

**Investigating the Correlation Between Functional Connectivity in Auditory-Motor  
Regions During Naturalistic Listening and Gait Synchronization Performance in  
Rhythmic Auditory Stimulation**

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### Abstract

Gait impairments are an important societal problem, significantly influencing quality of life, injuries, and mortality. A promising gait intervention called Rhythmic Auditory Stimulation (RAS) asks gait-disordered patients to synchronize their footsteps to auditory cues, including music, to improve stride length, variability, and velocity. However, responses to RAS are highly variable across individuals, and RAS' effectiveness may depend on people's ability to accurately synchronize to the musical beat. Previous studies have shown that auditory and motor brain areas are co-activated and functionally connected when perceiving auditory information. Here, we investigated whether this neural auditory-motor coupling underpins differences in synchronization accuracy during gait. Participants completed a functional magnetic resonance imaging (fMRI) scan, which included functional scans of passive music listening. Using functional connectivity analysis, we investigated the connectivity strength between auditory and motor areas. On a separate day, participants walked on a pressure-sensor walkway, where they had to synchronize to musical stimuli 10% faster than their baseline walk cadence (steps/min). Gait analysis focused on changes in synchronization accuracy compared to baseline by matching participants' walking cadences to the music's tempo (beats per minute). We correlated each cadence-matching value to the functional connectivity values. We hypothesize that participants who synchronize more accurately (i.e., walking cadence matches the stimuli's tempo relatively well) will have stronger auditory-motor connectivity in the brain, particularly between the supplementary motor area (SMA) and the superior temporal gyrus (STG). Examining gait synchrony's association with brain connectivity will provide insight into rehabilitation therapies and enhance understanding of their effectiveness on gait-disordered populations, such as those with Parkinson's Disease.

*Keywords:* rhythmic auditory stimulation; gait synchronization; auditory-motor coupling; naturalistic listening; fMRI

**Investigating the Correlation Between Functional Connectivity in Auditory-Motor Regions During Naturalistic Listening and Beat Synchronization Performance in Rhythmic Auditory Stimulation**

When listening to music, we are often tempted to move along to the beat by spontaneously tapping our feet, nodding our heads, or even breaking into dance movements (Chen et al., 2008). A musical beat is a consistent recurring pulse that can ignite our desire to follow and synchronize with it (Grahn and Rowe, 2013). The stronger or clearer the beat is, the easier it is for people to perceive and move along with it. Stronger beats have also been associated with greater brain activity in the basal ganglia and supplementary motor area (SMA), even during passive listening (Grahn and Brett, 2007; Grahn and McAuley, 2009). Undergoing rhythmic training has also been shown to enhance motor skills and responsiveness to auditory cues, allowing us to perform a variety of complex movements (Ross et al., 2016). Musical training can also modulate the encoding of complex sounds like music by improving neural synchrony in the brainstem (Russo et al., 2005).

The relationship between auditory and motor brain areas, along with the inherent ability of music to make people move to the beat, has led to rehabilitation therapies aimed at people with movement disorders. Among these is Rhythmic Auditory Stimulation (RAS), an auditory cueing intervention where gait-disordered patients, such as people with Parkinson's disease (PD), are encouraged to synchronize their footsteps to a metronome or a musical piece to improve gait impairments (Ready et al., 2022). A significant body of literature has shown that RAS can improve spatiotemporal gait parameters by increasing walking speed, taking longer strides, and enhancing stability (Burrai et al., 2024; Wang et al., 2022; Ghai et al., 2018; Spaulding et al., 2013).

Despite its benefits, RAS can be highly variable across individuals; studies have shown that some PD patients respond positively to RAS while others show either no or negative

responses (Dalla Bella et al., 2017). Since the goal of RAS is synchronizing to the beat, the variability in RAS's effectiveness could depend on one's sensorimotor timing skills, which refers to the ability to precisely coordinate sensory input with motor actions, enabling accurate timing in different movements (Dalla Bella et al., 2017). Sensorimotor timing skills are also highly variable among the general population (Dalla Bella, 2023); while "good beat synchronizers" can accurately and consistently synchronize to the beat, "poor beat synchronizers" or "beat deaf" individuals often fail to synchronize accurately. The inability to synchronize to musical beats can explain the variability in RAS effectiveness, as most PD patients with poor rhythmic abilities do not respond well to RAS treatment (Dalla Bella et al., 2018).

To understand the functional mechanisms behind differences in beat synchronization ability, researchers have pointed toward auditory-motor coupling in the brain. Naturalistic listening (i.e., passively listening to complex musical stimuli) has been shown to engage the motor system with connections to auditory areas, activating the dorsal premotor cortex (dPMC), SMA, basal ganglia, lateral cerebellum, and motor cortex (Ross et al., 2016; Karmonik et al., 2016). When there is damage to premotor and supplementary motor areas, studies have shown that one's timing ability is impaired, making it difficult to synchronize to musical beats (Grahn and Brett, 2007). Researchers predicted that bad synchronization tendencies may be due to potential disruptions between perceiving an auditory stimulus via auditory areas and producing the stimulus using motor areas of the brain (Sowiński and Dalla Bella, 2013). Therefore, many have concluded that the auditory system can play a role in influencing our motor output, allowing us to tap along to rhythms or synchronize footsteps to rhythmic stimuli (Zatorre et al., 2007). This connection between auditory input and motor output is what may play a key role in influencing people's ability to synchronize to a musical beat.

Researchers have utilized neuroimaging strategies to investigate the neural mechanisms of beat synchronization as participants perform rhythmic finger-tapping tasks (Chen et al., 2008; Cheng et al., 2022; Grahn and Brett, 2007; Mathias et al., 2020). When participants were asked to imitate beat-based rhythms, auditory regions like the STG and auditory cortex elicited strong connectivity with motor regions like the dPMC, SMA, and putamen (Grahn and Rowe, 2009; Chen et al., 2008). Specifically, the SMA has been shown to react bilaterally to more complex beat-based rhythms and is recruited not only during beat production, but also beat perception when no intentional movements are necessary (Kasdan et al., 2022; Chen et al., 2008). It is commonly known that the SMA is responsible for motor output and control, especially movements that are internally generated, such as involuntarily tapping to musical pieces (Wu et al., 2019). In fact, multiple music-listening experiments have identified motor responses from the SMA, confirming its involvement in music (Gordon et al., 2018). However, there is evidence that the SMA has a more expanded network in music processing, where it can be seen integrating multimodal information to prepare for and during a music performance (Tanaka and Kirino, 2017). Specifically on auditory-motor integration, there is a substantial body of literature investigating the connectivity between the SMA and STG due to the STG's role in melody, pitch, and rhythm processing, as well as its engagement in music performance settings (Koelsch et al., 2005; Overy et al., 2004; Tanaka and Kirino, 2019). As expected, both regions increase in functional connectivity when people listen (Wu et al., 2019) or perform music (Segado et al., 2021; Tanaka and Kirino, 2017).

Although many studies have investigated how auditory-motor coupling may underlie beat synchronization ability during music listening or finger tapping, little is understood about whether auditory-motor coupling underlies gait synchronization during RAS. One study addressed the association between brain activation and gait performance, and found that cortical motor areas like the SMA and cerebellum were activated when PD patients performed

RAS, but auditory-motor coupling was not incorporated (Nishida et al., 2021). Most importantly, these PD participants underwent RAS through gait imagery instead of actually walking, because it is impossible to simultaneously walk during a functional magnetic resonance imaging (fMRI) scan (Nishida et al., 2021). To circumvent this challenge, our study divided neuroimaging and gait into two separate sessions, where participants engaged in naturalistic listening tasks during the fMRI session, and walked to music at +10% of their preferred walking rate during the gait session. Increased stimuli tempos have been shown to encourage active synchronization, which can be beneficial for improving spatiotemporal gait patterns (Erra et al., 2019). Their gait synchronization accuracy will then be correlated with auditory-motor coupling, measured by the connectivity strength between the SMA (representing the motor region) and anterior/posterior STG (representing the auditory region) regions-of-interest (ROIs) of the brain.

In summary, people's responses to RAS are highly variable. We think this might be due to the individual strength of auditory-motor coupling. Therefore, investigating neural mechanisms in RAS performance helps us understand the high variability of responses to RAS treatment and ask what makes a person likely to have a good response from RAS. The present study aims to understand how auditory and motor systems interact with respect to gait synchronization by assessing the association between auditory-motor connections and synchronization accuracy. We hypothesize that people who synchronize more accurately to RAS cues (good beat synchronizers) will have stronger auditory-motor coupling during naturalistic listening than poor beat synchronizers.

## **Methods**

### ***Participants***

This experiment was part of a larger project known as the Open Multimodal Music and Auditory Brain Archive (OMMABA), which recruited 82 healthy young adults (30 males, 51

females, 1 non-binary) across Western University (London, Ontario, Canada) and McGill University (Montreal, Quebec, Canada). While the OMMABA study consisted of several experimental sessions, this study only included a subset of participants who participated in both the gait and fMRI sessions, resulting in a total of 34 participants (14 males, 20 females). 12 participants self-reported as musicians while 22 did not. All participants were screened for normal or corrected-to-normal vision and reported no history of neurological disorders. As part of the pre-screening process, an audiometric test with pure-tone thresholds from 250 to 8000 Hz was implemented to assess normal binaural hearing. Participants whose threshold exceeded 25 decibels had auditory deficiencies that may impact performance on auditory tasks, hence they did not proceed with the study. Participants provided informed and written consent, and were offered monetary compensation for their participation and time. All experimental procedures were approved by the Western University Non-Medical Research Ethics Board.

### ***Gait Stimuli and Materials***

The stimuli used in the gait session consisted of 10 non-lyrical music tracks sourced from previous studies (Leow et al., 2021; Von Handorf, Leung, Urian, & Grahn, in prep). Participants heard each musical track twice, once with a low-pitched metronome embedded in the music and once with no metronome overlaid. The metronome track was generated from a single bass drum sound sample (sourced from <https://www.freewavesamples.com>) and normalized to -18 LUFS. Ableton® was used to auto-align the metronome to an isochronous beat grid, followed by manual adjustments and verification by three trained musicians. The final tracks, consisting of both music and metronomes, were combined and re-normalized to -18 LUFS using a MATLAB 2022a script. To encourage active synchronization to the beat, the tempo of all tracks was modified in Audacity® (version 2.4.2; <http://audacity.sourceforge.net>) to be 110% of, or 10% faster than, each participant's baseline cadence (i.e., natural walking without stimuli) while preserving pitch. Since each participant had their own baseline cadence,

the 110% modified tempo was identical across one participant's stimuli but varied across participants depending on their walking speed. Therefore, songs and metronome tracks from 90 to 140 beats per minute (bpm) were prepared in Audacity to accommodate fast and slow walkers. Each trial will consist of a cadence value, which will be used to compare each participant's respective 110% tempo. This difference tells us how accurately people are synchronizing to the beat.

During each testing session, participants' gait was recorded using a built-in 16-foot Protokinetics Zeno® pressure sensor walkway gait mat spanning 579 x 90.2 centimetres and containing an active sensor region of 488 x 61 centimetres (Fig. 1). The stimuli files were generated by MATLAB2021b and the walk trials were run in conjunction with MATLAB2015b and the ProtoKinetics Movement Analysis Software (PKMAS) application. Stimuli were played over wireless headphones (Sennheiser® HDR 160) for all components of the study.

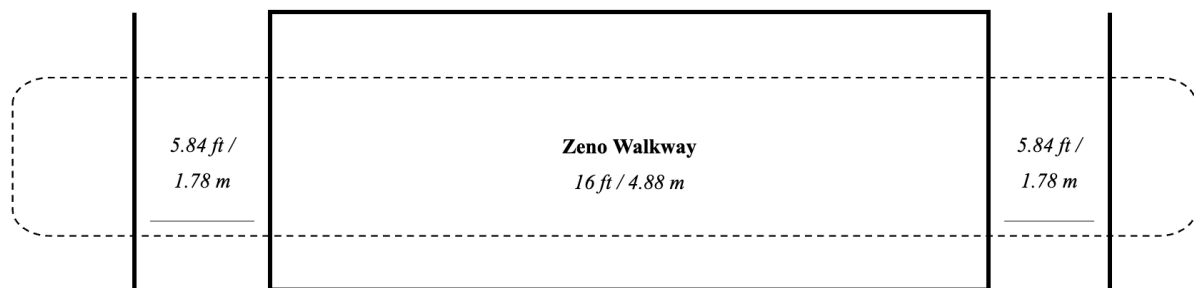
### ***Gait Procedure***

Participants were first instructed to walk for six lengths in a way that was comfortable and mimicked their natural everyday walk. Figure 1 illustrates the participants' walking trajectory on the pressure mat for two lengths (one back-and-forth), with the dotted lines showing the pathway. This procedure was done in silence, and the trial was immediately pre-processed afterwards to generate a personalized baseline cadence (number of steps per minute). Participants were asked to synchronize to musical stimuli 10% faster than their baseline cadence. To facilitate this, a file for each song with and without an embedded metronome was selected depending on their baseline cadence; for example, if a participant's baseline cadence is 103 steps/minute, all their musical stimuli were at 113 beats/minute. Participants also rated the songs on familiarity, groove, enjoyment, and beat salience (how strong the beat is) on a 1



to 100 Likert scale. Songs with the highest and lowest beat salience ratings were removed to equalize the level of beat strength across songs.

Participants then performed 20 RAS-cued walking trials, in which 8 songs contained an embedded metronome (“Music with Metronome” condition), 8 songs without any metronome embedded (“Music Only” condition), and 4 metronome tracks (“Metronome Only” condition). Following the same instructions as their baseline walk, participants walked to each song or metronome trial in a random order, completing six lengths each time. They were instructed to try their best to synchronize their footsteps to the beat of the stimuli. To ensure steady-state gait, participants started walking from the floor markings beyond the edges of the sensor mat. They walked beyond the mat every time before turning back. This allowed participants to take a few steps to find the beat before their footsteps were recorded, and prevented any accelerations or decelerations at the beginning, when turning, and at the end of a walk. Stimuli continued playing until they had completed all six lengths.



**Fig. 1.** Schematic diagram of the pressure-sensor Zeno walkway. Retrieved from Von Handorf, Leung, Urian, & Grahn, in prep

### ***Gait Analysis***

Participants’ walk trials were pre-processed on PKMAS and analyzed with R 4.4.1 (R Core Team, 2018). All partial footsteps (entering and exiting the mat) were excluded during the pre-processing phase. Since this study is only interested in synchronization accuracy, only cadence values were used for analysis and other spatiotemporal gait parameters (e.g. stride length, stride width) were not included.

Synchronization accuracy was measured using the equation in Figure 2. The absolute relative difference between the target tempo (baseline cadence +10%) and the observed participants' cadence for each trial was calculated. The score was then reversed so that a higher score corresponds to better synchronization accuracy. This process is computed for every walk trial and the scores were averaged across all 20 trials for each participant. This final synchronization score was used to correlate with our functional connectivity measures.

$$\text{Sync. Accuracy} = 1 - \frac{| \text{Cadence} - \text{Stimuli Tempo} |}{\text{Stimuli Tempo}}$$

**Fig. 2.** Equation for measuring gait synchronization accuracy.

### *fMRI Stimuli*

Musical stimuli were selected to encompass a diverse range of characteristics to facilitate a comprehensive analysis of auditory-motor coupling. Differences in genre, instrumentation, vocal presence, and familiarity were heavily considered in choosing the music. The finalized list of songs represented different musical styles, including rock, jazz, classical, rap, metal, folk, acapella, and music from diverse cultures. All selected musical pieces were sourced from MedleyDB 1.0 and 2.0, open datasets of multitrack recordings developed to support Music Information Retrieval research (Bittner et al., 2014; Bittner et al., 2016). All stimuli were normalized for loudness consistency to control for potential confounding caused by volume differences and presented in a fixed order across four 10-minute functional blocks.

### *fMRI Procedure*

Participants were placed in an MRI scanner and instructed to remain still. Participants completed several structural and functional MRI runs in one single session, where they listened to the musical stimuli without performing any explicit tasks. The OMMABA project included a T1-weighted anatomical scan, four functional music listening blocks, a fifth functional block

with naturalistic speech stimuli, a spin-echo field map, and a diffusion-weighted imaging scan. Only the music-listening runs were analyzed in this study. During each of these runs, participants passively listened to several music pieces and songs without performing any explicit tasks. Each block lasted approximately 10 minutes.

### ***fMRI Acquisition***

fMRI data were acquired using a SIEMENS MAGNETOM 7T investigational device with a 32-channel head coil at the Center for Functional and Metabolic Mapping in the Robarts Research Institute (Western University, London, Ontario, Canada). A whole-brain gradient-echo echo-planar imaging (EPI) interleaved sequence was employed to capture blood-oxygen-level-dependent (BOLD) signal changes. The imaging parameters for all four functional blocks were as follows: repetition time (TR) = 1500 ms, echo time (TE) = 24.00 ms, flip angle = 45°, field of view (FoV) = 207 mm (read) × 101.4% (phase), and voxel size = 1.5 × 1.5 × 1.5 mm. Data were collected with 88 slices in a transversal orientation, with an anterior-to-posterior phase encoding direction. Multi-band acceleration was set to factor 4, and GeneRalized Autocalibrating Partial Parallel Acquisition (GRAPPA) parallel imaging was used with an acceleration factor of 2 in the phase encoding direction, utilizing 36 reference lines. A total of 600 functional volumes were acquired per run.

### ***fMRI Preprocessing***

Raw data was first downloaded from the DICOM server and converted to Brain Imaging Data Structure (BIDS) format using Chris Rorden's *dcm2nii* function (version v1.0.20240202; Li et al., 2016). Preprocessing was performed using *fMRIPrep* 24.1.1 (Markiewicz et al., 2024; Esteban et al., 2019; RRID:SCR\_016216), which is based on *Nipype* 1.8.6 (Gorgolewski et al., 2011; Gorgolewski et al., 2018; RRID:SCR\_002502).

**Anatomical data preprocessing.** A total of 1 T1-weighted (T1w) images were found per participant within the input BIDS dataset. The T1w image was corrected for intensity

non-uniformity (INU) with N4BiasFieldCorrection (Tustison et al., 2010), distributed with ANTs 2.5.3 (Avants et al., 2008; RRID:SCR\_004757), and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped with a *Nipype* implementation of the *antsBrainExtraction.sh* workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using *fast* (FSL; Zhang et al., 2001; RRID:SCR\_002823). Volume-based spatial normalization to one standard space (MNI152NLin2009cAsym) was performed through nonlinear registration with *antsRegistration* (ANTs 2.5.3), using brain-extracted versions of both T1w reference and the T1w template. The following template was selected for spatial normalization and accessed with *TemplateFlow* (24.2.0; Ciric et al., 2022): *ICBM 152 Nonlinear Asymmetrical template version 2009c* (Fonov et al., 2009; RRID:SCR\_008796; TemplateFlow ID: MNI152NLin2009cAsym).

**Functional data preprocessing.** For each of the 5 BOLD runs found per subject (across all tasks and sessions), the following preprocessing was performed. First, a reference volume was generated using a custom methodology of fMRIPrep for use in head motion correction. Head-motion parameters with respect to the BOLD reference (transformation matrices and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using *mcflirt* (FSL; Jenkinson et al., 2002). The BOLD reference was then co-registered to the T1w reference using *mri\_coreg* (FreeSurfer), followed by *flirt* (FSL; Jenkinson and Smith, 2001) with the boundary-based registration (Greve and Fischl, 2009) cost-function. Co-registration was configured with six degrees of freedom. Several confounding time-series were calculated based on the preprocessed BOLD: framewise displacement (FD), DVARS and three region-wise global signals. FD was computed using two formulations following Power (absolute sum of relative motions; Power et al., 2014) and

Jenkinson (relative root mean square displacement between affines; Jenkinson et al., 2002). FD and DVARS are calculated for each functional run, both using their implementations in *Nipype* (Power et al., 2014). The three global signals are extracted within the CSF, the WM, and the whole-brain masks.

Additionally, a set of physiological regressors was extracted to allow for component-based noise correction (CompCor; Behzadi et al., 2007). Principal components are estimated after high-pass filtering the preprocessed BOLD time-series (using a discrete cosine filter with 128s cut-off) for the two CompCor variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components are then calculated from the top 2% variable voxels within the brain mask. For aCompCor, three probabilistic masks (CSF, WM and combined CSF+WM) are generated in anatomical space. The implementation differs from that of Behzadi et al. (2007) in that instead of eroding the masks by 2 pixels on BOLD space, a mask of pixels that likely contain a volume fraction of GM is subtracted from the aCompCor masks. This mask is obtained by thresholding the corresponding partial volume map at 0.05, and it ensures components are not extracted from voxels containing a minimal fraction of GM.

Finally, these masks are resampled into BOLD space and binarized by thresholding at 0.99 (as in the original implementation). Components are also calculated separately within the WM and CSF masks. For each CompCor decomposition, the  $k$  components with the largest singular values are retained, such that the retained components' time series are sufficient to explain 50 percent of variance across the nuisance mask (CSF, WM, combined, or temporal). The remaining components are dropped from consideration. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadratic terms for

each (Satterthwaite et al. 2013). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardized DVARS were annotated as motion outliers. Additional nuisance timeseries are calculated by means of principal components analysis of the signal found within a thin band (crown) of voxels around the edge of the brain (Patriat et al., 2017). All resamplings can be performed with a single interpolation step by composing all the pertinent transformations (i.e. head-motion transform matrices, susceptibility distortion correction when available, and co-registrations to anatomical and output spaces). Gridded (volumetric) resamplings were performed using *nitransforms*, configured with cubic B-spline interpolation.

### ***fMRI Analysis***

Analyses of fMRI data were performed using CONN release 22.a (Whitfield-Gabrieli and Nieto-Castanon, 2012; Nieto-Castanon and Whitfield-Gabrieli, 2022; RRID:SCR\_009550) and SPM release 12.7487 (Penny et al., 2011; RRID:SCR\_007037).

**Preprocessing.** Anatomical data were segmented into grey matter, white matter, and CSF tissue classes using SPM unified segmentation and normalization algorithm (Ashburner and Friston, 2005; Ashburner, 2007) with the default IXI-549 tissue probability map template.

**Denoising.** Functional data were denoised using a standard denoising pipeline (Nieto-Castanon, 2020) including the regression of potential confounding effects characterized by white matter timeseries (5 CompCor noise components), CSF timeseries (5 CompCor noise components), session effects and their first order derivatives (2 factors), and linear trends (2 factors) within each functional run, followed by bandpass frequency filtering of the BOLD timeseries (Hallquist et al., 2013) between 0.008 Hz and 0.09 Hz. CompCor (Behzadi et al., 2007; Chai et al., 2012) noise components within white matter and CSF were estimated by computing the average BOLD signal as well as the largest principal components orthogonal to the BOLD average within each subject's eroded segmentation masks. From the number of

noise terms included in this denoising strategy, the effective degrees of freedom of the BOLD signal after denoising were estimated to range from 375.9 to 394.8 (average 379.2) across all subjects (Nieto-Castanon, 2022).

**First-level analysis.** ROI-to-ROI connectivity (RRC) matrices were estimated by characterizing the functional connectivity between each pair of regions among 6 Harvard-Oxford atlas ROIs (Desikan et al., 2006): atlas.pSTG r (Superior Temporal Gyrus, posterior division Right), atlas.pSTG l (Superior Temporal Gyrus, posterior division Left), atlas.aSTG r (Superior Temporal Gyrus, anterior division Right), atlas.aSTG l (Superior Temporal Gyrus, anterior division Left), atlas.SMA r (Juxtapositional Lobule Cortex -formerly Supplementary Motor Cortex- Right), and atlas.SMA l (Juxtapositional Lobule Cortex -formerly Supplementary Motor Cortex- Left). Functional connectivity strength was represented by Fisher-transformed bivariate correlation coefficients from a general linear weighted-GLM model (Nieto-Castanon, 2020), estimated separately for each pair of ROIs, characterizing the association between their BOLD signal timeseries. To compensate for possible transient magnetization effects at the beginning of each run, individual scans were weighted by a step function convolved with an SPM canonical hemodynamic response function and rectified.

Finally, correlations between auditory-motor connectivity values and gait synchronization accuracy were examined to evaluate the hypothesized relationship between auditory-motor coupling and beat synchronization ability.

## Results

### *Consistency of Gait Synchronization Accuracy*

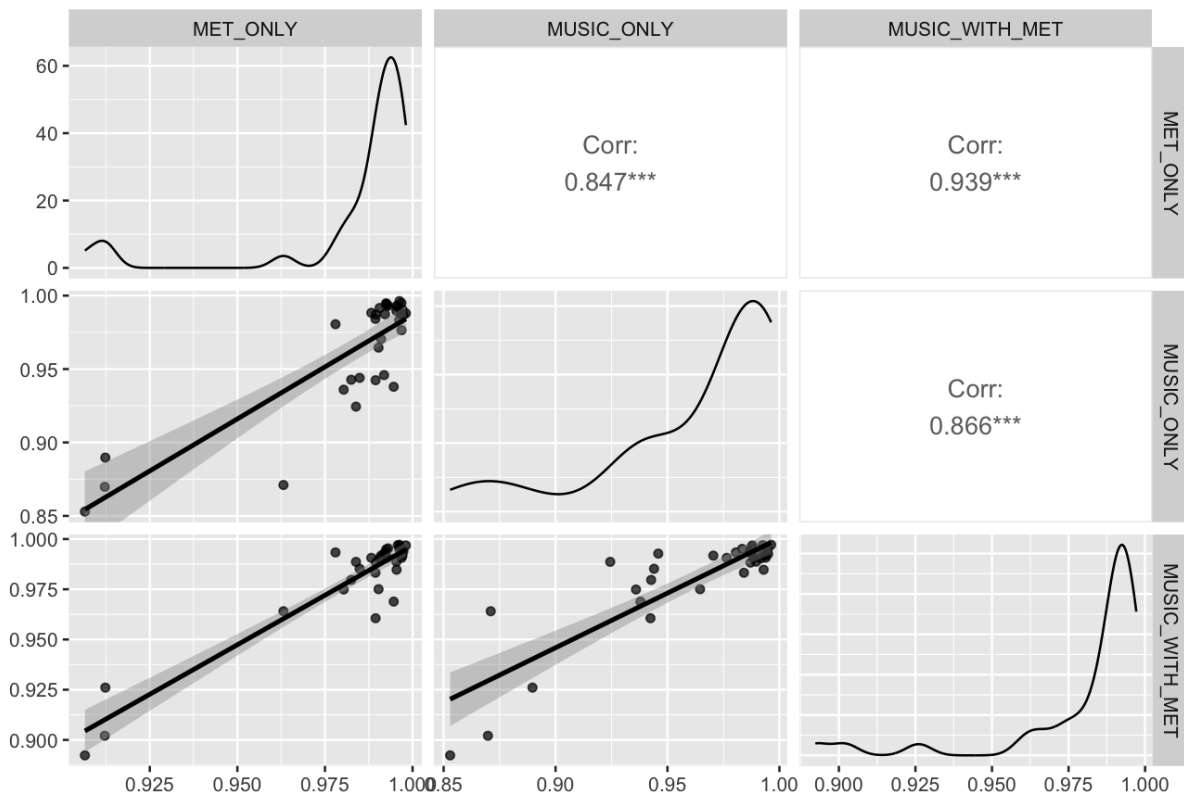
Before analyzing correlations between auditory-motor connectivity and gait synchronization accuracy, we first addressed the consistency of each measure. Inconsistent

measures can often lead to attenuated correlations or spurious effects, hence a higher consistency would suggest that our results are more likely to be valid. To investigate whether synchronization ability is consistent within individuals, we examined the correlations between our three song conditions—Music Only, Music with Metronome, and Metronome Only. Strong correlations would indicate that participants maintained consistent synchronization patterns regardless of whether a metronome was present, whereas weaker correlations would suggest greater variability in performance across conditions. Assessing these relationships allows us to perform subsequent analyses linking gait performance with functional connectivity in auditory-motor networks.

Figure 3 shows a correlation matrix for the means of synchronization accuracy across trials. Strong positive correlations were revealed across all conditions, with the highest correlation observed between the Metronome Only and Music with Metronome conditions,  $r(32) = .94$ ,  $p < .001$ . Such a strong correlation may be due to the involvement of the metronome across both conditions, making the music more beat-salient and easier to synchronize to. Nevertheless, the other two correlations—between Music Only and Music with Metronome, and between Music Only and Metronome Only—also reported significant positive correlations of  $r(32) = .87$ ,  $p < .001$  and  $r(32) = .85$ ,  $p < .001$  respectively.

These findings suggest that participants were highly consistent in their synchronization accuracy across conditions. While the scatterplots indicate a clear linear relationship, the density plots reveal that the data distribution is positively skewed, suggesting the presence of outliers with significantly lower accuracy values.

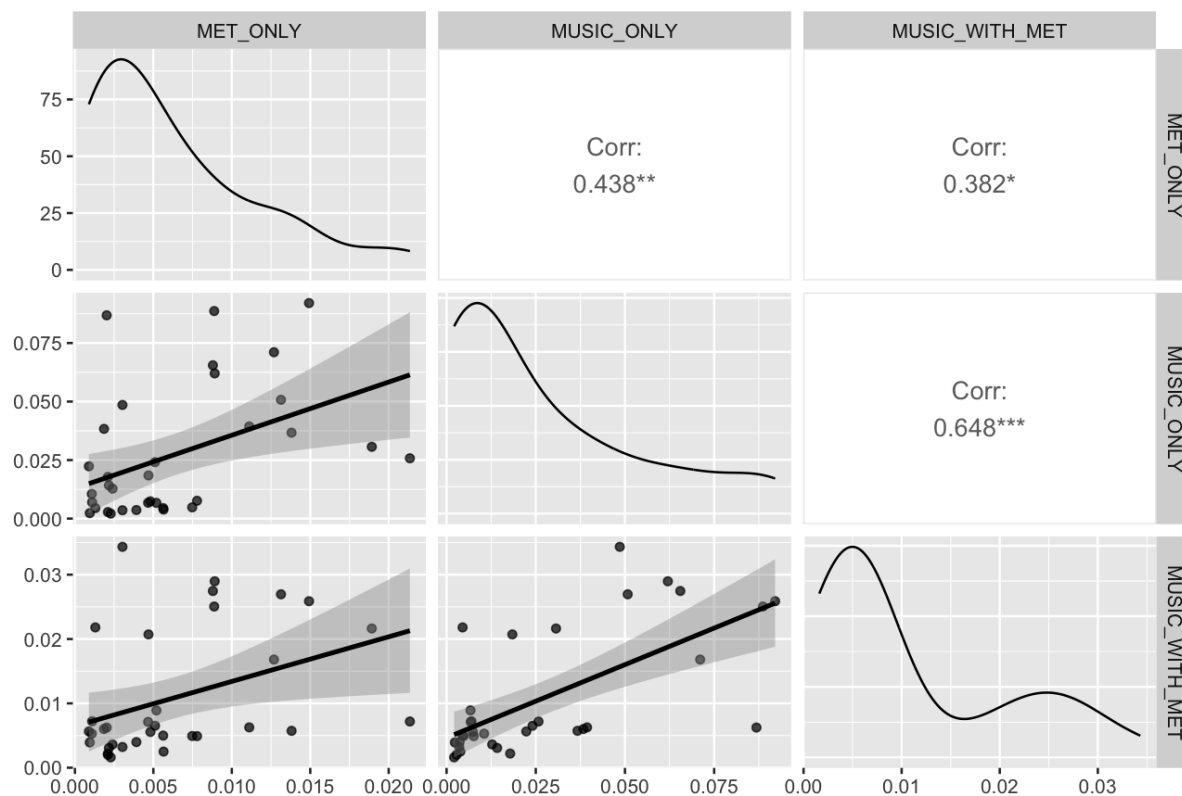




**Fig. 3.** Correlation Matrix of Synchronization Accuracy Means in Three Conditions.

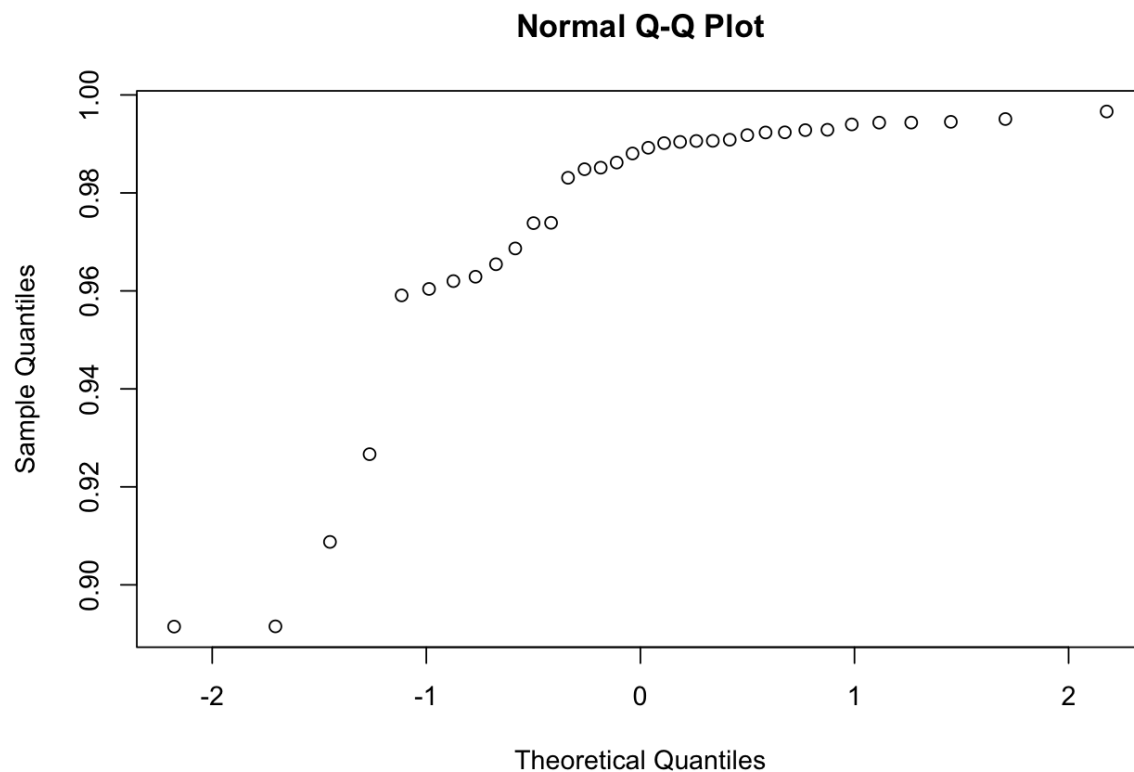
“MET” = *Metronome*. \*\*\* =  $p < .001$

In addition to correlating the means of all three conditions of every participant, another method of determining walking-to-music consistency is to observe how variable participants are walking across different song conditions (i.e., using standard deviation). Figure 4 shows a correlation matrix for the standard deviations of synchronization accuracy across trials. Moderate to strong positive correlations were observed between standard deviations from the three conditions but were weaker and more variable compared to the mean synchronization accuracy. Given this variability, standard deviation may be a less consistent measure for investigating synchronization across conditions, hence we have determined that taking participants’ mean (Fig. 3) is the optimal method for further analysis with functional connectivity.



**Fig. 4.** Correlation Matrix of Synchronization Accuracy Standard Deviations in Three Conditions. “MET” = Metronome. \*\*\* =  $p < .001$ , \*\* =  $p < .01$ , \* =  $p < .05$

Next we proceed to evaluate the assumptions necessary to conduct a correlational analysis. Despite deciding to take the mean synchronization accuracy of participants, skewed density plots in Figure 3 showed that extreme outliers were present in our gait data. We conducted a Shapiro-Wilk test and a *qqnorm* plot (Fig. 5), confirming that the non-normality was in part due to the presence of four outliers with synchronization scores lower than .94. The traditional criteria of identifying outliers beyond 2 standard deviations of the mean or 1.5 times interquartile range was met, identifying the same four participants. To address this, we removed these four participants and used nonparametric statistical tests (i.e., Spearman’s Rank Correlation) for subsequent correlational analyses with the connectivity measures.



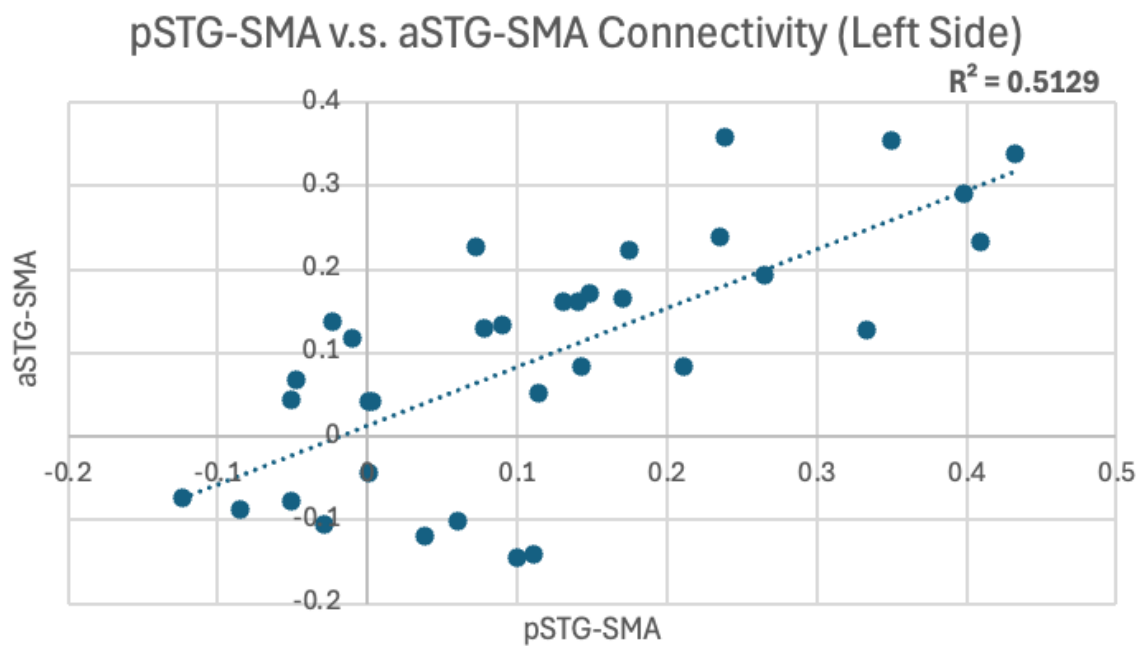
**Fig. 5.** Q-Q Plot of Participants' Gait Synchronization Means to Test for Normality

#### ***Consistency of Auditory-Motor Connectivity***

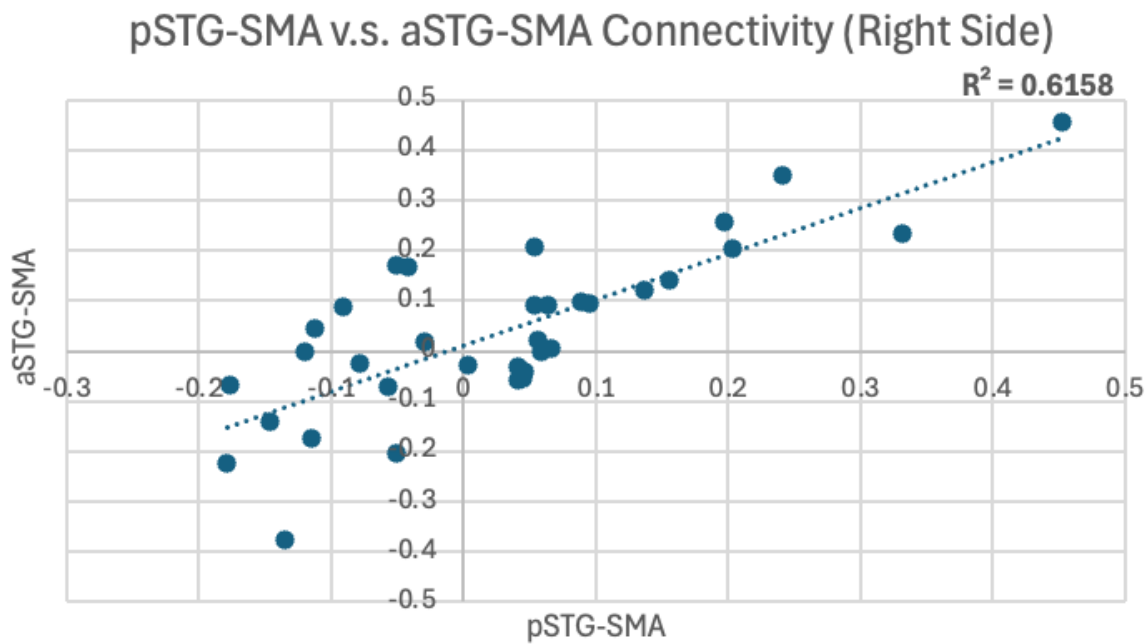
The consistency of connectivity strength was assessed in two ways—checking whether the posterior STG to SMA (pSTG-SMA) and anterior STG to SMA (aSTG-SMA) connectivities are correlated, and whether the left and right STG-SMA connectivities are correlated. These correlations were performed to evaluate whether specific subregions of the STG and hemispheric lateralization contribute uniquely or redundantly to auditory-motor connectivity, justifying the use of STG-SMA connectivity measures in subsequent analyses. A strong overall correlation would indicate that participants had consistent connectivity strengths between the STG and SMA, whereas a weak overall correlation could suggest STG-SMA may not be a good measure for addressing auditory-motor connectivity during passive music listening.

Figures 6 and 7 show the correlations between pSTG-SMA and aSTG-SMA on the left and right sides of the brain respectively. There was a strong positive correlation between the

left pSTG-SMA and left aSTG-SMA,  $r(32) = .72$ ,  $p < .001$  (Fig. 6). A strong positive correlation was also seen between the right pSTG-SMA and right aSTG-SMA,  $r(32) = .78$ ,  $p < .001$  (Fig. 7). These results indicate that selecting the STG and SMA as auditory and motor representations of the brain in this context is a consistent way of evaluating auditory-motor connectivity, as both locations of the STG (anterior and posterior) are strongly correlated when connected to the SMA.

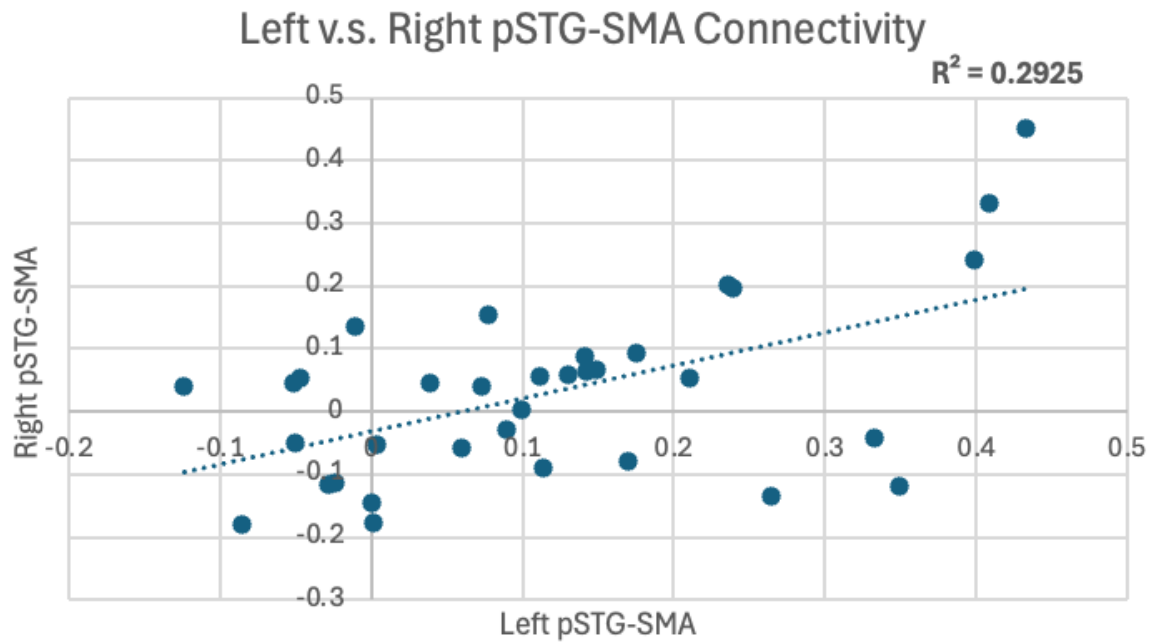


**Fig. 6.** Correlation between the **posterior** STG to SMA connectivity and **anterior** STG to SMA connectivity on the **left** hemisphere

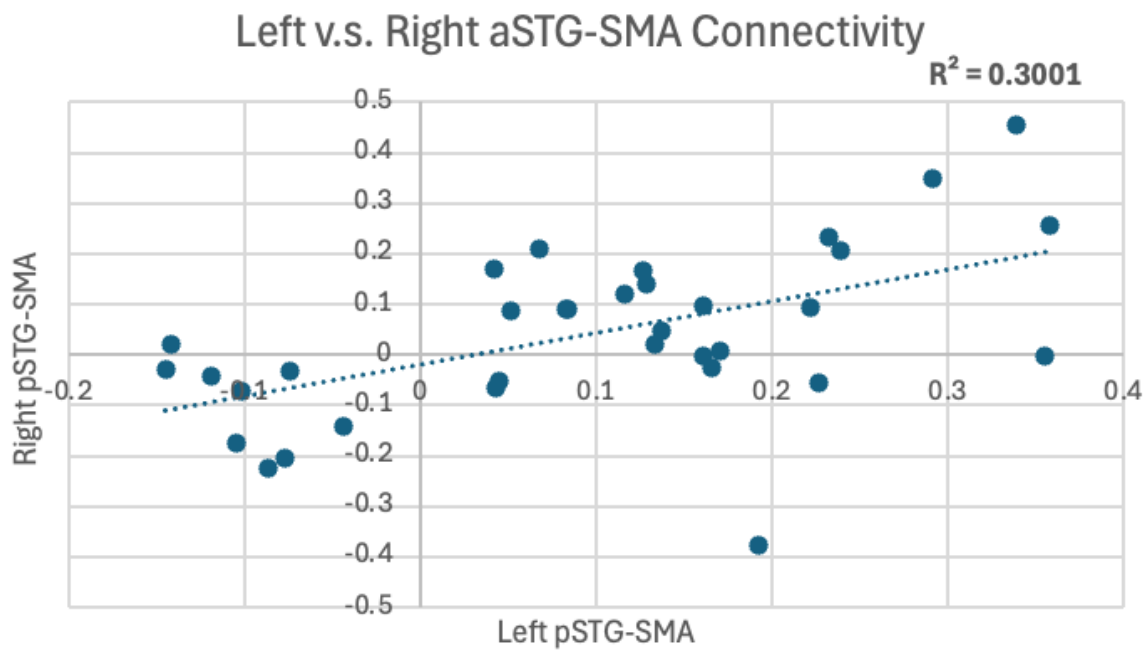


**Fig. 7.** Correlation between the **posterior** STG to SMA connectivity and **anterior** STG to SMA connectivity on the **right** hemisphere

To further validate the use of STG-SMA connectivity, we compared connectivity values between the left and right hemispheres. Figures 8 and 9 show correlations between left and right pSTG-SMA, and left and right aSTG-SMA respectively. There was a moderate positive correlation between the left and right pSTG-SMA,  $r(32) = .54$ ,  $p < .001$  (Fig. 8). A moderate positive correlation was also seen between the left and right aSTG-SMA,  $r(32) = .55$ ,  $p < .001$  (Fig. 9). Although the correlation coefficients when comparing left and right hemispheres were not as strong as comparing anterior and posterior STGs, these moderately strong correlations also reflect the consistency of using STG-SMA connectivity for further analyses.



**Fig. 8.** Correlation between the **left posterior** STG to SMA connectivity and **right posterior** STG to SMA connectivity

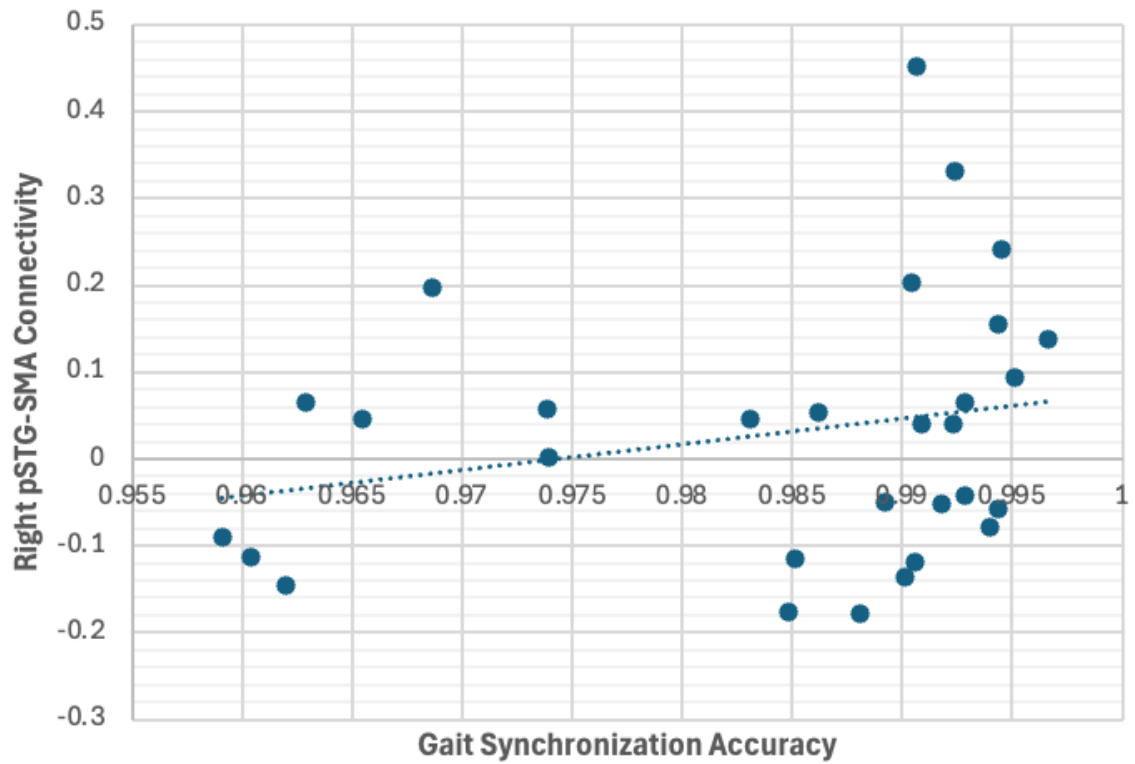


**Fig. 9.** Correlation between the **left anterior** STG to SMA connectivity and **right anterior** STG to SMA connectivity

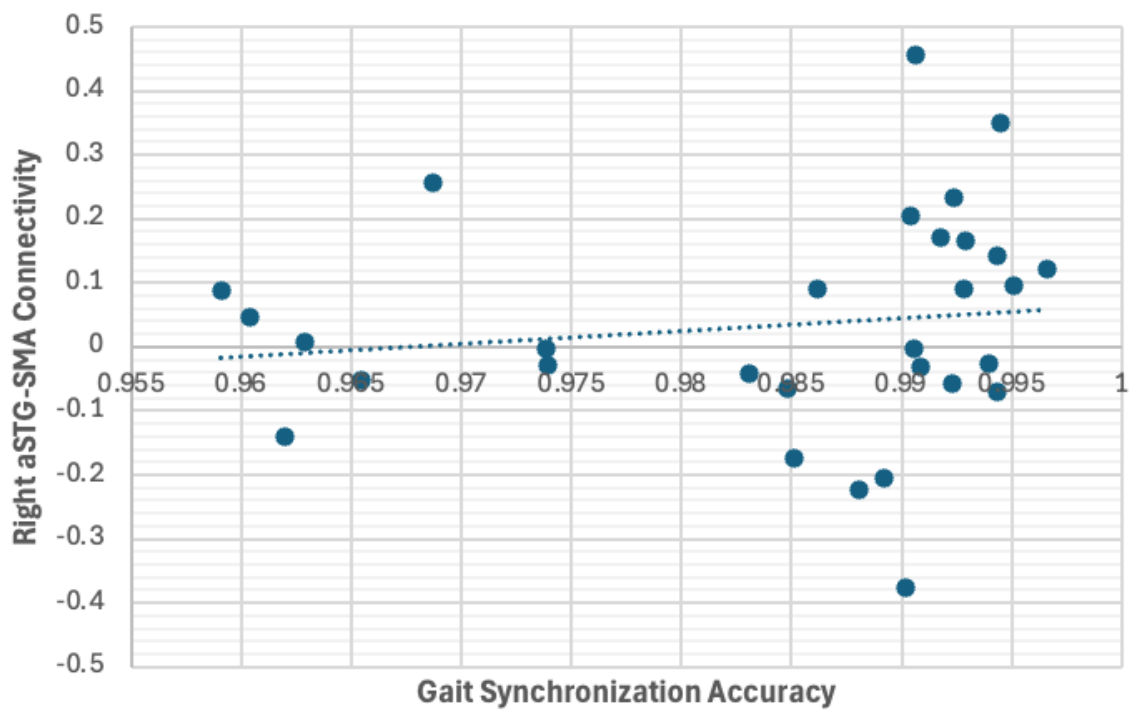
*Relationship Between Gait Synchronization and Auditory-Motor Connectivity*

Previous analyses indicate that both STG-SMA connectivity values and gait synchronization means are consistent measures. To examine the relationship between synchronization accuracy and auditory-motor functional connectivity, four Spearman's rank-order correlations were conducted between participants' mean synchronization accuracy and connectivity strength between the left and right SMA, and the left and right pSTG and aSTG subregions. Spearman's correlation is a nonparametric test that allows us to control for the lack of normality in the gait synchronization data; additionally, four participants identified as extreme outliers have been removed in this analysis.

A moderate positive correlation was nearly significant between synchronization accuracy and right pSTG-SMA connectivity,  $\rho(28) = .35$ ,  $p = .060$  (Fig. 10). Similarly, a moderate correlation between synchronization accuracy and right aSTG-SMA connectivity approached significance,  $\rho(28) = .33$ ,  $p = .073$  (Fig. 11). The left pSTG-SMA connection exhibited a weak positive correlation with synchronization accuracy and did not reach significance,  $\rho(28) = .27$ ,  $p = .146$  (Fig. 12). The correlation between synchronization accuracy and left anterior STG-SMA connectivity was the weakest and nonsignificant,  $\rho(28) = .23$ ,  $p = .216$  (Fig. 13). Although none of the correlations reached conventional significance thresholds, the observed effect sizes suggest a trend toward stronger associations between synchronization behaviour and right-lateralized auditory-motor connectivity, particularly in the pSTG.

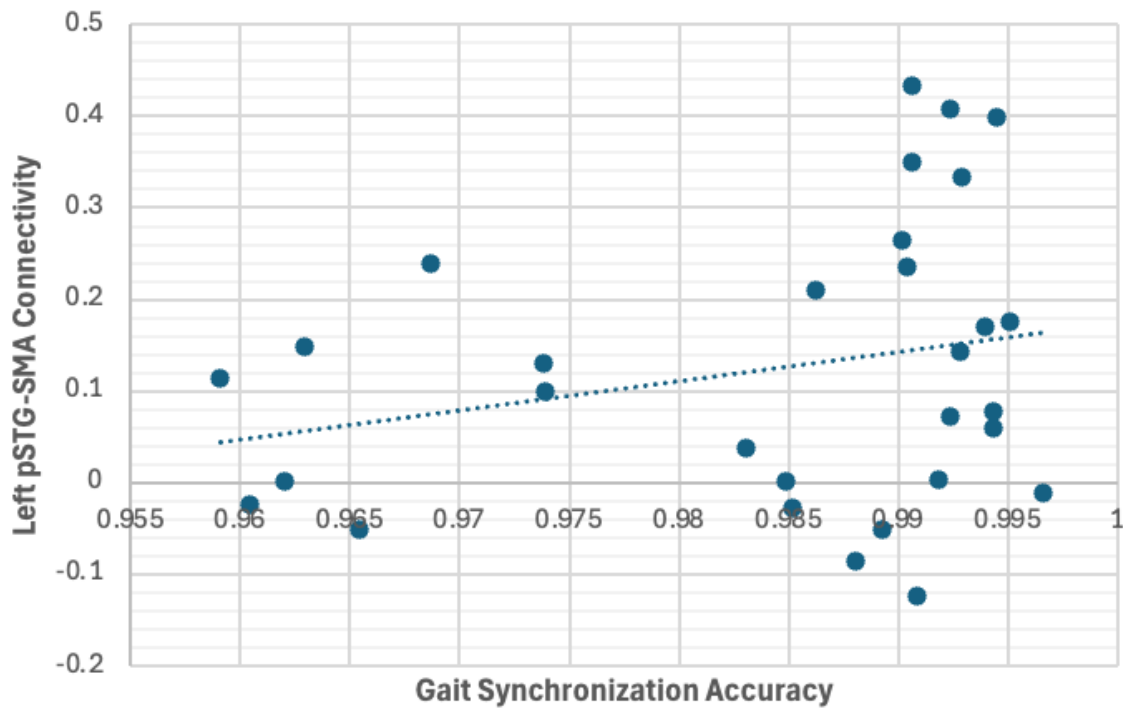


**Fig. 10.** Correlation between gait synchronization accuracy and the **right posterior STG-SMA** functional connectivity,  $\rho(28) = .35$ ,  $p = .060$ .

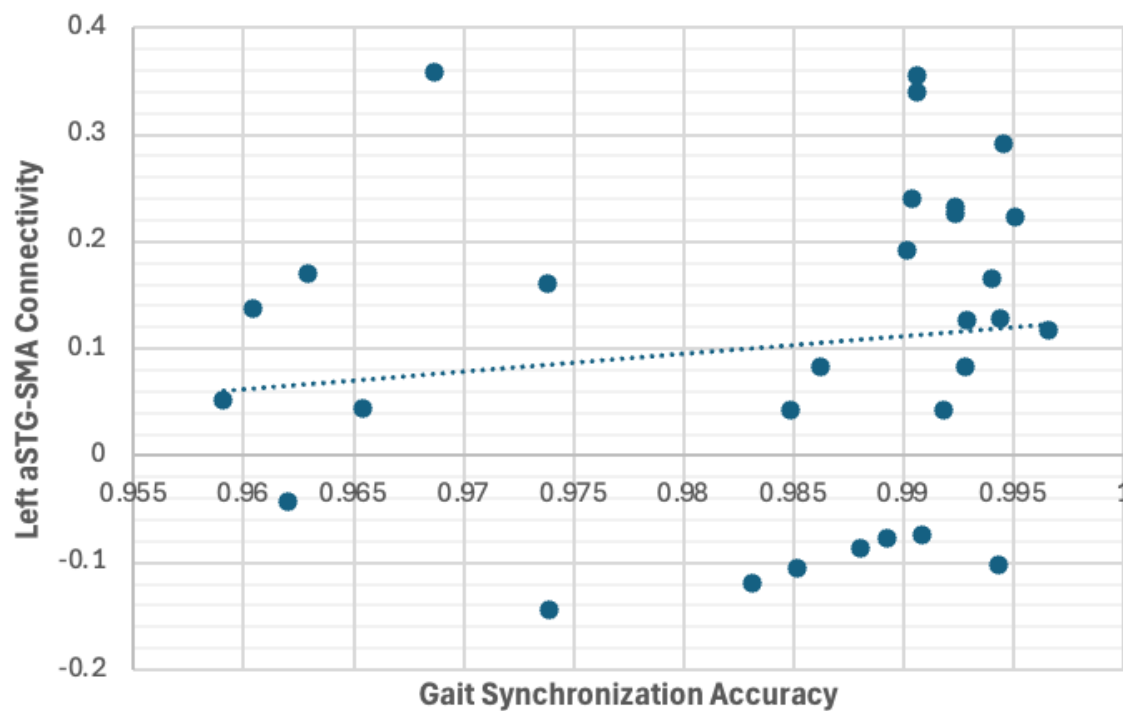




**Fig. 11.** Correlation between gait synchronization accuracy and the **right anterior STG-SMA** functional connectivity,  $\rho(28) = .33$ ,  $p = .073$ .



**Fig. 12.** Correlation between gait synchronization accuracy and the **left posterior STG-SMA** functional connectivity,  $\rho(28) = .27$ ,  $p = .146$ .



**Fig. 13.** Correlation between gait synchronization accuracy and the **left anterior STG-SMA** functional connectivity,  $\rho(28) = .23$ ,  $p = .216$ .

### Discussion

The current study explored the relationship between individual differences in auditory-motor brain connectivity during passive music listening and the ability to accurately synchronize gait to a musical beat. Employing the STG (posterior and anterior) as the auditory region and the SMA as the motor region, our central hypothesis predicted that stronger intrinsic functional connectivity between these areas would correlate with higher gait synchronization accuracy. We did not find significant correlations between functional connectivity and gait synchronization, but we found moderate positive correlations between synchronization accuracy and the right STG-SMA connections, as well as weak positive correlations between synchronization accuracy and the left STG-SMA connections. Our primary results, though insignificant, show promise in investigating the role of spontaneous neural dynamics in RAS behaviour.

### Functional Interplay Between STG and SMA

Although no statistically significant correlations were observed between STG-SMA functional connectivity and gait synchronization accuracy, the current study supports the relationship between the STG and SMA in auditory-motor integration. The posterior STG, in particular, has been associated with beat perception and temporal alignment, while the SMA is known to contribute to motor planning and internal timing, thus both regions are imperative in beat synchrony (Pecenka et al., 2013; Wu et al., 2019). Many studies have tested people's beat synchronization ability through rhythmic tapping tasks, but this study addresses possible sources of variability in RAS treatment for gait-disordered populations by exploring walking to music using RAS (Dalla Bella et al., 2017; Dalla Bella et al., 2018).

Although we see a huge variability in people's STG-SMA connectivity values when correlated to gait synchronization (as seen from a large range of connectivity values across participants with high synchronization accuracy), most displayed positive correlations between both areas, proposing that there is likely a positive functional relationship between the STG and SMA during passive music listening.

### **Relationship Between Connectivity and Synchronization Show Lateralization Trends**

Despite no statistically significant correlations, our primary results suggest meaningful trends. Moderate positive correlations between synchronization accuracy and right-lateralized auditory-motor connections—particularly between the posterior STG and SMA—approached significance. Alternatively, left-lateralized STG-SMA connections had weaker correlations. These findings indicate that individuals with stronger functional connectivity between the right auditory and motor regions had more accurate gait synchronization to music, supporting the idea that there is a functional dissociation between the left and right hemispheres (Suarez et al., 2008; Alluri et al., 2013). The most common distinction between left and right auditory cortices is that they are predominantly responsible for speech and music respectively. Previous studies found that listening to music without lyrics generated more right-lateralized responses, especially in the right STG, while the presence of lyrics recruited more left-hemispheric regions (Alluri et al., 2013). Other studies have revealed that the right STG is more sensitive to pitch perception and processing in music, while the left STG is more involved in controlled pitch evaluation across both music and language (Nan and Friederici, 2013). Domain-specific lateralization may be able to explain this study's results because higher correlations with auditory-motor connectivities in the right hemisphere indicate that music processing is more dominant on the right while speech is dominated on the left.

Furthermore, music lateralization studies have explored the avenue of musical training by comparing the brain activity of musicians and non-musicians. In general, musicians showed greater left hemisphere activation than non-musicians when passively listening to regular rhythms (Limb et al., 2006); in more complex stimuli where a temporal musical structure is lacking (scrambled/distorted music), there was still bilateral STG activation in musicians, but non-musicians showed activation only in the right STG (Matsui et al., 2013). These results show that musical training likely enhances left-hemisphere rhythmic auditory processing. Indeed, our study consists of more non-musicians than musicians, potentially explaining why right-lateralized connectivities are more correlated, but no conclusions regarding musical training can be made due to self-reporting and small sample sizes.

Overall, the observed correlational differences, when correlated to gait synchronization, support the idea that right-lateralized auditory-motor circuits may be more closely linked to rhythm-based motor behaviour, although further research is needed to confirm these relationships.

### **High Consistency of Individual Measures**

To ensure our correlations are true, we examined the internal consistency of both behavioural and neural measures to ensure their reliability. Gait synchronization accuracy was found to be highly consistent across conditions, particularly in terms of mean values, which strongly correlated between Music Only, Metronome Only, and Music with Metronome conditions. This suggests that individual synchronization tendencies were consistent regardless of whether musical beats were marked explicitly with a metronome or embedded within the musical structure. Similarly, auditory-motor functional connectivity measures also demonstrated strong consistency across participants. Correlations between STG-SMA connectivity values revealed consistent individual connectivity values across

anterior and posterior regions of the STG, as well as left and right hemispheres, indicating that these neural networks are sufficient to conduct further analyses. Together, these checks for consistency validated the suitability of both our behavioural and neural measures, suggesting that our primary results are true correlations between auditory-motor connectivity and gait synchronization.

### **Limitations**

Despite the insights gained from this study, several limitations must be acknowledged. Although moderate correlations were observed, the relatively small sample size may have limited statistical power, contributing to a failure to reach statistical significance. This was contributed by a highly skewed distribution in the gait synchronization data, in which four participants were excluded after conducting diagnostic tests for normality. Participant demographics may also not be fully representative of the issue we are trying to address. Since the rationale for conducting this study is to investigate the variability of RAS responses in gait-disordered populations, testing healthy younger adults may provide an insufficient or inaccurate understanding, as gait-disordered patients naturally find it more difficult to synchronize their walking due to their disease condition and aging. Future studies can build off this rationale and design by recruiting participants with PD and age-matched older adult healthy controls.

The definition and scope of “auditory-motor connectivity” is very narrow compared to neighbouring functional connectivity studies. Instead of using a seed-to-voxel analysis pipeline, ROI-to-ROI analyses were conducted, restricting the findings to only one auditory and one motor region. By implementing seed-to-voxel or full-brain analysis, researchers can set a primary seed in the auditory or motor cortex and visualize significantly more connections, such as the dPMC, putamen, and cerebellum, giving way to a better understanding of auditory-motor connectivity (Chen et al., 2008; Alluri et al., 2017).

In terms of gait synchronization, this study used cadence matching to measure people's synchronization ability. Despite its importance, cadence only takes the average walking speed across one trial and does not factor in the alignment of beat onsets in the music with step onset (first contact of each footstep). To fully quantify synchronization performance, RAS gait studies have explored the use of period-matching (overall step rate to pace of the auditory cue) and phase-matching (individual step onsets to beat onsets of the auditory cue; Leow et al., 2021; Von Handorf, Leung, Urian, & Grahn, in prep). We believe cadence matching was a good way to initially quantify synchronization accuracy, but an extension to this study can consider including period-matching and phase-matching analyses as well.

Finally, this study was unable to record brain responses and gait performance to music simultaneously as it is physically impossible to perform walking tasks during an MRI scan, which may contribute to the high variability in brain connectivity responses. Further research is encouraged to brainstorm and investigate how we can neurally address RAS variability in the most effective way.

### **Practical Implications**

These findings contribute to a growing body of literature aiming to understand the neural underpinnings of motor synchronization, with potential applications in music-based therapies for motor rehabilitation. Individuals with Parkinson's disease or stroke often exhibit impaired gait rhythmicity, and music-based interventions that harness RAS can improve motor timing (Thaut and Abiru, 2010). However, variable responses to RAS interventions are often observed and linked to individual differences in rhythmic ability, causing patients with poor rhythmic skills to not benefit from this treatment (Dalla Bella et al., 2017; Dalla Bella et al., 2018; Cochen de Cock et al., 2018). By identifying auditory-motor connectivity as a possible predictor of beat synchronization ability, this research provides a foundation for understanding the neural mechanisms underlying the high variability of responses to RAS treatment.

Clinically, such approaches could inform personalized treatment plans in RAS rehabilitation, further improving the efficacy of RAS by benefiting patients of varying levels of synchronization abilities.

### **Conclusion**

This study provides preliminary evidence linking auditory-motor connectivity to individual differences in gait-based synchronization accuracy. Using RAS procedures and functional connectivity, we observed that stronger right-lateralized STG-SMA connectivity corresponded to more accurate gait synchronization, suggesting a potential neural basis for rhythmic entrainment in naturalistic listening contexts. Although correlations did not reach significance, the consistency of right-hemisphere effects reflects a promising avenue for future research. These findings contribute to our understanding of how brain connectivity may support gait performance and give way to further investigation for motor rehabilitation strategies in gait-disordered populations.

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