Neural Mechanisms of Rhythm Perception: Current Findings and Future Perspectives

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Abstract

Perception of temporal patterns is fundamental to normal hearing, speech, motor control, and music. Certain types of pattern understanding are unique to humans, such as musical rhythm. Although human responses to musical rhythm are universal, there is much we do not understand about how rhythm is processed in the brain. Here, I consider findings from research into basic timing mechanisms and models through to the neuroscience of rhythm and meter. A network of neural areas, including motor regions, is regularly implicated in basic timing as well as processing of musical rhythm. However, fractionating the specific roles of individual areas in this network has remained a challenge. Distinctions in activity patterns appear between ''automatic'' and ''cognitively controlled'' timing processes, but the perception of musical rhythm requires features of both automatic and controlled processes. In addition, many experimental manipulations rely on participants directing their attention toward or away from certain stimulus features, and measuring corresponding differences in neural activity. Many temporal features, however, are implicitly processed whether attended to or not, making it difficult to create controlled baseline conditions for experimental comparisons. The variety of stimuli, paradigms, and definitions can further complicate comparisons across domains or methodologies. Despite these challenges, the high level of interest and multitude of methodological approaches from different cognitive domains (including music, language, and motor learning) have yielded new insights and hold promise for future progress.

Keywords: Rhythm; Functional magnetic resonance imaging; Magnetoencephalography; Electroencephalography; Music; Auditory; Timing; Neuroscience

1. Introduction

Research into rhythm has been approached/advanced with a variety of methodologies, including behavioral work in humans and animals, modeling, functional magnetic resonance

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imaging (fMRI), electroencephalography (EEG), and magnetoencephalography (MEG) techniques. Approaches from many domains (music, hearing, language, timing, and motor control) have led to a rich literature with relevance to rhythm and the underlying timing processes. I will consider the definitions, basic models, and latest experimental findings, focusing on neuroscientific methods, and the current state of understanding in musical rhythm. Finally, I will highlight the difficulties facing the field and how improved definitions and consensus will be crucial to moving forward.

2. Definitions

As the vocabulary used to describe important aspects of rhythm and timing is often used in different ways, I will begin by clarifying how they are used in this article. *Rhythm* is defined as the pattern of time intervals in a stimulus sequence. The rhythmic pattern is generally indicated by the onset of a stimulus (a tone, click, or other sound), and the time between onsets (interonset intervals) generally defines the lengths of the temporal intervals in the sequence. Often, listening to a musical rhythm gives rise to a sense of *pulse*, sometimes termed the *beat*. The pulse or beat is a series of regularly recurring psychological events that arise in response to a musical rhythm (Cooper & Meyer, 1960; Large, 2008). The time interval between beats is called the *beat period*, and it relates to *tempo*, the rate of the beat: A shorter beat period leads to a faster tempo. Although a sense of beat arises in response to a rhythmic stimulus, it is not purely defined as a stimulus property: Beat perception is a psychological response (Benjamin, 1984; Lerdahl & Jackendoff, 1983; London, 2004; Palmer & Krumhansl, 1990). For example, beats do not always have to coincide with stimulus onsets (as evidenced by our ability to mentally continue the beat through gaps or breaks in music). *Meter* refers to the temporal organization of beats, in which some beats are perceived as more salient than others, on multiple time scales (Epstein, 1995; Lerdahl & Jackendoff, 1983). For example, in a march rhythm, every other beat is accented (**1** 2 **1** 2), whereas for a waltz it is the first of every three beats (**1** 2 3 **1** 2 3). These patterns therefore differ in their perceived meter: The ''1''s are ''strong'' beats, and the others are ''weak'' beats. If we compare the time between each beat (regardless of strength) to the time between each strong beat, we have two levels of a *metric hierarchy.* Beats at each level of the hierarchy periodically coincide, but beats at lower levels of the hierarchy are at a faster tempo than beats at higher levels. *Meter perception* refers to our perception of the metric hierarchy: We perceive the pattern of strong and weak beats.

Entrainment (considered in more detail below) refers to the process of synchronizing our internal rhythmic processes to external regular, or periodic, cues (often the ''beats'') in stimuli. The internal rhythmic processes are usually characterized as *oscillators* with particular temporal frequencies (called *periods*). Stimulus onsets that occur at expected times are said to be ''in phase'' with the internal oscillator, whereas onsets that occur before or after the expected time are ''out of phase.''

3. Theories of timing

From a bottom-up perspective, timing is a logical place to begin investigating the neural instantiation of rhythm processing. Timing processes have been widely investigated in movement, language, perception, and memory (Eagleman et al., 2005; Ivry & Spencer, 2004; Mauk & Buonomano, 2004). The temporal range that is most relevant for rhythm are ''short'' time intervals, ranging from ∼200 to 2,000 ms (London, 2004). A number of theories of short interval timing exist with components that can be tested for their instantiation in the brain. However, despite this potential, there is still little consensus about the best way to model timing, with different researchers approaching theoretical timing models in different ways.

There are two popular classes of timing models for short intervals: interval models and entrainment models (for comprehensive reviews, see Grondin, 2010; McAuley, 2010). Interval models generally comprise three components: a clock that estimates duration, a reference memory that stores that duration, and a comparison mechanism to compare new durations to durations in the reference memory (Church & Broadbent, 1990; Gibbon, 1977; Treisman, 1963). Scalar expectancy theory (SET) is one of the most influential conceptualizations of an interval model (Church, Meck, & Gibbon, 1994; Gibbon, 1977; Gibbon, Church, & Meck, 1984; Rakitin et al., 1998). In SET, the clock is a neural ''pacemaker'' that continually emits pulses. Stimuli that mark the beginning of the to-be-timed interval trigger the closing of a gate that allows pulses to enter an accumulator. At the end of the interval, the gate opens. The number of pulses in the accumulator represents the code for the interval duration. More recent formalizations of interval models have replaced the pacemaker–accumulator conception of the clock with ''process-decay models,'' which track the decay of neural activity following signal onset, or oscillator/coincidence-detection models. The latter posit a collection of neural oscillators, each with a fixed oscillatory period. The oscillators are all synchronized by signal onset, then a ''coincidence-detector'' detects a specific combination of the periodic neural events (e.g., a measurement of each oscillator's phase) at the end of the duration. Durations are thus encoded by associating this combinatorial neural activity code with a particular duration (Church & Broadbent, 1990; Matell & Meck, 2000). Many of the tasks that have been used to test interval models involve judgments about ''standard'' and ''comparison'' pairs of intervals that are of an arbitrary length. In addition, much of the data for these models comes from the animal literature, and therefore the principles may not fully explain the range of more complex timing behaviors (such as tapping along to a rhythm) exhibited in humans.

In summary, interval models generally have an internal clock that is started and stopped by external stimulus onsets. The duration is stored in reference memory as a code, and each duration code is independent from other duration codes that are stored. To make timing comparisons, the duration codes for individual intervals are explicitly compared.

An alternative to interval models are entrainment models. Their basic assumption is that the timekeeper consists of one or more self-sustaining, entrainable oscillators that peak in amplitude at regular time intervals (Large & Jones, 1999; McAuley & Kidd, 1998). The time between peaks is the period of the oscillator, and it provides a referent for making judgments about timing. Peaks in amplitude represent expected time points for stimulus onsets, and

onsets can be on time, earlier, or later than expected. The oscillators in entrainment models do not have fixed, inflexible periods, and therefore should not be confused with the bank of fixed-period oscillators posited to fulfill the clock function by some interval-timing models described in the previous paragraph.

In the literature, entrainment models have been referred to as ''beat-based'' models; however, this is a misnomer. Beat-based models are a separate class of models that, like entrainment models, rely on oscillators with a specific period. However, they do not adjust their phase or period, or entrain in the true sense. The initial stimuli ''set'' the period and phase, and the oscillator cannot adjust if later stimuli are no longer in phase.

Entrainment models differ from interval models in several ways. First, in entrainment models, stimulus onsets will advance or delay an oscillator rather than start or stop an internal clock. Second, time intervals are represented implicitly by the oscillator's period rather than explicitly as a stored code. Third, successive duration estimates are not independent but depend on the oscillator's response to the previous stimulus onsets. Finally, with respect to duration/timing judgments, interval models involve explicit comparison of two stored duration codes, whereas entrainment models involve a comparison of stimulus onset relative to the oscillator phase.

A strength of the entrainment approach is that it accounts for effects of context: that is, how judgments of time intervals can be influenced by the events occurring prior to the time judgment (Point 3, above). This is supported by behavioral data showing that even when participants are explicitly told to ignore prior context intervals (e.g., ignoring a series of beeps that precede two final to-be-timed beeps), their judgments appear to be implicitly influenced by them. Entrainment model approaches have arguably also had more success in capturing ways that higher level features of temporal patterns, such as pulse and meter, can arise from the responses of entrainable neural oscillators to rhythmic stimuli (Large, 2000, 2008; Large & Kolen, 1994).

3.1. Neuroscience of timing

Studies on the neuroscience of timing measure brain responses to different dimensions. Commonly tested dimensions are as follows: attending to temporal versus nontemporal aspects of stimuli, use of subsecond versus suprasecond interval lengths, and perceptual (discrimination) versus motor (tapping) tasks. Generally, the stimuli and responses involve timing of single intervals (sometimes produced repeatedly), without considering rhythmic patterns composed of different time intervals or the temporal context in which these intervals occur.

Functional neuroimaging studies, as well as studies of brain-damaged patients, have linked components of timing processes to several cortical and subcortical regions, including the cerebellum, basal ganglia, parietal cortex, prefrontal cortex, premotor cortex, and supplementary motor area (SMA; Ferrandez et al., 2003; Macar, Anton, Bonnet, & Vidal, 2004; Nenadic et al., 2003; Rao, Mayer, & Harrington, 2001; Rao et al., 1997). Many of these areas are also traditionally thought to be involved in various aspects of movement. For example, the basal ganglia are a group of structures deep in the brain that have a role in

motor control, action selection, and learning (Graybiel, 2005; Graybiel, Aosaki, Flaherty, & Kimura, 1994; Mink, 1996; Redgrave, Prescott, & Gurney, 1999). The cerebellum allows coordination and fine-tuning of movement by integrating sensory and motor information (Diedrichsen, Criscimagna-Hemminger, & Shadmehr, 2007; Gao et al., 1996; Thach, 1998). Premotor area and SMA are strongly interconnected with the basal ganglia and cerebellum, and have roles in planning, voluntary control, and execution of movement (Boecker et al., 1998; Catalan, Honda, Weeks, Cohen, & Hallett, 1998; Gerloff, Corwell, Chen, Hallett, & Cohen, 1998; Grafton, Fagg, & Arbib, 1998; Picard & Strick, 1996). Several theories have been proposed to dissociate the different roles of these commonly activated motor areas in timing processes.

One approach to dissociating different motor area roles has been to compare the neural responses for directing attention to the temporal features of a stimulus (e.g., attending stimulus duration instead of stimulus pitch or color) versus directing attention to a particular point in time (e.g., expected time of stimulus appearance). The difference between this ''temporal orienting'' and ''temporal expectation'' has been investigated with cueing paradigms (Coull, 2004; Coull & Nobre, 1998). In an example of a temporal orienting paradigm, participants monitor a circle that appears for a particular duration, continuously changing color between red and blue. Subjects are cued to attend to the color or the duration. When directing attention to time (but not to color), the pre-SMA, premotor cortex, and basal ganglia were more responsive, suggesting these areas are involved in orienting to time. To measure temporal expectation, participants respond as quickly as possible to targets that are preceded by cues. The cues either correctly (''valid'') or incorrectly (''invalid'') predict the time of appearance of the upcoming target. Based on the cue, participants orient to that expected point in time, and when directing attention in this way, the left parietal cortex is active. This may be relevant to studies of entrainment showing that greater attention is allocated to times of pulse expectancy (Jones, Johnston, & Puente, 2006); the pulse expectancy may be mediated by the parietal cortex.

Another distinction has been made between systems required for the timing of suprasecond and subsecond durations (Ivry & Spencer, 2004; Lewis & Miall, 2003). In this framework, ''cognitively controlled'' timing, reliant in part on the basal ganglia, is the ''measurement of supra-second intervals not defined by movement and occurring as discrete epochs.'' This is contrasted with ''automatic'' timing, which relies on the cerebellum and involves ''the continuous measurement of predictable sub-second intervals defined by movement'' (Lewis & Miall, 2003). The distinction may be somewhat too simple, as subsecond timing can still require large amounts of cognitive control (e.g., during learning) and motor responses to suprasecond time intervals can be learned and become automatic. In addition, motor and perceptual mechanisms may be at least partially shared, as mentioned earlier. The distinction does, however, capture the intuitive sense that the timing of longer intervals is more cognitively demanding and less apt to induce movement than timing of shorter intervals, and aspects of the distinction are supported by reviews of the neuroimaging literature (Rammsayer & Ulrich, 2005; Wiener, Turkeltaub, & Coslett, 2009).

Finally, much timing research has focused on the specific role of subcortical areas, particularly the cerebellum and basal ganglia. Neuroimaging studies involving a variety of

different temporal tasks (memory-timed finger movement, tapping in response to temporally unpredictable stimuli, duration discrimination) show cerebellar activity (Kawashima et al., 2000; Lutz, Specht, Shah, & Jäncke, 2000; Teki, Grube, Kumar, & Griffiths, 2011), and a recent review suggests the cerebellar response is exclusive to subsecond intervals (Wiener et al., 2009). The basal ganglia are also directly involved in timing tasks. Patients with Parkinson's disease (who have impaired basal ganglia function) show impaired duration discrimination, time estimation, and synchronized finger tapping ability (Artieda, Pastor, Lacruz, & Obeso, 1992; Elsinger et al., 2003; Harrington, Haaland, & Hermanowitz, 1998; Malapani et al., 1998; Pastor, Artieda, Jahanshahi, & Obeso, 1992). Further confirmation comes from neuroimaging studies that show the basal ganglia are active in similar tasks to those that Parkinson's patients show deficits in, such as time estimation (Nenadic et al., 2003), duration discrimination (Ferrandez et al., 2003), and tapping intervals from memory (Lewis, Wing, Pope, Praamstra, & Miall, 2004; Rao et al., 1997).

Despite the fact that some temporal tasks appear to activate both the basal ganglia and the cerebellum, a series of recent studies provides evidence for a dissociation between interval-based (referred to by the authors as ''absolute'') and beat-based (''relative'') timing (Grube, Cooper, Chinnery, & Griffiths, 2010; Grube, Lee, Griffiths, Barker, & Woodruff, 2010; Teki et al., 2011). A variety of temporal discrimination tasks involving subsecond intervals were used (single interval duration discrimination, regularity detection, detections of deviation from isochrony, and rhythm discrimination). Some of these tasks permitted relative timing and some relied instead on the timing of arbitrary intervals without a beat context. fMRI showed greater cerebellar activity for absolute timing relative to relative timing, and greater basal ganglia activity for beat-based timing relative to absolute timing (Teki et al., 2011). They confirmed the role of the cerebellum by testing patients with cerebellar damage (Grube, Cooper, Chinnery, & Griffiths, 2009) as well as healthy participants who received transcranial magnetic stimulation (Grube, Lee, et al., 2010) over the cerebellum that temporarily impaired cerebellar function. Reduced performance was observed only for absolute timing tasks, not tasks that could use relative or beat-based timing. Thus, the cerebellum appears to be involved in the timing of arbitrary, subsecond intervals, consistent with a role in interval timing.

3.2. Theories of rhythm

Now we consider some of the approaches to modeling of rhythm. An important distinction in various models of rhythm is between the processing of rhythms that permit a metric coding (e.g., beat-based) and those that only afford a figural (grouping-based) coding (Essens & Povel, 1985; Hébert and Cuddy 2002; Povel & Essens, 1985). Povel and Essens (1985) refer to the former as metrical patterns and to the later as nonmetrical patterns. Much of the work on modeling of rhythm perception has focused on the induction of a beat and the perception of metrical structure (i.e., metric coding). These models range from rule-based approaches (Desain & Honing, 1999; Longuett-Higgins & Lee, 1982; Povel & Essens, 1985) to entrainment perspectives (Eck, 2002; Large & Jones, 1999; Large & Kolen, 1994).

An excellent summary of these approaches is found in McAuley (2010); some key points are summarized below.

Rule-based models of rhythm share some similarities with interval theories of timing. Rule-based models of rhythm tend to assume that people process rhythms by structuring their mental representation according to an internal clock. This internal clock is assumed to involve a pacemaker–accumulator mechanism that ticks out regular intervals that are aligned with particular stimulus onsets that correspond to beats.

One prominent rule-based model is the three-stage clock model of Povel and Essens (1985). In the first stage, accents (tone onsets with increased salience) are assigned to certain notes of the rhythm according to a set of rules (Povel & Okkerman, 1981). These rules are that accents occur on (a) temporally isolated tones, (b) the second in a group of two tones, and (c) the first and last tone in a run of three or more tones (Povel & Essens, 1985; Povel & Okkerman, 1981). In the second stage, all the intervals that ''fit'' with the accents in the rhythm (clock intervals) are generated. Some limits are applied (e.g., clocks that don't divide evenly into the rhythm or are very long). Finally, in a ''matching'' stage, the amount of counter (negative) evidence is calculated for each of the possible clock intervals, and the clock with the least negative evidence is determined to be the most likely induced beat. Negative evidence consists of clock pulses (predicted beats) falling on unaccented tones or during silence. In support of their model, Povel and Essens found that rhythms with ''best clocks'' that had less negative evidence were reproduced more accurately and judged to be simpler than rhythms with best clocks that had more negative evidence (Essens & Povel, 1985; Povel & Essens, 1985).

An overlooked factor in clock models is the role of repetition, as repetition of rhythmic patterns contributes to the perception of metrical structure (Temperley & Bartlette, 2002; but cf., Temperley, 2001). Also, the use of negative evidence heuristics versus positive evidence heuristics can lead to different predictions by clock models. Models that use negative evidence to determine clock likelihood tend to favor longer clock intervals: The longer the clock interval, the fewer instances of counter-evidence that can be accumulated (Povel & Essens, 1985). Models that favor positive evidence tend to favor shorter clock intervals: The shorter the clock interval, the more instances of onsets that coincide with the proposed clock that can be accumulated (Parncutt, 1994). Finally, another weakness of the internal clock approach is that it does not operate in real time and is therefore unable to make adaptive, online predictions during rhythm presentation. Instead, the models must consider the fit of all possible clocks across the entire rhythm before settling on a solution.

Real-time models have been created, however, mostly from an entrainment perspective (Eck, 2002; Large & Kolen, 1994; Large & Palmer, 2002; Toivanen & Snyder, 2003). These approaches model the entrainment of multiple self-sustaining internal oscillators to periodicities (e.g., different levels of the metric hierarchy) in the rhythm. Some newer entrainment models directly model the oscillators as neural oscillators in the brain (Large & Snyder, 2009). Neural oscillations in the brain result from the interaction of excitatory and inhibitory neural populations and are indicative of information processing (through communication between neurons) in the brain. The measure that is oscillating (periodically increasing and decreasing) is neural excitation or activity. The activity of different populations of neurons

can oscillate at different periods, and these periods can entrain to different levels of the metrical hierarchy. This ''neural resonance'' approach, with neural oscillators resonating to rhythmic stimuli, naturally gives rise to properties such as pulse and meter, which are aspects of rhythms that have not been easily accounted for by other types of models (Large & Snyder, 2009). The plausibility of this approach is supported by recent work (Sumbre, Muto, Baier, & Poo, 2008), which shows that a rhythmic stimulus can entrain neuronal groups, and that the neurons carry on responding at the entrained interval after the stimulus has stopped, exhibiting a ''memory'' of the interval. When exposed to the entrained interval, zebrafish larvae show correlations between their neural activity and tail-flipping behavior. Thus, even for primitive animals, neural entrainment to a stimulus can give rise to rhythmic behavior.

4. Neuroscience of rhythm

Despite the obvious relationship between time intervals and rhythms (sequences of time intervals), some prominent differences prevent straightforward application of basic timing models to rhythm processing. Rhythms are composed of multiple intervals, often of different durations, whereas most models of timing focus on single durations. In addition, in timing, the subsecond/suprasecond distinction is used in many studies, and recent attempts have been made to link this distinction to a larger one: distinguishing cognitively controlled and automatic timing mechanisms (Lewis & Miall, 2003), thought to activate different networks in the brain. Rhythm perception, however, requires perception of intervals in both categories, as durations in rhythm can span from approximately 100 ms to 2 s (Parncutt, 1994; Warren, 1993). In addition, some rhythms elicit perception of salient periodicities at different metric levels (metrical hierarchies), and these periodicities also span the subsecond and suprasecond domain. Therefore, the distinction used in timing investigations may be too simple for useful application to rhythm processing, or perception of musical rhythm may require integration of automatic and cognitively controlled processes.

4.1. fMRI studies

To move on from investigating single durations or supra- versus subsecond distinctions in basic timing research, several recent neuroimaging experiments have investigated perception and reproduction of musical rhythms. These studies generally show substantial overlap with the timing literature of activated brain areas: premotor cortex, SMA, cerebellum, and the basal ganglia (Bengtsson et al., 2009; Chen, Penhune, & Zatorre, 2008; Grahn & Brett, 2007; Lewis et al., 2004; Mayville, Jantzen, Fuchs, Steinberg, & Kelso, 2002; Schubotz & von Cramon, 2001; Ullén, Forssberg, & Ehrsson, 2003). The overlap may suggest that rhythm processing shares neural substrates with timing, and that the two processes are not completely independently mediated in the brain. There is also convergent neuroimaging evidence in support of behavioral data (Ivry & Hazeltine, 1995) for similarities in the mechanisms underlying perception and production of rhythm, as similar activations have been observed across studies

of perception and production (Schubotz, Friederici, & von Cramon, 2000). However, a word of caution is warranted: Overlapping activation in fMRI studies can arise from activation of different (but interleaved) neural subpopulations in the same brain region, so overlapping activation cannot be taken as conclusive evidence of genuine overlapping function (Peelen, Wiggett, & Downing, 2006). Newer fMRI analysis techniques, such as multivariate pattern analysis and representational similarity analysis (Kriegeskorte, Mur, & Bandettini, 2008), or paradigms using ''neural adaptation'' (Henson & Rugg, 2003; Sammler et al., 2010) are potentially sensitive to neural differences at the finer spatial scale of neural populations and represent worthwhile future avenues of investigation.

A key part of rhythm perception is perception of the beat. One proposal that has been made posits a basal ganglia role in generating an internal sense of pulse, or ''feeling the beat.'' Two fMRI studies examining beat perception reported that basal ganglia activity increased for regular rhythms that induced perception of a beat compared with similar rhythms that did not induce a beat (Grahn & Brett, 2007; Grahn & Rowe, 2009). A follow-up study in Parkinson's disease patients (for whom basal ganglia function is impaired) found a specific impairment in discriminating changes in the same beat-inducing rhythms (Grahn & Brett, 2009). Further evidence for a basal ganglia role in generating an internal sense of pulse comes from studies comparing auditory and visual rhythms. In general, visual rhythms (e.g., squares flashing on a screen) do not easily evoke a sense of the beat in the way that auditory rhythms do. However, when a visual rhythm is presented *after* the same rhythm is presented auditorily, a sense of beat can be induced for the visual rhythm (McAuley & Henry, 2010), possibly by relying on an internal representation of the beat that was formed during the auditory presentation. A recent fMRI study compared brain responses with visual rhythms presented either after or before similar auditory rhythms to examine the difference between visual rhythms that were perceived to have a beat and visual rhythms that were not perceived to have a beat. Activity in the basal ganglia during visual rhythm presentation significantly predicted whether that visual rhythm induced a beat (Grahn, Henry, & McAuley, 2011), suggesting that the basal ganglia may be responsible for beat perception across different modalities.

A final concept that is emerging from the neuroimaging literature is that rhythm perception relies on interactions between the auditory and motor systems. At least two studies have found increased coupling (representative of greater interaction or communication) of neural activity between auditory and premotor cortex during rhythm processing (Chen, Zatorre, & Penhune, 2006; Grahn & Rowe, 2009). Auditory–motor coupling may also be influenced by musical training. Chen et al. (2008) found that although left hemisphere auditory–motor coupling was present in musicians and nonmusicians, only musicians showed significant coupling in the right hemisphere. Grahn and Rowe (2009) found greater coupling was stronger for musically trained individuals in both hemispheres.

4.2. MEG/EEG studies

EEG and MEG studies are particularly relevant to rhythm and meter processing as they have better temporal resolution than fMRI studies. Several studies have tested for distinguishable

neural components related to meter processing and rhythm processing. One approach entails changing a repeating rhythmic sequence in order to either disrupt the rhythmic pattern but leave the overall metrical structure (pattern of ''strong'' and ''weak'' beats) intact, or to change the metric structure but leave the surface rhythm as similar as possible. For example, Geiser, Ziegler, Jancke, and Meyer (2009) measured event-related potential (ERP) responses to changes in meter perception by inserting or deleting a note from a repeating rhythm, which shifted the metric structure from having a regular pattern of strong and weak beats to an irregular pattern of strong and weak beats. The changes in the surface *rhythm*, on the other hand, were created by substituting two faster notes in the place of one slower note without shifting the pattern of strong and weak beats (the metric structure). A less technical illustration of these types of shifts may be the two approaches that are possible when singing the Happy Birthday song to someone with a very short name (Mary) and a very long name (Englebert Humperdink). One can sing each syllable at the same rate for both names, therefore requiring more time to sing the long name and adding extra beats to the song (changing the meter). Or one can speed up the syllable rate of the long name to fit it in the same space of time as the short name (substituting lots of fast notes in for two slower ones, changing the rhythm, but not the meter). Returning to the experiment, participants therefore heard a continuously repeating rhythm that occasionally had a metric change or a rhythmic change. The experimenters manipulated participants' attention by having them either press a button to the meter and rhythm changes, or press a button to pitch changes that were unrelated to the meter and rhythm. Rhythmic and metric perturbations were always present, but neural responses could be examined when these perturbations were attended (rhythm/meter task) or not attended (pitch task). In agreement with previous work (Jongsma et al., 2005; Vuust et al., 2005), they found a negative ERP component about 100–150 ms after the perturbation. In the *rhythm* condition, this deflection occurred regardless of participants' focus of attention. Metric changes, however, only elicited the negative deflection when they were attended. The authors suggest that encoding of metrical hierarchies is more complex and attention-demanding than encoding of surface rhythmic patterns. One caveat, however, is that the meter violations in this study were more difficult to detect than the rhythmic violations (particularly for nonmusically trained participants). It is therefore possible that the detection of this particular type of metric violation requires more attention, not all metric encoding per se.

In fact, using a different paradigm, Ladinig, Honing, Haden, and Winkler (2009) showed that a metric representation *was* present even when participants were not attending. In their paradigm, participants heard repeating rhythms, but instead of changing the rhythms, omissions occurred (silent gaps in the music where a note should have been). The gaps occurred either where metrically strong beats or where metrically weaker beats should have been. Acoustically, the two types of omission are identical (they are both silence), but if participants have a metric representation, then the omission of the metrically strong beat should be more salient than omission of the metrically weak beat. Behaviorally, the authors found this to be the case: Participants were better at detecting omissions of strong beats than weak beats when asked to respond when they occurred. In addition, they found a larger ERP

change (in the mismatch negativity component) for the strong beat omissions relative to the weak beat omissions. This was maintained even when participants were told to ignore the rhythms and instead listen to white noise presented at the same time, and respond when the white noise changed in intensity. Having a moderately challenging task that requires attention to a different auditory stream is a much stronger control condition than directing attention to different aspects of the same stream (or watching a silent movie, which is often used to direct attention away from stimuli in ERP studies). However, even with this strong control, the authors find that metric representations do not require attention to be formed, thus reaching a different conclusion from Geiser et al. (2009). These two studies highlight how paradigm and stimulus differences can lead to empirically supported but opposite conclusions.

One key consequence of listening to rhythm is the setting up of psychological expectancy. We expect salient events to occur more often ''on the beat'' than ''off,'' and we make predictions about how rhythmic patterns will continue on the basis of what has come before. The neural components elicited by violation of rhythmic expectancy were recently investigated using MEG, which is similar to EEG but measures magnetic field changes instead of electrical changes that result from neural firing (Vuust, Ostergaard, Pallesen, Bailey, & Roepstorff, 2009). Participants listened to repeating rhythms that sometimes contained salient violations of rhythmic expectancy. The researchers expected to observe event-related components reflecting error processing (induced by the violation of expectancy) and a separate component related to subsequent (re)evaluation of the internal model of the rhythmic sequence. The error term was predicted to be encoded by the mismatch negativity component (MMNm). As evaluation should occur after the error, the authors predicted that after the MMNm, they would observe a P3am component, usually associated with the evaluation of a change for subsequent behavioral action. Their predictions were confirmed: A mismatch negativity (MMNm) and a subsequent P3am component were both observed and were strongest for the condition with the biggest expectancy violation. Consistent with behavioral work (Kung, Tzeng, Hung, & Wu, 2011; Palmer & Krumhansl, 1990) and ERP work (Geiser, Sandmann, Jancke, & Meyer, 2010; Jongsma, Quiroga, & van Rijn, 2004), musicians showed greater sensitivity than non-musicians; musicians showed responses for milder violations, with larger, earlier MMNm peaks. The authors suggest this reflects a better internal representation of the metrical structure in the musicians that enables them to make more precise predictions about incoming stimuli. Their brains therefore respond more strongly and more quickly than nonmusicians' brains to any deviation from their predictions.

Investigations of neural oscillatory processes in the rhythm domain have revealed interesting changes in neural oscillations in the higher frequency beta (13–30 Hz) and gamma (>30 Hz) ranges. As mentioned earlier, the neural oscillations are thought to reflect communication between different brain regions and are modulated by various sensory and cognitive processes. For example, oscillations in the beta band have been strongly associated with motor tasks and are observed in sensory and motor cortices (Salmelin, Hamalainen, Kajola, & Hari, 1995), as well as basal ganglia and cerebellum (Baker, 2007; Salmelin & Hari, 1994). Oscillations in the gamma band frequency have been associated with attention and memory (Jensen, Kaiser, & Lachaux, 2007), anticipation, and feature-binding processes

(Bhattacharya, Petsche, & Pereda, 2001). Certain entrainment model approaches to rhythm processing posit that entrainment of neural oscillations to rhythmic stimuli (neural resonance) is key to giving rise to our psychological sense of rhythm and meter.

Oscillatory brain responses were measured in a study of rhythmic expectancy and metric encoding that used an isochronous sequence of tones (Snyder & Large, 2005). Every other tone was physically accented, which gave rise to a strong perception of a beat on the accented tone. Evoked neural responses to occasionally omitted tones were much greater for tones that were expected ''on the beat'' compared with ''off the beat.'' The authors also found increases in induced oscillatory activity at the time of the omitted accented tone. The increased oscillatory activity in the absence of the stimuli was interpreted as reflecting a temporal expectancy, induced by the metrical interpretation, and thus provides a potential neural marker of pulse, or beat expectancy. These findings are in line with predictions of neural resonance theories of timing.

Iversen et al. (2009) extended the findings of Snyder and Large (2005) using MEG. They measured brain responses evoked by a repeating rhythmic pattern of two tones followed by a rest. Listeners were instructed to impose different metrical interpretations on the rhythm by mentally placing emphasis on either the first tone or the second tone. As the stimulus was the same in both conditions, differences in brain activity reflected the internally imposed metrical interpretation. The metrical interpretation changed early evoked oscillatory neural responses to the tones, specifically in the upper beta range (20–30 Hz). The beta response was stronger when a tone was imagined to be the beat, compared with when it was not. A second experiment established that the beta increase was very similar to that observed when the tones were physically (rather than mentally) accented. As beta responses are closely linked to motor processing, these findings may parallel those found in fMRI studies: Activity in the motor system correlates with the metric interpretation of rhythms, even in the absence of overt movement. However, the exact relationship between neural synchrony and fMRI activation is only beginning to be investigated (Lachaux et al., 2007; Zumer, Brookes, Stevenson, Francis, & Morris, 2010), so strong conclusions about the relationship cannot yet be drawn. Fujioka, Trainor, Large, and Ross (2009) have also found increased beta and gamma oscillations during processing of the beat. They reported that gamma band synchrony increased immediately not only after each tone in a sequence of regularly presented tones but also after an unexpected omission, suggesting an association with anticipation. Taken together, the findings of these different groups provide converging evidence that increases in the induced beta and gamma band synchrony could be neural markers of endogenously generated pulse and meter.

5. Benefits of using neuroscience methods to study rhythm

Brain imaging techniques have been criticized for being unnecessarily expensive and not contributing to discrimination between psychological models (Coltheart, 2006; Page, 2006). In addition, they pose problems in requiring participants to keep still, sometimes in noisy environments, and the novelty and complexity of the preprocessing and statistical analysis

may lead to flaws in the analysis being overlooked. For example, a large number of different statistical procedures have been developed for multiple comparisons correction (across different brain areas in fMRI, or time windows in EEG/MEG), and many researchers may not be familiar with the details of every method. However, despite these issues, neuroscientific techniques do have some undisputable advantages over behavioral techniques. One advantage is that when overt behavior cannot be measured, the brain's response may still provide measurable information: It gives another dependent variable to test. A recent study of newborns illustrates this advantage (Winkler, Haden, Ladinig, Sziller, & Honing, 2009). Infants (2 or 3 days old) listened to simple rhythms while their brain responses were measured with EEG. Every so often, an omission of part of the rhythm occurred. In some cases, this omission did not disrupt the feel of the beat in the rhythm, but other times it did. The researchers wanted to know whether the newborns could ''feel the beat'' and therefore also tell when the beat was disrupted. Although it is not possible to ask a newborn to press a button, their brains answered for them. A clear difference was observed in their EEG measurements when listening to an omission that disrupted the beat when compared with an omission that did not disrupt the beat. The authors suggested that beat perception may be innate. This may or may not prove to be true; infants can hear in the womb from about 6 months, and this prenatal learning may play a role. In addition, infants' rhythm perception is influenced by being ''bounced'' in time with music (Phillips-Silver & Trainor, 2005), so any prenatal movement on the part of the mother may need to be taken into account. The fact that rhythm perception can be influenced by culture suggests that any innate predispositions are also shaped by subsequent experience (Cross, 2001; Gerry, Faux, & Trainor, 2010; Iversen, Patel, & Ohgushi, 2008; Soley & Hannon, 2010), but the Winkler et al.'s (2009) study does illustrate how neuroscience can provide data in situations where behavioral measures are difficult to obtain.

An additional important use of neuroscientific methods is when behavioral results do not allow two competing models to be distinguished. One example of this concerns the debate about interval-based versus beat-based models of timing (Keele, Nicoletti, Ivry, & Pokorny, 1989; McAuley & Jones, 2003; Pashler, 2001; Schulze, 1978). As mentioned earlier, beat-based models have largely been superseded by entrainment models (one can think of a beat-based model as inflexible entrainment model—the period is fixed once the beat-based timer starts), but the debate was framed at the time as beat-based versus interval-based, so I will use that terminology here. Interval-based timing has the advantage of parsimony: Many things that we time have no regular beat, so if a beat-based timing system were to exist, it would have to be in addition to some type of interval timing mechanism. One justification for having a beat-based timing system would be if it provides more accurate timing. To test whether accuracy was better for beat-based timing (thereby justifying the nonparsimonious existence of an additional timing system), Pashler (2001) conducted two experiments. In one study, participants heard a sequence of standard tones (all demarcating the same length interval) followed by two test tones. Participants compared the interval between test tones with the interval between the standards. If optimal precision was given by beat-based timing, performance should have been best in blocks in which the interval between standard and test reliably matched the standard interval (i.e., the onset of test interval tones occurred

''on the beat'' set up by the onsets of the standard tones). No such effect was observed. In another experiment, participants heard two test tones and reproduced the intertone interval by producing two keypresses. Entrainment to the beat was apparent; first-response latency clustered around the standard interval. However, responses occurring on or near the beat showed no better temporal accuracy than off-beat responses. This was taken as evidence that beat-based timing is unlikely to exist, as better temporal accuracy was not observed when beat-based timing could have been used. However, the conclusion may only hold for this particular paradigm. Other studies have shown an advantage for beat-based timing in different tasks (McAuley & Kidd, 1998; Schulze, 1978). One way of resolving these conflicting findings could be to show that a beat-based system exists but also can be active without *necessarily* improving performance. This could explain why, in some cases, the behavioral results do not distinguish between the predictions of beat-based and interval-based timing.

This is exactly what was attempted in a behavioral and fMRI study briefly mentioned earlier (Grahn & Brett, 2007). The results of the behavioral study indicated that when rhythms composed of multiple different interval lengths (similar to those that occur in musical rhythm) were reproduced, the rhythms designed to induce a beat were reproduced more accurately than those that did not induce a beat. The behavioral benefit suggested that a beat-based mechanism does exist and improves timing performance when more difficult temporal tasks are tested (as opposed to timing of single intervals). An fMRI study was conducted using the same stimuli. A specific network of areas (including the basal ganglia) was more active during perception of beat-inducing rhythms compared with other rhythms, even when the task was manipulated so that no significant behavioral performance differences occurred. This indicates that the beat-based system can be active without an observable behavioral benefit. Thus, the fact that some previous work does not find a behavioral beat-based timing benefit does not necessarily mean that such a mechanism was not active or used at the time.

6. Difficulties in neural investigations of rhythm processing

Rhythm has remained less tractable than pitch, harmony, and timbre when it comes to localizing specific neural substrates. This may be because rhythm is supported by some of the same processes that are involved in timing, and timing is a crucial component of many perceptual and motor functions. Therefore, time may be processed in a more distributed fashion across multiple brain areas, relative to timbre perception or other aspects of pitch processing. There may also be redundancy in timing networks across the brain, obscuring dissociations that exist between different timing systems. Redundancy would particularly affect neuropsychological studies that are conducted to determine how damage to an area affects a particular function. If another brain area can compensate for the functions of the damaged area, then the function of the damaged area may be obscured.

Another complication in the study of rhythm is the level of automatic processing of temporal features in sound. Many studies ask participants to direct their attention to certain aspects of stimuli in order to examine processing related to each aspect, such as monitoring musical sequences for a pitch deviant (attention to pitch) compared with a temporal deviant

(attention to time). However, temporal information may be implicitly processed, regardless of whether a participant is specifically attending to the temporal dimension (such as in Vuust et al.'s, 2009, study described earlier). In fact, because predicting the timing of a stimulus can facilitate better processing of other aspects of the stimulus, such as pitch (Jones, Moynihan, MacKenzie, & Puente, 2002), participants have an incentive to attend to time even when directed not to or when timing is not explicitly relevant to the task. The automaticity of attending to temporal features is supported by two recent neuroimaging studies that had two overlapping rhythm types but used very different tasks (Grahn & Brett, 2007; Grahn & Rowe, 2009). In the first study, participants had to indicate when a rhythmic change occurred. In the second, participants passively listened to the rhythms, monitoring for a pitch deviant. Nearly identical activation differences between different rhythm conditions were observed in both studies, despite the fact that temporal aspects of the stimuli were task-relevant in the first study but irrelevant in the second study.

An additional issue that is not necessarily specific to rhythm, but pertains to much of the neuroimaging literature, is determining the appropriate dimensions that any given neural area responds to. One proposed dimension is the degree to which rhythmic structure is present in a sequence (e.g., whether it can be metrically represented with strong/weak beats). However, the parameters that contribute to our perception of metric structure have not been fully described. It is fairly straightforward to generate rhythms that are likely to induce perception of meter. It is very difficult, however, to analyze a sequence of tones separated by, for example, randomly generated intervals, and model the metric structure that might be perceived at particular times by the listener. In addition, the human tendency toward categorical perception means that intervals differing in length by a small amount may be perceived as the same in one rhythm, and different in another (a very good illustration of this is found in Desain and Honing 2003).

A different dimension that has been used in multiple studies is the degree of ''temporal complexity.'' However, no unified definition for this exists. Each researcher formulates a new measure of complexity that may be clearly and sensibly defined, but unrelated to another researcher's definition. We actually have little idea of exactly what factors make a rhythm seem ''complex.'' The presence of integer ratios versus noninteger ratios has been suggested (Lewis et al., 2004; Sakai et al., 1999), and its simplicity is attractive. However, the tendency toward categorical perception mentioned above may render the mathematically complex 1:2.2:3.8 to be perceived the same as the mathematically simple 1:2:4. Beyond very simple sequences, it is unclear whether the integer/noninteger-ratio distinction is useful. One fMRI study showed activation differences between integer- and noninteger-ratio sequences, but never statistically compared the two conditions (Sakai et al., 1999), meaning that there may have been no reliable difference at all. Indeed, another study addressing this question showed that integer- and noninteger-ratio sequences could be rendered statistically indistinguishable in the brain, but significant differences between different types of integer-ratio sequences existed, based on their metric structure (Grahn & Brett, 2007).

Finally, other aspects of musical structure, such as melody, harmony, and timbre, also impact the perception of rhythm and meter. Many researchers in the field have examined the influences of various aspects of musical structure on rhythm and meter perception (Dawe,

Platt, & Racine, 1993, 1995; Ellis & Jones, 2009; Hannon, Snyder, Eerola, & Krumhansl, 2004; Huron & Royal, 1996; Povel & Okkerman, 1981; Repp, 2010; Temperley, 1963), but integration of all these findings into a single model has not been achieved (although see Parncutt, 1994). Additional basic research (along the lines of that done by the researchers cited above) that tests the mutual influences and boundaries of different grouping principles will need to be done to improve the information on which models can be based. In many ways, it is not surprising that neuroscience has not led to large breakthroughs in our understanding of rhythm, as much of the behavioral and computational groundwork remains to be laid.

7. Conclusions

Research into the neuroscience of rhythm perception and production has yielded interesting insights. Neural markers of anticipation of the beat and representations of metric structure have been found in EEG and MEG, especially in beta and gamma band synchrony. There is evidence for a specific network of neural areas that support beat perception, a process that is arguably crucial for musical rhythm perception. The distributed and overlapping nature of the activations observed for both timing and rhythm tasks lends support to theories that propose distributed processing, and also the idea that perception and production rely on similar mechanisms.

A wide variety of computational approaches have been utilized for models of timing and rhythm perception. There is still no consensus on the best approach, but recent studies have yielded some neuroscientific support for the predictions of neural resonance theory. Better definitions and greater consensus in terms of stimuli, tasks, and paradigms, as well as greater integration between neuroscience and modeling, will be critical to delineation of specific neurobiological components and mechanisms.

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