NEUROSCIENTIFIC INVESTIGATIONS OF MUSICAL RHYTHM

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ABSTRACT
Music occurs in every human society, unfolds over time, and enables synchronized movements. The neural mechanisms underlying the perception, cognition, and production of musical rhythm have been investigated using a variety of methods. FMRI studies in particular have shown that the motor system is crucially involved in rhythm and beat perception. Studies using other methods demonstrate that oscillatory neural activity entrains to regularities in musical rhythm, and that motor system excitability is modulated by listening to musical rhythm. This review paper describes some of the recent neuroscientific findings regarding musical rhythm, and especially the perception of a regular beat.

INTRODUCTION

The temporal structure of music enables synchronized movement, such as tapping one's foot, clapping, or dancing to the 'beat' of musical rhythms. Such movement is precisely timed to align with the periodic, salient beats in the music, and with the movements of other individuals. Given this relationship between musical rhythm and movement, it is perhaps unsurprising that the brain's motor system is heavily involved in the neural processing of auditory rhythms. However, it is a relatively recent discovery that the motor system is involved even in the absence of movement – subtle differences in the temporal structure or context of an auditory rhythm can elicit robust differences in motor system activity. These discoveries are the topic of this review paper, with a focus on findings from functional magnetic resonance imaging (fMRI). FMRI measures the change in oxygenated blood levels following neural activity [see 1, 2]. This 'blood-oxygen-level dependent' (or BOLD) signal is considered to be an indirect measure of brain activity, and therefore increases in BOLD are termed 'activations' in this review. Findings from patient studies, as well as electroencephalography (EEG), magnetoencephalography (MEG), and transcranial magnetic stimulation (TMS) studies will also be discussed.

Although much theoretic and empirical work has sought to explain why certain temporal patterns elicit movement (e.g., dancing) while others do not [3-5], and the evolutionary basis for human sensitivity to musical rhythm [6-7], this review will focus on the neural substrates of rhythm perception and the role of individual differences, expertise, and sensory modality.

RHYTHM AND BEAT IN THE BRAIN

When human participants listen to rhythms (i.e., auditory sequences) with or without a beat, widespread activity is observed in the cortical motor system, especially in the supplementary motor area (SMA) and premotor cortex (PMC), as well as subcortical regions such as the basal ganglia and cerebellum [8-14]. Rhythms that are composed of intervals that are integer ratios of one another, and have accents occurring at regular intervals, tend to elicit the perception of a regular, emphasized beat, and beats are usually organized in a metre (a temporal structure determined by the cyclical pattern of strong and weak beats; see Figure 1). Compared to rhythms without a beat, listening to beat-based rhythms elicits more activity in the SMA and the basal ganglia [10]. The importance of the basal ganglia in beat perception was highlighted in a study demonstrating that patients with Parkinson's disease have impaired perceptual discrimination of changes in beat-based rhythms compared to healthy controls, but not in nonbeat rhythms [15]. This deficit in sensitivity to the beat structure in rhythms is presumably due to the degeneration of dopaminergic cells in a part of the basal ganglia called the substantia nigra; the death of these cells deprives the basal ganglia of dopamine, causing dysfunction. Overall, these findings suggest that the basal ganglia not only respond during beat perception, but are crucial for normal beat perception to occur.

Figure 1. A depiction of rhythm, beat and metre. A rhythm is a sequence of auditory events, the onsets of which are separated by time intervals. The beat is the sequence of regular, salient time positions that are perceived in the rhythm. Metre is the hierarchical organization of beats into strong and weak (strong beats in the metrical structure are indicated in the top line).

In contrast to the basal ganglia, the cerebellum appears to play a different role in timing. Whereas the basal ganglia is important for beat perception and beat-based timing (i.e., timing of events relative to a regular and predictable beat), the cerebellum has been implicated in the perception of absolute time intervals (i.e., timing of events not relative to a beat). In one study, patients with cerebellar degeneration showed a deficit in absolute timing but not in beat-based timing [16]. A related study used TMS over the cerebellum to transiently disrupt function in that structure. After stimulation, participants performed worse in a single-interval timing task (i.e., a task that requires absolute timing), but not in a regularity (beat) detection task [17]. A subsequent fMRI study showed a dissociation between the cerebellum and basal ganglia (and the respective networks in which they operate) for absolute and beat-based timing: cerebellar regions and the inferior olive were more active for absolute timing, and regions of the basal ganglia, SMA, PMC, and other frontal cortical regions were more active for beat-based timing [18]. Both of these dissociable networks, however, are often active when hearing musical rhythms, suggesting that absolute and beat-based timing mechanisms are simultaneously engaged by rhythm processing.

THE TIME COURSE OF RHYTHM AND BEAT PERCEPTION

Beat perception is thought to have multiple stages: initially, when a rhythm is first heard, the beat must be detected, or found. ‘Beat-finding’ is followed by the creation of an internal representation of the beat, allowing the anticipation of future beats as the rhythm continues (‘beat-continuation’). One fMRI study attempted to determine whether the role of the basal ganglia in beat perception was selective for finding or continuing the beat. Participants heard short, consecutive rhythms that either had a beat or not. Basal ganglia activity was low during the initial presentation of a beat-based rhythm, during which participants were engaged in beat-finding. Activity was high when beat-based rhythms followed one after the other, during which participants had a strong and continuing sense of the beat, suggesting that the basal ganglia are more involved in beat-continuation than beat-finding [19].

Another fMRI study compared activation during initial perception of a rhythm, when participants were engaged in beat-finding, to subsequent tapping of the beat as they heard the rhythm again (synchronized beat-tapping). In contrast to the previous study, basal ganglia activity was similar during finding and tapping (along with PMC and other temporal and frontal regions) [20]. The difference with respect to the previous study may be the result of differences in experimental paradigms, stimuli, or analyses, therefore further work remains to be done to clarify the role of the basal ganglia in beat finding versus beat continuation.

The consideration of the time course of rhythm and beat perception is an important topic of future research, as music and beat perception necessarily unfold over time and different stages may rely on distinct neural mechanisms (e.g., finding the beat, continuing the beat, and even adapting the beat rate in response when a rhythm changes). Most fMRI methods have a temporal resolution of about 1-2 seconds, but through appropriate experimental designs can be used to investigate the distinct stages of rhythm and beat perception, although not responses to each individual note.

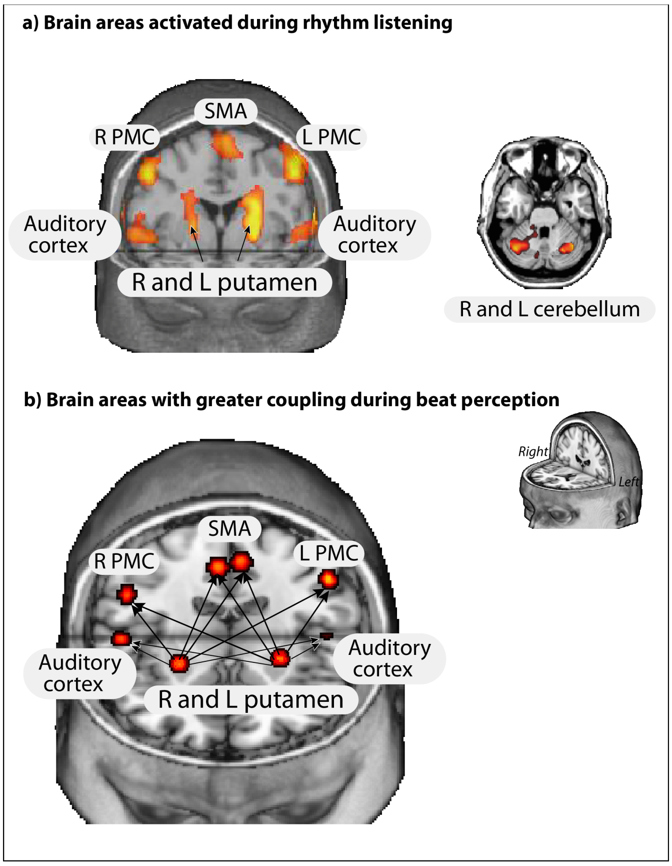

Figure 2. Neural regions that are a) active while listening to rhythms, and b) coupled (show greater correlation in activity) during beat perception [adapted from 10, 21]. PMC = premotor cortex, SMA = supplementary motor area, R = right, L = Left.

NEURAL CONNECTIVITY IN RHYTHM PERCEPTION

Individual brain regions do not act alone in the processing of musical rhythm, but rather function as networks. Using fMRI, the effective connectivity (the direct influence of one region's activity on that of another region) between the basal ganglia and several cortical areas, including the SMA, PMC and auditory cortex was found to be greater while participants listened to beat-based rhythms compared to nonbeat rhythms [21]. In another study, the functional connectivity (the non-directional correlation in activation) between PMC and auditory cortex was found to increase as the intensity of tones in beat positions of an isochronous sequence (or salience of the beat) increased [22]. Findings from these studies demonstrate that the connected activity, or coupling, between auditory and motor systems increases during rhythm and beat perception.

NEURAL OSCILLATIONS IN RHYTHM PERCEPTION

The studies discussed so far have used fMRI, which has poor temporal resolution – it is only sensitive to differences in activations occurring about 2 seconds apart. Although fMRI provides important insights about localization of neural activity due to its spatial resolution, other methods, such as EEG and MEG, provide insight regarding brain responses on a much finer timescale. The fine temporal resolution of these methods can capture the oscillatory nature of neural activity. Neural populations typically have synchronized, oscillatory activity due to feedback connections. Although their functional role is not fully understood, neural oscillations at particular frequency bands have been linked to attention [23], stages of sleep [24], and movement [25]. EEG and MEG studies have demonstrated particular patterns of oscillatory activity in response to auditory rhythms. For example, one study found that when listening to a tone sequence of isochronous, alternating strong and weak beats, neural activity in the gamma band of oscillatory frequencies (in this case defined as 20-60 Hz) was greater for strong beats than weak beats [26]. In addition, when a tone in the sequence was occasionally omitted, anticipatory gamma responses occurred in the gaps where tones were expected. These findings suggest that gamma responses may index the perception and expectation of beats

In a similar study, participants heard a simple, repeating pattern: two identical tones followed by a silent gap. Participants imagined one of the two tones to be accented (emphasized), and oscillatory activity in the beta band (20-30 Hz; note that this overlaps with the gamma range as defined in the study discussed immediately above) was greater for the tone with imaginary accents than for the other tone [27]. Beta activity therefore shows a similar pattern to gamma activity in the study described above, but for imagined accents, rather than physical accents (greater intensity). Beta activity also appears to be sensitive to the expectation of when a tone will occur. When listening to isochronous sequences with varying rates, beta activity decreases following the onset of tones, but rebounds with a time course that is specific to the rate of the isochronous stimulus tones. The relationship between the timing of the beta rebound and the rate of the stimulus tones suggests that beta activity indexes anticipation of the timing of the next tone [28]. Thus, overall, both beta and gamma have been implicated in anticipation of the beat, but future research may elucidate whether they have distinct roles.

Recent work has shown entrainment of neural oscillations to the rate of the perceived beat in auditory rhythms. When participants heard a continuous isochronous tone sequence and imagined it as having either a duple metre or a triple metre (imagining an accent, or emphasis, on every two or three tones, respectively) there was increased power in entrained oscillations at the rate of the imagined emphasis, in addition to the rate of the tones themselves [29]. This specific enhancement of neural entrainment to the metrical beat rates in auditory rhythms was subsequently shown to occur for rhythms that are not isochronous (as in music) [30], and to occur in distinct brain regions for perception of the rhythm and tapping of the beat while listening [31]. These studies demonstrate entrainment to the beat in the auditory and motor systems of the brain.

MOTOR SYSTEM EXCITABILITY

Although fMRI and EEG/MEG provide complementary information about the location and timing, respectively, of neural activity, they are correlational methods. That is, they can only demonstrate associations between a condition or task, and neural activity. They cannot, however, indicate whether a particular brain response is causally related to the observed behaviour. Other methods, such as TMS, allow one to causally (and transiently) influence neural processing, and observe whether behaviour is affected. Recent studies have begun to use TMS to investigate the dynamics of excitability in the motor system during rhythm perception. Applying single pulses of TMS to the primary motor cortex can elicit a muscle twitch, or motor evoked potential (MEP). MEPs vary in magnitude depending on the excitability in the motor system at the time of stimulation. Three studies have used single pulse TMS to investigate how the perception of rhythm can modulate excitability in the motor system. One study found that MEPs elicited when tone sequences gave a strong sense of beat were larger than when sequences did not give a sense of beat [32]. A different study found that listening to music that is rated as having a high degree of ‘groove’ (or inducing a desire to move) modulates excitability at the time of the musical beat [33]. Another study found that excitability was modulated in correlation with how closely the rate of an isochronous sequence matched the participant’s preferred tempo, determined by their spontaneous motor tempo (the rate at which they freely tapped) [34]. Together, these studies help show how the processing of rhythm by the brain’s motor system can extend directly to the muscles, providing a mechanism by which rhythm might influence movement.

The relationship between rhythm and the motor system has also been studied with behavioural methods, including measuring the accuracy of synchronizing one’s tapping with an auditory sequence [see 35], and theoretical and modelling approaches [e.g., 36). Rhythm's influence on the motor system is also exploited by movement rehabilitation in patients with motor disorders, such as Parkinson's Disease and stroke, using rhythmic auditory stimulation [see 37].

EXPERTISE AND INDIVIDUAL DIFFERENCES

The studies discussed thus far have usually manipulated rhythm structure in order to change perception (e.g., of the beat) in a general sample of participants. Individual differences among listeners, however, also influence rhythm and beat perception. Musical training is one difference that is commonly investigated. Musically trained and untrained individuals show similar coupling of activity between subcortical and cortical regions [21], and similar patterns of activity in the dorsal PMC, SMA, inferior parietal lobule and cerebellum, while listening to rhythms [38]. However, musicians show a greater increase in coupling between auditory cortex and the supplementary motor area when a beat is induced by the temporal structure of the rhythm, compared to when a beat is induced by regularly occurring volume accents [21]. Musicians also have greater activity in frontal regions and the cerebellum that covaries with the complexity of rhythms (defined by the metrical structure, varying from metrically simple to nonmetrical), compared to nonmusicians [38]. One study measured the contribution of several factors to individual differences in rhythm reproduction ability, including musical training, auditory short-term memory capacity, and sensitivity to the beat. All of these were found to be related to the ability to reproduce rhythms. Moreover, individual differences in these factors were associated with activity differences in response to hearing rhythms. Poor auditory short-term memory correlated with activity in auditory cortex, greater beat sensitivity correlated with activity in SMA and PMC, and musical training correlated with activity in both auditory and motor areas [39]. These findings underscore the importance of both motor and auditory systems in factors that lead to rhythmic ability. Another study found that while performing a temporal judgment task, individuals with strong beat perception had greater activity in the SMA, left PMC, insula, and inferior frontal gyrus compared to individuals with weak beat perception, who had greater activity in auditory cortex and right PMC [40]. In the normal human population there is a wide range of abilities and traits related to rhythm perception, and these studies only scratch the surface. Characterization of individual differences and their underlying causes needs to be addressed more comprehensively in the future.

AUDITORY SPECIFICITY OF BEAT PERCEPTION

The entrained behaviours associated with musical rhythms, such as dancing, do not generally occur in the real world for visual rhythms. Participants are much worse at tapping along with the beat of visual rhythms compared to auditory rhythms [41]. A few studies have tested the degree to which perception of a beat can be elicited by visual rhythms. In one study, participants were exposed to auditory and visual rhythms, and as expected, showed less sensitivity to the beat structure in visual rhythms. However, participants had a stronger sense of the beat in visual rhythms when they were preceded by identical rhythms in the auditory modality, suggesting that the timing mechanisms implicated in auditory beat perception can prime beat perception in other modalities [42]. Another study used a rhythm discrimination paradigm to show that sensitivity to the beat in rhythm can occur for visually presented rhythms, although overall performance is still worse for visual compared to auditory rhythms [43]. In that task, a rotating line was used to present the rhythms, and the added spatial information associated with each interval in the rhythm may have improved performance (i.e., compared to a simple flashing visual cue that always appears in the same spatial location). Other studies have used moving visual targets (such as a video of a finger tapping or a bouncing ball) and found that tapping in synchrony with these spatiotemporal visual stimuli was improved compared to purely temporal stimuli, but was still worse than for auditory stimuli [44, 45]. However, adding other visual information or using biological motion, may provide a means to more reliably induce beat perception from visual rhythms.

NONHUMAN PRIMATE STUDIES

The emerging research literature on rhythm and timing in nonhuman primates is bringing fresh insight to our understanding of the neuroscience of musical rhythm. Many studies have used a synchronization-continuation tapping task (in which monkeys were trained to synchronize their tapping with an isochronous auditory cue, then continue tapping at the same rate after the cue stopped) to compare rhythm and timing behaviour in humans and nonhuman primates. Rhesus monkeys and humans have similar performance when reproducing single intervals, but humans are far superior when synchronizing with sequences of multiple intervals [46]. Nonhuman primates are also worse at continuing tapping at the same rate after synchronizing with sequences of sounds, although there is preliminary evidence of at least one chimpanzee that shows some ability to do so [47]. One study found two populations of cells in the medial PMC of Rhesus monkeys that may provide distinct timing information during performance of the synchronization-continuation tapping task. The activity of some cells was sensitive to the duration of the interval being tapped, and the activity of other cells was sensitive to the time elapsed from the previous tap [48]. These two types of sensitivity could be used in conjunction with temporally precise movements, such as those required for musical rhythm production. A subsequent study showed that these mechanisms in the medial PMC are also used in the production of more complex, multiple-interval rhythms [49]. Distinct frequencies of oscillatory activity in the basal ganglia of Rhesus monkeys were found to relate to different aspects of rhythmic behaviour: activity in the gamma band (30-70 Hz) was more involved during synchronization of tapping, whereas activity in the beta band (13-30 Hz) was more involved in the continuation of tapping [50]. These results further implicate possible oscillatory mechanisms in cortical motor regions and the basal ganglia of humans that could underlie the particular roles these neural regions have for timing and movement synchronized to sound (such as required for the perception and production of musical rhythm). Behavioural work with nonhuman primates and other species will also help determine the degree to which beat perception is required for human-like synchronization-continuation [see 6, 7].

FUTURE DIRECTIONS

The future is promising for the neuroscience of musical rhythm. New and improving techniques (e.g., transcranial direct current stimulation, functional near-infrared spectroscopy), integration of existing techniques (e.g., computational modelling and neuroimaging), and the ongoing expansion of the research field (e.g., into animal research), will provide new insights into this topic.
Future research must face the persistent issue of stable and defined terminology. The use of ‘beat’, ‘pulse’, and ‘complexity’, for example, are not fully agreed upon in the literature, and the research community will benefit from standardizing the relevant terminology. Accounting for individual differences is becoming an increasingly apparent issue, with a wide range of rhythm abilities present in the normal population [39, 51].

The common comparison of musically trained and untrained groups (often based on a median split of years of musical training) is only an imprecise first step, insufficient to account for the variety of ways individuals can differ in their perception and processing of rhythm.

Future research will need to directly address the ‘bottom-up’ and ‘top-down’ influences on rhythm perception, and their inevitable interactions. For example, stimulus parameters like the temporal structure of intervals influence beat perception directly [3, 5], as do intensity dynamics in rhythms (i.e., compared to temporal structure alone) [21], but top-down influences of experience (e.g., culture, expertise) and of attention/intention (for paradigms requiring participants to intentionally impose a metrical beat structure onto rhythms) also influence beat perception. The interactions between these factors are largely uncharacterized, yet are critical for a complete understanding of the phenomena of interest.

Currently, the research literature is largely separated by methods, and future approaches could, for example, attempt to integrate across methods by accounting for entrained neural oscillations [e.g, 5], distinct timing mechanisms [19], and temporal expectation and probabilities in rhythms [e.g., 52] through convergent technical and theoretical methods.

CONCLUSIONS

Overall, recent neuroscientific investigations of the perception, behaviour, and neural processing related to musical rhythm have demonstrated the essential involvement of the brain's cortical and subcortical motor system. FMRI, EEG, TMS, and other methods have contributed to understanding the neural substrates, oscillatory frequencies, and excitability dynamics in relation to musical rhythm. Future work will likely focus on characterizing the exact neural pathways by which auditory and motor systems mutually influence each other during rhythm perception, and using this information to create neurobiologically plausible models of rhythm and beat perception.

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