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Moving to the Beat: Examining excitability of the motor system during beat perception with transcranial magnetic stimulation

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Abstract

Moving along to the beat of music is a universal human trait. It is a behaviour that displays the interaction between auditory and motor systems during beat perception. While several studies demonstrate that motor structures are involved in beat perception, the time course of motor system excitability during beat perception is not well understood. To examine the time course of motor system excitability in beat perception, we stimulated the motor cortex with transcranial magnetic stimulation (TMS) and measured the amplitude of the corresponding motor evoked potentials from the first dorsal interosseous (FDI) muscle while participants listened to rhythms that induced a strong, weak, or no sense of beat. The amplitude of the resultant MEPs is an index of motor excitability. Using TMS allowed for causal interpretations of the effect of beat perception on motor system excitability. It was found that there were numerical differences in motor excitability between conditions: excitability was greater for rhythms with a stronger sense of beat. Moreover, as predicted, the trends we observed suggest that motor system excitability may increase in anticipation of the induced beat. These findings support the need for different, more sensitive, approaches in determining the dynamics of motor system excitability.

Moving to the Beat

Humans have an innate tendency to move along or dance to music. When doing this we are synchronizing our movements to the beat. The beat is a regular pulse in the music that provides temporal structure. The beat can be emphasized through regular tones in music, however, regular tones are not necessary for an individual to perceive a beat.

Beat perception is an astounding process as it is universal and innate. It allows us to predict when the next beat will occur and prepare a motor response such as a clap or a hip shake to happen on the beat. These pre-planned motor behaviours in response to rhythms are behavioural evidence of motor systems being involved in the processing of music, and the beat in particular. This study looks to further our understanding of what is occurring in the motor network, during beat perception.

Auditory-Motor Link

The link between the auditory and motor systems is demonstrated both by behavioural responses as well as imaging studies that show the cortical interactions between these two systems. The main cortical structures of the motor system consist of the primary motor cortex (M1), supplementary motor area (SMA), and premotor cortex (PMC). Their projections to the basal ganglia and cerebellum result in activations of these two subcortical structures during motor tasks (Schubotz, Friederici, & Cramon, 2000; Chen, Penhune, & Zatorre, 2008). The motor system is not only involved in the timing of movements but is also involved in the perception of time without movement (Schubotz et al., 2000). For example, passive watching or listening to temporal sequences activates the same motor areas as actually reproducing temporal sequences (Schubotz et al., 2000). Schubotz et al. (2000) examined time perception by having participants perform a go/no go task based on temporal information in auditory and visual

rhythms. The functional magnetic resonance imaging (fMRI) results showed that the SMA, PMC, basal ganglia, and cerebellum had greater activity compared to baseline (passive listening / watching of rhythms), thus demonstrating that these structures are important not just for motor timing, but also for time perception.

The motor system is also involved in perceiving and producing temporal sequences called rhythms (Grahn & Brett, 2007). Rhythms with a strong sense of beat (metric simple) are more accurately reproduced than rhythms that have a weaker sense of the beat (metric complex) or no sense of beat (nonmetric). Activity in the SMA and basal ganglia is greater for metric simple rhythms; this is evidence that the SMA and basal ganglia are relevant for beat perception as these structures are involved in the processing of perceptual stimuli.

Not only is there increased activity within motor structures during the processing of rhythms, but the functional connectivity (association of activity in anatomically separate structures) between auditory and motor structures increases as the strength of beat increases; this highlights the involvement of the motor system in beat perception. Grahn & Rowe (2009) used fMRI to observe the functional connectivity of structures as participants listened to metric simple and nonmetric rhythms. Connectivity between the superior temporal gyri (which contains the primary auditory cortex), the SMA, PMC, and basal ganglia increased when participants were listening to metric simple rhythms. This auditory-motor connectivity was greater for musicians (five or more years formal training) than nonmusicians, suggesting that musical experience may affect how an individual processes rhythms and the beat. It is for this reason that musical experience should be taken into account when studying auditory-motor links and beat perception.

Synchronization during Beat Perception

While fMRI has superb spatial resolution to examine what brain structures are involved in a task, the temporal resolution of electrophysiological methods has provided insight into how cortical electrical activity changes over time; such studies have shown that auditory neural activity synchronizes to auditory stimuli. Steady-state evoked potentials (steady-state EPs) can be recorded using EEG to illustrate electrocortical activity that is entrained to a periodic stimulus. Therefore, a periodic stimulus such as a beat could evoke a steady-state EP that is of the same frequency as the presented beat (Nozaradan et al., 2011). Three conditions were examined in this study: listening to the pseudo-periodic beat, imagining the beat in a binary meter (emphasis on every second beat, like a march,) or ternary meter (emphasis on every third beat, like a waltz). The results showed that the frequency of the steady-state EPs matched the frequencies of both the actual and imagined meters, showing synchronization to an internally generated or imagined pulse on top of the actual stimuli heard. This is important as it is likely a similar mechanism allows for the synchronization of neural activity to internalized timing of beat perception.

To be able to coordinate a movement to an oncoming beat, one must be able to predict when the next beat will occur. Predictive synchronization was identified in a magnetoencephalography (MEG) study by Fujioka et al. (2012). This study used isochronous auditory rhythms, which are rhythms where tones are presented at regular intervals. The frequency of the tone onset in the isochronous rhythms was manipulated to create varying tempo conditions. Frequency changes in the beta band, one of five intrinsic frequency bands that allow for control over the timing of neural firing, were recorded during passive listening of the rhythms. The rise of beta band amplitude depended on the tempo; this rise was taken as evidence of internalized timing to predict the next tone onset. Beat perception relies on internalized

timing. Dancing or clapping along to the beat relies on not only predicting the next tone, but also planning a movement. For the present study we hope to identify if excitability in the motor system synchronizes to the beat in a similar predictive fashion to beta band activity in the auditory system.

Neural Excitability and TMS

Most tools of cognitive neuroscience rely on indirect measures and inferences of brain activity; transcranial magnetic stimulation (TMS), on the other hand, allows for causal conclusions to be made about the role of a brain area in a particular cognitive process by enhancing or disrupting a select area of a neural network by generating action potentials in cortical regions. TMS application to the primary motor cortex generates an action potential resulting in a motor evoked potential (MEP), or muscle twitch. The excitability of a cortical region will affect the amplitude of the motor evoked potential; this means that the generation of larger motor evoked potentials is representative of increased excitability in the motor cortex. It is important to note that the primary motor cortex itself is not directly involved during beat perception; instead the excitability is increased as a result of greater activity in the SMA, PMC, and other associated motor areas involved in the planning of movement. Stimulation of TMS to the primary motor cortex allows for a behavioural measure, which can not be achieved as clearly by stimulating associated motor structures.

MEPs and Beat Perception

Cameron and colleagues (2012) found that motor system excitability, as measured by MEP amplitude, was influenced by the beat perception of rhythms. TMS stimulations were applied either on the beat or off the beat in metric simple and metric complex rhythms. MEP amplitude was significantly greater for metric simple compared to metric complex rhythms when

the TMS was applied on the beat. This difference, however, did not apply when TMS was randomly applied, suggesting that motor system excitability may fluctuate during beat perception as opposed to being statically increased for metric simple rhythms.

As previously mentioned, musical training may affect auditory-motor communication as well as processing of auditory stimuli. In a study examining motor cortex excitability in response to groove, it was found that excitability was influenced by musical training (Stupacher et al., 2013). Groove is a characteristic of music which has to do with the degree a rhythm or piece makes a person want to move or dance. It was found that musicians had greater MEPs during high groove, as opposed to low groove, conditions and it is important to note that this was emphasized when stimulation occurred on the beat. This illustrates that musical experience may affect motor system excitability during rhythm and also beat perception. It is for this reason that during this study all participants were asked to indicate the amount and type of musical experience they had; the focus of this study is to examine "normal" motor excitability during beat perception before examining individual differences and effects of training or impairment.

The possibility of motor system excitability being anticipatory to the beat was studied by Wu, Cameron & Grahn (2015) by presenting TMS at precise asynchronies leading up to the beat; not just on beat and off beat. TMS stimulations were presented 20, 15, 10, 5 and 0% asynchrony to the beat and no significant interaction between time and metricality (sense of beat) were found; yet again a significant difference in motor system excitability was found between metric simple and metric complex rhythms.

The time course of motor system excitability during beat perception was examined in this study by gathering a sample of MEPs across the entire beat interval. Since musical experience can affect beat perception (Grahn & Rowe, 2009; Cameron & Grahn, 2014) participants were

asked about previous musical training and experience. Participants listened to metric simple, metric complex, and nonmetric rhythms while MEPs were measured from the first dorsal interosseous (FDI) muscle of the hand as a measure of motor system excitability.

It was predicted that motor system excitability would be greater for metric simple rhythms compared to metric complex and non-metric as found in previous literature (Cameron et al. 2012, Wu, Cameron 2015). Based on evidence of synchronization of neural activity during the listening of isochronous tone sequences it was hypothesized that motor system excitability may fluctuate in a similar anticipatory manner. Therefore it was predicted that: 1) MEPs would be greater overall during the metric simple compared to the metric complex and non-metric, and 2) that MEPs would increase in anticipation of the beat in metric simple trials.

Method

Participants

Seventeen participants (4 male) participated in the experiment. Participants were at least eighteen years old, with a mean age of 22.5, and normal hearing. Participants were recruited through posters displayed across campus (Western, University) and upon showing interest in the study participants were emailed a TMS pre-screening form for possible TMS exclusion criteria. TMS exclusion criteria includes but is not limited to pregnancy, epilepsy, metal implants, or a history of migraines. A musical experience questionnaire was completed after informed consent to the study regarding number of years and type of music and/or dance training. A typical testing session was approximately two and a half to three hours.

Auditory Stimuli

Auditory stimuli consisted of rhythms of either metric simple, metric complex, or nonmetric. The tone used in all the rhythms was a 6 ms sound clip of a generic snare drum (sample

from music production software). This tone was kept constant in pitch, volume, and duration for all rhythms. In metric simple rhythms a tone onset always occurred on the beat position and all tones occurred at integer ratios of 1, 2, 3, or 4. While tones in metric complex rhythms also occurred at integer ratios of 1, 2, 3, or 4 tone onsets only occurred on some of the beat positions. A similar construction of metric simple and metric complex rhythms was also used by Cameron (2012) and Wu (2015).

Although metric complex rhythms do not have a distinct beat it is hypothetically possible to sense a beat; due to this uncertainty we added a non-metric condition as no beat can be sensed from these rhythms. The non-metric rhythms were constructed by altering the intervals between tones of the metric simple rhythms. One third of intervals were decreased by ½ of one unit, one third of intervals were kept the same, and one third of the intervals were increased by ⅓ of one unit. This process created rhythms with irregular timing between tones while keeping the number of tones and length of the rhythms the same as the metric simple and metric complex rhythms. This method was also used by Grahn & Schuit (2012), and showed that reproduction of non-metric rhythms is significantly poorer than reproduction of metric simple rhythms.

There were 13 rhythms for each metric condition (simple, complex, non-metric) and each rhythm was played once at 700 ms and once at 900 ms resulting in a total of 78 rhythms. Rhythm length was between 35 seconds and 45 seconds depending on tempo condition. Participants listened to all 78 rhythms in a randomized order. Headphones were used to play all musical stimuli to eliminate any background noise, and experimenter bias.

Materials and Procedure

Participants sat relaxed in a chair with their feet planted on the ground. They were told to sit still and listen to the rhythms while receiving TMS and that they would verbally provide a

beat salience rating from 1 to 7 after each trial; 1 represented "I could not sense a beat, I would not be able to tap along" to 7 which represented "yes I knew where the beat was I could have tapped along". The beat salience rating was included to determine if participants were noticing a difference in beat salience between metric simple, metric complex and non-metric rhythms, and additional benefit of this was that it increased the likelihood that participants were paying attention to the rhythms. First electromyography (EMG) equipment, which would record the MEPs, was set up by placing a positive and negative electrode on the first dorsal interosseous muscle of the participant's right hand as well as a reference electrode on the styloid process of the ulna.

TMS was delivered using a Magstim high-speed magnetic stimulator with a figure-eight coil. M1 was located by first determining the center point of the skull by measuring the participant's head from nasion to inion, and from ear to ear, and then 2 cm anterior and 5 cm to the left from this center-point. The motor hotspot for the first interosseous muscles was determined by adjusting the intensity and location of the TMS coil by examining the resulting MEP measurements. Initial TMS pulses were set at 30% of the Magstim system and adjustments were then made in increments of 5% so that a minimum of 5 out of 10 stimulations evoked an MEP of at least 50 μ V; this was defined as motor threshold level. Stimulation intensity for the task was set at 110% motor threshold for each participant.

Stimulation sets were pre-paired with rhythms to control for beat and tone asynchrony. Beat asynchrony was consistent across conditions as each metric style had 100 stimulation time points evenly across the inter-beat interval. Stimulations occurred every five to seven beat intervals, for a total of six to eight stimulations per rhythm. Tone asynchrony was limited to ½ of the inter-beat interval, in other words a stimulation could only occur if a tone had been present

in the last possible tone position. Therefore the time between tone and TMS pulse could not exceed 175 ms or 225 ms for rhythms played at a tempo of 700 ms and 900 ms respectively. These same time limits were applied for tone asynchrony in the non-metric rhythms. Rhythms and their corresponding stimulation set were randomly selected and presented using MATLAB. After each rhythm participants were asked to verbally rate how salient the beat of the rhythm was and experimenter input of the rating into a keyboard cued the next trial to begin after a two second delay. A two minute break was offered after every ten trial; additional or longer breaks were given if requested by the participant.

Two behavioural tasks were also conducted to validate the differences between the three rhythm types as well as to allow for comparisons of motor excitability and individual differences behaviourally. The beat tapping task required participants to tap along to the beat of rhythms selected from the TMS task. Participants were presented two rhythms from each metric/tempo condition in a randomized order for a total of four rhythms for each rhythm type. Rhythms were listened to with headphones and the beat was taped on the "m" key of a laptop. Performance on the task was evaluated by examining how regular a participant's tapping was within a trial (coefficient of variation of inter-tap intervals), how close a participant tapped to the theoretic beat position relative to the tempo the rhythm (proportion asynchrony to the beat), and when the first tap of the trial occurred as this may provide information of how quickly a participant felt they sensed the beat. Coefficient of variation of the inter-tap interval, proportion asynchrony to the beat, and first tap time were calculated using E-Prime® 2.0.

Participants were also given a rhythm reproduction task in which they listened to rhythm clips (samples from those used in the TMS task) and attempted to tap back the tone onsets. This particular task was used by Grahn & Brett (2007) in which it was found that the type of rhythm

used affected the participants ability to accurately reproduce the rhythms during the task; metric simple was the easiest to reproduce whereas non-metric was the most difficult. Although the rhythms in the task were samples from the TMS task they were slowed down to tempos similar to those used in the Grahn & Brett study. Five clips were chosen for each beat condition: two at a tempo of 920 ms, one at 1000 ms and two at 1080 ms. The slower tempos also ensured that difficulty in reproduction came from rhythm perception and not due to constraints in speed of tapping. Rhythms were played twice before the participant was prompted to tap back the rhythm. If the participant successfully tapped the rhythm the next rhythm was presented. If they did not tap it correctly the failed rhythm was repeated twice again before the next tapping attempt. After three failed attempts the trial was marked as a fail and a new rhythm was presented. A successful trial was defined as all taps being within 20% of the true tone onsets of the rhythm.

It was hoped that this study could reproduce the findings of the Grahn & Brett study; that performance of both tasks would be better when listening to rhythms with a stronger sense of beat.

Data Analysis

MEPs were recorded through Signal software and this output was then run through a MatLAB script that auto-selected the peaks of the MEP and calculated the resulting amplitude. Data from four participants were excluded from analysis due to more than 25% of MEPs being deleted. MEPs were deleted if they did not exceed threshold level of 50 μ V or exceeded 3 standard deviations of the mean (calculated for each individually). The majority of deleted trials for participants were the result of being lower than 50 μ V (96% of deleted trials across all participants) which could result from head or coil movements. For participant data that was

included in the analysis the range of deleted MEPs was from 2.5-21.6% with an average of 12.2% of trials deleted.

For each participant MEP data was collapsed across tempo (as this was a control aspect and there was no significant effect of tempo, F(1,12) = 0.938, p = 0.352) and grouped into 8 bins spanning the inter-beat interval. Sense of beat will be from here on out referred to as metricality, as it is the manipulated metricality of a rhythm that gives rise to a person's perception of the sense of beat (Grube & Griffiths, 2009). A two-factor repeated measures analysis of variance (ANOVA) was conducted to examine the effect of metricality (metric simple, metric complex, and non-metric) and time (8 bins) on normalized MEP amplitudes. Repeated measures ANOVAs are particularly susceptible to violating the assumption of sphericity of ANOVAs; corrections such as Greenhouse Geisser and Huynh-Feldt reduce type 1 error and provide a more accurate significance value. All reported statistics are Huynh-Feldt corrected values, which are generally regarded as a more liberal correction compared to Greenhouse Geisser corrections, which we decided were appropriate given the natural variability of TMS induced MEPs. Behavioural scores were each analyzed using a repeated measures one factor ANOVA with the three levels of metricality and significant results were followed up with paired t-tests. A p-value of 0.05 was used for all statistical tests of significance. Formal music training ranged from 0 to 14 years for the included participants (M = 4.32, SEM = 0.96); most of this training occurred as part of the music curriculum in public education. Musical experience was not used as a covariate for analysis as only 2 of the 13 included participants were still actively practicing music. IBM SPSS software was used for all statistical analysis.

Results

MEP Amplitude

The effect of metricality on MEP amplitude was numerically different as predicted with MEPs being greater when listening to metric simple rhythms (M = -0.43, SEM = 0.13) compared to metric complex (M = -0.56, SEM = 0.12) and non-metric (M = -0.82, SEM = 0.20). The effect of metricality on MEP amplitude was marginally significant, F(1.73, 20.77) = 3.23, p = 0.066. The effect of bin number on MEP amplitude was also only marginally significant, F(5.53, 66.34)= 2.02, p = 0.081, as was the interaction of metricality and bin number on MEP amplitudes, F(9.66, 115.86) = 1.72, p = 0.087. Observed trends in the data as seen in Figure 1 however do show that motor system excitability, represented by normalized MEP amplitudes, was numerically greater for rhythms with a greater metricality (metric simple > metric complex > non-metric). MEPs for metric complex and non-metric rhythms displayed less of a trend across the inter-beat interval (appeared more random and variable) whereas metric simple rhythms displayed a trend increasing before the beat. Despite the results not being statistically significant the overall observed trends are as predicted: 1) metric simple would have greater MEP amplitudes compared to metric complex and non-metric and 2) MEP amplitudes would increase before the beat for metric simple rhythms.

Behavioural Tasks

Metricality had consistent effects on behavioural task outcomes; this verifies that the rhythms used in the study did indeed vary in their sense of beat.

Beat Rating.

As previously mentioned a beat salience rating was given after each trial in the TMS task; the rating was from 1 (low salience) - 7 (high salience). Metricality had a significant effect on beat salience ratings, F(1.34, 16.07) = 50.01, p < 0.001. Ratings were significantly greater for metric simple rhythms (M = 5.29, SEM = 0.25) than for metric complex rhythms (M= 4.65,

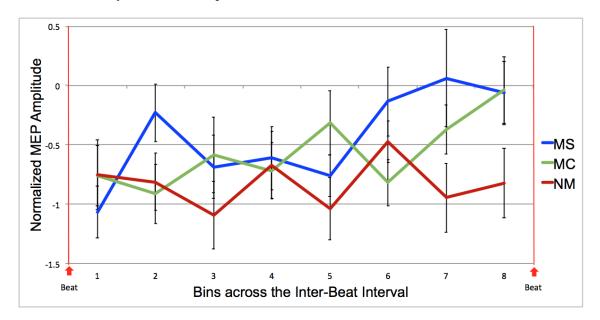


Figure 1. Normalized MEP amplitudes across 8 time bins along the inter-beat interval for each metrical condition (collapsed across the two tempo conditions). MEP amplitudes were normalized around the mean for each participant. Error bars represent the standard error of the mean.

SEM = 0.23), t(12) = 5.09, p < 0.001, and non-metric rhythms (M = 2.85, SEM = 0.22), t(12) = 7.89, p < 0.001. The difference in ratings was also significant between metric complex and non-metric rhythms, t(12) = 6.34, p < 0.001. These differences have been illustrated in Figure 2.

Beat Tapping.

Three measures were collected from the beat tapping task: proportion asynchrony to the beat, 1st tap time, and coefficient of variation of the inter-tap interval (CV ITI). The overall effect of metricality on proportion asynchrony to the beat was marginally significant, F(2, 24) = 2.73, p = 0.085. Numerically the differences of proportion asynchrony to the beat or beat tapping accuracy was in the predicted direction as seen in figure 3; accuracy was best for metric simple rhythms (M = 0.186, SEM = 0.007), than metric complex rhythms (M = 0.197, SEM = 0.005) and least accurate for tapping non-metric rhythms (M = 0.200, SEM = 0.006).

Metricality affected how long participants listened to the rhythm before beginning to attempt to tap the beat, F(1.15, 13.79) = 4.68, p = 0.044. Participants began to tap significantly sooner for metric simple rhythms (M = 4319, SEM = 741) than metric complex (M = 5601, SEM = 866), t(12) = -4.30, p = 0.001, and non-metric rhythms (M = 7069, SEM = 1399), t(12) = -2.55, p = 0.026, as seen in figure 4. The difference of first tap in metric complex and non-metric rhythms was not significantly different, t(12) = -1.36, p = 0.200.

Coefficient of variation of the inter-tap interval (CV ITI) was a measure for how regular a participant tapped regardless of the relation to the beat. A significant main effect of metricality was not found for this measure of beat tapping, F(2,24) = 1.167, p = 0.328. Meaning that metricality did not affect how regular the participant tapped; this may have been a result of participants being instructed to stay consistent with their tapping and avoid changing tempos.

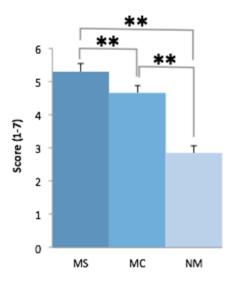


Figure 2. Beat salience ratings (mean \pm SEM). Rating scores of beat salience were given after each trial during the TMS task. Rhythms with more regularity and tones on beat positions elicited a greater sense of beat. Paired samples t-test, **p < 0.001.

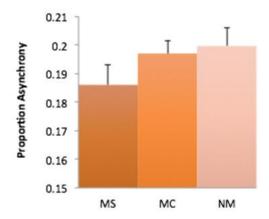


Figure 3. Proportion asynchrony to beat (mean \pm SEM) during beat tapping task while listening to metric simple, metric complex, and non-metric rhythms.

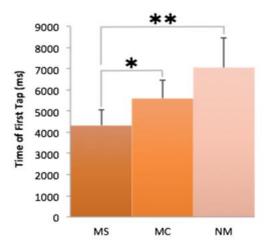


Figure 4. Time of first tap (mean \pm SEM) during beat tapping task for metric simple, metric complex, and non-metric rhythms. Participants began the tapping task significantly sooner when listening to metric simple rhythms compared to metric complex or non-metric. Paired samples t-test, *p value < 0.05, **p value < 0.001.

Rhythm Reproduction.

Metricality had a significant effect on rhythm reproduction scores, F(2,24) = 13.46, p < 0.001. Individual scores were calculated by percent of rhythms that were accurately reproduced (taps within 20% of tone onsets). Scores were significantly better for metric simple rhythms (M= 0.80, SEM = 0.072) compared to metric complex (M = 0.63, SEM = 0.087), t(12) = 2.269, p = 0.043 and non-metric rhythms (M = 0.43, SEM = 0.067), t(12) = 5.196, p < 0.001, as illustrated in figure 5. A significant difference in rhythm reproduction was also found between metric complex and non-metric rhythms, t(12) = 2.944, p = 0.012.

Discussion

The purpose of this study was to examine fluctuations in motor system excitability across the inter-beat interval and determine if metricality influenced these dynamics. This was done by having participants listen to rhythms that varied in metricality and by measuring motor excitability at 100 time points across the inter-beat interval. The results, although only marginally significant, show that there is a numerical difference in motor system excitability, as indexed by TMS induced MEPs, when listening to the three different rhythm types. Such differences are in line with knowledge that there is increased activity in the motor system when listening to rhythms that are in greater metricality and thus induce a greater sense of beat (Grahn & Brett, 2007; Chen, Penhune, & Zatorre, 2008). Although this method was limited in measuring excitability from M1, which it self is not active during beat perception, modulation of excitability of M1 is thought to be due to activity in upstream motor system areas, like the SMA and PMC. Therefore the amplitude of MEP as a result of stimulating M1 can be reasonably interpreted as an index of overall excitability in the motor system as a result of activation of upstream motor areas during beat perception. There also appears to be an anticipatory growth of motor system excitability before the beat for metric simple rhythms as predicted. MEP amplitudes for metric

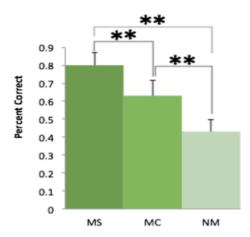


Figure 5. Percentage of rhythms (mean \pm SEM) accurately reproduced for metric simple, metric complex, and non-metric . Five rhythms were presented for each metricality. Accuracy of rhythm reproduction was significantly better for rhythms with a greater sense of beat (MS > MC > NM). Paired samples t-test, **p < 0.001.

complex rhythms were also greater in the last time bin compared to the earlier time bins. This could be a result of metric complex having some metric structure and enabling participants to perceive a weaker sense of beat (Grahn & Brett, 2007; Chen, Penhune, & Zatorre, 2008), further studies will be needed to examine how metric complex rhythms are processed. The anticipatory pattern displayed during metric simple rhythms was predicted based on evidence from MEG studies that show that activity in the auditory system fluctuates in an anticipatory manner when listening to isochronous rhythms (Fujioka et al., 2012). Such anticipation was also predicted from behavioural evidence people are not just reacting to the beat but planning their movements to occur in time with the beat (Patel & Iversen, 2014).

Previous TMS studies examining motor system excitability and beat perception have also experienced difficulties with MEP variability within and between subjects. While Cameron et al. (2012) found a statistical difference in motor system excitability between rhythms with a greater metricality and rhythms with lesser metricality, 1 of 4 of the study's participants actually displayed the reverse pattern. Wu et al. (2015), like the present study, was unable to find statistically significant results in terms of a main effect of metricality or interaction between metricality and time before the beat (examined up to 20% before the beat). The present study and the Wu et al. (2015) were both interested in characterizing the dynamics of motor system excitability leading up to the beat, both utilized similar methods and analysis; repeated measures ANOVA, to examine if a statistically significant interaction of metricality and time existed. Lack of significant results in both studies may very likely be result of high variability of MEP responses along with analysis not sensitive enough to capture fluctuations and differences in motor system excitability across time. Increased control in TMS stimulations, larger sample size,

greater resolution of time points, and more sensitive analysis are all likely to be beneficial in determining the link between motor system excitability and beat perception.

TMS is a very sensitive technique with the induced electric field being dependent on coil location, angle and rotation all relative to an individual's brain/skull structure (Laakso, Hirata, & Ugawa, 2013). Individualized coil placement (ex. MRI or fMRI guided) is still quite time consuming and expensive (Bijsterbosch, Barker, Lee, & Woodruff, 2012). While such a practice could be beneficial in reducing variability of MEPs and number of lost MEPs, this approach is not as necessary due to TMS eliciting a clear behavioural response upon correct stimulation. The use of a head support and coil secured in a stand may reduce the loss and variability of MEPs. The current method of the researcher holding the TMS coil was utilized to reduce strain and discomfort for the participant, in particular due to the long testing phase, as well as allow for coil micro-adjustments in response to participant's head movements, however this does mean that coil placement may have varied between stimulations. Variability could also be reduced in approaches of data analysis, such as the use of a sliding window. This approach could smooth out variability however still allow for enough resolution to allow for the observation of trends across the inter-beat interval. The smoothed data could then be analyzed with curve fitting approaches that would be more sensitive to the dynamics and changes of motor system excitability.

The behavioural tasks verified that there was a difference in the ability to sense a beat between the three different rhythm types and this was shown by the affect it had on the participants' task performance. This study was unique in not only examining the entire beat interval but also examining motor excitability in non-metric rhythms in addition to metric simple and metric complex. The difference in effect of non-metric rhythms compared to metric complex

rhythms is seen in overall MEP amplitudes as well as in performance on the behavioural tasks. It was clear that metric complex rhythms provide some metric information and level of beat perception shown by performance scores being less than metric simple but greater than nonmetric. Important to note is that the non-metric condition was also added as it is unclear to what degree individuals perceive a beat in metric complex rhythms. Metric complex rhythms can be compared to syncopated rhythms (commonly found in jazz, samba and reggae music) as both produce expectancy violations from a greater emphasis off the beat than on the beat than traditional rhythms. Musicians have been found to enjoy syncopated rhythms more than unsycopated rhythms (Keller & Schubert, 2011) and also would likely have more experience studying unsycopated rhythms than non-musicians. Therefore a musician may perceive metric complex rhythms as sounding like a syncopated rhythm and perceive the rhythm with more structure and beat than a person without musical experience. A perception of a greater sense of beat from metric complex rhythms could result in differences in motor system excitability. Individual differences in short term memory capacity, beat sensitivity, and musical training have all been associated with differences in performance on rhythm reproduction tasks as well as different patterns of brain activity during beat perception (Grahn & Schuit, 2012). These differences in brain activity would likely translate into differences in motor excitability found in M1.

A curve fitting analysis could also be applied to study individual differences in motor system excitability during beat perception. An individual's motor system excitability curve for when they are listening to metric complex rhythms could be compared to curves that result when they listen to metric simple and non-metric rhythms; this would be one way of analyzing if an individual processes metric complex rhythms as having a greater (more like metric simple) or

weaker metricality (more like non-metric). Based on the information found in this study further research could be done to determine if individuals with more musical experience or better performance on the behavioural tasks would perceive the metric complex rhythms more like the metric simple than the non-metric rhythms, and to see if excitability would be increased in anticipation before the beat.

To be able to explain how people are able to synchronize their movements to an aspect of auditory stimuli, further understanding of the dynamics of motor activity and excitability during beat perception are needed. Beat perception has been described as a predictive process (Patel & Iversen, 2014), the current results suggest that motor system excitability may be anticipatory to the beat; which could be a key aspect in the predictive nature of beat perception. This anticipatory pattern of motor system excitability could possibly also play role in the motor system acting as a time mechanism for timed movements and time perception (as illustrated by Schubotz et al. (2000)). The value of this study and other studies examining motor system excitability during beat perception is that it furthers our understanding of the interaction between the auditory and motor system.

Conclusion

The findings of this study suggest that motor system excitability may fluctuate in an anticipatory fashion to the beat. MEP amplitudes were numerically greater for rhythms that were of greater metricality. While the resulting MEP amplitudes were not different in a statistically significant way the observed patterns were as predicted based on previous findings examining motor system excitability and dynamics in the auditory system. In combination with the other studies that have found an effect of metricality on motor system excitability this study provides a

basis for continued study and analysis in capturing the dynamics of motor system excitability during beat perception.

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