical model captures universal properties of neural oscillation, generic behaviors that are expected to be observed in all neural oscillators, despite differences in neurophysiology or network organization[62,63]:

$$\frac{dz}{dt} = z(\alpha + i\omega + (\beta + i\delta)\,|z|^2) + c\,s(t) + \text{h.o.t.} \tag{1}$$

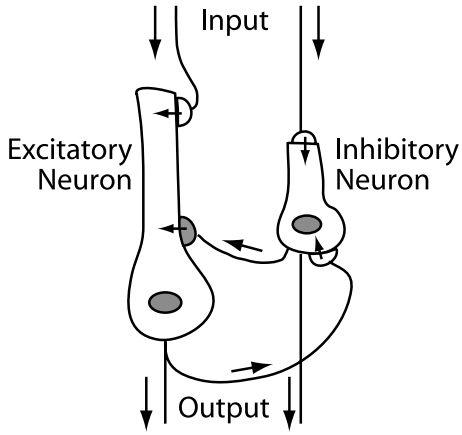

Figure 1. Neural oscillation. A neural oscillation can arise from the interaction between excitatory and inhibitory neural populations. (Adapted from Hoppensteadt and Izhikevich.[63])

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 discussed later. The transformation also produces higher-order terms (abbreviated h.o.t.) that are not presented in Equation 1, but are important in understanding the behavior of the system, as explained below. 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 1 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.

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

The polar formulation reveals 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 analysis of this model are described next.

Universal Properties

Universal properties of neural oscillation are revealed in the canonical form (Equations 1 and 2). These properties are generic, and thus are expected to be observed in all neural oscillators, despite differences in neurophysiology or network organization. The following focuses 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 2, with $s(t) = 0$]. In this case the oscillator can display two behaviors depending upon the bifurcation parameter, α. As illustrated in Figure 2A, 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. This bifurcation is called the Andronov–Hopf bifurcation. If one continues the expansion of higher-order terms (h.o.t.), one finds other bifurcations, such as the Bautin bifurcation,[64] that also lead to

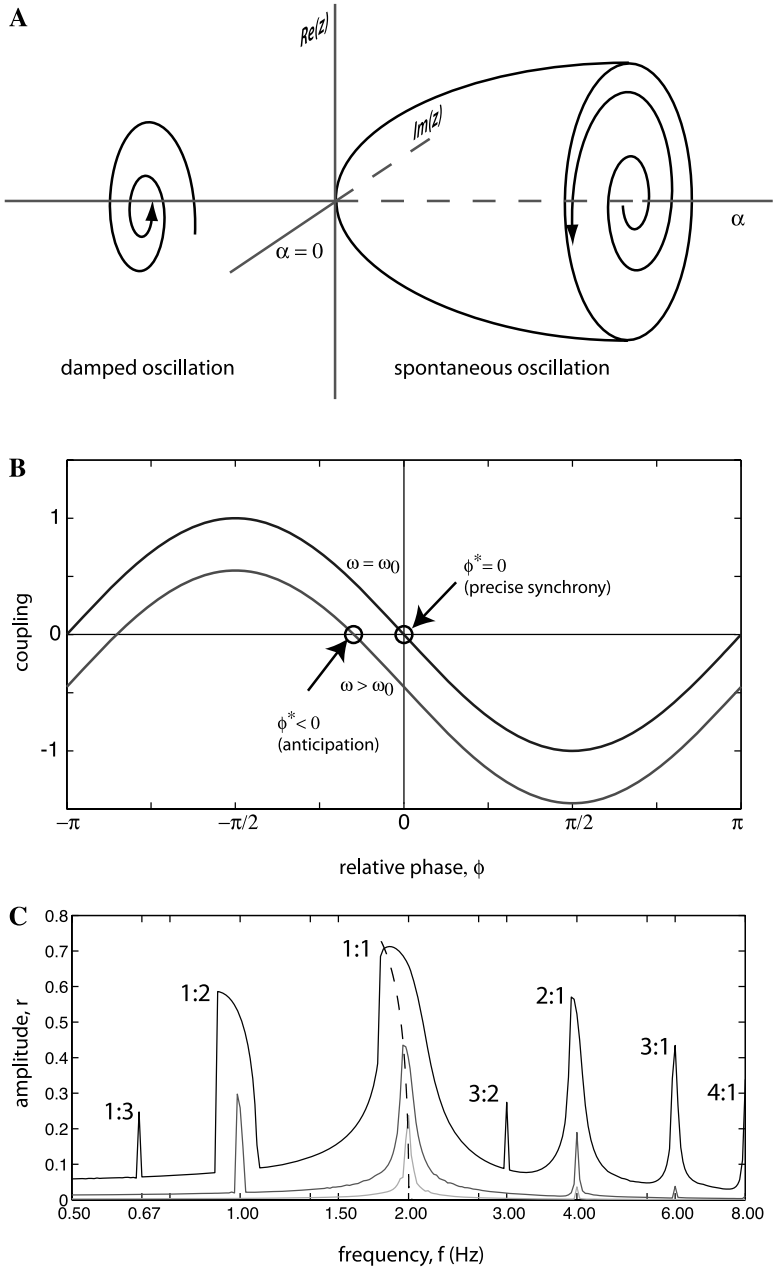

Figure 2. Three universal properties of nonlinear oscillation: spontaneous oscillation, entrainment, and higher-order resonance. (**A**) Spontaneous oscillation. When the bifurcation parameter crosses zero, a spontaneous oscillation is generated, as energy is added into the system. (**B**) Entrainment. Entrainment of phase is brought about by stimulus coupling. (**C**) Higher-order resonance. The amplitude response of a nonlinear oscillator bank stimulated with a sinusoid at 2 Hz, at three different amplitudes. (From Large.[10] Reprinted by permission.) (In color in *Annals* online.)

spontaneous oscillation. The capacity for spontaneous oscillation may explain the experience of endogenous periodicity,[11] and the ability of listeners to maintain a pulse after a stimulus ceases.[25]

Entrainment

When a stimulus is present, spontaneous oscillation continues; however, stimulus coupling affects the oscillation's phase. Figure 2B plots coupling as a function of relative phase (the phase of the oscillator relative to the phase of the stimulus) 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 1 and 2), and depicted in Figure 2B, 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.[18] 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, and the oscillation anticipates the stimulus. The capacity for 1:1 synchrony is observed in both linear and nonlinear models. Entrainment of nonlinear oscillators also predicts more general forms of synchrony. The terms that describe this behavior, however, are the higher-order terms of Equations 1 and 2. Higher-order terms describe the capacity for antiphase and multi-frequency (e.g., 1:2, 3:2, 3:1) modes of coordination with rhythmic stimuli, described in more detail next.

Higher-order Resonance

Figure 2C presents the results of three simulations of an array of nonlinear oscillators,[65] based on Equation 1, similar in concept to a bank of linear filters.[66,67] The frequencies of the oscillators in the array lie along a logarithmic frequency gradient, varying from 0.5–8.0 Hz, approximating the human range of pulse perception.[18] The stimulus is not a rhythm, but a sinusoid with a frequency of 2 Hz (period 500 ms); thus no frequencies other than 2 Hz are present in this stimulus. In these simulations, higher-order terms are included (abbreviated h.o.t. in Equations 1 and 2) to illustrate 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, excellent frequency selectivity is achieved. As stimulus amplitude increases, frequency selectivity deteriorates on account of 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, perhaps explaining the anticipation tendency.[18] Most importantly, oscillations arise at frequencies that are not present in the stimulus. This is because of nonlinear stimulus coupling, which is captured 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 at a given frequency 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.[47,49] 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.[65,68] Coupling between oscillators in a multifrequency network[45,69]

may also explain the subdivision effects that have been observed in synchronization experiments.[39,51]

Summary

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. The theory holds that listeners experience dynamic temporal patterns (i.e., pulse and meter), and that they 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 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 is not a computational theory in the sense that pulse and meter are held to be computed by special-purpose mechanisms. However, computer models of pulse and meter can be created based on the general theory.

Neural Correlates

Functional imaging studies support the notion that rhythmic information is represented across broad cortical and subcortical networks in a manner that is dependent upon task and rhythmic complexity.[70–73] It is known that metrical rhythms are easier to remember and reproduce than more syncopated rhythms,[74,75] and it has been observed that metrical rhythms result in characteristic patterns of functional brain activation.[70] Grahn and Brett[72] observed improved reproductions for metric rhythms, and observed that these rhythms also elicited higher activity in the basal ganglia and supplementary motor area, suggesting that these motor areas play a role in mediating pulse and meter perception. Chen *et al.*[73] showed that both performance and neural activity were modulated as musicians and nonmusicians tapped in synchrony with progressively more syncopated auditory rhythms. In perception, secondary motor regions were recruited in musicians and nonmusicians, while the dorsal premotor cortex appeared to mediate auditory–motor interactions. Of interest, the dorsal auditory pathway is implicated in rhythm performance, regardless of the modality in which the rhythms are trained and paced.[76] In short, both auditory and motor areas are implicated in both rhythm *perception* and rhythm *production*. A set of brain areas including the dorsal auditory pathway, dorsal premotor cortex, supplementary and pre-supplementary motor areas, the cerebellum, and basal ganglia are implicated. But what is happening in this distributed network, and are these results consistent with the hypothesis of neural resonance?

Using electroencephalography (EEG), Snyder and Large[77] observed that peaks in the power of induced beta- and gamma-band activity 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 brain activity matched the main predictions for pulse and meter. Zanto *et al.*[78] tested the synchrony of high-frequency activity 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 that observed in motor synchronization studies,[37,39] and asymmetric responses were observed to early versus

late tones (cf. Refs. 54 and 79) Moreover, recent magnetoencephalography studies have found subharmonic rhythmic responses in the beta-band when subjects were instructed to impose a subjective meter on a periodic stimulus,[80] and anticipatory beta-band responses for periodic and metrical sequences, but not for randomly timed sequences in primary auditory cortex.[81] Thus beta- and gamma-band responses to auditory rhythms in EEG and MEG correlate with predictions of neural resonance. Oscillatory brain activity as a neural correlate of temporal expectancy is in line with previous results from a variety of perceptual and cognitive experiments, suggesting that this type of brain activity can reflect object representations as opposed to mere sensory encoding of stimulus features.[82]

To date, computational simulations of neural resonance to rhythm have been derived from mathematical models of single-neuron action potentials or from models of alternating excitatory and inhibitory activity. As observed by Eck,[79] the timescale of such neural processes may not provide a good match to the time scale of musical pulse and meter. Therefore, it is necessary to consider whether neural resonance is truly a plausible theory of pulse and meter. A clue to the answer may come from the above EEG and MEG findings of beta- and gamma-band activity that anticipate rhythmic sequences.[77,78,80,81] Such observations could indicate bursts of activity in cortical neurons, which can also arise from a neural circuit such as that illustrated in Figure 1.[61] Moreover, bursts of high-frequency activity could explain communication between different cortical areas.[83] For example, oscillatory activity in the beta range is widely observed in sensorimotor cortex in connection with motor behavior in humans[84,85] and nonhuman primates.[86–89] Synchrony of beta oscillations is often observed between different areas of sensorimotor cortex,[87,88] and between motor cortical and muscle activity.[87] Moreover, synchronized beta oscillations may bind multiple sensorimotor areas into a large-scale network during motor behavior and carry causal influences from primary somatosensory and inferior posterior parietal cortices to motor cortex.[83] We propose that anticipatory rhythmic bursts of beta activity may enable communication between auditory and motor cortices in rhythm perception and motor coordination. Rhythmic bursts of higher-frequency gamma activity may also enable functional communication between different cortical regions.

Bursting is a dynamic state where neurons repeatedly fire groups, or *bursts*, of action potentials, and each burst is followed by a period of quiescence before the next occurs.[61] Interburst periods, the time interval between one burst and the next one, are 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 bursting is not currently available. Nevertheless, burst oscillation is currently receiving a great deal of attention in the computational neuroscience literature, and mathematical analyses have shown that bursting displays key properties we have relied upon to predict pulse and meter.[61,90] Figure 3 shows a computational simulation of burst oscillation[91] responding to a simple rhythm, displaying both entrainment to the sequence and persistence in the absence of a stimulus event. Thus, two timescales would be involved: the timescale of the high-frequency oscillations that underlie coordination between different neural areas, and the timescale of the rhythmic bursting that underlies coordination with the rhythmic stimulus. The picture that emerges is one of rhythmic communication, via bursts of high-frequency activity, between different neural areas as they resonate to rhythmic patterns.

Future studies should determine whether communication between auditory and motor areas during rhythm perception and production occurs through inter-area synchronization of beta activity of the type observed recently.[77,78,80,81] Such a finding could help explain activation of sensory and motor

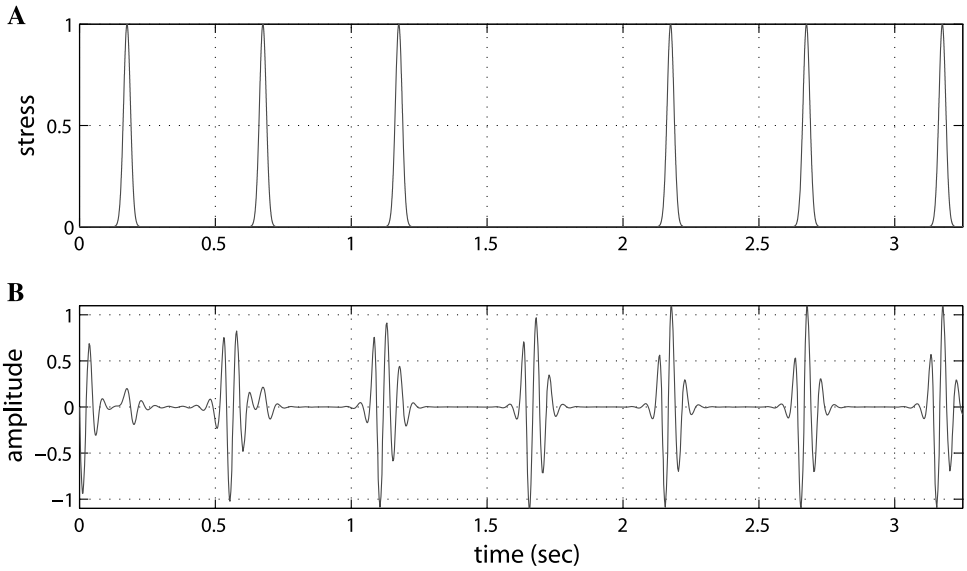

Figure 3. Response of a burst oscillator[91] to a rhythmic pattern. (**A**) Continuous time series representation of event onsets. (**B**) Bursts of activity entrain to the stimulus and are observed in the absence of a stimulus event. (From Large 2008.[10] Reprinted by permission.) (In color in *Annals* online.)

areas in rhythm perception and production tasks.[70–73,76] Mathematical and computational analysis of distributed bursting models could establish generic predictions (or families of predictions[61]) for patterns of spatiotemporal neural activity, depending on task, stimulus modality and so forth. Complementary neuroimaging techniques could identify temporal activity in distributed neural areas, as well as patterns of causal interactions between areas.[83] Such a research program has a realistic chance of identifying—perhaps for the first time—precise correlates of dynamic neural activity underlying a well-studied cognitive phenomenon. Such oscillations may embody dynamic attending to a rhythmic stimulus, such that the oscillations at both timescales serve to configure the neural network responsible for responding in a given task situation.

Acknowledgments

We gratefully acknowledge the support of the Air Force Office of Scientific Research (Grant FA9550-07-C0095), and the J. William Fulbright Foreign Scholarship Board in support of E.W.L.

Conflicts of Interest

The authors declare no conflicts of interest.

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