Perspectives on Rhythm Processing
In Motor Regions of the Brain

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ABSTRACT: From established musicians to musically untrained children, music seems to have a universal, automatic impact on the movement of the human body. Sensing a beat in rhythm may compel some individuals to move. Through neuroimaging techniques and investigation of neurological patient groups, researchers have discovered that several movement areas of the brain respond to rhythms, whether regular, musical rhythms or irregular rhythms. In addition, a specific response to rhythms with a beat is routinely observed in the basal ganglia, a crucial set of brain structures for movement control. These new findings about the brain's response to rhythm have led researchers to investigate the possible mechanisms through which music may affect movement. Beat-based rhythms may increase activity in the basal ganglia and consequently improve basal ganglia function in disorders such as Parkinson's disease. Alternatively, it is possible that other, intact, brain regions may compensate for impaired function. Although much research remains to be done, current findings about how rhythm relates to the control of movement may have implications for therapeutic approaches to rehabilitation.

The field of music therapy is expanding, both in terms of research into mechanisms underlying therapy and strategies to improve practical implementation. In recent decades, neuro-scientific investigations into the relationship between music processing and other perceptual and cognitive processes have accelerated, yielding insights that may interest music therapists. Although pitch, melody and intensity are all elements of music that have been investigated, here we discuss the neuroimaging and neuropsychological investigations of rhythm, focusing first on conceptual issues and definitions, and then moving to studies that have often highlighted the importance of two subcortical brain structures: the basal ganglia and the cerebellum.

One of rhythm's most fascinating features is the way it can spontaneously induce movement, even in very young infants (Hannon & Trainor, 2007; Hannon & Trehub, 2005; Soley & Hannon, 2010). Sensitivity to musical rhythm appears to be unique to humans; in particular, we are unusual in our ability to rapidly identify a central feature of rhythm called the 'beat.' The beat is the regular time interval that we may tap along to and against which other time intervals in the rhythm can be measured (Large & Palmer, 2002; London, 2004). The presence of beat structure in rhythm is important for perception and behavior, as it improves timing performance accuracy and the ability to discriminate changes in rhythmic sequences (Drake & Gerard, 1989; Grube & Griffiths, 2009; Hebert & Cuddy, 2002; Patel, Iversen, Chen, & Repp, 2005;

Ross & Houtsma, 1994). Because of humans' special rhythmic abilities, a variety of researchers are investigating how the brain responds to rhythm, with particular interest in the role of activation of functional motor areas.

As many of the words associated with rhythm and timing are used in different ways across different fields, we first clarify how they are used here. 'Rhythm' is defined as the pattern of time intervals in a stimulus sequence. A rhythmic pattern is generally indicated by the onset of a stimulus (a tone, click or other sound). Inter-onset-intervals (the time intervals between stimulus onsets) define the lengths of the time intervals in the sequence. The relative importance of onsets compared to offsets is illustrated by the fact that we can recognize the same rhythm whether played by plucking a string (which produces a brief sound) or bowing (which produces a more sustained sound). Listening to a rhythmic pattern often gives rise to a sense of 'pulse,' sometimes termed the 'beat.' The pulse or beat is a series of regularly recurring, equivalent *psychological* events that arise in response to a musical rhythm (Cooper & Meyer, 1960; Large, 2008). The beat is psychological because it is not defined as a stimulus property, even though it generally arises in response to a rhythm (Benjamin, 1984; Lerdahl & Jackendoff, 1983; London, 2004; Palmer & Krumhansl, 1990). The psychological internalizing of pulse is why we can sense a pulse even when music is rhythmically complex or has "offbeats" (many note onsets not occurring on the beat). Individual pulses or beats are frequently perceived to possess differing degrees of accent, or stress, which gives rise to meter, sometimes termed metrical structure. 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 every third beat (**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. Most beat-based rhythms are also metrical. In summary, rhythms can induce an internal pulse, and internal organization of these pulses can lead to the perception of a recurring pattern of relative pulse strengths called meter.

The previous terminology is influenced by music theoretic conceptions of rhythm and timing. Another set of terms is derived from psychological conceptions of timing, particularly the difference between the types of timing we engage in when the sequence has a clear beat compared to when the sequence is irregular, with no clear beat (irregular sequences are uncommon in popular music). When a beat is present, we are said to engage in 'relative' timing, as all the time intervals are measured relative to the beat (e.g., an interval may be 1/2, 1, 2, or 3 times the length of the beat interval). Relative timing

is therefore sometimes called 'beat-based' timing. However, when there is no beat present, we must use absolute timing, sometimes called duration-based timing (Grube, Cooper, Chinnery & Griffiths, 2010; Grube, Lee, Griffiths, Barker, & Woodruff, 2010; Teki, Grube, Kumar & Griffiths, 2011a). The durations of each interval in the rhythm must be measured and stored in memory separately as they occur. They cannot be related to and remembered by using a beat (Teki et al., 2011a).

Evidence is growing that relative (or beat-based) and absolute (or duration-based) timing appear to be controlled by partially distinct brain mechanisms. Understanding the different brain mechanisms is important, as patients with different disorders may have problems in one system that can be compensated for by the other. Evidence suggests that a subcortical brain area called the basal ganglia is important for relative or beat-based timing, whereas a different subcortical area called the cerebellum is important for absolute or duration-based timing (Grahn & Brett, 2007; Grahn & Brett, 2009; Grube, Cooper, et al., 2010; Teki et al., 2011a). To begin, we will direct our attention to relative/beat-based timing and review the literature investigating the brain mechanisms underlying beat-based rhythm processing.

Neuroimaging of Relative or Beat-Based Timing

Several studies have been conducted using functional magnetic resonance imaging (fMRI) to examine how the brain responds during beat perception. When a brain area is more active, it consumes oxygen and glucose, thus requiring increased blood flow to that region to replenish oxygen and energy stores. Functional magnetic resonance imaging works by detecting changes in blood oxygenation and flow that occur, and active brain regions can be shown on a structural picture of a brain (Devlin, 2012).

One series of studies has implicated the basal ganglia and the supplementary motor area in beat-based timing (Grahn & Brett, 2007, 2009; Grahn & Rowe, 2009, 2013; Teki et al., 2011a). Grahn & Brett (2007) created short rhythms that were either beat-based or nonbeat-based (irregular). Participants heard the different rhythms while being scanned using fMRI. Participants were asked not to move any part of their body during the experiment (confirmed by visual observation), and no tapping was required, therefore the observed brain activations were elicited purely by listening to the rhythms. Even so, several brain areas associated with the control of movement were activated during the perception of both beat-based and nonbeat-based rhythms, including the supplementary motor area (SMA), premotor cortex (PMC), the basal ganglia, and the cerebellum.

These data are consistent with other imaging studies that find responses in motor areas during rhythm perception (Bengtsson et al., 2009; Chen, Penhune, & Zatorre, 2008), even when no movement is required. To isolate brain areas that responded specifically to the beat, the activity to beat-based and nonbeat-based rhythms was compared. The basal ganglia and supplementary motor area (which are highly interconnected structures; see Alexander, Crutcher, & DeLong, 1990), as well as the superior temporal gyri (auditory cortex) showed increased activity in response to the beat-based rhythms. Thus, only a subset of interconnected motor structures (as well as auditory structures) showed greater response to the beat-based rhythms, whereas the other motor structures (PMC and cerebellum) were equally responsive to all types of rhythms. Other work has also confirmed that regular and irregular sequences are processed differently, finding greater basal ganglia activity for isochronous, regular tone sequences compared to irregular tone sequences (Geiser, Notter, & Gabrieli, 2012).

Interestingly, BG activity does not appear to correlate with the speed of the beat, but instead shows maximal activity around the beat rate that humans find ideal (~500–700 ms), then decreases as rates become too fast for a beat to be felt (up to ~160 ms) (Riecker, Kassubek, Groschel, Grodd, & Ackermann, 2006; Riecker, Wildgruber, Mathiak, Grodd, & Ackermann, 2003). This suggests that the basal ganglia are not simply responding to any perceived temporal regularity in auditory stimuli, but are most responsive to regularity at the frequency that best induces a sense of beat.

Activity in the basal ganglia that is induced by beat perception also appears to be affected by the degree of 'internal' generation of the beat that is required when processing beat-based rhythms (Grahn & Rowe, 2013). In a rhythm, the beat can be induced in a variety of ways. Increasing the loudness of tones that occur on the beat is a very clear external signal that induces beat perception (Chen et al., 2008). Perceiving the beat through loudness changes requires almost no internal generation of the beat, as it is very salient, even if one is barely attending to it. A more subtle strategy involves creating a temporal pattern, without any loudness changes, by simply varying the lengths of the different intervals used in the rhythm in a way that emphasizes a regular beat. For example, the theme to the *William Tell Overture* has a clear beat without large loudness changes. Perceiving the beat through duration changes is more subtle than through loudness changes and often requires some internal generation of and attention to the beat.

There is a third type of beat perception that is entirely internally generated, sometimes called 'subjective accenting.' This is the imposition of a beat percept onto a series of identical isochronous tones such that it sounds more like a rhythm instead of just a series of monotonous sounds. An example is when we hear a clock as a tick-tock tick-tock pattern of sound, even though the sound is actually tick-tick-tick-tick. We internally emphasize certain sounds in the pattern to make a beat or even a rhythm, despite the fact that all the sounds in the sequence are the same (Brochard, Abecasis, Potter, Ragot, & Drake, 2003; Potter, Fenwick, Abecasis, & Brochard, 2009; Temperley, 1963). When this happens, the beat that is perceived is entirely internally generated, as all of the sounds are acoustically identical.

To examine how the role of internal generation influences basal ganglia activity, Grahn and Rowe (2009) tested beat-based and nonbeat-based rhythms that varied in how much internal generation was required; the rhythms had loudness changes, duration changes, or were acoustically identical tones. Earlier findings that the basal ganglia were more active during beat-based rhythms compared to nonbeat-based were replicated. In addition, for beat-based rhythms, the activity of the basal ganglia correlated with how much internal

generation of the beat was required: it was lowest for rhythms with the least internal generation (rhythms with loudness changes) and highest for those requiring the most internal generation (acoustically identical tones). Thus, the basal ganglia responded to the beat, but more so when internal generation was needed (Grahn & Rowe, 2009). Other work using synchronization-continuation paradigms confirms that internal generation activates the basal ganglia. During synchronization, participants tap along with a regular auditory tone. Then the tone stops and participants continue tapping at the same rate, but without the auditory signal. Basal ganglia and supplementary motor area activity is higher during continuation than synchronization (Lewis, Wing, Pope, Praamstra, & Miall, 2004).

Neuroimaging of Absolute or Duration-Based Timing

In addition to the basal ganglia, the cerebellum frequently responds during the perception of rhythm and has an important role in timing. In contrast to the basal ganglia's proposed involvement with relative timing, the cerebellum has been linked to absolute timing (Teki, Grube, Kumar & Griffiths, 2011b). Teki et al. (2011a) carried out an fMRI study of a variety of different timing tasks. Some could be accomplished by relative (beat-based) timing, whereas others relied on absolute timing (such as comparing two unrelated time durations). For relative timing, the results were consistent with previous work, showing activation in the basal ganglia, supplementary motor area, and premotor cortex. In contrast, absolute timing resulted in activation of several cerebellar structures.

These imaging results provide support for the notion that two distinct timing networks exist; one for relative timing that relies on the basal ganglia and interactions with supplementary motor and premotor cortex, and one for absolute timing that relies on cerebellar networks (Teki et al., 2011a). In support of this distinction, Grahn and Rowe (2013) found that listening to nonbeat rhythms (when absolute timing is required because no beat is present) activated the cerebellum. Finally, Ramnani and Passingham (2001) showed that learning of an irregular rhythm resulted in increased cerebellar activity, which they interpreted as evidence for a cerebellar role in learning the arbitrary durations of the rhythm.

Other Neuroimaging Findings

An additional concept that is emerging from the neuroimaging literature is that rhythm perception relies on interactions between the auditory and motor systems. In addition to being more active during beat perception, the basal ganglia exhibit increased communication, or coupling, with other brain areas during beat perception (Grahn & Rowe, 2009). Specifically, beat perception leads to increased coupling between the basal ganglia and cortical motor areas including the supplementary motor area and premotor cortex. Grahn & Rowe (2009) suggested that a network including the putamen, SMA, and PMC is involved in the analysis of temporal sequences and the prediction or generation of a beat. They speculate that the ability to tap along to a beat is facilitated by the putamen, which forms predictions about when the beat will occur, and through greater coupling with motor areas, facilitates the

temporal coordination of movement in time with a beat. At least two other studies have found increased coupling of neural activity between the auditory and premotor cortex during rhythm processing (Chen et al., 2008; 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 that coupling was stronger for musically trained individuals in both hemispheres. However, it is not yet known if this coupling has consequences for behavioural measures of rhythm perception or accuracy of movement timing.

Because fMRI is a correlational method, one cannot conclude from the basis of these studies that the basal ganglia are *necessary* for relative or beat-based timing, or that that the cerebellum is *necessary* for absolute timing. However, work with neuropsychological patient populations can address this question. If dysfunction of a particular brain area is associated with deficits in a particular type of timing, then there is converging evidence with neuroimaging for that brain area being necessary for that type of timing. In the next section, we examine the neuropsychological patient evidence for a distinction between the basal ganglia and cerebellar roles in timing in patient work.

Beat-Based or Relative Timing: Patient Evidence

One neurological disorder that affects the basal ganglia is Parkinson's disease (PD). PD results from the death of dopaminergic neurons that project to the basal ganglia, thus affecting the functioning of the basal ganglia, leading to problems with movement, including tremor, slowed movement, loss of voluntary movement, and impaired posture and balance ("Parkinson's Disease," 2011). To test whether the basal ganglia were necessary for normal beat processing, Grahn and Brett (2009) tested PD patients and controls on discrimination of beat-based and nonbeat-based rhythms. The participants heard a rhythm two times, and then determined if a third rhythm was the same or different from the original rhythm. The authors predicted that if the basal ganglia are necessary for normal beat perception, PD patients should do worse than controls in discriminating the beat-based rhythms, due to their basal ganglia dysfunction. This prediction was supported. Both groups performed similarly when discriminating nonbeat-based rhythms, suggesting that even with dysfunctional basal ganglia, absolute timing function is intact. However, beat-based or relative timing capabilities were not preserved in the PD patients. In the control group, participants were significantly better at discriminating rhythms that had a beat compared to those without a beat, but in the PD group, this beat-based advantage was significantly reduced. These results demonstrate that PD patients did not benefit to the same degree from the presence of an underlying beat. Either PD patients are less able to use a beat structure to aid in their discrimination between rhythms, or they are impaired at initially extracting or finding the beat structure when listening to a rhythm. Either way, the evidence supports that the basal ganglia have a causal role in healthy beat processing (Grahn & Brett, 2009).

PD patients do not always show clear deficits in beat perception, however. In a study by Geiser & Kaelin-Lang (2011), patients were asked to identify whether a rhythm was metrical (beat-based) or non-metrical (non-beat-based) and found that patients were not significantly impaired relative to controls at correctly classifying the rhythms. However, there was a marginally significant interaction. Controls were better at identifying metric than nonmetric rhythms (82% vs. 74% correct), but PD patients showed similar performance for both conditions (77% vs. 78% correct). Thus, the data are consistent with earlier findings of a lack of benefit for beat-based rhythms, but the interaction in this study reached only marginal statistical significance.

Similar findings have come from Kotz, Schwartze, and Schmidt-Kassow (2009) who have focused on the basal ganglia's role in the temporal aspects of language processing. Patients with basal ganglia lesions that resulted in non-fluent aphasia showed better articulation when their speech was paced by rhythmic drumbeats (Stahl, Kotz, Henseler, Turner, & Geyer, 2011). The regular cues provided a grid to structure the incoming speech stream (Schmidt-Kassow & Kotz, 2008). The authors suggest that the basal ganglia are involved in the planning of speech production by acting as a pacemaker, in concert with the pre-supplementary motor area and the cerebellum, to provide temporal structure (Kotz & Schwartze, 2010). This temporal structure is used to guide articulation. When the basal ganglia pacemaker is compromised, the presence of external rhythmic cues helps patients compensate for the internal pacemaking deficit. Thus, the basal ganglia may provide important processing of temporal structure in both music and language, and external cues may help compensate for problems with temporal structure when the basal ganglia are compromised.

Beat-Based or Relative Timing: Patient Evidence

Turning to absolute timing, several studies have used non-correlational methods to assess the cerebellum's role. Patients with cerebellar degeneration (spinocerebellar ataxia type 6) show a significant deficit in absolute timing on a variable-interval task (Grube, Cooper, et al., 2010). In this task, participants compare durations of two arbitrary intervals that vary from trial to trial. Participants are therefore unable to create an internal long-term reference or use any form of beat to help time the stimulus. The ataxia patients are significantly impaired on this task. In contrast, they showed no deficit on relative timing tasks, including tests with beat-based rhythmic sequences. The evidence suggests that the cerebellum is necessary for normal absolute timing, but not relative timing.

Another noncorrelational method that has been used to assess the cerebellum's timing function is transcranial magnetic stimulation (TMS). TMS is a non-invasive method of exciting cortical neurons by inducing a weak electric current in the brain tissue with by a rapidly changing magnetic field. This magnetic field is generated by a coil placed at the surface of the scalp (Barker, Jalinous, & Freeston, 1985; Walsh & Cowey, 1998). The method is ideal for stimulating the brain structures near the surface, although deeper structures such as the basal ganglia are generally beyond reach. Since TMS can temporarily disrupt neuronal processing, it can be used to

conclude whether an area is necessary for a particular task to be successfully carried out in healthy brains. Grube, Lee, et al. (2010) tested participants on a variety of absolute and relative timing tasks both before and after TMS stimulation to the cerebellum. After stimulation, participants showed no difference from pre-stimulation performance on tasks that required the detection of a regular beat. However, their performance on absolute-timing tasks showed a large and significant deficit after TMS stimulation. The data provide further support for the role of the cerebellum in absolute timing perception, and its functional dissociation from relative timing perception (Grube, Lee, et al., 2010).

Although there are clear differences that are emerging in the neural areas that respond to beat-based/relative and nonbeat-based/absolute timing, there are also commonalities that emerge across investigations of rhythm perception and production. Previous behavioral work suggests that the underlying mechanisms involved in rhythm perception are very similar to the those involved in rhythm production (Ivry & Hazeltine, 1995), and neuroimaging studies have provided evidence to support this data by showing similar activations for rhythm perception and production (Schubotz, Friederici, & von Cramon, 2000). A network of areas are commonly activated across a variety of rhythm tasks, including the premotor cortex, SMA, cerebellum, and the basal ganglia (Bengtsson et al., 2009; Chen et al., 2008; Grahn & Brett, 2007; Lewis et al., 2004; Mayville, Jantzen, Fuchs, Steinberg, & Kelso, 2002; Schubotz & von Cramon, 2001; Ullén, Forssberg, & Ehrsson, 2003). The activity of each of these areas is modulated by the task or stimulus type. For example, the basal ganglia will respond to a certain degree to all types of rhythmic sequences, but responds most to beat-based sequences that require internal generation. The cerebellum also responds during many rhythm and timing tasks, but most significantly, when a beat cannot be detected.

Hypothetical Mechanisms of Therapeutic Benefits

In addition to continuing basic research in to rhythm processing, researchers are now tackling a more difficult question; through what mechanisms can music have an impact on movement, and how can these mechanisms help patients with movement disorders? Over the years, a number of studies have been conducted to investigate the benefits of music and rhythm on an individual's ability to coordinate movements. For example, synchronizing auditory cues with a patient's steps has been shown to improve various aspects of gait. While immediate effects of cueing may include facilitation of gait initiation, reduction of freezing of gait, and improved sit-to-stand speed, lasting effects of cueing therapy have been shown to include improved walking velocity, stride length, balance, and more (Benoit, Farrugia, Kotz, & Bella, 2012). Clinical evidence of these effects has been critically reviewed in a 2005 review article by Lim et al. They found that only one "high-quality" study had been conducted that was specifically focused on the effects of auditory rhythmical cueing. However, there was strong evidence for cueing positively influencing the walking speed of patients with Parkinson's disease. Currently, there are a few potential explanations for this effect.

One possibility is that as patients listen to a beat-based rhythm, activation of the basal ganglia is increased and the increase leads to improved function, whether it be speech abilities or motor abilities. The second possibility is that when patients have dysfunctional basal ganglia, other brain regions must compensate for this loss of function. Thus, music may have its therapeutic effect through compensatory intact systems such as the cerebellum and premotor cortex. As explained by Kotz et al. (2009), a dysfunctional BG can inhibit projections to surrounding brain regions that are involved in the synchronization of internal and external cues. With this inhibition, these brain regions may receive increased input from the cerebellum, compensating for the lack of signals coming from the basal ganglia (Kotz et al., 2009). External, predictable cues may therefore have their effect through the intact cerebellum, thus making up for the process that would normally occur naturally through the basal ganglia (Kotz et al., 2009).

Sarma et al. (2012) propose an alternate perspective for the role of cueing in the facilitation of movement. They propose that a motor plan in the prefrontal cortex needs to be activated by cueing in order to effectively trigger movement in PD patients. Patients are able to form the motor plan in the prefrontal cortex, but a trigger is required to put the plan into action. While the motor plan is normally activated by the expectation of movement, Sarma et al. (2012) suggest that either a predictably timed external cue or an internally generated cue will lead to the same activation. Increased activation leads to the suppression of pathological basal ganglia activity through direct pathways, and motor facilitation results (Sarma et al., 2012).

Conclusion

Advances in brain imaging research are becoming more relevant to the world of music therapy. As researchers continue to explore the neural underpinnings of rhythm perception, the mechanism for benefits of music and rhythm may become clearer.

While rhythmic auditory stimulation (RAS) has been shown to be successful in some patients, this is not always the case. As researchers broaden their understanding of the connection between rhythm and movement, they can start to improve these treatments in a way that leads to increased patient success. For example, now that studies have shown that internal generation of the beat leads to more activation in the basal ganglia than simply perceiving the beat (Grahn & Rowe, 2009), this information could be used to test whether more beneficial forms of rhythmic auditory stimulation can be created. While most studies in the past have focused on having patients walk to the beat of a metronome, future studies could use more complex rhythms that require increased internal generation of the beat by patients, and consequently increased activation of the basal ganglia.

In addition, as researchers further their understanding of how the brain perceives rhythm and how it relates to movement, these ideas can start to be applied to a larger array of movement disorders, as well as stroke patients. Stroke patients are much more variable in their motor symptoms because stroke affects different brain areas in different patients. Although this variability provides a challenge to rehabilitation and therapy, it also offers an opportunity to learn more about how damage to different brain areas leads to different capabilities being preserved or not. For example, how do strokes that affect the premotor cortex alter a patient's response to rhythm when compared to strokes that affect the supplementary motor area? These comparisons may enable us to make more fine-grained distinctions about the characteristics of musical rhythm that can be used to improve movement.

Finally, much of the past music therapy research focuses on the effects of synchronizing movements to the beat. However, many other features in music may influence movement, such as familiarity, preference, genre, or the energy levels of the music. Music therapeutic approaches can examine the contributions of these factors, perhaps providing neuroscientists with new questions to explore. As our conceptual understanding of these theories and techniques continue to grow, music therapy may be able to capitalize on these insights and further improve lives of patients around the world.

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