

Investigating a Beat Network Using Passive Listening and Functional Connectivity

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Abstract

Previous literature has shown a network of activation between motor and auditory cortices when listening to rhythms that elicited a strong perception of a beat (Chen et al. 2008; Grahn & Rowe, 2009). However, no research to this date has investigated these networks using a resting-state paradigm. The purpose of this thesis project is assess the functional connectivity between motor and auditory regions during the perception of a beat, with the goal of mapping a unique network of structures that are co-active during beat perception. To do this, we will administer a functional magnetic resonance imaging (fMRI) scan to 5 healthy participants while they passively listen to a metric simple rhythm or silence. Each condition will be 5-minutes in duration. To determine the functional connectivity between cortical regions 30 hypothesis driven structurally defined ROIs will be correlated and then compared. It was shown that motor and auditory regions showed high magnitude of connectivity with themselves when compared to regions in control networks (visual, default mode). However, the similar trend was observed in the silent condition, therefore we are unable to infer that this network of auditory and motor regions is related to the perception of a beat.

Neural Networks Associated in the Perception of a Beat

The ability to synchronize motor movements to a musical rhythm is a very complex task, as it requires the perceiver to simultaneously decipher audio information and coordinate muscle movements accordingly. However, this task seems to come easy to humans, shown by our ability to tap our feet to the rhythms of a musical piece with profound accuracy (Large, 2000).

Moreover, the ability to accurately synchronize motor movements to music seems to be a uniquely human ability, as apes, our closest genetic ancestors do not show this capacity (Zacro, 2009).

What Guides Our Perception of a Beat?

Music can be broken down into components such as rhythm, tempo and pitch. These components work together to provide the listener with a complete experience of music. This thesis project is focused on music's rhythmic structure.

The best description of rhythm comes from a quote from the famous jazz musician Miles Davis who says, "Music is the space between the notes. It's not the notes you play; it's the notes you don't play". Rhythm is defined as the arrangement of time intervals across the span of an auditory sequence (Grahn, 2009). In other words, what signifies a rhythm is the sequence of spaces between the notes of a musical piece. Listening to a rhythm usually leaves the listener with a feeling of an underlying pulse. This pulse is what is defined as the beat. The beat of a musical piece is a property of its rhythm and is subjectively perceived by the listener (Large & Palmer, 2002). Our perception of a beat is affected by the metrical structure of rhythm. The metrical structure of a rhythm is described as the order in which notes are organized across the sequence of a rhythm. The metrical structure of a rhythm can be quantified as the amount of notes that fall in a position of where the beat could be found, or rather the quantity of notes that

fall on the position of a persistent pulse. Operationally we define these different metric structures as being either metric simple, or metric complex. The structure of a metric simple rhythm will be organized in a way that the majority of beat positions are occupied with note (see Figure 1.). Metric simple rhythms have been shown to readily elicit a feeling of a beat (Grahn & Brett, 2007). Conversely, metric complex rhythms are organized as to leave many beat positions unoccupied by notes, thus making it much harder to perceive a feeling of a beat. It is crucial to point out that the perception of a beat is something that is inferred onto a musical rhythm. Furthermore, as shown by the variety of metrical structures, notes do not always fall in line with the beat, therefore the perception of a beat must be formed internally, to some extent. As a result, two observers may perceive completely different beats when listening to the same rhythm (Repp, 2007). Thus, the metricality of a rhythm only affects the ease in which someone is able to perceive a beat, it does not dictate the specific beat that is perceived. This is determined by the observer.

The Neural Substrates of Beat

Patel and Iversen (2014), propose the theory of “action simulation for auditory prediction” (ASAP). Their theory suggests that musical beat perception is based on the integration of auditory and motor planning regions of the brain. Moreover, their theory suggests that our perception of a beat is based on our ability to make predictions of when subsequent notes will fall. These predictive assessments of a rhythm rely on the interaction between cortical regions; such the basal ganglia (Grahn & Brett, 2007; Grahn & Rowe 2009), associated in timing and regions responsible for audition. This theory is given support by research that has shown the activation of motor system brain during the passive listening of music (Zattore, Chen, & Penhune, 2007; Cameron et al., 2012). Furthermore, this theory is supported anecdotally by the

ease in our ability to tap along to the beat of a musical stimulus with extreme precision, suggesting that we are wired to integrate motor movements with auditory stimuli.

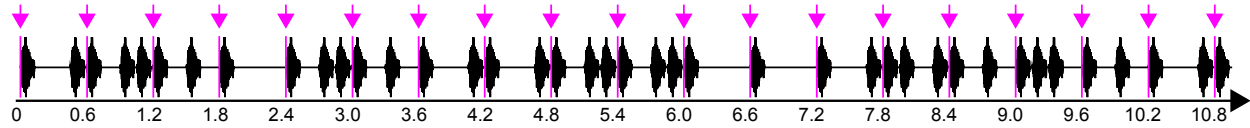


Figure 1. This figure depicts the arrangement of the concatenated macaque calls used in the simple rhythm condition. The X-axis represents a hypothetical measurement of time. The pink lines are the equally spaced points that mark the beat and the black notches represent are the sounds. As shown every pink line contained a sound eliciting a strong feeling of a beat.

A study by Chen et al. (2008), investigated the activation of cortical regions responsible for beat perception. In this experiment they manipulated the metrical parameters of rhythm, by exposing musicians and non-musicians to either metric simple or metric complex rhythms. They used functional magnetic resonance imaging (fMRI) to determine the regional activity during different metrical rhythms, and in between scans they had participants complete a beat tapping task that measured the ability to synchronize to a rhythm. Performance on the task indexed the ability to perceive a beat. The result of the tapping task showed that synchrony of tapping increased in conditions with a metric simple structure. It was also observed that higher performance predicted a higher levels of activity in regions of the motor cortex responsible for motor planning (premotor cortex, cerebellum & supplementary motor area) during the exposure to metric simple rhythms. This suggests that an increased ability to perceive a beat is related to increased recruitment of the motor cortex in beat perception. These results align with the hypothesis that motor planning is related to our ability to perceive a beat.

Further work conducted by Grahn & Rowe (2009) investigated the neural substrates that are related to the metrical structure of rhythm. In their study they aimed to determine what

cortical regions are simultaneously active during the perception of a beat by administering an fMRI scan to participants that listened to either rhythms that had a metrically simple or complex tone sequence. Before scanning, participants rated “how clear was the beat?”. The results of the experiment showed that in the metric strong conditions, participants rated the beat as more clear. Further, they also observed that in metric simple conditions there was a higher correlation of activity between the putamen, premotor cortex (PMC), supplementary motor area (SMA), and auditory cortex compared to the metric complex conditions. The correlated activity of these regions during the exposure to a metric simple condition provides support for the existence of a specific neural network related to beat perception. This study provided further support for the integration of motor-specific regions of the brain into a neural network during the perception of a beat.

Taken together, these two studies suggest that motor regions such as the PMC and SMA are associated with beat perception. Additionally, the correlated activity of these regions with the auditory cortex (Grahn & Rowe 2009), suggests the existence of a functional connected network related to beat perception. Though, no research to date has investigated the neural networks of beat perception using a completely passive listening paradigm. Implementing a passive listening paradigm would eliminate the possibility that any activity observed during listening is due to extraneous factors elicited from task demands. Thus this work is needed in order to isolate the specific neural network for beat perception, and conducting this research would allow us to infer with a greater degree of certainty the existence of a functional neural network that is exclusively related to beat perception.

Resting-State Functional Connectivity

In contrast to most fMRI studies that have investigated the cortical activity during the completion of a cognitive task, resting-state fMRI research investigates the cortical activity of someone at rest. To determine the functional connectivity, a series of regions of interest are either functionally driven, through the observation of activity during a task, or hypothesis driven and based on the finding of previous research. An example of a functional connectivity analysis would then correlate the activity observed in all the ROIs across the time course of rest. This work has provided a platform for work on resting-state functional connectivity. Research in this field aims to determine how multiple cortical regions that are anatomically separated, but functionally connected, are coactive over the time course of a resting condition. Interestingly, resting state networks show overlap with previously established functional networks (i.e. visual-motor network). This has provided extensive support for the existence of connections between cortical regions. However, as it stands, no research has investigated the neural networks corresponding to beat perception using a passive listening paradigm.

Dynamic Functional Networks

The brain is a dynamic system and functional networks wax and wane over time. Networks observed during resting-state fMRI have been demonstrated to be more or less coupled over the course of a few seconds (Hutchison et al. 2013). This temporal variation in functional networks presents a problem to the previous findings by Chen et al. (2008), and Grahn and Rowe (2009), as in their experiments they observed activity in a network of motor and auditory regions during listening to 14-20 second stimuli, and their functional analyses did not allow for the possibility that connectivity might vary as a function of time. If these networks are prone to dynamical shifts, then observations need to be made across an extended time series. Although it

is outside the scope of this thesis project, a paradigm with prolonged exposure adds a novel feature to the study of functional connectivity related to beat perception, and it affords us with the future opportunity to examine reorganization of functional neural networks underlying perception of beat.

The Present Study

The present study aims to provide further support for a specific neural network associated with beat perception. To do this a simple rhythm will be presented to participants for 5-minutes, while participants lay passively in an fMRI scanner. There will also be a silent condition, in which participants will be instructed to lay in silence for 5-minutes. It is hypothesized that we will observe an increase in connectivity between the striatal regions (basal ganglia, putamen), premotor cortex, and auditory cortex in the metric simple conditions when compared to the silent condition. Furthermore, it is suspected that regions associated with beat perception will show less connectivity with regions that are not related to beat perception (ie. visual regions). The confirmation of these hypotheses will expand on previous work conducted by Chen et al. (2008) and Grahn and Rowe (2009), and provide more support for the existence of a neural network responsible for beat perception.

Methods

Participants

A total of 5 participants (2 males, 3 females) partook in the experiment after the necessary fMRI protocol was discussed and written informed consent was obtained. Ages of participants ranged from 23-36 years ($M = 25.5$, $SD = 4.4$). Participants had between 0 and 23 ($M = 7.8$, $SD = 6.5$) years of musical practice. All participants were right handed and self-reported as possessing normal hearing.

Materials

Demographic Questionnaire. Participants were given a questionnaire which contained a battery of 24 questions. Demographic information such as age, sex, handedness, highest education, and native language was obtained through this questionnaire. Information concerning music training such as, years of training, musical skill, instrument of practice, and hours of daily practice was also obtained. Lastly, information regarding hearing capacity was also obtained through an abbreviated version of the Speech and Spatial Qualities of Hearing scale (SSQ) (Gatehouse & Noble, 2004).

Stimuli. To induce a feeling of a beat participants passively listened to a rhythmic stimulus. The stimulus was constructed of a series of concatenated macaque call sounds. Macaque sounds were manipulated using Praat software (v6.0.1.2). Using this software each sound was truncated using the PSOLA plugin which allowed for the temporal qualities of each sound to be manipulated while keeping the spectral qualities consistent (see Figure 2). Each macaque call was condensed into a base duration of 135ms. The rhythm was constructed as to replicate a metric simple structure, in which the inter note interval was based on multiples of 150ms. This induced a feeling of a consistent pulse and thus made it easy for the participant to perceive a beat (for a visual depiction of the rhythm see Figure 2). Participants were also exposed to 5min. of silence in which there was no auditory stimulus was provided and the participant was simply asked to lay still in silence. The order that conditions (metric simple rhythm or silent) were presented was counterbalanced across participants.

Procedure

fMRI Experimental Design. Before entering the scanner signed consent was obtained. Following the acquisition of consent, participants filled out a questionnaire where demographic

information as well as information on musical ability was obtained. The questionnaire also contained an abbreviated version of the speech and spatial hearing questionnaire (SSQ) allowing for the determination of any hearing deficits. Immediately after filling out the questionnaire each participant was informed of standard functional magnetic imaging (fMRI) protocol, and all items that possessed ferromagnetic properties were removed. After participants were cleared to enter the MRI room the MR technician escorted them into the scanner. Once inside the scanner participant's heads were fixated using foam block, and the head coil was then attached. Participants were then told to lay as still as possible and attend to the auditory stimuli. A visual fixation was provided in the form of a smiley face. However, participants were given the option to close their eyes during the scan. Structural scans were obtained, which took ~10 minute. Following this, functional scans were obtained while participants listened to rhythms.

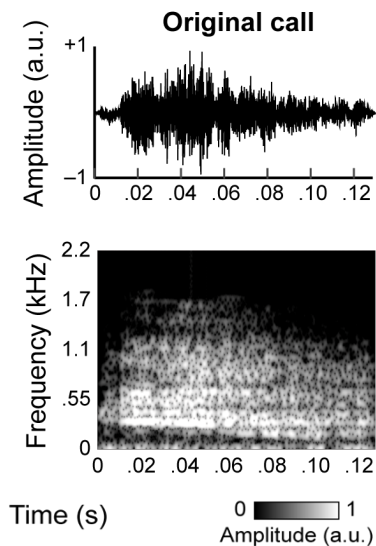


Figure 2. This image depicts the spectral qualities of the macaques call. A truncated version of this was concatenated to form our rhythmic stimuli. The image at the top is the macaque call in wave format which shows the amplitude of the sound (y-axis) across time (x-axis). The image at the bottom is a spectrogram of the sound, showing the frequency (y-axis) across time (x-axis) as amplitude which is shown in the whiteness of each region.

Rhythms were presented diotically using fMRI compatible earphones (Sensimetrics model S14) using the standard Comply™ foam tips which attenuate ~25dB of scanner noise.

MRI noise was also attenuated using foam blocks. Each condition lasted 5 minutes with a ~3-minute break in between conditions. At the end of the experiment participants were reimbursed for their time at a pro-rated rate of \$25 per hour. Between MRI information, questionnaire completion and scanning, the experiment took roughly 2 hours.

Image Acquisition. A 7-T Seimens Syngo MRI scanner and a 32-channel receive; 8-channel transmit head RF coil was used to acquire 240 echoplanar imaging (EPI) volumes for each rhythmic condition. Every EPI had 40 slices, matrix size 128 x 128, echotime (TE) of 20 ms, repetition time (TR) of 1.25 s, field of view 25.6 x 25.6 cm, flip angle of 35°, slice thickness 2.5 mm, in-plane resolution 2 x 2 mm. Each EPI volume was obtained using multiband acquisition with the multiband acceleration factor of 2, multi-slice mode interleaved. High-resolution magnetization-prepared rapid-acquisition gradient echo (MPRAGE) anatomical images (TR of 6000 ms, TE of 1.94 ms, flip-angle of 4°, inversion time of 800 ms, 0.8 x 0.8 x 0.8 mm voxels) were obtained and used for anatomic localization and co-registration. Total time spent acquiring the anatomical and functional images was ~20 minutes.

Image Preprocessing. SPM12 (SPM12; Wellcome Department of Imaging Neuroscience, London, UK) was used to preprocess all the EPIs. The first 3 EPI volumes of each condition were discarded as to compensate for stabilization of the magnet field. Slices contained in a single EPI volume were then synchronized by interpolating the time-course of the middle slice. Images were then realigned using the mean EPI volume as the reference. The EPI volumes were then co-registered with MPRAGE image. The MPRAGE image was deformed and normalized to the T-1 Montreal Neurological Institute (MNI) template image, and the normalization parameters used on the MPRAGE image was then applied to the EPI volumes. EPI volumes were spatially smoothed using a Gaussian kernel of full-width half maximum 8 mm.

Region of Interest (ROI) Definition and Model Design. A total of 30 different ROIs were selected based on a hypothesis driven structural definition (for a list of ROIs see Figure 3). ROIs were then subdivided into, “beat”, “control” and “default” network. ROIs were established using Automated Anatomical Labeling (AAL), an open source database of 116 structural brain regions all of which are based on the MNI template. Eighteen regions were selected as being apart of the “beat network”. The selection of regions in the basal ganglia (putamen and caudate), supplementary motor cortex and components of the pre-motor cortex (pre-central gyrus, paracentral lobule) was based on previous findings from Grahn & Brett, 2007 and Grahn & Rowe, 2009. Selection of inferior parietal and the thalamus was based on findings from Chen et al. 2008. Superior and inferior temporal gyrus was selected based on it being a structural landmark of primary auditory cortex (Grahn & Brett, 2007; Chen et al. 2008; Grahn & Rowe, 2009).

“Control regions” (calcarine sulcus and lingula) were selected as being related to the visual network (Beckmann et al., 2005). We selected only these two regions from the visual network because of their relation in primary visual processing, thus making them more exclusive to visual processing, whereas other components of the visual network may be more multimodal. Selection of region associated with the “default mode network” (precuneus, orbital medial frontal cortex, superior medial frontal cortex hippocampus) was based on a review paper on resting-state functional connectivity by van den Heuvel & Pol (2010). The default mode network was chosen as a second control network for it’s tendency to be arise during resting-state conditions, thus providing a sanity check for our silent condition.

Time courses extraction for all 30 ROIs was done using SPM12 (SPM12; Wellcome Department of Imaging Neuroscience, London, UK) and MarsBar (marsbar.sourceforge.net). A

subject specific general linear model (GLM) design matrix was constructed for each condition (silent, simple), in which the 237 EPIs (240 minus the 3 removed for stabilization of magnetic field) collected for each condition were coded as individual regressors. The data was processed using a standard high-pass filter of (1/128Hz). This was completed for each participant and each condition.

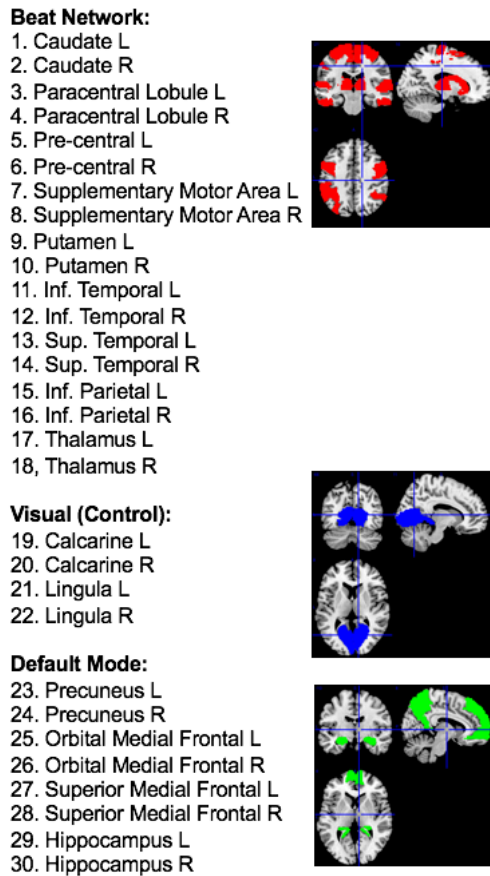


Figure 3. A depiction of all the ROIs used in this study. On the left, numbered from 1-30 are all the anatomical regions used. 1-18 are regions in the beat network, 19-22 are regions in the visual (control) network, and 23-30 are regions in the default mode network. To the right is a visual depiction of these network based on AAL structural images superimposed on to MNI images

Connectivity Analysis and Data Analysis. Using the GLM, the first-level analysis was completed, and the time course extraction for all 30 ROIs was done with MarsBar (marsbar.sourceforge.net). Extraction was completed for each participant and condition.

Resulting time-courses were then entered into a Pearson's-correlation, where the time courses activation of from all 30 ROIs was correlated in a pairwise fashion. This provided us with a measure of connectivity between ROIs. Correlation coefficients were then transformed into z scores using a Fisher Z transformation. To determine how the magnitude of connectivity of ROIs within the beat network differed from their connectivity with ROIs in the control networks, 3 separate network comparisons were made (beat v. beat, beat v. vision, beat v. default). Mean correlation for each network comparison was calculated for each participant, and each condition. These mean correlation coefficients were analyzed at the second-level using a 3 x 2 repeated measures ANOVA to determine how network comparisons (beat v. beat, beat v. vision, beat v. default) differed across conditions (simple, silence). A series of paired sample t -tests were used as a post-hoc test to access the differences in mean connectivity between each of the 3 comparisons.

Results

The analysis focused on the connectivity of ROIs within the beat network, and how correlated their activity was with other regions within the beat network as well with ROIs in the 2 control networks. This resulted in a total of 3 comparisons, for each a mean correlation was obtained. Connectivity was also compared across conditions, to determine how the communication between ROIs changed depending on whether participants were perceiving a beat or laying in silence. The results of a 3x2 (network comparisons [beat network v. beat network, beat network v. vision network, beat network v. default mode] X conditions [metric simple, silent]) repeated measures ANOVA showed a main effect of network comparison collapsed across conditions, $F(1, 4) = 20.83, p < 0.01$ (see Figure 3.). A series of post-hoc paired sample t -tests showed that ROIs in the beat network were significantly more correlated with

other ROIs in the beat network ($M = .54, SD = .12$), compared to ROIs in the vision network ($M = .45, SD = .15$), $t(9) = 2.9, p < .01$, and default mode network ($M = .34, SD = .13$), $t(9) = 11.3, p < .01$. There was also a main effect of condition, $F(1, 4) = 8.67, p < 0.05$, when average correlations were collapsed across network comparisons. No interaction was observed between conditions and mean correlation of networks with ROIs in the beat network, $F(1, 2) = .002, p = .99$. Thus the differences in mean correlation of between ROIs in the beat networks with ROIs in other networks cannot be said to be brought upon by the manipulation of listening conditions.

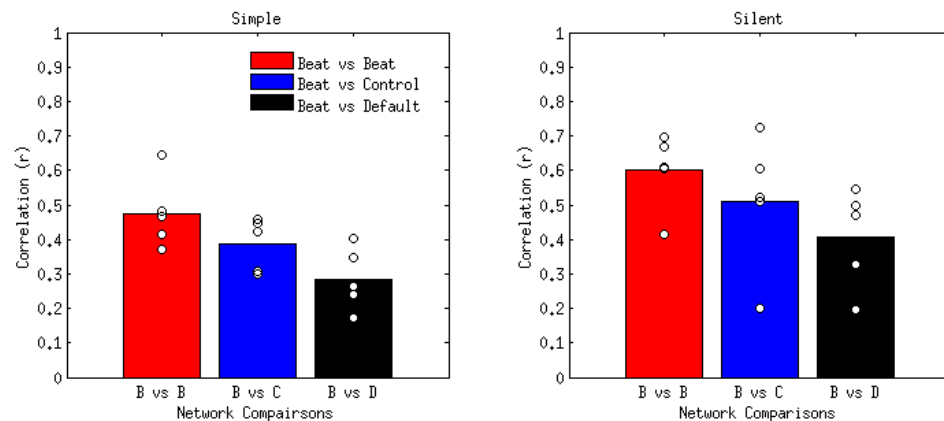


Figure 4. Mean correlation of activity between beat networks, visual (control) and default mode network, between rhythm and silent conditions. The left plot represents the rhythm condition, the right plot is the silent condition. The red bars are the mean correlation between 18 regions located in the beat network. The blue bars are mean correlations between beat regions and visual (control) regions. The green bars are mean correlations between beat regions and default mode regions. Single subject data is represented by the black dots above each bar. It is shown that regions in the beat network are less correlated with regions in visual and default mode regions, suggesting an independent beat network.

Discussion

Previous literature has documented that auditory and motor cortices form a functional connection during the perception of rhythms that elicit a strong sense of a beat (Grahn & Brett, 2007; Chen et al., 2008; Grahn & Rowe, 2009). In this experiment we observed how the magnitude of connectivity between regions previously established as being active during beat perception vary in relation to their connectivity with regions in the visual and default mode

networks. It was observed that across listening conditions, regions related to beat perceptions showed significantly higher connectivity with one another, compared to visual and default mode regions. These results corroborate previous findings in the literature and confirm our hypothesis of the existence of an exclusive functional network of cortices related to beat perception.

We also analyzed the magnitude of connectivity collapsed network comparisons and observed a higher amount of connectivity across all regions during the silent conditions when compared to the rhythm condition. This result, along with the observation that the same trends in network comparisons were observed in both the metric simple and silent condition, prevents us from confirming that this exclusive ‘beat network’ is in fact related to beat perception. However, there may be certain limitations related to the use of AAL structures to define the ROIs. As previously stated ROIs in the AAL database are based on structural parcellations of the brain. These parcellations are often non-specific definitions of cortical regions. For example, the ROIs we used to define the pre-motor cortex (supplementary motor cortex, paracentral lobule) covers a diffuse area of the motor cortex (see Figure 3). This may be problematic when trying to distinguish very specific parts of the motor cortex that are related to beat perception. Moreover, defining the pre-motor ROI based on a diffuse area of the motor cortex may explain why we see an overall increase in the magnitude of connectivity during the silent condition. Previous studies have shown that many sub-regions of the motor cortex show activation when participants are at rest (Biswal et al., 1995; Dwyer et al., 2014). Thus it may be the case that ROIs included as part of the beat network may also encompass regions that were also part of the default mode network and are driving the increase in connectivity during silence and decreasing the measures of connectivity during the metric simple condition.

Previous literature has used a functionally driven process where ROIs are defined based on condition-evoked activation, where selection of ROIs are based on mean voxel activation during a condition. However, in paradigms that implement a steady state condition this may be problematic as there is usually little or no material that defines the prime location of these ROIs that display activation (Marrelec & Fansson, 2011). This is especially true for research investigating functional connectivity of beat perception, given its novel nature. A study done by Marrelec & Fansson (2011), compared different ROI selection methods. They observed that each method produced different results on the spatial specificity of functionally active regions. Although the selection of ROIs is problematic, it is nevertheless recommended that future studies stray away from defining ROIs based on AAL templates, as they may not produce the specificity needed to locate regions that are functionally related to beat perception.

A future analysis on this data set could explore how patterns of connectivity change between conditions. It was observed that mean connectivity between ROIs was significantly higher in the silent condition. However, this merely tells us that overall the average connectivity in the silent condition was higher and nuances in the patterns of connectivity between ROIs may exist that are indistinguishable by assessing differences in mean connectivity. To determine how these patterns fluctuate we could systematically move the coefficients from each condition's correlation matrix into two separate vectors; each representing the pattern of connectivity in each condition. Correlating these two plots would then tell us how connectivity patterns differ for each condition, further informing where the differences between each condition remain.

Beyond the said limitations of this study, the result provides a solid foundation for future work investigating the functional networks corresponding to beat perception. More specifically, this work may provide future implications for studying if beat perception exists in other non-

human species. To date, the majority of work investigating beat perception in other species has used behavioural measures such as synchronization tasks (Patel et al. 2009), or electrophysiological measures (Selezneva et al., 2013). If it is found that a specific network of functionally connected cortices related to beat perception exists, it may act as a biomarker to inform neuroimaging work on non-human species. Fore knowing what regions to look at would guide this research.

Moreover, there may be clinical implications to the mapping of a specific beat network. A recent study identified a rare disorder in which individuals are unable to perceive a beat in auditory stimuli (Palmer, Lidji, & Peretz, 2016). These beat-deaf individuals are unable to synchronize any motor movements to a musical beat, and struggle to discriminate between rhythmic stimuli. As a result, beat-deaf individuals are prevented from ever learning to play a musical instrument, or participating in a music related activities. Additionally, language deficits in speech production may also be linked to the deficits in rhythm discrimination (Wiedland et al., 2015), suggesting that deficits in beat perception may have far reaching consequences. There is current research that show divergences in electrophysiological behaviour suggesting some kind of neurological defect, however there is no research specifying where these deficits exist. Mapping out a functional network related to beat perception may facilitate a better understanding of where these deficits lay, and potentially aid in the development of a treatment for this disorder.

Overall, the findings in this study suggest that auditory, motor and basal ganglia regions form distinct functionally connected network, shown by a higher rate of coupling with each other compared to other regions. Further research with different methods in ROI selection is suggested in order to determine if this motor-auditory, basal ganglia network is related to beat perception.

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