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Modulation of Motor Excitability by Metricality of Tone Sequences

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When listening to music, humans tend to synchronize their movements with the perceived beat (e.g., foot-tapping). Brain areas associated with motor function have been closely linked to the perception of beat and rhythm, but the mechanism of this temporal auditory–motor coupling is not fully understood. To investigate how auditory rhythms affect movement, we applied single-pulse transcranial magnetic stimulation (TMS) to primary motor cortex, eliciting motor-evoked potentials (MEPs) in ankle-driving muscles of the lower leg, while participants ($N = 4$) listened to metrically strong or weak tone sequences or music. When TMS pulses were delivered synchronously with perceptible beats in the metrically strong tone sequences, MEPs had greater amplitude than for metrically weak sequences. In contrast, for music that gave a strong or weak sense of the underlying beat, there were no differences in MEP amplitude. These results demonstrate that the pure metrical structure of an auditory rhythm presented as generic parametrically varied tone sequences can influence motor excitability but that the picture may be more complex for real recordings of musical pieces.

Keywords: metricality, rhythm, motor excitability

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Humans tend to synchronize their movements with periodic, that is, rhythmic or regular, auditory stimuli. In Western music, rhythm (the succession of events over time) is usually organized into a hierarchical structure, known as "meter," which allows the listener to perceive, and synchronize their movements to, a regular "beat." Every human culture known has produced music incorporating periodicity (Wallin, Merker, & Brown, 2000), implicating music-oriented auditory–motor coupling as a universal human behavior.

Behavioral, neuroimaging, and electrophysiological studies have investigated aspects of rhythm and meter processing and associated auditory–motor coupling. Metricality, or the degree to which rhythms imply a particular meter, can enhance the precision of temporal encoding and ratings of perceived rhythmicity (Grube & Griffiths, 2009), and the periodic beat induced by metrical rhythms coincides with increased attention (Jones, Moynihan, MacKenzie, & Puente, 2002). Motor areas of the brain (including premotor and supplementary motor cortical areas, and basal ganglia) are involved in processing of auditory rhythm, and their activity is modulated by the presence of a perceptible beat and by rhythmic complexity (Chen, Penhune, & Zatorre, 2008; Grahn & Brett, 2007; Teki, Grube, Kumar, & Griffiths, 2011). Electrophysiological research shows that beat perception modulates endogenous neural activity at the frequency of the beat, and in Beta and Gamma bands (Abecasis, Brochard, Granot, & Drake, 2005; Fujioka, Trainor, Large, & Ross, 2009, 2012; Iverson, Repp, & Patel, 2009; Nozaradan, Peretz, Missal, & Mouraux, 2011; Snyder & Large, 2005). Thus, previous research suggests that auditory rhythms may influence neural Beta and Gamma band activity in motor areas of the brain. These neuroimaging and electrophysiological findings, however, have not been extended from brain sources to muscle activity: how auditory rhythm specifically modulates motor activity is not well understood.

Transcranial magnetic stimulation (TMS) is a useful method for inferring causal relationships between brain areas and functions. TMS uses a transient magnetic field to influence the neural function of the underlying cortical area. Thus, TMS can probe auditory–motor coupling by directly stimulating motor areas of the brain as participants listen to auditory stimuli. In particular, the application of TMS to primary motor cortex can elicit motor-evoked potentials (MEPs), or muscle twitches. Changes in the size of MEPs reflect changes in excitability of the motor system. Changes in motor excitability, as measured by TMS-elicited lip MEPs, owing to auditory (speech) stimuli have been shown

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(Watkins & Paus, 2004), providing a methodological basis for investigating musical and rhythmic stimuli.

Wilson and Davey (2002) used rock music and TMS pulses timed to coincide or alternate with musical beats to elicit MEPs from the lateral gastrocnemius (LG) and tibialis anterior (TA) muscles of the lower leg as participants listened to beat-based rock music or white noise. In that study, the normal, "resting-state" correlation of MEP size between LG and TA muscles found while participants listened to white noise was absent or reduced in 11 of 12 participants while they listened to music. Because this correlation disappears when extensor and flexor muscles are executing a movement, Wilson and Davey suggested that this music-induced elimination of correlation represents motor preparation via corticospinal drive induced by the music.

The present study aims to test the influence of the metricality of music and generic parametrically controlled auditory rhythms on implicit motor processing in TA and LG muscles. The stimuli included excerpts of real-world music: a set of complex highly variable stimuli with high ecological validity, containing beat-based and non–beat-based sections. In addition, we used sequences of pure sine tones that were systematically varied in their metricality: a set of basic stimuli with highly controlled temporal properties. To investigate whether the influence of metrical strength for either stimulus type occurs in a temporally generalized fashion (i.e., an increase in excitability during the entire listening period) or a temporally precise fashion (i.e., an increase in excitability only at the time points coinciding with the beats), we compared randomly timed vs. beat-synchronized TMS pulses.

Based on the apparent universal tendency to synchronize movements with musical rhythm, and specifically with periodic metrically salient points, we hypothesized that the amplitude of MEPs elicited by stimulation of primary motor cortex would be greater when participants were listening to strongly compared with weakly metrical stimuli and for TMS pulses synchronized with the metrical beat compared with randomly timed pulses.

Methods

Participants

Informed signed consent was obtained from six volunteer participants (four female, mean age 24.67 years) recruited from the London, UK area. All participants were of Western cultural background (UK, US, or Canada) and had fewer than 4 years of formal musical training.

Stimuli

Music stimuli consisted of 8 excerpts of commercial recordings of popular songs ranging from about 60s to about 80s in length. Each excerpt contained roughly equal length sections, which subjectively strongly implied a beat or weakly so (or not at all). Selections were made based on the subjective opinion of experimenters, with the criteria of containing sections for which it would be easy to tap your foot to the beat, and sections for which it would be difficult or impossible to tap your foot. An example excerpt is the Beach Boys' song "Wouldn't It Be Nice" from 1:05 through 2:00. In the second half of that excerpt, the music gradually changes into a rubato (rhythmically flexible) section where the music provides a weaker sense of beat compared with the first half. Thus, the first half of this excerpt is considered metrically strong and the second half metrically weak.

Tone sequences were composed of 28 metrically strong and 28 metrically weak individual tone sequences, respectively, each of which was composed of sine tones, as used by Grube and Griffiths (2009), randomly concatenated into 90s rhythmic sequences. Metrical strength of the individual sequences was determined using the model of Povel and Essens (1985), based on the phenomenal accentuation of tones owing to their temporal spacing and the induction of a metrical beat by the regular occurrence of such accents. Sequences were composed of 7 or 8 sinusoidal tones with a duration of 100 ms, and a frequency of 200 Hz, distributed in time over 16 units of 200 ms each, to either induce a strong metrical beat, by having an accented tone occurring every fourth unit, or not (Figure 1). Importantly, all individual sequences had an accented tone on the first and the 13th unit, i.e., the first and the last of four metrical beats. The difference in metrical strength was created by the presence of accented tones on the second and third downbeat in the metrically strong sequences and absence of tones in those positions in the weak ones. The sequences used here were chosen based on behavioral ratings out of the larger total number of sequences fitting these criteria (Grube et al., unpublished data). Although the presence of a metrical beat can be reliably perceived for the strong, but not the weak, individual sequence, the perceived metricality of our longer sequences would presumably be greater, especially for those that are metrically strong, owing to their continuous nature. It is possible that some participants were able to perceive the beat in the metrically weak tone sequences. However, based on subjective listening by expert musicians, the metrically weak tone sequences were considered to require substantial effortful attention in order to establish an ongoing perception of a

Figure 1. Schematic representation of examples of metrically strong and metrically weak tone sequences. Illustrated is one random-order concatenation of six individual sequences for either category; the beginning of each sequence is denoted by numbers 1 to 6. Each individual sequence comprised 16 units, with an underlying beat of 200 ms per unit. In order to induce a metrical beat of 4 in the listener, the strong sequences had a phenomenally (purely due to temporal spacing) accented tone on every fourth unit, i.e. coinciding with the "downbeat" (denoted by ►). The weak sequences had an accented tone on the first and last downbeat of each of the individual sequences, but no tones on positions of the hypothetical second and the third downbeats. All individual sequences ended on their final downbeat. Dots denote silent units.

metrical beat, and thus would be unlikely to induce a metrical beat perception in most listeners. Three different sequences were created for each type of tone sequence, each composed using the same set of 28 individual sequences, half of them composed of 7 and 8 tones, respectively.

Each tone sequence and music excerpt was played twice for each participant, once with TMS pulses coinciding with metrical beats and once with randomly timed TMS pulses.

Procedure and Equipment

TMS was delivered using a Magstim Super Rapid TMS machine (Magstim Company, Ltd., Dyfed, Wales). Participants received a description of the procedure and were given a brief session to become familiar with the TMS methods to be used, to minimize discomfort with the physical sensation of TMS. Participants sat in a chair with their feet relaxed and flat on the floor. Electrodes were placed over the right LG and TA muscles, as well as over the bone of the ankle and shin as references. MEPs were recorded using the BioSemi system (Biosemi, Amsterdam, Holland). TMS was applied to the left medial primary motor cortex with stimulation intensity starting at 30% of maximum and increasing incrementally by 5% steps until a 50 μV MEP was apparent in the raw electromyographic (EMG) signal of the TA muscle for at least 5 of 10 TMS pulses. The resulting intensity level was taken to reflect the motor threshold.

Participants were instructed to sit still, relax, and to listen to the auditory stimuli. Rather than using a task to direct attention to the stimuli, passive listening was preferred to mimic the real-world contexts in which humans synchronize movement (e.g., dance, clap) with musical rhythm. Stimuli were presented through stereo headphones, in random order to prevent any potential order effects. One experimenter (DC) held the figure 8 TMS coil over the site, on the scalp, at about the central sulcus, slightly left of the midline, where the intensity of motor threshold was established. Pulses were delivered at 110% of the intensity of motor threshold. Pulses were delivered automatically according to a schedule either locking stimulation times to coincide with a metrical beat in the stimuli or randomizing them within 1000 ms of those beat-synchronized time-points. About 4 to 5 seconds separated each pulse. Because music-synchronized motor actions anticipate the ongoing beat and their initiation typically precedes it, in order to reach their target (i.e., foot tapping the floor or hands clapping together) coinciding with the beat, beat-synchronized pulses were delivered 100 ms before the beat, to coincide with corticospinal drive functioning to synchronize impact of movements with beat. For music stimuli, beat onsets were determined by isolating the peaks at metrical points in the waveform, typically coinciding with bass drum or snare drum notes. For both music and tone sequences, metrical beats to which TMS pulses were timed were those occurring in all four positions within the metrical cycle. During tone sequence trials, 18 or 19 TMS pulses were delivered, for a total of 224 for that type of stimuli per participant, and between 8 and 20 during music trials, for a total of 226 per participant. Anecdotally, participants sat still through the testing procedure with ease, and avoided voluntary movements that would have influenced EMG recordings.

Data Preprocessing

EMG recordings of LG and TA electrodes were averaged, and the resulting signal was analyzed to isolate MEP time windows based on the identification of the gradient of the artifact in the signal elicited by the TMS pulse itself. The MEP amplitude was calculated as the difference between maximum and minimum points in the signal within a 100 ms window postartifact. Preprocessing was conducted using Matlab software (Mathworks, MA, USA).

Analysis

Two participants' data were excluded owing to insufficient MEPs caused by excessive head movement. For these two participants, $<$23% of TMS pulses resulted in an MEP of $>$50 μV, compared with $>$72% for each of the four participants whose data were included in the analysis. Analyses of variance (ANOVA) were applied to MEP data to compare differences in mean MEP amplitude due to metrical strength (strong vs. weak), pulse-timing (beat-synchronized vs. random), and participant, for tone sequences and music excerpts separately. The use of individual participant as a fixed factor, compared with using traditional repeated measures ANOVA, reduces the ability to generalize our findings to the greater population, but increases the sensitivity of our tests because it considers all MEPs as data points, rather than only the means of conditions for each participant. This was deemed best practice considering the small number of participants and exploratory nature of our study. Statistics of individual participants were also considered, and follow-up contrasts were conducted using Tukey's test of Honestly Significant Differences, to correct for multiple comparisons. An alpha level of .05 was used for all tests of statistical significance. Statistical analyses were conducted using the R language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria).

Results

Tone Sequences

Analyses revealed a significant two-way interaction of metrical strength and pulse-timing, $F(1, 892) = 26.039$, $p < .0001$, and a three-way interaction of metrical strength, pulse-timing, and participant, $F(1, 880) = 11.289$, $p < .0001$. Main effects for metrical strength, pulse-timing, and participant were not significant. Beat-synchronized MEPs had significantly greater amplitude for metrically strong tone sequences compared with metrically weak ($p < .05$). No significant metricality-based difference was found for MEPs elicited at random asynchrony from metrical beats ($p > .05$). For metrically strong tone sequences, beat-synchronized MEPs had significantly greater amplitude than randomly timed MEPs ($p < .05$). For metrically weak tone sequences, randomly timed MEPs had significantly greater amplitude than beat-synchronized MEPs ($p < .0001$). These differences are apparent in Figure 2.

The significant interaction of metrical strength, pulse-timing, and individual participant indicates the influence and interaction of metrical strength and pulse-timing varies between participants.

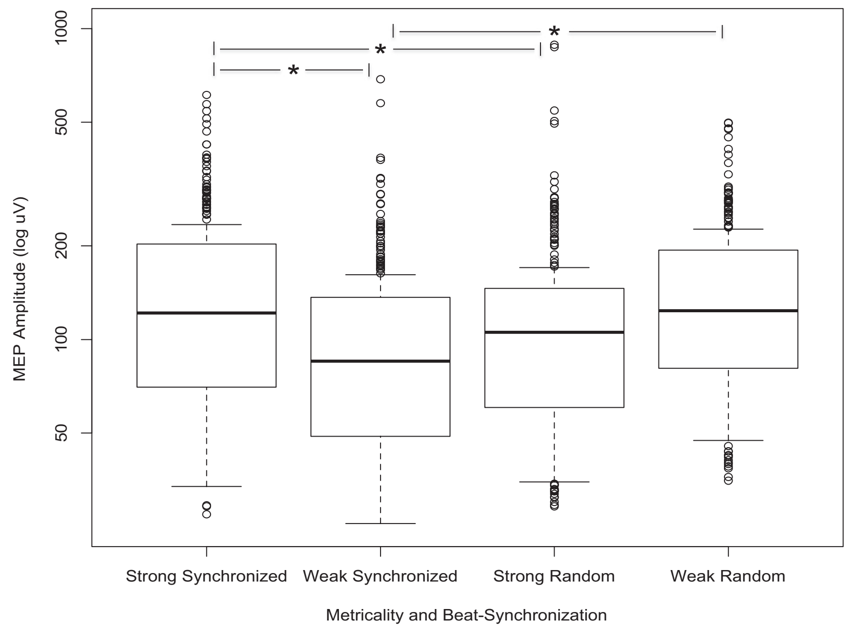

Figure 2. MEP amplitude across all conditions of tone sequences, for all participants. Bold lines indicate the mean. Upper and lower edges of boxes indicate upper edges of third and first quartiles, respectively. Whiskers indicate the most extreme data point within 0.3 times the interquartile range. Circles represent more extreme values. Statistically significant differences ($p < 0.5$) in mean MEP amplitude found by Tukey's test of Honestly Significant Differences (HSD) following ANOVA are indicated by *.

MEPs from three of four participants had greater beat-synchronized MEP amplitude for metrically strong tone sequences compared with weak, and this difference was statistically significant for two of those. For one participant, beat-synchronized MEP amplitude was significantly greater for metrically weak tone sequences compared with metrically strong. Figure 3 shows the beat-synchronized MEP amplitudes for metrically strong and weak tone sequences for each participant. The statistics for differences in MEP amplitude owing to metrical strength for both beat-synchronized and randomly timed pulses for each participant are shown in Table 1.

Music

No significant main effects or interactions were found for metrical strength, TMS pulse-timing, or participant on mean amplitude of MEPs elicited while participants listened to music excerpts. In addition, the amplitude of MEPs elicited while listening to music excerpts were not significantly different from those elicited during tone sequences, $t(1808) = 1.49$, $p > .05$.

Discussion

This study aimed to investigate motor processing of the metrical aspects of rhythm, by comparing MEPs elicited by single pulse TMS while participants listened to metrically strong and weak rhythmic tone sequences and music. Our findings show that for the present small sample of participants, changes in excitability of the motor system can occur owing to the metrical strength of rhythmic tone sequences. Based on the present data, differences in excitability owing to auditory rhythms can be concluded to occur in the motor system, and to be temporally locked to the metrical beat of perceived auditory rhythms. This finding is consistent with previous research implicating motor systems (Chen, Penhune, & Zatorre, 2008; Grahn & Brett, 2007; Teki, Grube, Kumar, & Griffiths, 2011) and temporally dynamic brain responses in processing of rhythmic auditory stimuli (Abecasis, Brochard, Granot, & Drake, 2005; Fujioka, Trainor, Large, & Ross, 2009, 2012; Iverson, Repp, & Patel, 2009; Nozaradan, Peretz, Missal, & Mouraux, 2011; Snyder & Large, 2005).

Although generalization and interpretation of our data are limited owing to the analysis of data from only four participants and the use of participant as a fixed factor instead of within a repeated measures design, effects may nevertheless reflect auditory–motor processing thought to underlie the synchronized and periodic movements of musical behavior. An overall picture recently emerging from research on the neural processing of rhythm suggests that motor systems subserve the processing of rhythm, meter, and the internal beat induced by auditory input (music), to which humans tend to synchronize their movements. Our experimental design and the methodological constraints of TMS did not allow direct reliable investigation of brain areas other than primary motor cortex, but our results are consistent with a hypothesis of motor excitability being modulated by the communication within an auditory–motor network, including other motor areas, in particular those like the striatum, supplementary and pre-motor areas that are activated by a regular beat (Chen, Zatorre, & Penhune, 2006; Grahn & Rowe, 2009; Teki, Grube, Kumar, & Griffiths, 2011).

The temporal specificity of modulated motor excitability is demonstrated by the difference in MEP amplitude for TMS pulses

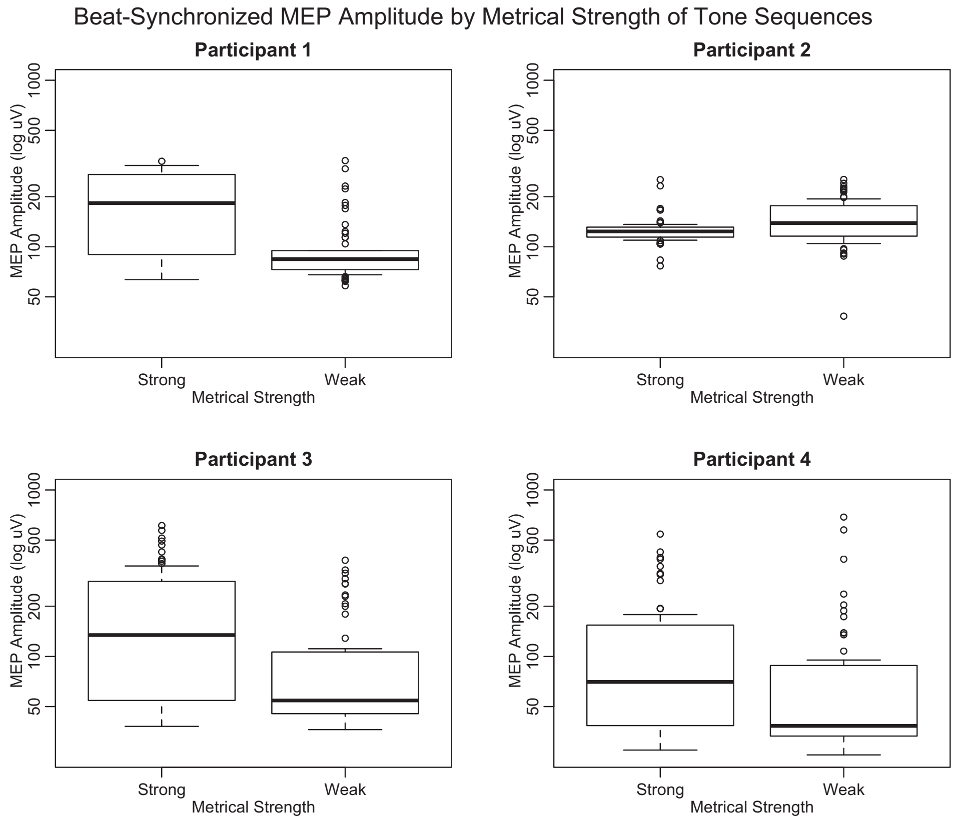

Figure 3. Single-subject data for beat-synchronized MEP amplitude by metrical strength of tone sequences. Bold lines indicate the mean. Upper and lower edges of boxes indicate upper edges of third and first quartiles, respectively. Whiskers indicate the most extreme data point within 0.3 times the interquartile range. Circles represent more extreme values.

delivered on the metrical beat vs. TMS pulses delivered at points unrelated to the metrical beat, in metrically strong tone sequences. This is consistent with the metrical beat-synchronized nature of music-oriented movement as well as findings of brain responses specific to the metrical beat as discussed above. We expected and found an increase in MEP amplitude timed to the beat for tone sequences that strongly induce the perception of a metrical beat. This effect of larger MEPs for beat-synchronized TMS was not expected for the metrically weak tone sequences, as these convey little information regarding the underlying beat. However, the finding of the opposite effect of increased amplitude for randomly timed versus beat-synchronized MEPs was unexpected. It is possible that owing to some degree of nonperiodic predictability, or local pseudoperiodicity within short rhythmic phrases that accidentally induced a metrical beat over short periods of time within or across individual sequences, anticipatory neural activity would allow dynamically, but not periodically, occurring motor facilitation, which could be captured by random TMS pulses better than those synchronized to an unrelated periodicity.

Table 1
Differences Due to Metrical Strength (Strong > Weak) in Mean MEP Amplitude

	Beat-synchronized pulses		Randomly timed pulses	
Participant	μV	*p*	μV	*p*
1	76.67	<0.0001	4.13	0.99
2	−20.18	0.017	12.15	0.2
3	88.34	0.0005	93.80	0.0002
4	31.80	0.5	−15.04	0.9

Note. Differences in MEP amplitude due to metrical strength for individual participants, elicited while listening to tone sequences. *p* values are adjusted for multiple comparisons using Tukey's HSD.

The overall high degree of variability in MEP amplitude, and differences in effects between individual participants, may reflect a number of factors. The use of participant as a fixed factor highlighted the variability between participants, in terms of the effect of experimental condition on MEP amplitude. How attention or effort to find and maintain a perceptible beat may influence motor excitability is not known, and we did not control or systematically test it here. Participants were instructed to listen attentively, but no specific instructions or task were given regarding the perception of the rhythm, meter, or "the beat" in either type of stimuli (so as to most closely resemble the real-world situations in which passive listening results in music-synchronized movements), and we cannot preclude the possibility that some participants paid greater attention or put greater listening effort into finding a beat than others. Our tone sequences differed in metrical strength, but both strong and weak tone sequences contained metrical information and an underlying beat. It is plausible that some participants may have tried and been able to perceive a beat in the metrically weak tone sequences, adding to variability. This is possible in particular owing to the randomized presentation of strong and weak tone sequences and music excerpts, which could lead to carry-over effects and reduce differences between conditions (Kidd, Boltz, & Jones, 1984). Individual differences in performance on a beat perception task have been shown to correlate with activity in auditory and motor areas of the brain (Grahn & McAuley, 2009). Thus, individual differences in perceptual abilities may also account for some of the variability in effects across participants. For example, in Participant 2, beat-synchronized MEP amplitude was more variable and mean amplitude was greater for metrically weak tone sequences compared with metrically strong. It is possible that, if MEP amplitude is modulated by perception of and attention to the beat, effortful entrainment in metrically weak conditions could provide such a pattern of results. However, without behavioral or perceptual response data from participants such interpretations remain speculative.

Individual differences in effects and variability may also arise from possible relationships between cognitive or emotional factors and motor excitability. It is plausible that changes in attention, arousal, and subjective preference owing to metrical strength may vary between participants. Changes in premotor cortex activity owing to preference of musical rhythms have been implicated (Kornysheva, von Cramon, Jacobsen, & Schubotz, 2010), suggesting that subjective aesthetic preference may have a role in modulating motor excitability while listening to musical rhythms. Such differences may contribute to beat-synchronized or temporally generalized differences in motor excitability. Participant 3 showed MEP modulation for metrically strong compared with weak tone sequences when TMS pulses were randomly timed as well as when beat-synchronized. The use of a task to direct the subject's attention to the tone sequences, or the collection of responses and measures of preference and arousal, could provide means to investigate such individual differences in further research.

Contrary to our hypothesis, we did not find differences in MEP amplitude relating to differences in metrical strength in music excerpts. Our expectations were that, as real-world music would elicit greater preference, attention, and emotional and cognitive engagement compared with the basic tone sequences, MEP modulation by metricality would be more evident for the musical conditions. The lack of randomly timed or beat-synchronized enhancement of motor excitability based on metrical differences in the music may be due to a sufficiently small effect of metrical strength relative to other factors, such as arousal, valence, familiarity, emotional engagement, and participants' subjective preference, which may influence motor excitability. These factors may underlie the anecdotal reports of some participants that music trials were preferred compared with tone sequences. This possibility is consistent with findings of preliminary research showing increased generalized motor excitability in stroke patients listening to self-selected (i.e., preferred) music, and increased anticipatory temporally specific motor execution for patients listening to a periodic tone (Raghavan, Aluru, & Leung, 2011). The mechanism underlying the effects found for the tone sequences may be the same that underlie everyday music-oriented motor behaviors, only undetected for those stimuli in this study. Future investigation could account for these factors using participant-selected music that would vary more systematically in arousal, mood, and preference.

Our stimulus design may also contribute to the fact that experimental manipulation of metrical strength and pulse-timing significantly interacted in their influence on MEP amplitude for the tone sequences but not the music excerpts. Tone sequences varied systematically with defined metricality-based differences in their rhythmic structure (Povel & Essens, 1985) that lead to known previously described differences in their processing and subjective perception (Grube & Griffiths, 2009), whereas the music excerpts were selected by subjective choice of the experimenters. This method of stimulus selection is liable to bias and subjective perception, and does not necessarily eliminate the presence of (or degree of presence of) metrical information, that is, sections of music excerpts intended to inhibit synchronized foot-tapping may contain adequate metrical information for the facilitation of motor excitability. Future work could examine the physical rhythmic structure and quantify the content metrical information of music excerpts in a more systematic manner and allow a more thorough investigation.

Our study extends the findings of Wilson and Davey (2002), and incorporates the implications of their research into known aspects of rhythm and meter processing, by using sequences defined by metrical strength and with known cognitive and perceptual correlates. Anecdotally, some participants reported no awareness of the existence of two types (i.e., metrically strong and weak) of tone sequence trials. A lack of explicit perception of the difference in metricality in the tone sequences underscores the automatic nature of the processing of the metrical beat and the tendency to synchronize movements with the beat, even without an explicit perception. Future research can expand on our design and stimuli to investigate the neural basis of the translation of metric auditory cues into motor excitability and action.

Conclusion

Our study demonstrates temporally specific modulation of motor excitability due to the metrical information in rhythmic auditory sequences occurring in some listeners. Our use of TMS allows for causal interpretations of auditory–motor relationships, and specifically the effect of metrical strength on motor excitability. When TMS pulses were delivered synchronously with perceptible metrically salient beats in the metrically strong tone sequences, MEPs had greater amplitude than for metrically weak sequences. Our results are consistent with expectations regarding the universal tendency to move along with music and known brain processing of rhythm and meter. The use of individual participant as a fixed factor in our analyses demonstrates considerable differences in the observed effects between individuals. This study provides a basis for future TMS research on motor processing associated with auditory rhythm and music.

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