DISSERTATION

INVESTIGATING THE NEURAL MECHANISMS OF RHYTHMIC ENTRAINMENT AND AUDITORY PRIMING USING EEG

Submitted by

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ABSTRACT

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A body of literature on rhythmic entrainment, the synchronization of behaviors to rhythmic stimuli in the environment, shows auditory rhythmic cuing can improve motor performance in neurotypical and clinical populations. This is thought to be driven by underlying communication, i.e., functional connectivity, between auditory and motor brain regions. Surprisingly, some clinical research shows rhythmic entrainment interventions, designed to enhance motor performance, may improve cognitive performance as well. However, it is unclear if improved cognitive performance during rhythmic entrainment reflects changes in functional connectivity. Evidence from cognitive neuroscience suggests rhythmic auditory stimuli may direct attentional resources through the synchronization of certain neural oscillations with the rhythmic pulse. Neural oscillations are repetitive patterns of brain activity which can be measured noninvasively at the scalp using electroencephalography (EEG). Measuring how neural oscillations from spatially distinct brain regions synchronize with each other reflects changes functional connectivity. Before functional connectivity during rhythmic entrainment can be studied, research is first needed to establish connectivity patterns when processing auditory rhythmic stimuli (auditory condition) and during self-paced rhythmic motor performance (motor condition), which was the goal of Study 1. Overall, the results of Study 1 provide evidence that the auditory condition may promote more efficient functional connectivity with increased activation in localized brain regions, while the motor condition may utilize long-range low-

frequency neural oscillations to suppress activity in task-irrelevant brain regions to sustain attention. A recent EEG study by our lab compared the neural oscillations of participants who listened to auditory rhythmic stimuli presented for a little over five minutes (auditory-first group) to participants who completed a self-paced rhythmic motor task for about minutes (motor-first group) prior to tapping along to auditory rhythmic cues (rhythmic entrainment condition). One important finding was a greater "priming effect" in the auditory-first group, who showed reduced neural resources needed during rhythmic entrainment compared to the motor-first group. Thus, auditory priming, compared to motor priming, may result in a more efficient use of neural resources during rhythmic entrainment. However, the optimal duration of auditory priming to promote efficient brain and behavior function is unknown. Therefore, the goal of Study 2 was to determine how different durations of auditory priming affect brain efficiency in neurotypical individuals, as measured using EEG. Overall, the results of Study 2 found that a duration of about two minutes may be optimal for auditory processing of rhythmic stimuli. However, more research is needed to confirm if auditory priming reduces neural resources needed during rhythmic entrainment compared to no priming and if auditory priming improves motor performance. Rhythmic entrainment and auditory priming are both important principles of rhythm-based interventions used in rehabilitation. A better understanding of their neural mechanisms in neurotypical individuals provides a necessary foundation for future research examining these processes in clinical populations and as a component of clinical interventions.

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Chapter 1: Literature Review

This literature review is primarily from a neuroscience perspective. The first section reviews potential mechanisms underlying rhythmic entrainment and auditory priming and applications to clinical interventions. The second section provides background on electroencephalography (EEG) methods to measure brain oscillations and connectivity and reviews existing literature on the neural correlates of rhythmic auditory and motor processes. Together, both sections provide a rationale for the overall purpose of this dissertation: investigating the underlying neural mechanisms of rhythmic entrainment and auditory priming using EEG to measure functional connectivity and neural resource allocation.

Rhythmic Entrainment

Rhythmic entrainment is when any action (e.g., motor, speech, cognition) synchronizes to rhythmic stimuli in any modality, e.g., auditory, visual, tactile (Ross & Balasubramaniam, 2014). For example, moving in time to music when playing musical instruments or dancing requires coordinating movement with rhythm (Burger et al., 2014). Even for those with no musical training, synchronizing repetitive cyclical movements with auditory rhythmic cues, such as tapping a finger or walking along to a metronome, often increases the fluidity and consistency of the movement (see reviews: Repp & Su, 2013; Thaut et al., 2015; Zatorre et al., 2007). Synchronizing movement to auditory rhythm, also known as auditory-motor entrainment (Thaut et al., 2015), involves two basic processes: 1) the sensory and temporal processing of rhythm in auditory stimuli and 2) motor planning and control of rhythmic patterns in movement. In addition, auditory-motor entrainment may enhance underlying interactions between auditory and motor processes.

Processing Auditory Rhythmic Stimuli

The neural processing of auditory rhythmic stimuli can be grouped into three general categories: the sensory perception of rhythm, timing mechanisms, and neural entrainment. Each of these processes are strongly tied to perception-action mechanisms – perceiving cues in the environment and using that information to direct thought or behavior. Thus, all three mechanisms are also linked to motor processing.

Sensory Perception of Rhythm. The sensory perception of rhythm involves auditory perception integrated with motor processes. First, listening to auditory rhythm requires the orienting to the auditory stimulus (Westman & Walters, 1981) and perceiving the stimulus through the auditory network, including the primary auditory cortex, secondary auditory regions in the insula, and the superior temporal gyrus (Sadaghiani et al., 2009). However, passive listening to auditory rhythms also activates motor brain regions including the basal ganglia, cerebellum, supplementary motor area (SMA), and premotor cortex (PMC; Cameron & Grahn, 2016; Grahn & Brett, 2007; Grahn & Rowe, 2012; Janzen & Thaut, 2018; Repp & Su, 2013; Zatorre et al., 2007). Further, passive listening to rhythms increases communication between auditory and motor brain regions (Morillon & Baillet, 2017). This coupling between auditory and motor regions is thought to be driven by an automatic mechanism in which the brain uses environmental cues to improve the timing and spatial trajectory of movement (for review, see Zatorre et al., 2007). However, more research is needed to understand the integration of auditory and motor processes in rhythm perception.

Timing Mechanisms. Time perception is important for a range of cognitive skills including speech/language, attention, and sensory perception (Wiener et al., 2010). Unlike sensory processing, a large body of evidence suggests that the perception of time does not have

dedicated neural regions or pathways but is an intrinsic part of all neural processing (Ivry & Schlerf, 2008). Time is an important dimension of sensory stimuli which is typically measured by the interval between stimuli or the duration of the stimuli (Paton & Buonomano, 2018). In auditory modalities, music specifically, rhythm is the temporal element. Thus, timing mechanisms are inherent to processing auditory rhythms. Auditory rhythms also provide timing cues. For example, when rhythmic sequences are predicable, this can increase the ability to judge the passage of time accurately (McAuley & Jones, 2003). Therefore, processing auditory rhythms may enhance time perception. As timing mechanisms are driven by properties inherent to neurons (Paton & Buonomano, 2018), the mechanisms underlying time perception of rhythmic stimuli can be studied by examining patterns of neuronal firing in relation to rhythmic stimuli.

Neural Entrainment. An oscillation is any system or process with regular repeated patterns or periodic events. Auditory rhythmic stimuli are an example of an environmental oscillation. Brain oscillations, the naturally occurring rhythmic patterns of electrical activity in the brain (Herrmann et al., 2005), provide a representation of the timing of rhythmic activity inherent to neuronal firing. Brain oscillations can be measured noninvasively at the scalp using neuroimaging methods such as magnetoencephalography (MEG) and electroencephalography (EEG). A body of evidence suggests that rhythmic entrainment may be driven by the synchronization of brain oscillations to the external rhythms such as rhythmic auditory stimuli in a process known as *neural* entrainment (Haegens & Zion Golumbic, 2018; Large & Jones, 1999). Using MEG or EEG, researchers have found that during passive listening to auditory rhythmic stimuli, brain oscillations fluctuate in time with the stimuli (Henry et al., 2014; Henry & Obleser, 2012; Lakatos et al., 2013; Snyder & Large, 2005). During neural entrainment, brain oscillations anticipate the auditory stimuli (Fujioka et al., 2012) and continue to follow a

consistent pattern even when beats are randomly omitted (Fujioka et al., 2009), suggesting rhythm processing involves endogenous timekeeping driven by brain oscillations. Neural entrainment is a dynamic process, as the brain adapts internal representations over time to enhance to perception of environmental stimuli (Bauer et al., 2018). Further, neural entrainment occurs even when the auditory rhythmic stimuli is below the level of conscious perception (ten Oever et al., 2014), suggesting neural entrainment is automatic.

Evidence suggests neural entrainment can be enhanced with musical training (Harding et al., 2019). Importantly, increased neural entrainment may facilitate improved accuracy (Arnal et al., 2011) and response times (Stefanics et al., 2010) on target detection tasks. Thus, interventions which improve neural entrainment mechanisms may also improve cognitive and motor function. An important step in developing and refining such interventions is conducting research to better understand the unique neural processes underlying the perception of auditory rhythms and if those processes can be enhanced through rhythmic movement.

Motor Planning and Control of Rhythmic Motor Patterns

Rhythmic movement is an inherent part of many basic motor patterns such as walking. Rhythmic movement processes can be categorized by somatosensory processes, timing mechanisms, and spatial organization. All three of these processes work together and are driven by feedback loops between motor processes and the environment.

Somatosensory Processes. Self-paced movement is driven primarily by the somatomotor network (SMN) in the cortex which includes the primary motor, primary somatosensory and motor planning regions (Seitzman et al., 2019), as well as the striatum (Choi et al., 2012) and the cerebellum (Buckner et al., 2011). In the biomechanics literature, it is well known that cyclic motor behaviors, such as tapping a finger repetitively or walking, are driven by neural central

pattern generators which can be influenced by sensory input (Rand et al., 1988) in what Janata and Grafton (2003) called a "perception-action cycle" (p.682). Therefore, cyclic motor behaviors may be enhanced by environmental cues. Given the speed and precision in which the brain processes auditory stimuli compared to other forms of stimuli (Hove et al., 2013; Thaut et al., 2015), auditory rhythmic cues may be ideal for improving motor performance.

Movement Timing. The timing of movements is essential to motor planning and control. Thus, areas of the brain involved in spatial perception, such as the parietal cortex (Bueti & Walsh, 2009), primary and secondary motor regions (Wiener et al., 2010), and the basal ganglia and cerebellum (Coull et al., 2011) are also involved in time perception. Overall, timing mechanisms serve to synchronize action with sensory information and maintain an internal tempo in a dynamic attentional process (Janata & Grafton, 2003). Movement timing also depends greatly on recognizing and organizing spatial patterns (for review, see Paton & Buonomano, 2018).

Spatial Organization. Rhythmically timed movement, such as playing a musical instrument, requires spatial organization (for review see Zatorre, 2007). Spatial processing is primarily driven by the dorsal visual processing stream which includes projections from the parietal cortex to 1) the prefrontal cortex to support eye movement and spatial working memory, 2) the premotor cortex to support visually guided action, and 3) the medial temporal lobe to support navigation (Kravitz et al., 2011). One study found that visuospatial working memory was correlated with the temporal organization of motor sequences such that participants with greater visuospatial working memory capacity had a faster rate of learning and organized sequences into longer "chunks." In the same study, temporal processes, measured as the consistency of timing control on a rhythmic finger tapping task, were not related to the temporal organization of motor

sequences (Bo & Seidler, 2009). This is likely because the temporal/rhythmic control of movement uses different brain regions than spatial control of movement (Bengtsson et al., 2004). However, one study found a task requiring both temporal and spatial movement activated additional brain regions, the medial cerebellum and the superior colliculus, which may be involved in the *integration* of temporal and spatial information in motor tasks (Bengtsson et al., 2004). Auditory rhythmic cues may improve the spatial organization of rhythmic movements by helping the brain integrate temporal and spatial information more efficiently. Auditory beats may provide temporal landmarks which allow the brain to plan an efficient movement trajectory within a known timeframe (Janzen & Thaut, 2018; Nozaradan, 2014; Zatorre et al., 2007). This is one of several theories to describe the synchronization of behavior to rhythm.

Theories of Rhythmic Entrainment

Researchers studying the synchronization of movement to rhythm have approached the phenomenon from different theoretical frameworks or models. Such theories are not necessarily contradictory (Repp, 2005), but instead provide different perspectives on the relationship between behavior and the environment. For example, researchers using *information processing models* tend to represent motor performance e.g., finger taps, as discrete events and focus on the behavioral alignment between movement and the external rhythm (Repp, 2005). Researchers using *dynamic systems models* are more likely to describe the synchronization of repetitive rhythmic movements to environmental stimuli as a process involving the interaction between two oscillatory systems (Janata & Grafton, 2003; Repp, 2005).

Information Processing Models for Sensorimotor Synchronization. Whole-body entrainment to complex auditory stimuli, such as music, is physically and rhythmically complex (Burger et al., 2014). Therefore, researchers often use finger tapping paradigms to study the basic

behavioral patterns and neural correlates of the synchronization of movement to rhythm, i.e., sensorimotor synchronization (see reviews: Repp, 2005; Repp & Su, 2013). One approach to finger tapping paradigms follows the information processing model in which sensory stimuli and motor performance are defined by two components: period and phase (see Figure 1.1). The *period* is the time interval between two stimuli, e.g., auditory beats, or two behavioral responses, e.g., finger taps. In music, this is called the tempo, which is measured in beats per minute. During sensorimotor synchronization, the period between taps is a similar duration to the period between the stimuli with little variability across trials. The *phase*, also called the *phase synchronization error* or *phase asynchrony*, is the time interval between the tap and the stimulus presentation. Participants tapping a finger along to a metronome will typically tap slightly before the beat in a process known as the anticipation tendency or *negative mean asynchrony* (see reviews: Aschersleben, 2002; Repp, 2005; Repp & Su, 2013). Across time, participants are thought to systematically adjust their sensorimotor synchronization performance by shortening or lengthening the period between finger taps to match the period between the beats or by shifting their taps to decreases the phase synchronization error in a process called *dual-process error correction.*

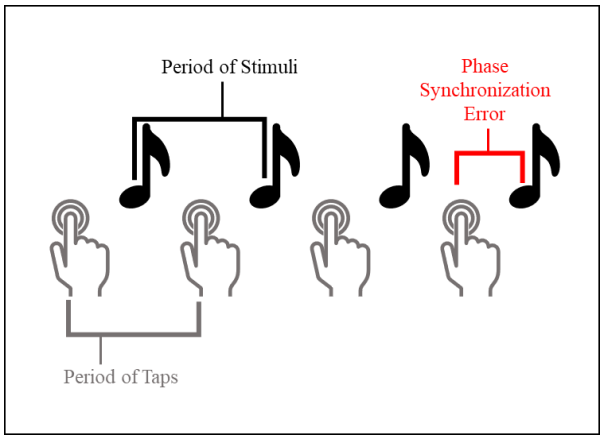

Figure 1.1. The period and phase in sensorimotor synchronization. The period of taps is the time between taps. The period of the stimuli is the time between stimulus presentations. The phase synchronization error, also called asynchrony, is the time between the tap and the tone. In sensorimotor synchronization, the tap tends to precede the tone, which is referred to as a negative mean asynchrony.

Dual-Process Model of Error Correction. While there are several information processing models of varying complexity (for review, see Repp, 2005), the *dual-process model of error correction* (Mates, 1994a, 1994b) is foundational in sensorimotor synchronization literature. In the dual-process model, sensorimotor synchronization occurs through two simultaneous forms of error correction: period correction and phase correction. Period correction is when the rate/tempo i.e., period, of tapping increases or decreases to match the external rhythmic period. Some researchers have suggested period correction is usually a more intentional process involving action planning as it requires awareness of a tempo change (Kubovy & Van Valkenburg, 2001; Repp, 2005; Repp & Su, 2013). However, Thaut and colleagues found that period correction occurs even when changes in tempo are below the level of conscious perception (Thaut et al., 1999; Thaut et al., 1998), suggesting it may sometimes be automatic. Phase correction is a process where the interval between the taps i.e., the period, does not change, but shifts in time, so the taps are closer in alignment to the external cue (i.e., the phase is shorter). Phase correction is thought to be a more automatic process to regulate behavior (Repp,

2005; Repp & Su, 2013). The degree of period or phase correction can be measured by changes in the mean and variability of the interval between the taps i.e., the inter-tap interval, and the mean and variability of the phase asynchrony. There is evidence that period and phase correction result from separate neurological processes. For example, researchers using repetitive transcranial magnetic stimulation (rTMS) found that, in participants who performed a sensorimotor synchronization task, inhibition of the superior temporal parietal junction (STP) increased phase error but did *not* affect period error (Malcolm et al., 2008). Thus, the STP may regulate anticipatory behavior relative to the environment, which is separate from maintaining a consistent tempo/pacing across time.

Error correction varies based on individual differences (Repp, 2005). For example, inter-tap interval variability varies with age, with children having the most variability, which decreases into adolescence but remains stable from adulthood to old age (Drewing et al., 2006). Musicians also tend to have less variable inter-tap intervals than non-musicians (Pressing & Jolley-Rogers, 1997; Repp & Penel, 2002) and a smaller negative mean asynchrony compared to non-musicians (see reviews: Aschersleben, 2002; Repp & Su, 2013), suggesting musical training may improve the accuracy and consistency of sensorimotor synchronization.

Researchers have proposed various theories describing the underlying mechanisms and neural correlates of the dual-process model of error correction. One such theory is a dual-process model for timing perception, which complements the dual-processing model of error correction. Teki, Grube, and Griffiths (2012) proposed that timing perception involves a "beat-based" (i.e., phase-based) mechanism and a "duration-based" (i.e., period-based) mechanism. The beat-based mechanism is responsible for measuring time intervals relative to beats and is controlled by a striato-thalamo-cortical system involving the striatum, thalamus, premotor cortex, supplementary

motor area (SMA), dorsal prefrontal cortex, and dorsolateral prefrontal cortex (DLPFC; Teki et al., 2011). The duration-based mechanism measures the absolute timing of successive intervals to monitor and optimize movements by recruiting an olivio-cerebellar network involving the inferior olive and cerebellar nuclei including the dentate nucleus (Teki et al., 2011). The beat-based and duration-based networks interact via multiple loops along with the thalamus, supplementary motor area (SMA), pre-SMA, and the cerebral cortex (Teki et al., 2012). This model suggests the traditional dual process model of error correction may not fully capture the complex and iterative nature of sensorimotor synchronization.

Dynamic Systems Theories and Entrainment. Some researchers describe the synchronization of movement to rhythm as a dynamic and continuous process involving two or more oscillations. Thus, researchers who take a dynamic systems approach tend to focus on interactions, coupling, or *entrainment* rather than sensorimotor synchronization or error correction, although there may be some overlap in terminology (Repp, 2005). The most formalized dynamic systems theory is Dynamic Attention Theory (DAT; Jones, 1976, 1987, 1990; Large & Jones, 1999; McAuley & Jones, 2003), which describes how external and internal rhythms interact to direct attention. According to DAT, internal oscillations, such as brain oscillations, allow us to quickly recognize patterns and guide attention to environmental stimuli. The internal oscillations entrain to rhythmic patterns in the environment, which improves our ability to predict upcoming events and thus more easily coordinate movement with the environment (Jones, 1976). The process is dynamic in that endogenous oscillations maintain a general rhythmic structure while simultaneously adjusting based on changes in the environment (Large & Jones, 1999). This model provides an overarching framework for describing interactions between auditory and motor processes.

Auditory-Motor Interactions. Under the DAT umbrella is the theory of integration, or coupling, between sensory and motor systems (for review, see Repp & Su, 2013). Due to the precision and speed of auditory processing, auditory-motor interactions may be stronger than other sensory-motor interactions (Thaut et al., 2015). For example, Jäncke et al. (2000) found stronger positron emission tomography (PET) activation in motor brain regions during auditory-paced tapping compared to visually paced tapping, supporting the theory that auditory and motor processes are uniquely coupled and strongly linked.

A body of evidence using a synchronization-continuation paradigm suggests that rhythmic entrainment may enhance auditory-motor interactions. In a basic synchronization-continuation paradigm, participants tap a finger in time to auditory rhythmic stimuli for some duration (the synchronization task) and then continue tapping at the same pace after the auditory stimuli is removed (the continuation task). This paradigm is commonly performed during a functional magnetic resonance imaging (fMRI) recording. While one such study found similar fMRI activation patterns during both the synchronization and continuation tasks (Jantzen et al., 2004), others have found greater activation in motor brain regions during the synchronization task compared to the continuation task (Gerloff et al., 1998; Lewis et al., 2004), suggesting auditory-motor entrainment enhances auditory-motor interactions.

The Dual-Pathway Model of Auditory Processing. Studies of the neural underpinnings of speech may provide a potential model for auditory-motor interactions more broadly. For example, Hickok & Poeppel (2004) proposed that speech processing involves two primary types of interactions: 1) auditory-conceptual interactions via a ventral processing stream and 2) auditory-motor interactions via a dorsal processing stream. While the ventral stream maps sound onto meaning, the dorsal stream maps sound onto articulatory-based representations related to

speech production. A similar dual-pathway model of auditory processing has been proposed by Rauschecker (2011; see Figure 1.2). In Rauschecker's model, a ventral pathway is responsible for the perception of vocalization and speech and a dorsal pathway is responsible for localizing sounds and involves spatial processing and sensorimotor integration.

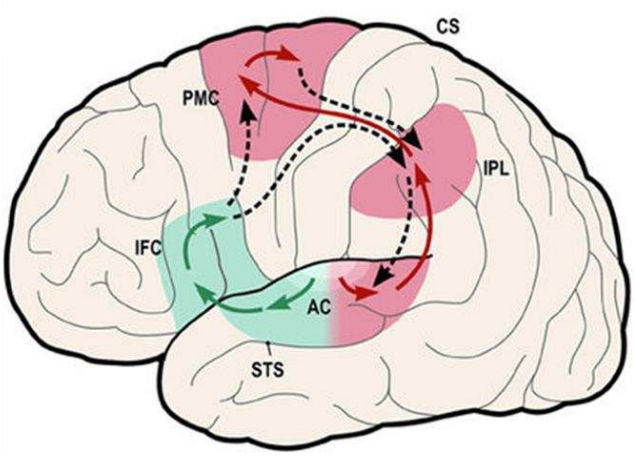

Figure 1.2. *The Dual-Pathway Model of Auditory Processing*. The ventral pathway (green) and dorsal pathway (red) of the dual-process model of auditory processing. AC, auditory cortex; CS, central sulcus; IFC, inferior frontal cortex; IPL, inferior parietal lobule; PMC, premotor cortex; STS, superior temporal sulcus. Image adapted from Rauschecker (2011) to include only the image of the human brain and not the primate brain, licensed under the Creative Commons Attribution 3.0 Unported license: https://creativecommons.org/licenses/by/3.0/legalcode

As tapping to a beat likely involves the internal pairing of sound and with motor representations, a dorsal stream for speech/auditory processing may also be involved in rhythmic entrainment. In fact, Warren et al. (2005) proposed a dorsal pathway may be responsible for auditory-motor transformations in general, not just those specific to speech. In Warren et al.'s model, auditory input travels via the ascending auditory pathways and the primary auditory cortex to the posterior superior temporal plane where the auditory information undergoes a template-matching process based on past experiences. From there, the template-matched auditory sequence is transformed in the dorsal pathway into motor sequences which can be used to generate motor responses via the prefrontal, premotor, and motor cortices. In addition, auditory

feedback can improve performance monitoring. Thus, the dorsal pathway is a bidirectional loop. While the dorsal pathway is largely automatic, higher-order tasks involving rhythmic tracking (Thaut et al., 1999) or adapting to abrupt changes (Stephan et al., 2002) may recruit additional prefrontal brain regions. Overall, a dual-pathway model integrates a dual-process information processing model and dynamic systems theories of rhythmic entrainment, which can more readily be applied to practical and clinical applications of rhythmic entrainment.

Clinical Applications of Rhythmic Entrainment

Clinical applications of rhythmic entrainment tend to integrate information processing and dynamic systems theories. For example, Thaut et al. (2015) defined rhythmic entrainment as the synchronization of the auditory period and movement period, using terms from information processing literature. But rather than represent beats and movements as a series of discrete time points, Thaut et al. modeled the rhythmic beats as markers for a time window (auditory period) within which the movement trajectory (movement period) occurs. The overarching purpose of Thaut and colleagues' model of rhythmic entrainment was to provide a foundation for clinical applications. Therefore, the primary outcomes of interest include characteristics of the movement trajectory e.g., stride length variability or the smoothness of arms movements, which tend to improve during rhythmic entrainment (Thaut et al., 2014; Thaut et al., 1996).

One prominent clinical application of rhythmic entrainment is in music therapy interventions. Music therapy is the clinical and evidence-based use of music interventions to accomplish individualized goals within a therapeutic setting by a board-certified music therapist (American Music Therapy Association, 2013). Neurologic Music Therapy (NMT) is a specific set of therapeutic music techniques developed by music therapists, neurologists, and neuroscientists based on neuroscience evidence of the effects of music on non-musical brain and

behavior function (Thaut & Hoemberg, 2014). Other rehabilitation therapists can also use rhythm- and music-based interventions utilizing the principles of rhythmic entrainment.

Rhythmic-Cueing Interventions to Improve Motor Skills

Studies of clinical interventions using rhythmic cueing to improve motor skills can be grouped into gait training, training functional movements, and movement to music/dance. Rhythmic cueing for gait training is often a protocolized intervention explicitly based on rhythmic entrainment principles. The use of rhythmic cues to train functional movements such as reaching, standing, or sequences of movements is often based on rhythmic entrainment principles, but may incorporate other musical elements e.g., pitch. Interventions utilizing movement to music or dance have been shown to improve motor skills in some clinical populations. While movement to music and dance interventions are often not explicitly based on rhythmic entrainment principles, rhythmic cues are inherently a fundamental component.

Gait Training. An NMT technique called Rhythmic Auditory Stimulation (RAS) is a manualized protocol for gait training using rhythmic cues, often embedded in live patient-preferred music, to improve stride length, gait speed, and evenness of gait (Thaut & Hoemberg, 2014). Thaut and colleagues have conducted clinical research with patients with Parkinson's disease (Thaut et al., 1996) and acquired brain injury/stroke (Thaut & Abiru, 2010) to support the efficacy and effectiveness of RAS. A Cochrane review of music interventions for acquired brain injury found moderate evidence to support to use of rhythm to increase walking speed and stride length, but low evidence to support the use of rhythm to improve other aspects of walking (Magee et al., 2017). Additionally, there is some evidence that singing (Harrison et al., 2017) and internal cueing (mental singing) may be more effective for gait training than external cueing (music listening) in healthy older adults and people with Parkinson's disease (Harrison et al.,

2018, 2019). Therefore, interventions utilizing self-paced rhythmic cues may be as effective as external auditory rhythmic cues at improving gait characteristic in those with Parkinson's disease. More research on the underlying mechanisms of rhythmic entrainment is needed to understand when external versus internal cueing is ideal for gait training interventions.

Functional Movement Training. The most extensive research on rhythmic cues for functional movement training is research on the use of rhythmic cues to provide a temporal structure for training upper extremity movements. RAS for functional movement training has been shown to improve upper extremity movement in stroke patients (Jeong & Kim, 2007; Thaut et al., 2002). A specific protocol called bilateral arm training with rhythmic auditory cueing (BATRAC), has produced positive neural and functional outcomes in some patients with chronic stroke (Luft et al., 2004; Whitall & Waller, 2013; Whitall et al., 2000). Studies of both RAS for upper extremity movement and BATRAC have primarily used a metronome to cue the timing of movement, but in practice the use of rhythm for functional movement often involves more complex stimuli or music.

Patterned Sensory Enhancement (PSE) is an NMT which uses rhythmic cueing along with pitch, harmonic, and dynamic cues to facilitate a wide range of motor patterns (Thaut & Hoemberg, 2014). While rhythm provides the temporal cues, the other musical elements can provide spatial and force cues. For example, an ascending scale can cue an upward movement, such as lifting an arm. Dissonant chords or a louder dynamic can cue greater force or effort for movement. Among NMTs, PSE is considered best practice for training discrete movements and movement sequences. However, there is limited and contradictory evidence.

Some studies have found that PSE improved motor outcomes in children with disabilities, including improved sit-to-stand performance in children with spastic diplegia (Peng et al., 2011)

and improved gross motor function in children with cerebral palsy compared to exercise with no music (Wang et al., 2013). However, a recent thesis project found PSE may decrease postural control in people with Parkinson's disease (Lai, 2019). While PSE is often used in group exercise with older adults, there is evidence to suggest PSE does not improve motor outcomes (Clark et al., 2012) or is just as effective as exercise with background music (O'Konski et al., 2010). Therefore, it is not clear if melody and harmony in PSE provide additional benefits to improving motor performance beyond using rhythmic cues alone. Overall, more research is needed to support the efficacy and effectiveness of PSE along with a better understanding of the role of rhythmic entrainment in PSE.

Movement to Music and Dance Interventions. Clinical interventions involving structured and improvisational movement to music may improve motor skills (for review, see Sihvonen et al., 2017). For example, one small study found that nine older adults saw improvements in gait following a 9-week Jaques-Dalcroze Eurhythmics intervention, which involved multitasking and coordinated movement to music (Ferguson-Stegall et al., 2017). In addition, dance-based interventions have been shown to improve motor skills in people with Parkinson's disease (Devlin et al., 2019; Hackney & Earhart, 2009a, 2009b). However, more clinical evidence is needed to support the use of movement to music in motor rehabilitation (for review, see Sihvonen et al., 2017). Further, a better understanding of the underlying neural mechanisms of auditory-motor entrainment is needed to optimize rhythmic interventions aimed at improving movement skills.

Rhythmic-Cueing Interventions to Improve Speech and Language Skills

Deficits in rhythm perception are also associated with deficits in language skills (Cumming et al., 2015; Gordon et al., 2015). A body of evidence also supports a link between

musical training and improved language skills (for review, see Patel, 2011). Together, this evidence suggests that rhythm-based interventions may improve speech and language skills in clinical populations. Such interventions include manualized protocols such as Rhythmic Speech Cueing (RSC) and Melodic Intonation Therapy (MIT), as well as singing interventions.

Rhythmic Speech Cueing. The NMT intervention Rhythmic Speech Cueing (RSC), uses rhythmic cues to facilitate the rate and rhythm of speech (Thaut & Hoemberg, 2014). Some limited evidence suggests RSC may be effective with certain populations with speech difficulties. One study with 20 patients with Parkinson's disease found that RSC may be effective in improving speech intelligibility in people with severe dysarthria, but the benefits for those with mild to moderate dysarthria may be limited (Thaut et al., 2001 as cited in Thaut & Hoemberg, 2014). A small pilot study with three patients with traumatic brain injury (TBI) found that auditory metronome cueing (i.e., RSC), singing, and visual timing cues all significantly improved speech intelligbility in two participants. While RSC had the best results for those two participants overall, there was not a significant difference between conditions (Pilon et al., 1998). In people who stutter, rhythmic stimulation or rhythmic speech was found to be as effective as other techniques (auditory masking, chorus reading, and whispering) in improving speech fluency. However, chorus reading was the best at maintaining speech naturalness and reducing self-judged speech effort (Ingham et al., 2012). For those with apraxia of speech, rhythm-based interventions may be an effective treatment (for review, see Ballard et al., 2015). For example, a study with 10 patients with apraxia of speech found that a metrical pacing technique improved the rate and fluency of speech more than a non-rhythmic control treatment (Brendel & Ziegler, 2008). However, another study found that a rate/rhythm treatment for patients with aquired apraxia of speech and aphasia did not show any benefit over repeated practice alone in

improving sound production accuray (Wambaugh et al., 2012). Overall, the studies supporting RSC to improve speech in clinical populations are limited and have mixed results. Randomized controlled trials with larger sample sizes are needed to support the effectiveness of rhythm-based interventions to improve speech and language skills. Further, a basic understanding of the mechanisms shared by rhythm and speech are needed to develop and improve interventions.

Melodic Intonation Therapy. Melodic Intonation Therapy (MIT), developed by Speech Language Pathologists and used by music therapists, is an intervention which uses rhythmic and melodic cues to facilitate the expression of simple phrases in people with non-fluent i.e., Broca's, aphasia. MIT involves two primary components: rhythm tapping of the left hand and intoning words and simple phrases to a melody designed to follow natural prosody of speech. As non-fluent aphasia results specifically from lesions in the left hemisphere of the brain, MIT is designed to engage homologous speech and motor regions in the right hemisphere to retrain language skills (Schlaug et al., 2010). While rhythmic tapping is likely an important component of MIT, one cross-over design study with three participants with Broca's aphasia found that the combination of rhythm and pitch in MIT resulted in more generalization of speech skills than the use of rhythm alone (Zumbansen et al., 2014). Overall, the effectiveness of MIT is limited specifically to non-fluent aphasia and more research is needed to differentiate the role of rhythm and melody in improving speech outcomes.

Singing Interventions. There is clinical and neuroimaging research supporting the benefits of singing to improve speech and communication skills in people with neurological disorders including Parkinson's disease, stuttering, aphasia, and autism (for review, see Wan et al., 2010). However, the singing techniques used in these studies vary widely, making it difficult to determine which components of singing (rhythm, melody, group participation) affect speech

and language skills and to what degree. The goals of singing interventions also vary widely based on the population and the individual. Like RSC, singing interventions may improve the pacing of speech in some populations. For example, singing may be an effective intervention for improving respiratory function in patients with spinal cord injuries (Tamplin et al., 2011).

Rhythmic cues in singing may improve language skills. For example, one study where people with Parkinson's disease sang chants to enhance auditory rhythmic stimulation resulted in improvement in vowel phonation and reading (Di Benedetto et al., 2009). However, it is unclear to what extent these effects were driven by rhythmic entrainment mechanisms. A Cochrane review of evidence supporting music therapy interventions in people with acquired brain injury found the quality of evidence supporting the use of music to improve communication was very low (Magee et al., 2017), suggesting more research is needed overall.

Rhythmic-Cueing Interventions to Improve Cognitive Skills

There is some cognitive neuroscience evidence that rhythmic entrainment may improve attention and perception processes (Conway et al., 2009; Miller et al., 2013). Some clinical evidence also suggests music therapy may improve cognitive functions such as memory, attention, and executive functions (Thaut, 2010). However, it is unclear if rhythmic entrainment interventions can improve cognitive skills. For example, one study measured cognitive skills before and after four different 30-minute group music therapy sessions aimed at improving cognitive skills in participants with brain injury. Following the first session, which utilized "rhythmic synchronization exercises" to improve sustained and focused attention, participants did not show any significant improvements in attention post-intervention. However, participants did demonstrate improvement in executive function skills following the third session utilizing music improvisation exercises (Thaut, Gardiner, et al., 2009). There is some evidence that

rhythmically cued or musically cued gait training, though designed to improve motor skills, may improve cognitive task performance such as perceptual skills (Benoit et al., 2014) and dual tasking (Rochester et al., 2005) in people with Parkinson's disease. However, the mechanisms underlying these improvements are not fully understood. Overall, more evidence is needed to support the use of rhythmic cueing to improve cognitive skills in neurotypical and clinical populations, including a better understanding of the underlying neural mechanisms of rhythmic entrainment and their potential link to attention and cognitive processing.

Auditory Priming in Rhythm-Based Interventions

Priming is when prior experience changes the processing of a stimulus e.g., reduces neural resources, and often improves subsequent performance e.g., faster reaction times or improved accuracy (Henson, 2003). Movement-based priming may be effective in augmenting the physical and neurological effects of therapeutic interventions (Stoykov et al., 2017; Stoykov & Madhavan, 2015). Additionally, Crasta et al. (2018) demonstrated a more significant neural priming effect following an *auditory* priming task compared to a motor priming task. Results from this study suggest auditory priming may enhance the neural effects of rhythmic entrainment more than motor priming. A clinical study with patients with Parkinson's Disease found that auditory-paced finger tapping may be an effective priming tool for gait training. Participants first participated in three 1-minute blocks of a finger tapping training involving tapping an index finger along to a metronome at a pace 20% faster than their pre-training gait cadence. Participants who participated in the finger tapping training significantly improved gait velocity and cadence compared to participants who participated in a rhythmic arm swinging training or no training (Janzen et al., 2019). While this initial research suggests auditory priming may be

beneficial for neural processing and motor performance, more research is needed to understand the underlying neural mechanisms and effects on behavior.

Conclusion

Rhythmic entrainment is a dynamic process involving interactions between sensory and motor systems, possibly driven by a dorsal processing stream in the brain for auditory processing. Thus, rhythmic entrainment may be a useful tool for promoting improved brain and behavior function in a wide range of domains. However, overall evidence of the effectiveness of rhythmic entrainment interventions is still in the early stages. In addition, the effects of rhythmic entrainment on brain and behavior function are not fully understood. Studying rhythmic entrainment in neurotypical populations is imperative for future research with clinical populations and the advancement of clinical applications. Further, measuring brain oscillations during rhythmic tasks in neurotypical populations may be useful for understanding the relationship between external and internal rhythms in sensory, motor, and cognitive processes.

Brain Oscillations and Brain Connectivity

EEG Oscillations and Time-Frequency Measures

Brain oscillations are "rhythmic fluctuations in the [firing] of neurons or populations of neurons" (Cohen & Grafman, 2014, p. 54) which represent either 1) interactions between excitatory and inhibitory activity, 2) pure excitatory activity, or 3) pure inhibitory activity (Cohen & Grafman, 2014; Schnitzler & Gross, 2005). Due to the arrangement of neurons in vertical columns (Vanderah et al., 2016), brain oscillations can be measured noninvasively by placing electrodes on the scalp to measure magnetic activity using MEG or electrical activity using EEG (Cohen & Grafman, 2014). EEG electrodes record changes in the voltage of electrical signal at the scalp across time i.e., the EEG signal (Stern et al., 2001). The EEG signal at one site

reflects the summation of activity from multiple localized or spatially distant brain regions (Cohen & Grafman, 2014; Coles & Rugg, 1995; Varela et al., 2001). While EEG oscillations can be observed in the "raw" i.e., unfiltered signal, they can also provide information about stimulus or event processing. For event processing, if a person is presented with a stimulus (e.g., a tone) or asked to respond to a stimulus (e.g., press a button) multiple times, the EEG signal can be segmented around the stimulus or task event and averaged to obtain a signal, the event-related potential (ERP), which is thought to reflect the brain's unique response to the stimulus or event (Polich, 1993; Stern et al., 2001). The EEG signal can be measured from one EEG electrode i.e., EEG site, or compared across multiple EEG sites.

EEG oscillations are measured using time-frequency methods and contain three types of information: frequency, power, and phase. Frequency is how fast the signal cycles and is measured in hertz (Hz). EEG oscillations are typically grouped into specific *frequency bands* including delta (0–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (15–30 Hz), lower gamma (30–80 Hz), and upper gamma (80–150 Hz). Each frequency band is associated with various cognitive processes, for example, alpha is sometimes considered an "idling rhythm" but is also associated with somatosensory processing (Pfurtscheller & Lopes da Silva, 1999). In general, faster frequencies (e.g., gamma) tend to reflect activity from smaller more localized neuronal populations. Slower frequencies (e.g., delta and theta) tend to reflect activity from larger and more spatially separated neuronal populations (Schnitzler & Gross, 2005; von Stein & Sarnthein, 2000). Power is the amount of energy or intensity contained in the signal and is the amplitude of the signal squared. Phase is the position of the oscillation in time and is measured in radians (0-2 π) or degrees (Cohen & Grafman, 2014).

Frequency, power, and phase information can be extracted from EEG oscillations using time frequency methods, such as a Fourier transform or continuous wavelet transform. A Fourier transform converts the time-based EEG signal in a frequency-based signal. A Fourier transform provides a measure of the average power or phase of each frequency band averaged within a time window (Cohen & Grafman, 2014; Im, 2018; Zhang, 2019). A continuous wavelet transform, using complex Morlet wavelets, allows measurement of changes in the power and phase of frequencies over time (Cohen & Grafman, 2014; Zhang, 2019). Complex Morlet wavelets are created by combining the sine wave of a specific frequency band with a Gaussian wave to create a template. The template is compared to the EEG signal at each time point within the averaged segment window to determine when and how much of that frequency band is contained in the EEG signal at each time point.

Using the averaged EEG signal across trials, the power of each frequency band can be measured relative to the phase of the stimulus of event. If the phase of the signal aligns with the stimulus/event across trials, the power is considered phase-locked to the stimulus/event. Correspondingly, *evoked power* is a measure of changes in EEG power which are correlated and phase-locked the stimulus/event. Thus, evoked power is thought to reflect brain processing which is directly related to the stimulus/event (e.g., sensory registration or cognitive evaluation). *Total power* contains both phase-locked and non-phase locked EEG power across trials. *Induced power* is stimulus/event related changes in EEG power which are time-locked, but not phase-locked across trials. Thus, induced power is thought to reflect brain processes which are related to but not directly evoked by the stimulus/event, e.g., cognitive control, working memory, or preparation (Cohen & Grafman, 2014; Herrmann et al., 2005; Roach & Mathalon, 2008). In addition to measuring power across trials, phase of EEG oscillations relative to the

stimulus/event can be measured across trials independently of power using phase locking factor (PLF; Roach & Mathalon, 2008) also called intertrial phase clustering (ITPC; Cohen & Grafman, 2014). PLF measures the consistency in the timing of brain activity across trials.

Frequency Bands in Rhythmic Entrainment. Research using time-frequency methods reveals which frequency bands may be involved in rhythmic entrainment. This research includes studies from three general paradigms: 1) passive listening to rhythmic auditory tones, i.e., auditory-only paradigms, 2) self-paced rhythmic finger tapping, i.e., motor-only paradigms, and 3) finger tapping paced to auditory-rhythmic tones, i.e., combined paradigms.

Frequency Bands in Auditory-Only Paradigms. Studies which have examined brain oscillations during auditory-only paradigms provide evidence of the involvement of beta and gamma band activity. Induced beta band activity around 20 Hz tends to decrease after the auditory stimulus presentation (Fujioka et al., 2009). Additionally, beta oscillations may represent a mechanism for predictive timing. For example, the timing of beta activity changes based on the rate of the rhythmic auditory stimuli such that it reaches its peak right before the next stimulus presentation (Fujioka et al., 2012). This evidence suggests that beta activity during passive listening to rhythmic tones may reflect underlying motor preparation.

One EEG study found that while evoked gamma follows the stimulus onset, induced gamma preceded the evoked gamma, and in some cases preceded the stimulus. Thus, evoked gamma may represent auditory processes, while induced gamma may represent anticipatory processes. In this study, gamma power was the greatest at fronto-central EEG sites (Snyder & Large, 2005). Additionally, when participants listened to rhythmic auditory tones with random omissions, gamma activity around 40 Hz consistently peaked just prior to stimulus onset or

omission, providing further evidence that gamma activity reflects underlying anticipatory process (Fujioka et al., 2009).

Frequency Bands in Motor-Only Paradigms. Self-paced finger tapping involves alpha, beta, and gamma band activity. During self-paced finger movement, there is a decrease in alpha band activity in the 10-12 Hz range (sometimes referred to as mu) about 2 seconds prior to movement which is associated with somatosensory processing. Like alpha, beta band activity (~14-20 Hz) also decreases prior to movement but also sharply increases post-movement. Beta band activity during self-paced finger tapping is associated with motor processes (Hari & Salmelin, 1997; Pfurtscheller & Lopes da Silva, 1999). One study found finger movement (abduction) was slower when preceded by a peak in beta activity (Gilbertson et al., 2005). Hari and Salmelin (1997) found that 10 Hz (alpha/mu) activity was bilateral during finger movement, but 20 Hz (beta) activity was contralateral during movement. Finally, induced gamma increases slightly before movement onset (Pfurtscheller & Lopes da Silva, 1999) suggesting gamma may reflect anticipation in motor as well as auditory processes.

Frequency Bands in Combined Paradigms. Two EEG studies used finger tapping paced by rhythmic auditory stimuli i.e., combined paradigms, to examine brain oscillations in the beta band. One study found that individual musical tempo preference was correlated with beta (13-25 Hz) during auditory-paced tapping, suggesting beta band activity may reflect an endogenous rhythmic process (Bauer et al., 2018). Another study found that beta activity (14-38 Hz) was time-locked with muscular activity when taps were synchronized with the auditory stimuli (Nijhuis et al., 2021), suggesting beta may assist with the motor coordination and timing.

Crasta et al. (2018) examined frequency bands spanning theta, alpha, beta, and gamma at an EEG site C3 during passive listening, self-paced rhythmic tapping, and auditory-paced

rhythmic tapping tasks. Overall, results found that auditory-paced tapping may decrease neural resources needed for motor performance and anticipation/predictive timing and increase sensorimotor processing compared to self-paced rhythmic tapping. Additionally, neural resource allocation during auditory-rhythmic paced tapping was more efficient (lower power and PLF) following passive listening compared to following self-paced tapping (Crasta et al., 2018). The Crasta et al. (2018) study will be discussed in more detail in Study 1 and Study 2.

Brain Connectivity

Historical Background: Disconnection and Connectionist Theories. Early studies of the human brain in the 19th century focused on localizing brain regions responsible for specific functions (Friston, 2011; Sutterer & Tranel, 2017), the earliest being the pseudoscientific theory of phrenology developed by Franz Joseph Gall (Catani & Ffytche, 2005; Getz, 2018). The decades following saw a continued focus on "localizationist" approaches to researching brain function. This period saw a rise in animal studies and case studies in which researchers identified localized brain regions corresponding to specific functions. For example, Pierre Paul Broca (1824-1880) and Carl Wernicke (1848-1905) discovered brain regions associated with language production and language comprehension, respectively (Bell, 2018; Friston, 2011; Friston et al., 2019; Sutterer & Tranel, 2017). Wernicke, despite discovering one of the most well-known brain regions, was one of the first neuroscientists to support the idea that *connections* between brain regions, rather than localized activity, underlie complex brain functions. Therefore, Wernike is often considered the father of connectionist theory (Absher & Benson, 1993; Sutterer & Tranel, 2017). Today, both simple and complex cognitive functions can be explained by integration among segregated and specialized brain regions i.e., brain connectivity (Friston, 2011).

Types of Brain Connectivity. Generally, brain connectivity measures include structural, functional, and effective connectivity. *Structural* connectivity includes the physical connections of white matter tracts, groups of neurons in specific brain regions, and connections between individual neurons at the level of the synapse. *Functional* connectivity provides a measure of co-dependency between brain activity from spatially separate brain regions. *Effective* connectivity represents the direct influence of one brain region on another. In other words, functional and effective connectivity represent correlation and causation, respectively (Cohen & Grafman, 2014; Friston, 2011). Brain connectivity can take place at different levels anatomically, including the point of connection between individual neurons i.e., at the synapse (Stiles & Jernigan, 2010), within populations of neurons in one brain region, or as neural networks/systems across spatially separated brain regions (Friston, 2011; Tsvetanov et al., 2016).

Neural Networks. Studies of brain connectivity are often aimed identifying neural networks across spatially separated brain regions. Structurally, brain regions are primarily made of grey matter (cell bodies) which are connected by white matter tracts i.e., bundles of axons. In addition to structural connections, networks are classified by their function or specialization. For example, there are neural networks designated for motor planning and execution (Okawa et al., 2017) auditory processing (Patel & Iversen, 2014; Rauschecker, 2011), and attention (Petersen & Posner, 2012). Rhythmic entrainment likely involves interactions between motor, auditory, and attention networks.

Neural Networks in Rhythmic Entrainment. As discussed previously, a possible mechanism underlying rhythm entrainment is auditory-motor interactions (Thaut et al., 2015). This hypothesis is further supported by evidence that rhythm perception is driven by functional connections between auditory and motor brain regions (Patel & Iversen, 2014). In addition to

auditory and motor networks, rhythmic entrainment may also involve attention networks. For example, one MEG study found that rhythmic entrainment involved different cortico-cerebellar networks depending on the amount of attention the task required (Thaut, Stephan, et al., 2009). One network involving motor areas was maintained throughout. A second network involving visuomotor coordination areas activated during tempo changes outside of conscious awareness. A third network involving prefrontal brain areas activated during large tempo changes, suggesting conscious attention was required. Findings suggest that, in addition to auditory-motor interactions, rhythmic entrainment may involve dynamic interactions between orienting (unconscious) and executive (conscious) attention networks (Petersen & Posner, 2012), which fluctuate based on task demands. However, the specific role of attention networks and their potential interactions with auditory and motor networks in rhythmic entrainment is unclear.

Measuring Brain Connectivity. There are various neuroimaging techniques which can measure brain connectivity in neurotypical and clinical populations. Measures of structural connectivity depict white matter tracts such as diffusor tensor imaging (DTI) and fiber tractography (Mukherjee et al., 2008). One notable use of diffusion imaging is the Human Connectome Project, aimed at mapping structural and functional human brain connections in neurotypical adults (Cole et al., 2010; Sotiropoulos et al., 2013). Structural connectivity can support functional and effective connectivity findings. For example, findings from structural imaging which show the brain has more short and closely interconnected neurons than long-range neurons support functional and effective models of highly localized yet vast global communication in the brain (Schnitzler & Gross, 2005).

Measures of functional and effective connectivity provide insight into how the brain adapts and utilizes anatomical connections across time in specific contexts (Friston, 2011).

Functional and effective brain connectivity can be calculated using brain data from many types of neuroimaging including PET, fMRI, MEG, or EEG. fMRI measures have high spatial resolution and can more accurately show where in brain neural events occur (Camprodon & Stern, 2013; Logothetis, 2008). However, the BOLD response takes a few seconds, reducing the ability to accurately measure when events are processed in the brain (Hall et al., 2016). On the other hand, the changes in electrical signals recorded using EEG reflect changes in the brain on the order of milliseconds, which may be preferable for studying functional and effective connectivity (e.g., Mohammad-Rezazadeh et al., 2016). Further, the high temporal resolution of EEG is advantageous for studying the effects of temporally based stimuli, such as rhythm, on changes in brain connectivity (Herholz & Zatorre, 2012).

EEG Oscillations to Measure Functional Brain Connectivity. Time-frequency measures of EEG oscillations across two or more EEG sites provide a measure of functional connectivity (Cohen & Grafman, 2014). In time windows where the signal is expected to be relatively stationary, connectivity measures can be performed on Fourier transformed data. However, to examine changes in connectivity at each time point in a segment, connectivity measures should be performed using continuous wavelet transformed data. In either case, power and phase information can be used to measure connectivity. Power-based measures of connectivity indirectly provide a measure of underlying functional relationships and ignore timing information. Phase-based measures of connectivity provide information about the similarity in the timing of brain oscillations across the brain. If phases of the EEG signal between two EEG sites are synchronized, this is thought to represent a functional coupling between two different neural populations (Cohen & Grafman, 2014; Varela et al., 2001).

Phase-based connectivity methods use the phase information to measure the similarity in the timing of EEG signals between EEG sites. Phase locking value (PLV; Lachaux et al., 1999), also called Inter-site Phase Consistency (ISPC; Cohen & Grafman, 2014) measures the similarity of phase between sites regardless of the power of the signal. Coherence is another phase-based connectivity measure where the phase values are weighted by power (Cohen & Grafman, 2014). Both PLV and coherence are prone to spurious results due to *volume conduction*. Ideally, PLV or coherence reflects communication between spatially distant brain regions. However, the brain generates large electrical fields which are measured by more than one electrode. Therefore, higher PLV or coherence between two electrodes could reflect brain activity from the same underlying source. Further, the electrical fields "spread" when passing through the skull. Thus, volume conduction is most common at EEG sites which are closer in proximity.

There are several methods to control for volume conduction including a current source density (CSD) transformation. Where changes in electrical activity at each electrode are typically compared to a common reference signal, e.g., another electrode, CSD creates a "reference-free" signal which attenuates the effects of volume conduction (Tenke & Kayser, 2012). Further, EEG signals due to volume conduction will have zero phase lag between the signals. Therefore, measures such as phase lag index can help determine true connectivity of PLV measures. For coherence measures, the *imaginary* part of coherency can also control for volume conduction. A wavelet transformed signal produces a complex number containing a *real* part and *imaginary* part (square root of the negative real part). By definition, the imaginary part must be time-lagged and is thus more likely to reflect connections between unique sources (Nolte et al., 2004).

EEG Measures of Brain Connectivity During Rhythmic Entrainment. Very few studies have examined EEG measures connectivity during auditory pace tapping i.e., rhythmic

entrainment. However, some studies have examined EEG measures of connectivity during passive listening to rhythmic auditory tones or self-paced finger tapping. These studies will be discussed in the introduction to Study 1. While these studies provide some insight into functional connectivity during rhythmic entrainment, more evidence is needed.

Disruptions to Brain Connectivity

Common neurologic conditions which result from disruptions to brain connectivity include stroke, multiple sclerosis, Parkinson's disease, and traumatic brain injury (TBI; Khan et al., 2017). Structurally, disruptions to brain connectivity can occur at the synaptic level and to both short- and long-range connections (Sharp et al., 2014). Additionally, either decreased connectivity and increased connectivity could result in disruptions to brain and behavior function. For example, TBI is characterized by decreased long distance connections and increased localized connections. These abnormal connectivity patterns result in imbalanced and inefficient functional communication in the brain associated with a wide range of motor, sensory, and cognitive deficits (Hayes et al., 2016; Sharp et al., 2014). Thus, understanding the effects of rhythmic entrainment and priming on functional connectivity and neural resource allocation may impact future research and the development of rhythm- and music-based interventions to target disruptions to brain connectivity following brain injury.

Conclusion

Time-frequency measures of EEG oscillations may reflect the allocation of neural resources in response to sensory stimuli or during a task. The similarity of the phase of EEG oscillations across EEG sites can provide a measure of functional connectivity. Time-frequency measures and phase-based measures of functional connectivity may be useful for examining neural resource allocation and functional communication between brain regions during rhythmic

entrainment auditory priming. Findings may be relevant to future research aimed at developing interventions to target inefficient use of neural resources or disruptions to brain connectivity for those with neurologic-based injury or impairment.

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Chapter 2: Study 1

Introduction

Movement in time to rhythmic auditory stimulation has been shown to produce immediate and short-term positive effects on motor function in neurotypical and clinical populations (for review, see Thaut et al., 2015). However, less is known about the potential lasting effects of rhythmic auditory stimulation interventions on brain and behavior function. Learning new skills (Sampaio-Baptista et al., 2015) or recovery after injury (Corbetta, 2010) is often characterized by lasting changes in communication between brain regions, i.e., functional connectivity, along with adaptive improvements in behavior function. Therefore, measuring functional connectivity before, immediately after, and weeks to months after rhythmic auditory stimulation interventions may be one way to measure effectiveness. However, a better understanding of functional connectivity during rhythmic tasks is necessary in order for future research examining lasting therapeutic effects to be put in context of connectivity during rhythmic tasks. Functional improvements during or immediately following rhythmic tasks may be driven by interactions between auditory and motor systems (for review, see Zatorre, 2007). However, research differentiating the auditory processing of rhythmic stimuli from rhythmic movement is necessary to understand potentially complex auditory-motor interactions. Thus, this study aims to examine and distinguish between functional connectivity during a passive rhythmic auditory listening task and a self-paced rhythmic motor task. Time-frequency analysis of this dataset has been published previously (Crasta et al., 2018).

Rhythmic Entrainment and Auditory-Motor Entrainment

In physics, *entrainment* is when two oscillating systems synchronize, such as when the pendulums of two clocks mounted on the same wall swing together in time (Pantaleone, 2002). In humans, *rhythmic* entrainment is when internal rhythmic processes (e.g., neural oscillations, central pattern generators) or rhythmic behaviors (e.g., tapping a finger, walking) entrain to external rhythmic cues (Cameron & Grahn, 2016; Thaut et al., 2015). More specifically, *auditory-motor* entrainment is the mechanism by which motor patterns automatically synchronize to auditory rhythmic cues, which rehabilitation therapists, including music therapists, can use to rehabilitate motor function in those with neurologic-based motor impairments (Thaut et al., 1999). In addition to improvements in motor control, rhythmic cueing may also improve behavioral performance, such as response time, accuracy, and visual orienting, on cognitive tasks (Miller et al., 2013), possibly by improving anticipation and timing mechanisms (Nobre & van Ede, 2018). Improvements across both motor and cognitive domains suggest that auditory-motor entrainment may involve neurological pathways shared by both motor and cognitive processes. However, it is not fully understood how moving in time to auditory rhythm affects functional connectivity. Further, it can be difficult to disentangle the effects of rhythmic auditory cueing from rhythmic movement. Given the short timescale of rhythmic processes, the high temporal resolution of electroencephalography (EEG) measures of connectivity may be an appropriate method to begin to answer these questions.

The Intensity and Consistency of Neural Oscillations during Rhythmic Tasks

Neural oscillations can be measured at the scalp using EEG. EEG measures of neural oscillations, even when measured from a single electrode, i.e., a single EEG site, represent neural activity from multiple widely distributed and interacting neural sources, i.e., specialized groups

of neurons or brain regions (Herrmann et al., 2005; Schnitzler & Gross, 2005; Varela et al., 2001). Neural oscillations contain different frequencies, measured in hertz (Hz). Neural oscillations are often grouped into frequency bands including delta (0–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (15–30 Hz), lower gamma (30–80 Hz), and upper gamma (80–150 Hz), each associated with different cognitive processes (Cohen & Grafman, 2014; Herrmann et al., 2005). In general, neural oscillations at faster frequency bands (i.e., beta and gamma) reflect activity from small, localized neuron populations and slower frequencies (i.e., delta, theta, and alpha) reflect activity from neuron populations which are larger and more spatially separate (Schnitzler & Gross, 2005; von Stein & Sarnthein, 2000). Time-frequency measures provide information about the intensity or consistency of specific frequency bands across time (Cohen & Grafman, 2014). Intensity is measured using power, which is the amplitude of the signal squared (Cohen & Grafman, 2014). The consistency of frequency bands is measured as the similarity of the phase of neural oscillations, the degree to which the peaks and valleys of the signal align across trials (Cohen & Grafman, 2014).

The power of neural oscillations can provide information about underlying sensory and motor processes during rhythmic tasks. For example, delta and theta band activity has been associated with the anticipation (Arnal & Giraud, 2012, Stefanics et al., 2010) and detection (ten Oever et al., 2014) of auditory stimuli. Alpha band activity is associated with somatosensory processing during self-paced finger tapping (Hari & Salmelin, 1997; Pfurtscheller & Lopes da Silva, 1999) and finger tapping paced by auditory tones (Pollok, Gross, et al., 2005; Pollok, Südmeyer, et al., 2005). The lower frequencies of the beta band (14-20 Hz) are associated with motor processing during self-paced (Gilbertson et al., 2005; Haegens & Zion Golumbic, 2018; Thaut et al., 2015) and auditorily paced (Bauer et al., 2018; Stavrinou et al., 2007) finger

movements. However, beta band activity around 20 Hz has been linked to both motor and auditory processing when passively listening to rhythmic tones, suggesting beta oscillations may facilitate motor preparation for synchronizing movements to sound (Fujioka et al., 2009). In addition, beta band activity has been found to synchronize with auditory rhythmic stimuli such that the power of the signal decreases after each stimulus onset and reaches a maximum just before the onset of the next stimulus sound (Fujioka et al., 2012). Gamma band activity (above 30 Hz) may help bind sensory information and facilitate sensorimotor integration during self-paced tapping (Pfurtscheller & Lopes da Silva, 1999) and may represent the processing of anticipation and timing information during passive listening to rhythmic tones (Bauer et al., 2018; Fujioka et al., 2009; Snyder & Large, 2005).

Measuring the phase synchrony of neural oscillations across trials, e.g., inter-trial coherence or phase locking factor (PLF), can provide information about how auditory and motor rhythmic tasks affect the consistency of brain responses across time. For example, there is stronger inter-trial coherence when listening to rhythmic stimuli with consistent time-intervals compared to non-rhythmic stimuli with variable time intervals (Will & Berg, 2007). Increased inter-trial coherence even occurs when auditory stimuli are below perceptual detection i.e., it does not produce an evoked response, suggesting that processing auditory rhythms is automatic and separate from overt perception of auditory stimuli (ten Oever et al., 2014).

A recent study in our lab (Crasta et al., 2018) examined the effects of auditory and motor rhythmic condition on the intensity and phase synchrony of neural oscillations across trials. Half of participants participated in an auditory condition in which they passively listened to rhythmic tones. The other half of participants participated in a motor task in which they pushed a button at a rhythmic pace, which was demonstrated briefly by the experimenter. Crasta et al. (2018)

compared time-frequency measures at a single EEG site, C3, between conditions. First, these researchers visually and descriptively compared the time frequency plots to identify frequency bands within critical time windows which served as regions of interest (ROIs) which appeared different between groups/conditions. Then, these ROIs were statistically compared between groups/conditions. The ROIs identified were associated with sensorimotor processing, motor processing, and anticipation/predicting timing. Time-frequency measures included evoked power (power time locked to the event), total power (power regardless of its relationship to the stimulus), and phase locking factor (PLF), the consistency of brain oscillations across trials, (Cohen & Grafman, 2014). Evoked power and PLF ROIs included a window of 20-45 Hz (high beta and low gamma) from 10-60 ms following the event (i.e., auditory stimulus or finger tap) representing motor processing and a window of 4-20 Hz (theta, alpha, and low beta) from 60-250 ms representing sensorimotor processing. The ROI representing anticipation and predictive timing was measured using total power for 13-16 Hz (low beta) from 50-150 ms. Overall, the researchers found different patterns of neural resource allocation between the auditory and motor conditions. Specifically, there was greater evoked power and PLF in the motor ROI during the motor-only precondition but greater evoked power and PLF in the sensorimotor ROI during the auditory-only precondition. In the current study, EEG measures of connectivity were used to measure the similarity of the neural oscillations across EEG sites in the same dataset.

Neural Oscillations to Measure Brain Connectivity

Analyses which measure the consistency of the power or phase of neural oscillations *across* EEG sites are considered measures of connectivity (Cohen & Grafman, 2014). EEG measures of connectivity reflect the communication between widely distributed underlying brain regions (Varela et al., 2001). There are several phase-based measures of connectivity including

phase synchronization across sites and inter-site coherence. Coherence provides a measure of the degree of phase synchronization (the timing of the peaks and valleys) weighted by the power (amplitude squared) of the EEG signal between two EEG sites, which is thought to reflect functional connectivity, or interdependency, between underlying spatially distinct sources/brain regions. However, coherence does not provide a measure of effective connectivity and cannot be used to infer any causal influences between sources (Cohen & Grafman, 2014; Friston, 2011).

Coherence results are often prone to spurious effects due to volume conduction. In other words, high coherence values may result from a signal from the same underlying source observed at multiple sites simultaneously rather than coordination between two spatially distinct sources. If effects are due to volume conduction, there is no time lag between the signals (Cohen & Grafman, 2014). All complex values/numbers, including coherency, contain a *real* part and *imaginary* part, i.e., the square root of the negative real part. Coherence is a real number, which can reflect simultaneous and time-lagged signals. The *imaginary* part of coherency inherently captures only signals which are time-lagged. Therefore, the imaginary part of coherency can help control for spurious effects due to volume conduction (Nolte et al., 2004).

There is some limited evidence of how rhythmic auditory and motor processes affect brain connectivity as measured using phase-based measures of connectivity, .e.g., phase synchronization and coherence across sites. Some studies have examined phase-based connectivity during self-paced finger tapping. For example, Pfurtscheller & Lopes da Silva, 1999 found high coherence of gamma during self-paced tapping between site EEG C3 and a "mid-frontal area" near the SMA. To our best knowledge, no studies have examined EEG phase-based connectivity during passive listening to rhythmic tones. However, Fujioka et al. (2012) used magnetoencephalography (MEG) to examine the coherence of beta activity of five brain

locations with the whole brain following tone presentations. Overall, the researchers found a decrease in whole-brain beta coherence with the right and left auditory cortices but an increase in whole-brain beta coherence with sensorimotor areas. Findings suggest functional coordination between auditory and motor systems when listening to auditory rhythmic stimuli.

A body of evidence from neuroimaging studies provides evidence of auditory, motor, and frontal brain regions involved in rhythmic tasks in neurotypical (e.g., Thaut et al., 2009) and clinical (e.g., Cerasa et al., 2006) populations. However, there is limited evidence about the functional connectivity between brain regions during rhythmic tasks. Therefore, the overall purpose of this study was to examine how functional connectivity patterns during auditory and motor rhythmic tasks qualitatively and quantitatively differed from a rest condition and from each other. Qualitative differences included observable differences in the visualizations of connectivity patterns. Quantitative differences were tested using statistical modeling.

Research Questions

This study will answer the following research questions:

1. Is functional connectivity: a) during the auditory condition qualitatively and quantitatively different from functional connectivity during the rest condition and b) during the motor condition qualitatively and quantitatively different from functional connectivity during the rest condition?

    Hypothesis 1a: The auditory condition will elicit more localized connectivity at higher frequencies (beta and gamma) following the stimulus compared to the rest condition.

    Hypothesis 1b: The motor condition will elicit more long-range connectivity at lower frequencies (delta, theta, and alpha) following the stimulus compared to the rest condition.

Hypothesis 1c: Inter-site coherence will discriminate between a) the auditory condition and the rest condition and b) the motor condition and the rest condition.

2. Is functional connectivity during the auditory condition qualitatively and quantitatively different from functional connectivity during the motor condition?

Hypothesis 2a: The auditory condition will elicit more localized connectivity at higher frequencies (beta and gamma) compared to the motor condition.

Hypothesis 2b. The motor condition will elicit more long-range connectivity at lower frequencies (delta, theta, and alpha) compared to the auditory condition.

Hypothesis 2c: Inter-site coherence will discriminate between the auditory condition and the motor condition.

Method

This study used an exploratory method to identify qualitative and quantitative differences in functional connectivity EEG measures between a passive rhythmic auditory task (i.e., auditory condition) compared to an eyes-open (i.e., rest) condition, a self-paced rhythmic motor task (i.e., motor condition) and a rest condition, and between the auditory and motor conditions. Time-frequency analyses of the dataset for this study have been published previously (see Crasta et al., 2018). Ethical approval was obtained from the Institutional Review Board of Colorado State University and all participants provided written consent before the study session.

Participants

Participants included 39 neurotypical adults, ages 18–39 years (M = 23.51 years, SD = 4.93; 17 males, 22 females). Participants were recruited by word-of-mouth from the university where data collection took place. All participants completed a self-report screening questionnaire developed by the lab to exclude for history of neurologic injuries, disabilities, and family history

of psychological disorders (see Figure A1). No participants were excluded due to these exclusionary criteria. All participants also completed a self-report measure of musical experience expertise (see Figure A2). Participants self-reported their experience playing musical instruments and ranked their overall music expertise as no musical expertise, novice, moderate, or expert musical expertise, which was subsequently coded on a Likert scale from 1–4 for later analysis. Twenty-two out of 39 participants reported experience playing a musical instrument. A total of 9 participants reported having no musical expertise, 11 self-reported as a novice, 14 as having moderate musical expertise, and 5 as musical experts.

Participants were randomly assigned to one of two conditions: the *auditory group* (n = 20; M = 24.8 years, SD = 4.68; 7 males, 13 females) or the *motor group* (n = 19; M = 22.16 years, SD = 4.95; 10 males, 9 females). Groups were not significantly different in age, t (37) = 1.72, p = 0.095. Out of the 22 participants who played instruments, 13 were in the auditory group and 9 were in the motor group. Although both groups had a range of self-reported musical expertise along the 1–4 Likert scale continuum, the groups were significantly different in musical expertise, t (37) = 2.527, p = 0.016, with the auditory group (M = 2.75, SD = 0.85) having more musical expertise than the motor group (M = 2.00, SD = 1.00) overall.

Procedure

First, all participants completed a *rest* condition in which they stared at a fixation point for three minutes. Following the rest condition, the *auditory* group participants completed a passive rhythmic auditory task in which they listened to 400 presentations of auditory tones presented every 800 ms through ER3A binaural ear tips (Etymotic Research). Tones were generated using a 1kHz sinusoidal wave set to 70 decibels sound pressure level with a 50 ms duration and 10 ms rise/fall time and presented using E-Prime 3.0 software (Psychology

Software Tools, 2016). The *motor* group participants completed a rhythmic motor task in which they pushed a button with their right index finger 400 times at a rate of 800 ms between taps following the experimenter briefly modeling the rate of tapping with 5 taps and demonstrating the appropriate finger position. Participants in both groups were given a short break halfway through.

EEG Recording

Participants completed all tasks during an EEG recording. A BioSemi ActiveTwo (BioSemi, 2016) EEG Acquisition System with 64 pin-type Ag/AgCl sintered active-electrodes recorded an electrical signal at the scalp for each channel with a sampling rate of 1024 Hz with a bandwidth of 0-268 Hz. Four flat electrodes recorded electrooculograms (EOGs); two placed on the left supraorbital and infraorbital regions recorded vertical eye movements (i.e., eye blinks) and two placed lateral to the external canthus of each eye measured horizontal eye movements (i.e., eye saccades). Data recorded from flat electrodes placed on the left and right earlobes were used as the offline reference. Two additional flat electrodes were placed on the left and right mastoids. A Common Mode Sense (CMS) active electrode and Driven Right Leg (DRL) formed a feedback loop which served as the online reference and ground (https://www.biosemi.com/faq/cms&drl.htm).

Data Reduction

EEG data were analyzed using BrainVision Analyzer, Version 2.2.0 software (Brain Products GmbH, 2019). A band-pass filter removed frequencies below 0.1 Hz and above 80 Hz. To accommodate lower frequencies in subsequent wavelet analyses, data were segmented from -2500 ms to 2500 ms around each marker. For the eyes open rest condition, 400 markers were placed every 800 ms beginning approximately 900 ms into the recording. For the auditory

condition, the marker for segmentation was the auditory stimulus. For the motor condition, the marker for segmentation was the button press. The segmented data were baseline corrected using a baseline of -200 ms to 0 ms prior to the event. Next, vertical eye movements were removed from trials with a regression method (Segalowitz, 1996) using a custom MATLAB script. Following the eye regression, another baseline correction relative to -200 ms to 0 ms prior to the event onset was conducted. Next, artifact rejection at all EEG sites and the vertical eye channel removed segments with voltage deviations of ± 200 microvolts. For this study, a threshold of ±200 microvolts was selected to maintain at least 75% of segments (Im, 2018). A current source density (CSD) transformation of each segment was performed to control for volume conduction by creating a reference-free signal (Tenke & Kayser, 2012). The parameters for the CSD transformation (Perrin et al., 1989) was set as the order of the splines at 3, the maximal degree of the Legendre polynomial at 10 and the lambda smoothing parameter set to the default 1e-5. The parameters for the CSD transformation were determined based on visual inspection of topographical maps of the preprocessed data for one participant chosen at random from the auditory group to ensure parameters captured scalp regions with maximal power. The parameters for CSD transformation are primarily affected by the electrode density and sampling rate; however, the CSD transformation can also be affected by noise in the data (Kayser & Tenke, 2015). Therefore, the CSD parameters were confirmed with 4 additional participants, 2 from each group, for both the task and rest conditions. To conserve computational time and resources, only sites from a 32-channel montage based on the modified 10-20 system (American Electroencephalography Society, 1994) were selected for connectivity analysis (see Figure 2.1).

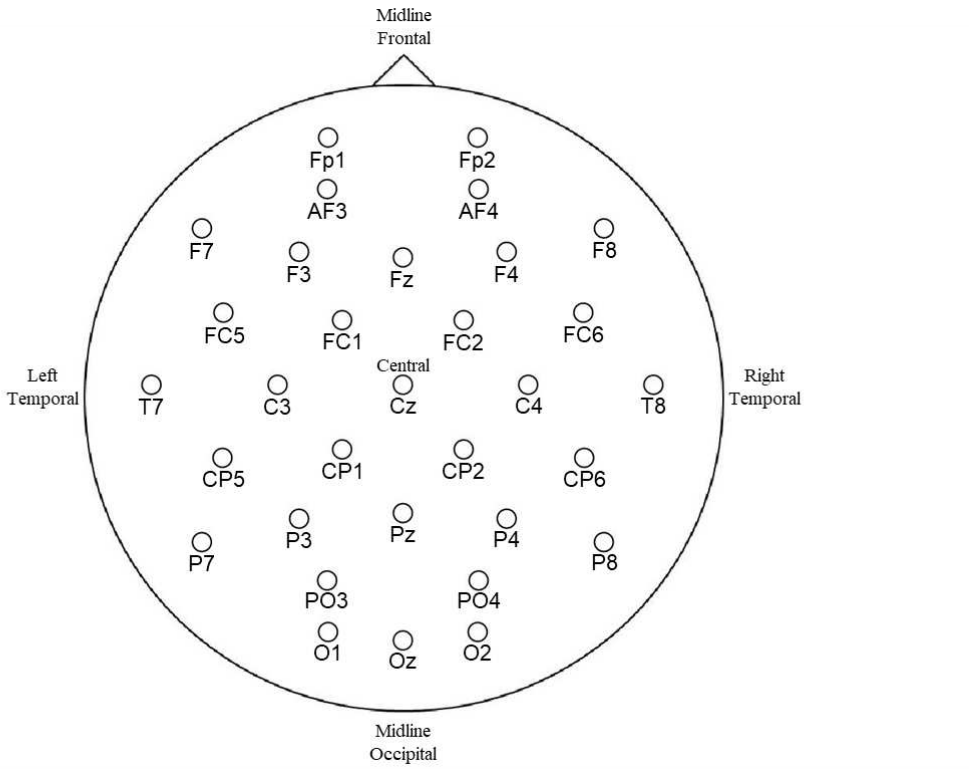

Figure 2.1. 32-channel montage based on the modified 10-20 system used in the connectivity analysis. Frontal, central, and occipital locations are labeled at midline and temporal locations are labeled on the right and left sides of the head.

Data Analysis

Behavioral Measures. Behavioral measures for the motor condition included the inter-response interval (IRI) mean and variability (Crasta et al., 2018). The IRI was calculated as the time between each tap. IRIs of greater than 1200 ms were considered missed taps and IRIs of less than 200 ms were considered double taps. The IRIs for missed taps and double taps were removed. The percentage of taps missed was calculated as the number of missed taps divided by 400. The IRI mean provides a measure of the average rate of tapping and the IRI standard deviation provides a measure of the variability of tapping rate across trials.

Functional Connectivity Analyses. Four EEG measures of functional connectivity were calculated and visually inspected including magnitude squared coherence (Cohen & Grafman,

2014), the imaginary part of coherency (Nolte et al., 2004), phase locking value (Lachaux et al., 1999), and phase lag index (Stam et al., 2007). Of these, only the results for the imaginary part of coherency (IMC) are reported here as the other three measures were not found to have salient visual results. IMC results in values from -1 to 1, with values closer to -1 or 1 indicating lower variability (i.e., better coherence) between signals. In addition, a positive or negative value indicates the direction of the relationship. A positive value indicates the phase of signal from first site leads while a negative value indicates that the second site leads. IMC controls for the effects of volume conduction as it only accounts for coupling between signals which are time-lagged (Nolte et al., 2004).

To calculate IMC, first, the CSD-transformed, i.e., "reference-free" EEG signal underwent a complex Morlet wavelet transformation resulting in a signal containing amplitude/power, frequency, and phase information at each time point (Cohen & Grafman, 2014). The Morlet wavelet transformation was performed across the entire -2500 ms to 2500 ms segment from 1–60 Hz with linear frequency steps and a constant of 5, resulting in one wavelet layer for each frequency (a total of 60 wavelet layers) at 32 channels. The wavelet data were segmented from -400 ms to 400 ms around each event resulting in segments 819 datapoints in length (approximately 800 ms). From there, IMC values were calculated across 496 channel pairs, which were all unique channel pairs among the 32 EEG sites. The resulting output for each channel pair was the average connectivity value at each of the 819 datapoints for each frequency layer (1–60 Hz). Connectivity values were exported from Analyzer using a generic export which could be imported into MATLAB 2020b for further analyses. Finally, using a custom MATLAB script (see Appendix B), connectivity measures were averaged into 50 ms bins from -400 ms to 400 ms around the event (a total 16 total bins) and into 5 frequency bands: delta, theta, alpha,

beta, and gamma (see Table 2.1). The steps outlined above were conducted for each of the four conditions (auditory, motor, rest-auditory group, and rest-motor group).

Table 2.1. *Frequency Bands for Wavelet Analysis.* The frequency range and total number of wavelet layers in each of the five frequency bands averaged for visual inspection and subsequent statistical analyses.

Frequency Band	Frequency Range	Number of Wavelet Layers
delta	1 – 4 Hz	4
theta	5 – 7 Hz	3
alpha	8 – 12 Hz	5
beta	13 – 30 Hz	18
gamma	31 – 60 Hz	30

Visual Inspection of Band-Channel Pairs Maps

Band-channel pairs maps of the standardized IMC were visually inspected for qualitative differences between conditions across time. Prior to mapping and visual inspection, IMC values were standardized using the "zscore" function in MATLAB. The Z-transformation distribution was based on the mean and standard deviation across all pairs within a single bin. The standardized values were then grand averaged for each condition within each group. Band channel pairs were mapped which met a threshold of ±0.6 standardized IMC. Most of the channel pairs with the highest IMC values were short-distance pairs. Therefore, the threshold was determined by rank-ordering the data and selecting a cutoff which captured at least one long-distance channel pair in at least one 50 ms bin for each frequency band.

Using a custom MATLAB script (see Appendix B), channel pairs at the ±0.6 threshold of standardized IMC for each frequency band in each 50 ms bin were mapped onto a 2D representation of a 32-channel modified 10-20 map (American Electroencephalography Society, 1994) for each condition for a total of 320 maps (see figures in Appendix C). To identify qualitative differences between the auditory and rest condition (Research Question 1a), the motor

and rest condition (Research Question 1b), and the auditory and motor condition (Research Question 2), band-channel pair maps of each time-frequency bin were visually inspected to select critical time-frequency windows for each comparison. Critical time-frequency windows of 2-3 adjacent frequency bands were selected based on the following observable criteria in the task condition: 1) distinct patterns of connectivity which remained consistent across bins, 2) high coherence values, 3) notable differences between the conditions. IMC values were then averaged and standardized for each frequency band in each time window for subsequent visualization statistical analyses. Band-channel pair maps of standardized IMC averaged within the critical time-frequency windows were created using a threshold of ±0.6 with 2–3 frequency bands combined in one map.

Statistical Analyses

Discriminant analysis was used to determine if the IMC values of unique channel pairs could discriminate between 1) the task and rest conditions within each group and 2) between the auditory and motor conditions. Discriminant analysis is like a linear regression, but with a categorial outcome variable. The Box's M statistic tested the assumption of homogeneity of covariance between conditions. However, discriminant analysis is robust to violations of the homogeneity assumption when the ratio between groups is less than 1.5 (Stevens, 2012), which is true for this dataset. The canonical correlation provided an index of the overall model fit. The square of the canonical correlation is reported as the percentage of the variance explained by the model. Significance of the overall model was indicated by Wilks' Lambda, which represents the percentage of variance not accounted for in the model. The alpha level for significance was calculated as .05 divided by the number of discriminant analyses conducted for each comparison. As there were four discriminant analysis distinguishing between auditory and rest conditions,

significance was determined using a Bonferroni-corrected alpha level of .0125 (.05/4). As there were three discriminant analysis distinguishing between auditory and rest conditions and between the auditory and motor conditions, significance was determined using a Bonferroni-corrected alpha level of .017 (.05/3) for those analyses. The individual coefficients (weights) provide an index of the importance of each predictor. The structure matrix correlations (loadings) rank the importance of each predictor, with an absolute value above .3 indicating the variable accounts for at least 9% of the variability in the function. Classification results provide a percentage of original cases which were correctly classified by the model. The percentage of cases correctly classified after cross-validation indicates the generalizability of the model to a larger population.

To answer the first research question and determine if functional connectivity patterns were quantitatively different between the task (auditory or motor) and rest conditions, discriminant analyses were conducted for each critical time-frequency window (described in Results section): four to discriminate between the auditory and rest condition and three to discriminate between the motor and rest condition. To determine the predictor variables, the top 5 unique pairs from each condition were selected, such that there were no duplicate pairs between conditions, for a total of 10 predictor variables. First, the standardized IMC values for each condition were rank-ordered within each critical time-frequency window and the five band-channel pairs with the highest values were identified. Next, any duplicate band-channel pairs between the task and rest condition, which were more likely to represent underlying connectivity which was not task-specific, were removed from the list. Finally, the band-channel pairs with the next greatest standardized IMC values were identified. This process was repeated until 5 unique band-channel pairs were identified in each condition.

To answer the second research question and determine if functional connectivity was quantitatively different between the two task conditions, three discriminant analyses were conducted to discriminate between the auditory and motor conditions – one for each critical time-frequency window identified by visual inspection. To select predictor variables, the top 5 band-channel pairs were selected from each condition after removing band-channel pairs which had a standardized IMC value of at least ± 0.6 in the rest condition. As substantial overlap was observed between the band-channel pairs maps between the rest and task conditions in each group, this process helped ensure that comparisons between the auditory and motor conditions represented differences in task-specific brain activity. Finally, it was confirmed that band-channel pairs were not duplicated between the auditory and motor conditions. As self-reported music expertise was significantly different between groups, the level of musical experience was an additional predictor.

Results

Motor Performance

As participants in the motor group self-paced their tapping during the motor condition, the inter-response interval (IRI) mean and standard deviation for the motor condition served as behavioral measures. Participants in the motor group were asked to pace their tapping around 800 ms for 400 trials (two blocks of 200 trials). For each participant, the time between the last tap of the first block of 200 and the first tap of the second block of 200 was not included in the calculation. Seven participants had "missed taps" (IRI greater than 1200 ms): One participant had 12 (3%) missed taps, one had 5 (1.25%) missed taps, two had 4 (1%) missed taps, and three had 1 missed tap (0.25%). One participant had one "double tap" (IRI less than 200 ms). After removing missed and double taps, the mean IRI was 806.58 ms (*SD* = 87.17) and the mean IRI

variability was 66.65 ms (*SD* = 28.76). Overall, participants, on average, tapped slightly (6 ms) slower than the desired IRI of 800 ms, but IRI varied across participants. Participants varied their IRI across trials by about 67 ms on average.

Auditory Condition versus Rest Condition

Based on visual inspection of the band-channel pair maps of the IMC across all 50 ms bins (see Appendix C), the auditory condition appeared to have the greatest differences compared to the rest condition in three critical time-frequency windows: 1) delta and theta band IMC from -200 to 100 ms, 2) theta and alpha band IMC from 250 to 500 ms (i.e., 250 to -300), 3) alpha and beta band IMC from 50 to 250 ms, and 4) beta and gamma band IMC from -200 ms to 200 ms. Discriminant analyses revealed that out of the four critical time-frequency windows, the theta and alpha 250-500 ms critical time-frequency window was able to differentiate between the auditory and rest conditions.

The critical time-frequency window delta and theta at -200 to 100 ms was selected as it showed the strongest delta and theta band IMC at long-distance channel pairs in the auditory condition. The channel pairs AF4-CP6 for delta and AF3-T8 for theta were both prominent during the -200 to 100 ms window. The rest condition had 16 band-channel pairs which met threshold and the auditory condition 18 pairs which met threshold. There was one overlapping band-channel pair between the conditions (theta at FC1-Cz). The top 5 unique band-channel pairs for the rest condition included delta IMC at T8-P4 and theta IMC at FC2-C4, Fz-FC2, F3-Fz, and O1-Fz. The top 5 unique band-channel pairs for auditory condition included delta IMC at AF4-CP6 and Fp2-FC2, and theta IMC at AF3-T8, O1-O2 and CP6-CP2. A Box's M of 124.21 was significant (F = 1.61, p = .003), violating the assumption of equality of covariance matrices. The discriminant analysis model explained 40.70% of the variance between the conditions

(Wilks' Lambda = 0.59, χ^2 (10) = 17.23, p = .069), which was not significant. The group classification showed that 80.0% of the original cases were correctly classified overall and 60.0% of cases were correctly classified after cross-validation. Descriptive statistics, discriminant function coefficients, and structure matrix correlations for each predictor are listed in Table 2.2.

Table 2.2. Predictors in discriminant analysis differentiating between the auditory and rest conditions. Freq. Band = frequency band, Weight = standardized canonical coefficient, Loading = structure matrix correlation, M = Mean, SD = standard deviation, IMC = imaginary part of coherency.

Predictors		Auditory Condition IMC			Rest Condition IMC			Model Contribution	
Freq. Band	Channel Pair	Raw Score	Z Score		Raw Score	Z Score			
-200 to 100 ms		M	M	SD	M	M	SD	Weight	Loading
delta	AF4-CP6	0.0250	0.851	1.046	-0.0017	-0.047	0.961	0.711	.554
	Fp2-FC2	0.0216	0.735	1.399	-0.0002	-0.006	1.070	0.569	0.369
	T8-P4	-0.0079	-0.276	1.273	-0.0320	-0.909	1.942	0.056	0.239
theta	AF3-T8	0.0346	0.916	1.552	>0.0001	0.012	1.232	-0.338	0.400
	O1-O2	0.0326	0.863	1.878	0.0055	0.138	0.904	-0.061	0.305
	CP6-CP2	0.0298	0.789	1.283	-0.0260	-0.586	1.316	0.411	0.656
	FC2-C4	-0.0245	-0.655	1.064	-0.0378	-0.859	0.894	-0.134	0.129
	Fz-FC2	-0.0238	-0.637	0.771	-0.0327	-0.741	0.673	0.106	0.090
	F3-Fz	0.0132	0.346	1.004	0.0311	0.730	1.085	-0.359	-0.228
	O1-Fz	0.0121	0.318	1.062	0.0307	0.719	1.048	-0.817	-0.236
250 to 500 ms									
theta	F4-Cz	-0.036	-0.955	0.961	-0.025	-0.514	1.228	0.306	0.169
	FC6-T8	-0.032	-0.849	1.015	-0.003	-0.054	1.028	0.698	0.329
	F3-CP6	0.030	0.792	1.064	0.013	0.292	1.258	-0.186	-0.181
alpha	P8-PO4	0.044	0.805	1.572	0.019	0.335	1.308	0.049	-0.137
	Oz-PO4	-0.041	-0.793	1.582	-0.027	-0.516	1.380	0.029	0.079
	P7-Cz	0.014	0.251	1.900	0.053	0.978	1.388	0.983	0.184
	FC1-CP1	0.032	0.584	1.154	0.045	0.823	1.187	-0.564	0.086
	P3-P7	0.020	0.351	1.387	0.045	0.817	1.291	0.328	0.147
	AF4-Fz	0.003	0.046	0.889	0.041	0.748	0.863	1.428	0.338
	PO3-Oz	0.024	0.435	1.800	0.040	0.733	1.512	0.352	0.076
50 to 250 ms									
alpha	PO3-PO4	0.055	1.025	1.888	0.047	0.812	1.575	0.209	0.111
	O1-PO4	0.050	0.934	1.446	0.020	0.343	1.133	0.253	0.414
	FC1-CP1	0.039	0.718	1.073	0.049	0.851	1.198	-0.12	-0.107
beta	F4-F8	-0.037	-1.350	2.427	-0.023	-0.713	1.335	-0.316	-0.296
	T7-F4	0.028	0.966	1.797	-0.005	-0.188	0.721	0.74	0.766
	CP5-P7	0.028	0.960	1.844	0.026	0.767	1.343	0.127	0.109
	FC6-T8	-0.011	-0.434	1.579	-0.035	-1.081	1.568	0.188	0.374
	P8-O2	0.020	0.681	0.957	0.034	1.040	1.516	-0.343	-0.257
	FC5-CP5	-0.018	-0.676	1.177	-0.029	-0.901	1.624	0.394	0.144
	C4-T8	0.019	0.633	1.884	0.028	0.848	1.700	0.281	-0.109
-200 to 200 ms									
beta	F4-F8	-0.034	-1.453	2.787	-0.024	-0.955	1.787	-0.164	0.241
	F3-F7	-0.026	-1.087	1.320	-0.012	-0.482	1.316	0.707	0.52
	F7-T7	0.025	1.025	1.523	0.022	0.794	1.552	0.109	-0.17
	FC6-T8	-0.014	-0.589	1.483	-0.030	-1.179	1.614	-1.02	-0.431
	P8-O2	0.019	0.746	1.294	0.030	1.116	1.818	-0.036	0.266
gamma	F7-T7	0.029	1.196	1.903	0.023	0.857	1.627	-0.209	-0.217
	F8-FC6	-0.027	-1.113	2.516	-0.021	-0.807	2.502	0.669	0.138
	FC5-CP5	-0.010	-0.418	2.169	-0.029	-1.099	2.579	-0.519	-0.324
	FC6-T8	-0.023	-0.957	1.721	-0.028	-1.059	1.364	0.621	-0.074
	FC6-C4	-0.024	-0.978	2.590	-0.028	-1.051	2.752	-0.027	-0.031

The critical time-frequency window theta-alpha band at 250 to 500 ms was selected as it showed distinct theta and alpha band IMC connectivity to frontal sites during the auditory condition. The auditory task showed higher theta IMC overall with more pairs crossing midline between temporal and fronto-central sites, shown in Figure 2.2 by thicker orange lines between left frontal and right temporal sites and between right frontal and left temporal sites. The rest condition had greater IMC with left parietal sites (e.g., P7-Cz) and the auditory condition had greater alpha IMC with right parietal sites (e.g., P8-PO4). The rest condition had 31 band-channel pairs which met threshold and the auditory condition had 48 pairs which met threshold. There were 6 overlapping band-pair between the conditions (alpha at O1-Oz, PO3-PO4, P3-O1, FC2-C4, and P4-PO4 and theta at FC1-Cz). The top 5 unique channel pairs for the rest condition included alpha IMC at P7-Cz, FC1-CP1, P3-P7, AF4-Fz, PO3-Oz. Of these, theta at FC6-T8 was the most discriminating (see Table 2.2). The top 5 unique channel pairs for the auditory condition included theta IMC at F4-Cz, FC6-T8, and F3-CP6 and alpha IMC at P8-PO4 and Oz-PO4. Of these, theta at FC6-T8 was the most discriminating (see Table 2.2). A Box's M of 65.68 was not significant ($F = 0.85$, $p = .772$), meeting the assumption of equality of covariance matrices. The discriminant analysis model explained 59.60% of the variance between the conditions (Wilks' Lambda = 0.41, χ^2 (10) = 29.94, $p < .001$), which was significant. The group classification showed that 90% of the original cases were correctly classified overall and 87.5% were correctly classified after cross-validation. Overall, what was most discriminating for this window was fronto-central alpha connectivity at rest and fronto-temporal theta connectivity during the auditory condition.

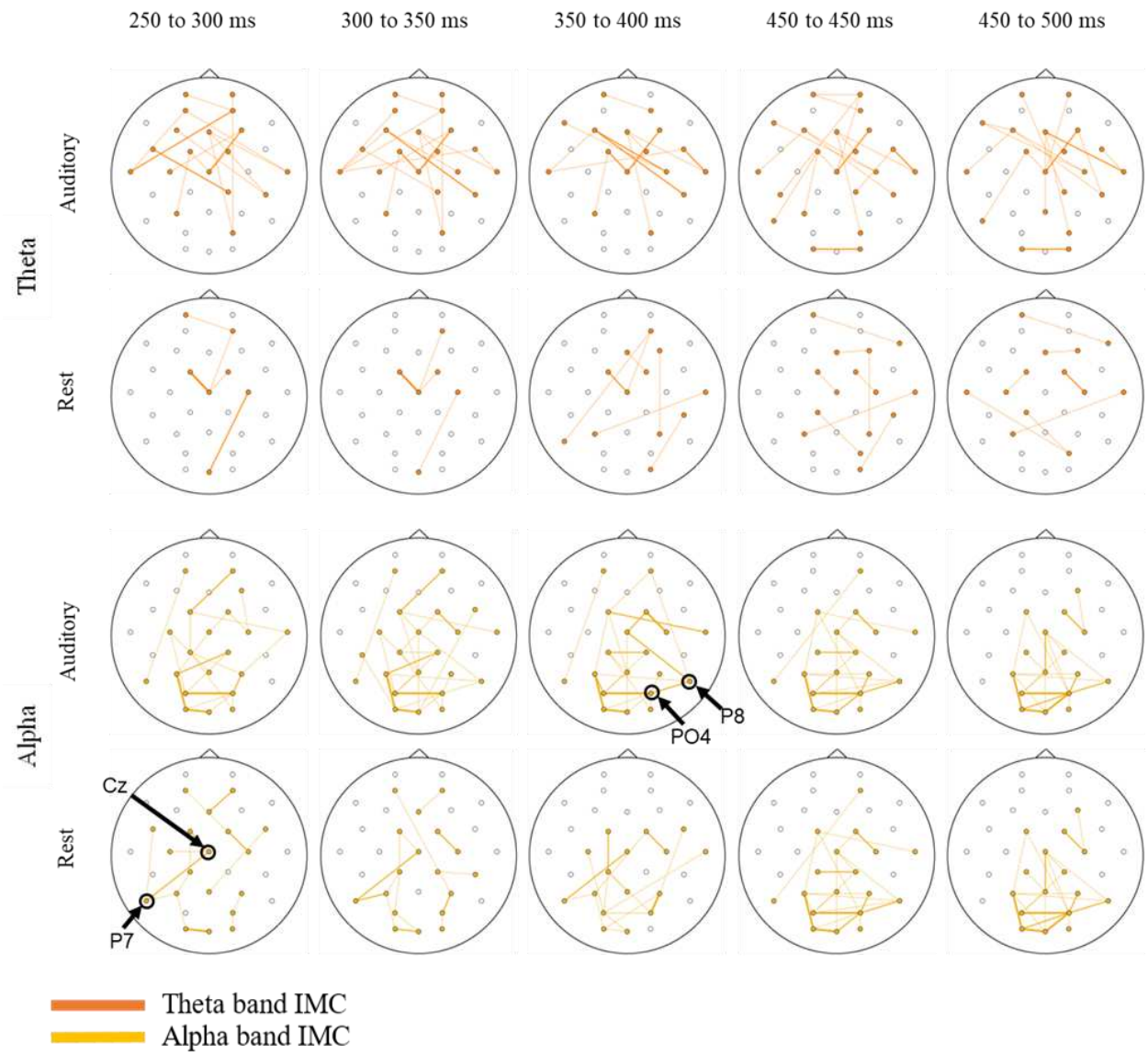

Figure 2.2. Band-channel pair maps in 50 ms bins for standardized IMC at a threshold of ±0.6, withing the critical time-frequency window theta-alpha band at 250 to 500 ms comparing the auditory and rest conditions. Sites within notable channel pairs are indicated.

The critical time-frequency window alpha-beta at 50 to 250 ms was selected at it showed long-distance connectivity in the alpha and beta bands during the auditory condition: alpha at frontal and fronto-central sites and for beta from T7 to bilateral frontal sites (T7-AF3, T7-AF4, and T7-F4), see Figure 2.3. The rest condition had 33 band-channel pairs which met threshold and the auditory condition had 50 pairs which met threshold. There were 2 overlapping pairs

between the conditions (alpha at O1-Oz and beta at T7-CP5). The top 5 unique band-channel pairs for the rest condition included alpha IMC at FC1-CP1 and beta IMC at FC6-T8, P8-O2, FC5-CP5, and C4-T8. The top 5 unique band-channel pairs for the auditory condition included alpha IMC at PO3-PO4 and O1-PO4 and beta IMC at F4-F8, T7-F4, and CP5-P7. A Box's M of 108.09 was significant ($F = 1.40$, $p = .0270$, violating the assumption of equality of covariance matrices. The discriminant analysis model explained 24.11% of the variance between the conditions (Wilks' Lambda = 0.759, χ^2 (10) = 9.11, $p = .522$), which was not significant. The group classification showed that 70.0% of the original cases were correctly classified overall and 42.5% were correctly classified after cross-validation.

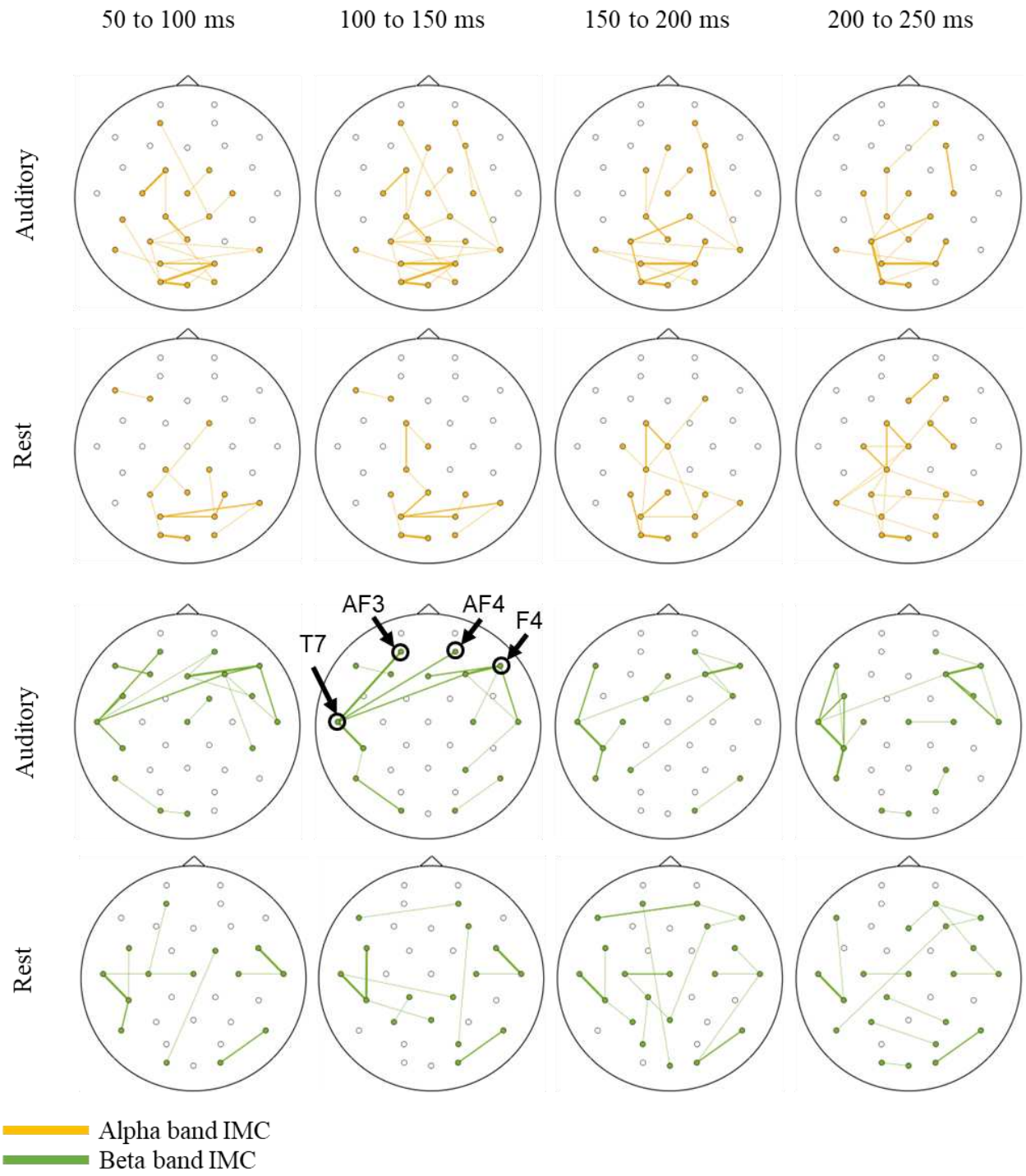

Figure 2.3. Band-channel pair maps in 50 ms bins for standardized IMC at a threshold of ±0.6, withing the critical time-frequency window alpha-beta at 50 to 250 ms comparing the auditory and rest conditions. Sites within notable channel pairs are indicated.

The critical time-frequency window beta and gamma at -200 to 200 ms was selected as it showed a pattern of left-lateralized connectivity to prefrontal and parietal sites in the beta and gamma bands during the auditory condition. The rest condition had 48 band-channel pairs which met threshold and the auditory condition had 55 pairs which met threshold. There were 7 overlapping pairs (beta at T7-CP5 and gamma at T7-CP5, AF4-Fz, Fz-F4, Fz-F8, C4-T8, and F8-T8). The top 5 unique band-channel pairs for the rest condition included beta IMC at FC6-T8 and P8-O2 and gamma IMC at FC5-CP5, FC6-T8, and FC6-C4. The top 5 unique band-channel pairs for the auditory condition included beta IMC at F4-F8, F3-F7, and F7-T7 and gamma IMC at F7-T7 and F8-FC6. A Box's M of 50.66 was not significant ($F = 0.66$, $p = .976$), meeting the assumption of equality of covariance matrices. The discriminant analysis model explained 17.06% of the variance between the conditions (Wilks' Lambda = 0.83, χ^2 (10) = 6.162, p = .801), which was not significant. The group classification showed that 67.5% of the original cases were correctly classified overall and 40.0% were correctly classified after cross-validation.

Overall, the critical time-frequency window of standardized IMC for theta and alpha band at 250 to 500 ms was able to distinguish between the auditory and rest conditions, with fronto-temporal theta IMC characterizing the auditory condition and fronto-central alpha IMC characterizing the rest condition. Visually, there were prominent differences in beta IMC, but the discriminant analysis was not significant for either critical time-frequency window including beta. Band-channel pair maps of the standardized IMC averaged within each critical time-frequency window and the location of band-channel pair predictors to discriminate between the auditory and rest conditions are shown in Figure 2.4.

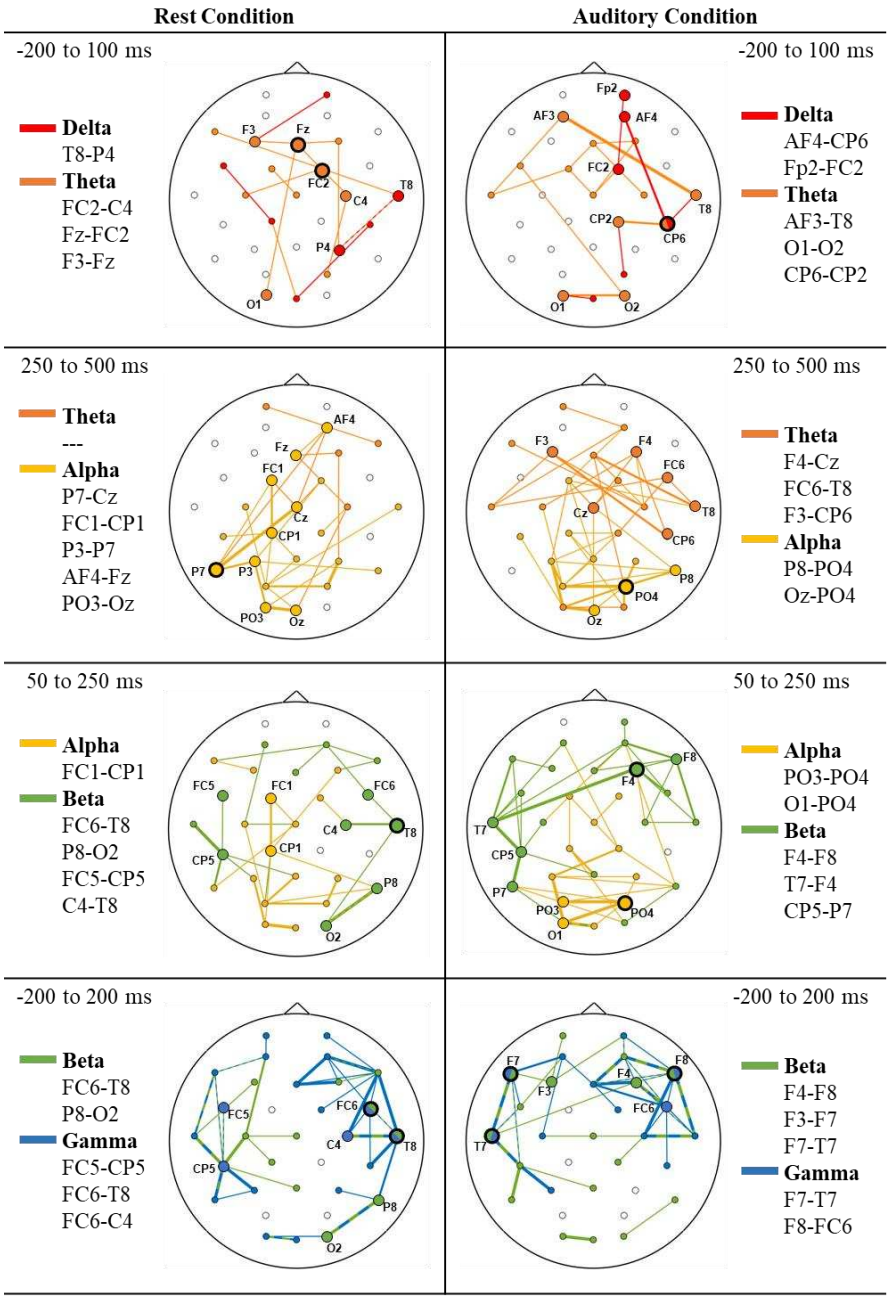

Figure 2.4. Band-channel pair maps comparing the auditory and rest conditions within the auditory group for standardized IMC at a threshold of ± 0.6 averaged within four critical time-frequency windows: 1) delta and theta band IMC at -200 to 100 ms 2) theta and alpha band IMC at 250 to 500 ms (i.e., 250 to -300), 3) alpha and beta band IMC at 50 to 250 ms, and 4) beta and gamma band IMC at -200 ms to 200 ms. For each critical time-frequency window, the top 5 unique channel pairs for each condition (those included in the discriminant analysis) are listed, with the corresponding sites labeled in the band-channel pair map. Color indicates the frequency band (red = delta, orange = theta, yellow = alpha, green = beta, and blue = gamma). Thicker lines indicate greater standardized IMC values.

Motor Condition versus Rest Condition

Based on visual inspection of the band-channel pair maps of the IMC across all 50 ms bins (see Appendix C), the motor condition appeared to have the greatest differences compared to the rest condition in three critical time-frequency windows: 1) delta, theta, and alpha band IMC at -150 ms to 150 ms, 2) theta and alpha band IMC from at -350 to -100 ms and 3) beta and gamma band activity at -300 to 0 ms. Discriminant analyses revealed that out of the three critical time-frequency windows, delta, theta, and alpha from -150 to 150 ms was able to distinguish between the motor and rest conditions.

The critical time-frequency window delta, theta, and alpha at -150 to 150 ms was selected as it showed long-distance IMC during the motor condition including delta IMC for F3-P7, theta IMC branching from T7 across midline, and alpha IMC branching from P7 across midline (Figure 2.5). The motor condition also showed prominent short-distance delta band-channel pairs at frontal sites. The rest condition had 25 band-channel pairs which met threshold and the motor condition had 74 pairs which met threshold. There were 7 overlapping band-channel pairs (theta at FC1-Cz and alpha at Oz-O2, P4-PO4, O1-Oz, Pz-Cz, FC1-Cz, and C4-CP6). The top 5 unique band-channel pairs for the rest condition included delta IMC at Fp1-CP1, theta IMC at Oz-PO4, and alpha IMC at F4-C4, FC2-Cz, and F8-Cz. Of these, theta at Oz-PO4 and alpha at F4-C4 and F8-Cz were the more discriminating. The top 5 unique band-channel pairs for the motor condition included delta IMC at AF3-F3, theta IMC at FC2-Cz and FC1-Fz, and alpha IMC at P4-P8 and P3-PO3. Of these, delta at AF3-F3, theta at FC1-Fz, and alpha at P4-P8 were the most discriminating. A Box's M of 138.32 was significant ($F = 1.76$, $p < .001$), violating the assumption of equality of covariance matrices. However, discriminant analysis is robust against violations of the homogeneity of variance assumption. The discriminant analysis model

explained 63.20% of the variance between the conditions (Wilks' Lambda = 0.37, χ^2 (10) = 30.98, $p < .001$), which was significant. The group classification showed that 89.5% of the original cases were correctly classified overall and 76.3% were correctly classified after cross-validation. Overall, what was most discriminating for this window was occipital-parietal theta and frontal alpha connectivity during the rest condition and frontal delta and theta and parietal alpha connectivity in the motor condition. Descriptive statistics, the discriminant function coefficients, and structure matrix correlations for each predictor are listed in Table 2.3.

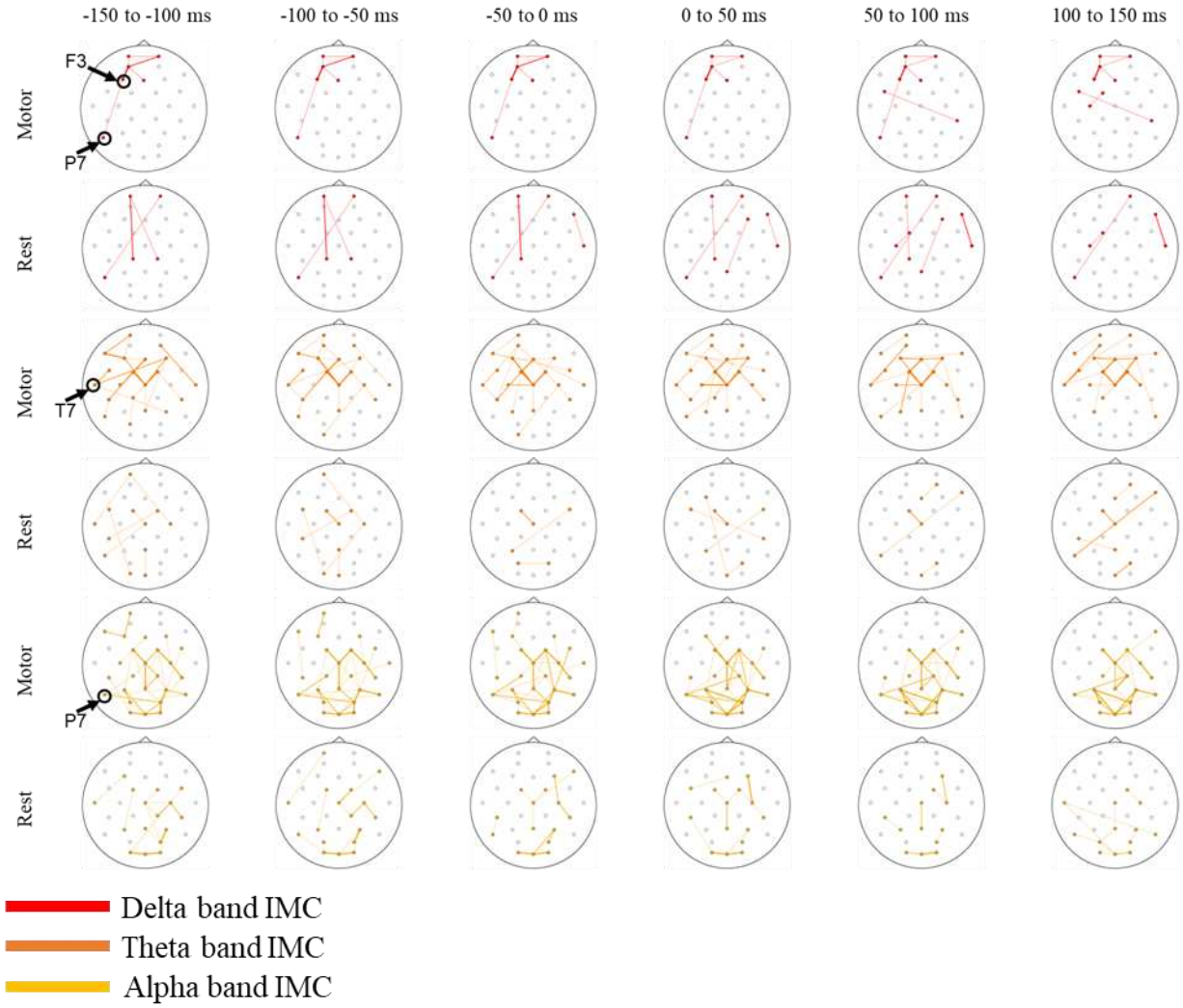

Figure 2.5. Band-channel pair maps in 50 ms bins for standardized IMC at a threshold of ±0.6, withing the critical time-frequency window delta-alpha at -150 to 150 ms comparing the motor and rest conditions. Sites within notable channel pairs are indicated.

Table 2.3. Predictors in discriminant analysis differentiating between the motor and rest conditions. Freq. Band = frequency band, Unstd = unstandardized, Weight = standardized canonical coefficients, Loading = structure matrix correlation, M = Mean, SD = standard deviation, IMC = imaginary part of coherency.

Predictors		Motor Condition IMC			Rest Condition IMC			Model Contribution	
Freq. Band	Channel Pair	Raw Score	Z Score		Raw Score	Z Score			
-150 to 150 ms		M	M	SD	M	M	SD	Weight	Loading
delta	AF3-F3	0.041	1.180	2.100	0.018	0.340	0.817	0.443	0.206
	Fp1-CP1	-0.001	-0.020	1.142	-0.039	-0.720	1.894	-0.326	0.177
theta	FC2-Cz	-0.061	-1.690	1.247	-0.032	-0.530	1.012	-1.241	-0.4
	FC1-Fz	0.044	1.230	1.427	0.011	0.220	1.292	0.465	0.292
	Oz-PO4	-0.008	-0.220	1.301	-0.041	-0.700	1.211	0.696	0.151
alpha	P4-P8	0.052	1.050	1.410	0.021	0.330	1.089	0.496	0.225
	P3-PO3	0.051	1.040	1.492	0.014	0.220	1.095	0.134	0.245
	F4-C4	-0.030	-0.660	1.463	-0.053	-0.860	2.015	0.612	0.044
	FC2-Cz	-0.046	-1.020	1.230	-0.047	-0.760	1.147	-0.361	-0.086
	F8-Cz	-0.029	-0.640	1.014	-0.045	-0.740	1.242	0.821	0.032
-350 to -100 ms									
theta	FC2-Cz	-0.052	-1.458	0.961	-0.038	-0.612	1.211	0.445	0.623
	FC1-Cz	-0.051	-1.416	1.044	-0.039	-0.618	0.950	0.745	0.644
	FC1-Fz	0.042	1.193	1.284	0.018	0.320	1.491	0.118	-0.505
	F3-Fz	0.023	0.648	1.096	0.047	0.790	0.738	0.208	0.122
alpha	P4-PO4	0.072	1.465	1.698	-0.004	0.658	1.369	-0.657	-0.421
	Pz-Cz	0.054	1.098	2.039	0.008	0.599	1.383	-0.071	-0.231
	FC2-Cz	-0.044	-0.969	1.341	-0.038	-0.921	1.286	-0.02	0.029
	C4-CP6	-0.045	-0.978	1.870	-0.020	-0.829	1.753	0.858	0.066
	FC2-C4	-0.043	-0.935	1.631	-0.010	-0.728	1.521	-0.656	0.106
	Cz-C4	-0.030	-0.660	0.992	-0.003	-0.708	1.148	0.075	-0.036
-300 to 0 ms									
beta	F3-Fp2	-0.030	-1.179	2.305	-0.012	-0.335	1.470	1.184	0.245
	P7-O1	0.029	1.071	1.675	0.017	0.435	0.577	-0.309	-0.285
	P8-O2	0.022	0.822	1.205	0.017	0.450	0.886	-0.592	-0.198
	Fp1-Oz	0.005	0.182	0.720	0.028	0.730	1.450	0.572	0.269
	AF3-F3	0.020	0.735	2.769	0.027	0.726	1.890	-0.232	0.044
	F3-CP5	-0.014	-0.558	1.949	-0.025	-0.695	1.445	-0.694	-0.045
gamma	AF4-F8	0.028	0.844	1.006	0.010	0.283	1.068	-0.637	-0.304
	AF3-F7	0.028	0.836	1.279	0.016	0.456	1.338	-0.328	-0.163
	AF3-F3	0.017	0.533	2.623	0.027	0.750	2.929	0.462	-0.002
	F8-C4	0.018	0.536	2.014	0.025	0.685	1.572	1.104	0.046

The critical time-frequency window theta and alpha at -350 to -100 ms was selected as it showed short-distance IMC connectivity at left prefrontal sites in both theta and alpha and long-distance connectivity for theta in the motor condition. The rest condition had 19 band-channel pairs which met threshold and the motor condition had 64 pairs which met threshold. There were 2 overlapping pairs (alpha at Oz-O2 and O1-Oz). The top 5 unique channel pairs for the rest

condition included theta IMC at F3-Fz and alpha IMC at FC2-Cz, C4-CP6, FC2-C4, Cz-C4. The top 5 unique band-channel pairs for the motor condition included theta IMC at FC2-Cz, FC1-Cz, and FC1-Fz and alpha IMC at P4-PO4 and Pz-Cz. A Box's M of 109.18 was significant (F = 1.39, p = .032), violating the assumption of equality of covariance matrices. The discriminant analysis model explained 28.94% of the variance between the conditions (Wilks' Lambda = 0.71, χ^2 (10) = 10.60, p = .39), which not significant. The group classification showed that 78.9% of the original cases were correctly classified overall and 52.6% were correctly classified after cross-validation.

The critical time-frequency window beta and gamma at -300 to 0 ms was selected as it showed the strongest IMC and highest number of channel pairs at threshold for higher frequency bands. The the rest condition had 17 band-channel pairs which met threshold and the motor condition had 38 pairs which met threshold. There were 6 overlapping pairs (beta at Oz-O2, O1-Oz, FC5-P7, and AF3-FC1 and gamma at Fp1-F7 and F3-CP5). The top 5 unique channel pairs for the rest condition included beta IMC at Fp1-Oz, AF3-F3, and F3-CP5 and gamma IMC at AF3-F3 and F8-C4. The top 5 unique band-channel pairs for the motor condition included beta IMC at F3-Fp2, P7-O1, and P8-O2 and gamma IMC at AF4-F8 and AF3-F7. A Box's M of 109.82 was significant (F = 1.39, p = .03), violating the assumption of equality of covariance matrices. The discriminant analysis model explained 45.56% of the variance between the conditions (Wilks Lambda = 0.55, χ^2 (10) = 17.23, p = .042), which was not significant at Bonferroni-corrected alpha of .017. The group classification showed that 71.1% of the original cases were correctly classified overall and 65.8% were correctly classified after cross-validation.

Overall, the critical time-frequency window of delta, theta, and alpha at -150 to 150 ms was able to discriminate between the motor and rest condition, with frontal delta and theta IMC

and parietal alpha IMC characterizing the motor condition and occipical-parietal theta and frontal alpha characterizing the rest condition. While there were some visual differences for theta and alpha at -350 to -100 ms and beta and gamma at -300 to 0 ms, the discriminant analyses were not significant. Band-channel pair maps of the standardized IMC averaged within each critical time-frequency window and the location of band-channel pair predictors to discriminate between the motor and rest conditions are shown in Figure 2.6.

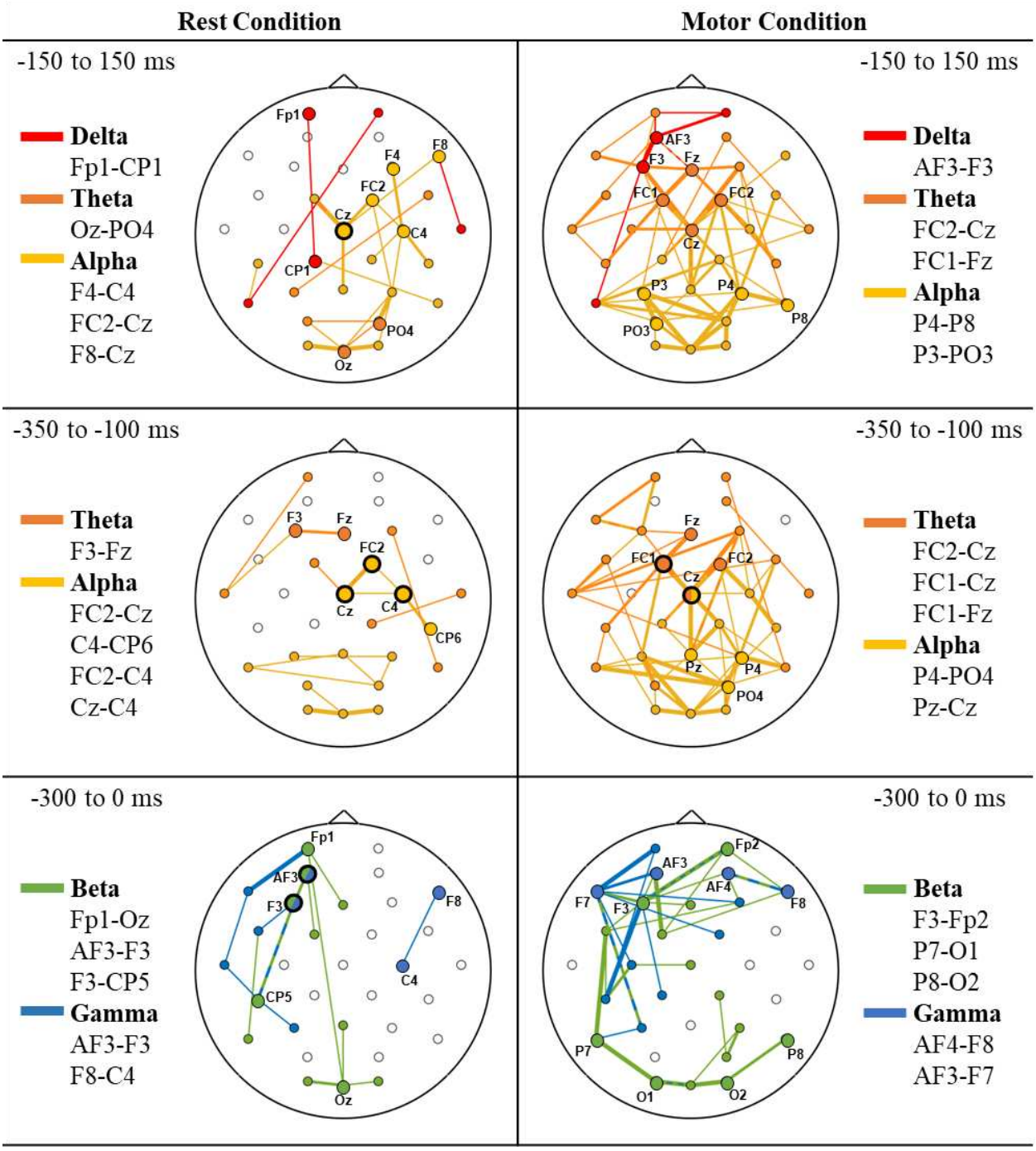

Figure 2.6. Band-channel pair maps comparing the motor and rest conditions withing the auditory group for standardized IMC at a threshold of ± 0.6 averaged within four critical time-frequency windows: 1) delta, theta, and alpha band IMC at -150 to 150 ms 2) theta and alpha band IMC at -350 to -100 ms, and 3) beta and gamma band IMC at -300 ms to 0 ms. For each critical time-frequency window, the top 5 unique channel pairs for each condition (those included in the discriminant analysis) are listed, with the corresponding sites labeled in the band-channel pair map. Color indicates the frequency band (red = delta, orange = theta, yellow = alpha, green = beta, and blue = gamma). Thicker lines indicate greater standardized IMC values.

Auditory Condition versus Motor Condition

Based on visual inspection of the band-channel pair maps comparing the auditory condition minus rest condition to the motor condition minus rest condition between groups, three critical time-frequency windows were selected: (1) delta and theta band from -200 to 100 ms, (2) alpha, beta, gamma from -200 to 0 ms, and (3) alpha, beta, and gamma from 0 to 200 ms. Discriminant analyses revealed that out of the three critical time-frequency windows, delta and theta band from -200 to 100 ms and alpha, beta, gamma from -200 to 0 ms were able to differentiate between the auditory and motor conditions.

The critical time-frequency window delta and theta from -200 to 100 ms was selected as it showed the strongest IMC in the slower frequency bands (delta and theta) in both the auditory and motor conditions, with distinctly different connectivity patterns between conditions. For the auditory condition, the delta IMC for the auditory condition was right-lateralized with the strongest IMC at AF4-CP6. For the motor condition, the strongest delta IMC were left-localized and included connections branching from AF3 to frontal sites as well as the pair F3-P7. There was stronger IMC overall in the motor condition compared to the auditory condition (see Figure 2.7). For the auditory condition, there were a total of 18 band-channel pairs at a threshold of ± 0.6 standardized IMC. Of these, 4 (22.22%) had a standardized IMC of ± 0.6 in the rest condition, which were removed. The top 5 band-channel pairs in the auditory condition included delta IMC at AF4-CP6 and Fp2-FC2 and theta IMC at AF3-T8, O1-O2, and CP6-CP2. Of these, delta at AF4-CP6 was the most discriminating (see Table 2.4). For the motor condition, there were a total of 31 band-channel pairs at a threshold of ± 0.6 standardized IMC. Of these, 1 (3.23%) had a standardized IMC of ± 0.6 in the rest condition, which was removed. The top 5 band-channel pairs in the motor condition included delta IMC at AF3-F3 and theta IMC at FC2-

Cz, FC1-Fz, F3-Cz, and F4-Cz. Of these, delta at AF3-F3 and theta at FC2-Cz and F4-Cz were the most discriminating (see Table 2.4). A Box's M of 140.55 was significant (F = 1.44, p = .012), violating the assumption of equality of covariance matrices. However, discriminant analysis is robust against violations of the homogeneity of variances assumption. The discriminant analysis model explained 55.35% of the variance between the conditions (Wilks' Lambda = 0.45, χ^2 (11) = 25.38, p = .008), which was significant. The group classification showed that 87.2% of the original cases were correctly classified overall and 76.9% were correctly classified after cross-validation. Overall, what was most discriminating for this window was right fronto-central delta connectivity in the auditory condition and left frontal delta and left fronto-central theta connectivity in the motor condition. Music expertise also discriminated between conditions. Descriptive statistics, the discriminant function coefficients, and structure matrix correlations for each predictor are listed in Table 2.4.

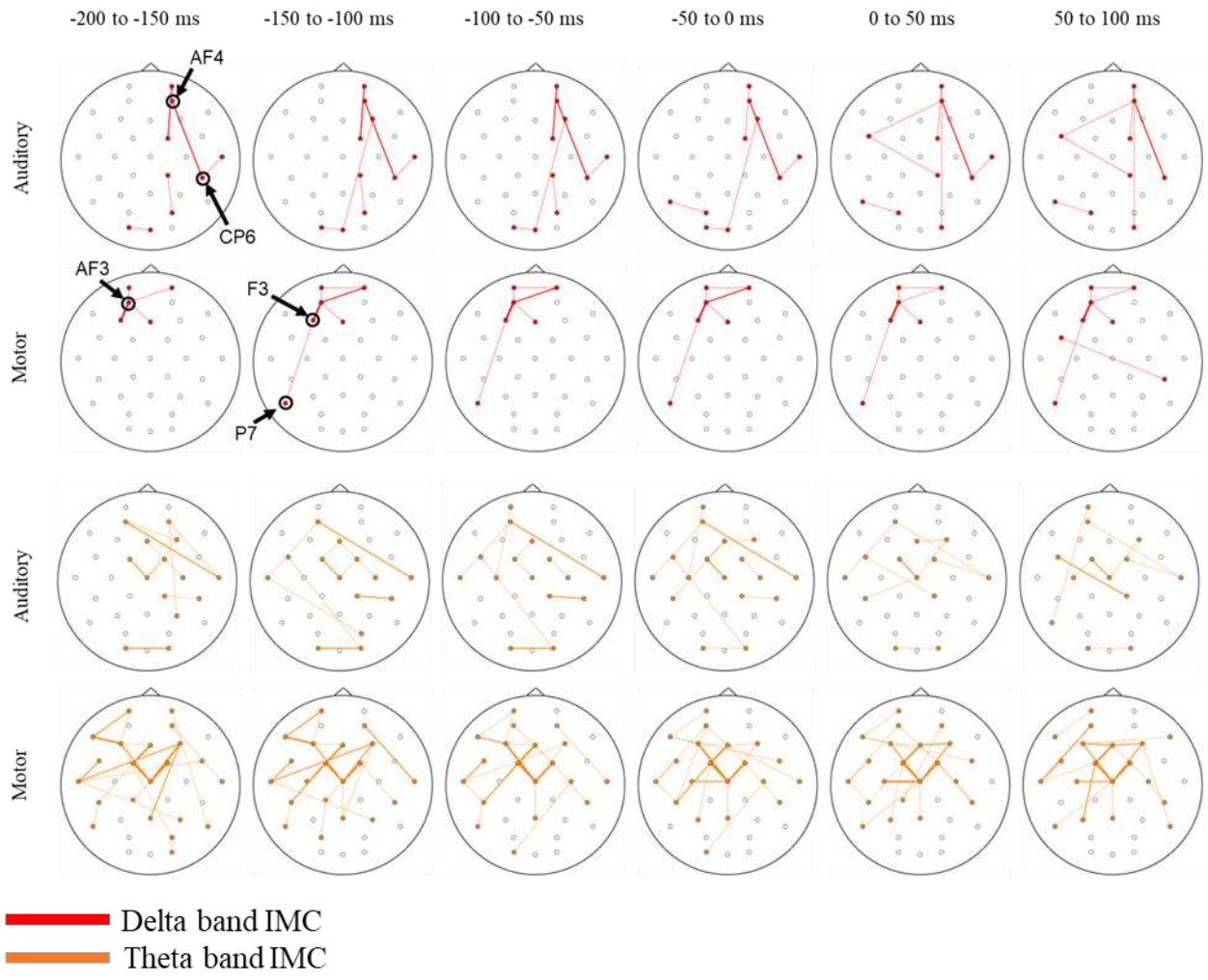

Figure 2.7. Band-channel pair maps in 50 ms bins for standardized IMC at a threshold of ±0.6, withing the critical time-frequency window delta-theta at -200 to 100 ms comparing the auditory and motor conditions. Sites within notable channel pairs are indicated.

Table 2.4. Predictors in discriminant analysis differentiating between the auditory and motor conditions. Freq. Band = frequency band, Unstd = unstandardized, Weight = standardized canonical coefficients, Loading = structure matrix correlation, M = Mean, SD = standard deviation, IMC = imaginary part of coherency.

Predictors		Auditory Condition IMC			Motor Condition IMC			Model Contribution	
Freq. Band	Channel Pair	Raw Score	Z Score		Raw Score	Z Score			
-200 to 100 ms		M	M	SD	M	M	SD	Weight	Loading
delta	AF4-CP6	.025	0.851	1.046	0.005	0.148	0.559	.470	.384
	Fp2-FC2	.022	0.735	1.399	-0.004	-0.101	1.233	.040	.292
	AF3-F3	-.001	-0.036	0.817	0.040	1.177	2.106	-.569	-.354
theta	AF3-T8	.035	0.916	1.552	0.013	0.378	0.920	.018	.193
	O1-O2	.033	0.863	1.878	0.001	0.034	1.110	.084	.246
	CP6-CP2	.030	0.789	1.283	0.002	0.049	0.982	-.008	.297
	FC2-Cz	-.024	-0.646	1.209	-0.060	-1.669	1.178	.727	.395
	FC1-Fz	.025	0.669	0.969	0.044	1.236	1.360	-.086	-.222
	F3-Cz	-.013	-0.340	0.663	-0.035	-0.972	1.253	.212	.293
	F4-Cz	-.026	-0.694	0.892	-0.033	-0.920	0.838	-.461	.120
music experience		2.750		0.851	2.000		1.000	.727	.373
-200 to 0 ms									
alpha	Cz-P8	-.055	-1.025	1.565	-.005	-0.143	0.886	-.459	-.338
	PO4-O2	.022	0.373	2.311	.055	1.074	2.150	.426	-.154
	FC2-C4	-.045	-0.841	1.683	-.048	-1.000	1.624	-.316	.047
	P4-P8	.022	0.371	1.195	.050	0.970	1.448	-.613	-.222
beta	F3-F7	-.027	-0.978	1.267	-.019	-0.687	2.138	.411	-.082
	F4-FC6	.026	0.905	1.546	-.004	-0.177	0.663	.469	.442
	F3-Fp2	-.023	-0.836	1.577	-.034	-1.221	2.070	-.089	.103
	P7-O1	-.004	-0.164	1.123	.029	0.989	1.646	-.637	-.404
gamma	Fp2-AF4	-.025	-0.921	2.602	-.011	-0.318	1.469	-.147	-.139
	F7-T7	.025	0.904	1.719	-.007	-0.200	1.537	.530	.332
music experience		2.750		0.851	2.000		1.000	.432	.397
0 to 200 ms									
alpha	O1-PO4	.052	0.965	1.598	-.010	-0.237	1.763	-.090	-.414
	P3-PO4	.035	0.650	1.132	.064	1.276	1.520	.213	.272
	Oz-P4	.023	0.423	1.170	.061	1.218	1.458	.336	.349
	P3-PO3	.027	0.485	1.286	.057	1.124	1.419	-.004	.274
	P3-Oz	-.014	-0.269	1.604	-.051	-1.072	1.416	.009	-.307
beta	F8-T8	.027	0.941	1.521	-.001	-0.075	0.882	-.394	-.470
	Fz-F8	-.025	-0.941	1.563	.003	0.092	0.682	.372	.492
	P7-O1	.019	0.663	0.829	.035	1.247	1.350	.301	.304
gamma	FC5-T7	-.025	-0.923	2.649	.007	0.204	3.469	.111	.212
	F4-F8	-.024	-0.898	2.186	.004	0.126	2.846	.027	.235
music experience		2.750		0.851	2.000		1.000	-.645	-.469

The critical time-frequency window alpha, beta, gamma at -200 to 0 ms was selected as it included observable differences in IMC patterns for faster frequency bands (alpha, beta, and gamma) leading up to event. For alpha, the motor condition had more channel pairs including frontal sites. For beta, the auditory condition included mostly short-range connections including frontal and temporal sites while the motor condition had channel pairs spanning frontal, central, parietal, and occipital sites. For gamma, the auditory condition had more short-range fronto-temporal pairs while the motor condition primarily included pairs branching from left frontal sites to right frontal sites or left parietal sites (see Figure 2.8). For the auditory condition, there were a total of 71 band-channel pairs at a threshold of ± 0.6 standardized IMC. Of these, 32 (45.07%) had a standardized IMC of ± 0.6 in the rest condition, which were removed. The top 5 band-channel pairs in the auditory condition included alpha at Cz-P8, and FC2-C4, beta at F3-F7, F4-FC6, and gamma at Fp2-AF4 and F7-T7. Of these, alpha at Cz-P8, beta at F4-FC6, and gamma at F7-T7 were the most discriminating (see Table 2.4). For the motor condition, there were a total of 72 band-channel pairs at a threshold of ± 0.6 standardized IMC. Of these, 16 (22.22%) had a standardized IMC of ± 0.6 in the rest condition, which were removed. The top 5 band-channel pairs for the motor condition included alpha at PO4-O2, FC2-C4, and P4-P8 and beta at F3-Fp2 and P7-O1. Of these, alpha at P4-P8 and beta at P7-O1 were the most discriminating (see Table 2.4). A Box's M of 133.56 was significant, $F(66,4339.45) = 1.37$, $p = .026$), violating the assumption of equality of covariance matrices. The discriminant analysis model explained 52.27% of the variance between the conditions (Wilks' Lambda = 0.48, $\chi^2(11) = 23.30$, $p = .016$), which was significant. The group classification showed that 84.6% of the original cases were correctly classified overall and 74.4% were correctly classified after cross-validation. Overall, what was most discriminating for this window was central-to-parietal alpha

and frontal and temporal beta and gamma connectivity in the auditory condition and parietal and occipital alpha and beta connectivity in the motor condition.

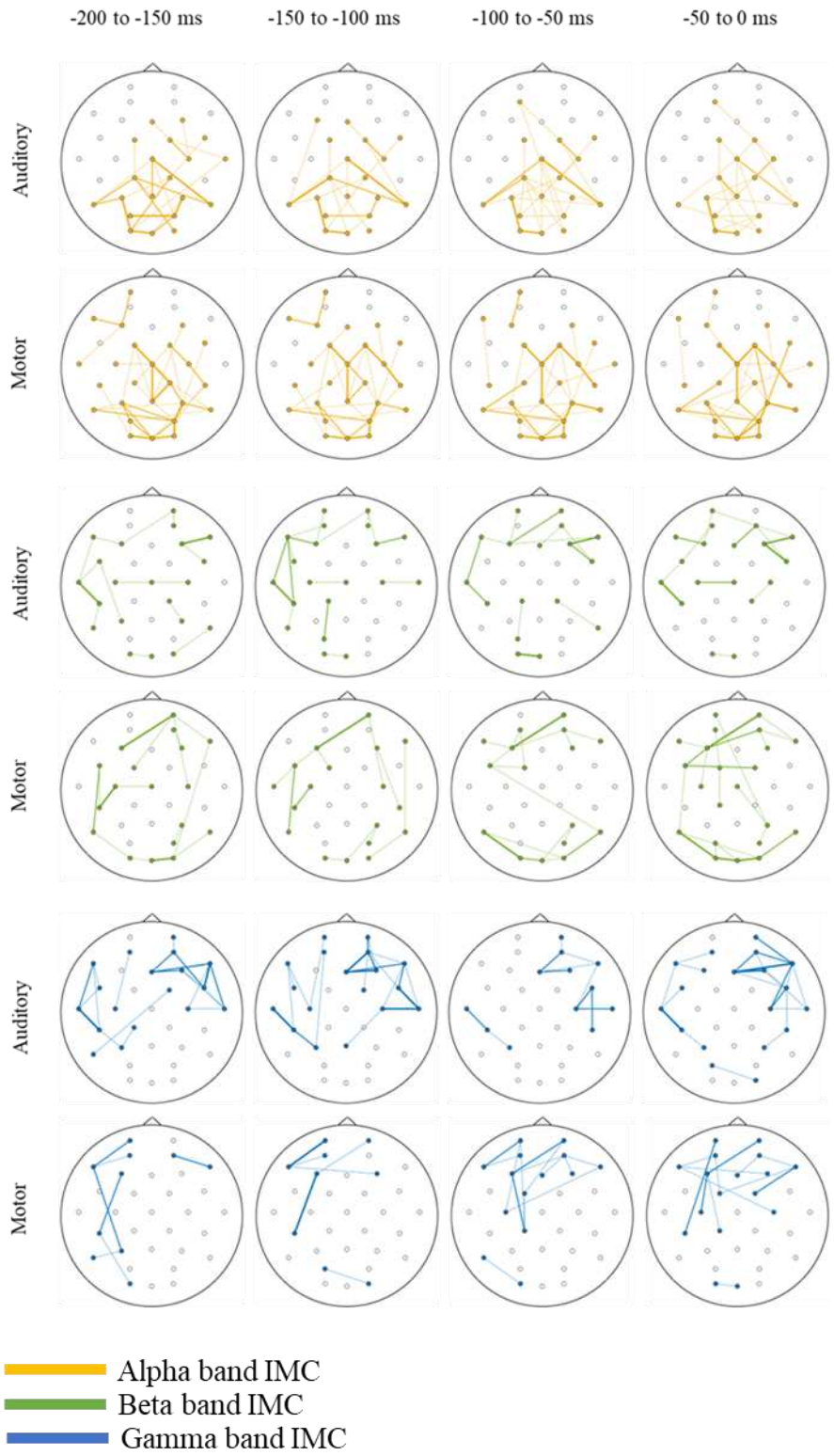

Figure 2.8. Band-channel pair maps in 50 ms bins for standardized IMC at a threshold of ±0.6, withing the critical time-frequency window alpha, beta, gamma at -200 to 0 ms comparing the auditory and motor conditions. Sites within notable channel pairs are indicated.

The critical time-frequency window alpha, beta, gamma at 0 to 200 ms was selected as it included observable differences in patterns of connectivity in faster frequency bands (alpha, beta, and gamma) following the event. For the auditory condition, there were a total of 75 band-channel pairs at a threshold of ± 0.6 standardized IMC. Of these, 32 (42.67%) had a standardized IMC of ± 0.6 in the rest condition, which were removed. The top 5 band-channel pairs in the auditory condition included alpha at O1-PO4, beta at F8-T8 and Fz-F8, and gamma at FC5-T7 and F4-F8. For the motor condition, there were a total of 57 band-channel pairs at a threshold of ± 0.6 standardized IMC. Of these, 16 (28.07%) had a standardized IMC of ± 0.6 in the rest condition, which were removed. The top 5 band-channel pairs in the motor condition included alpha at P3-PO4, Oz-P4, P3-PO3, and P3-Oz and beta at P7-O1. A Box's M of 109.77 was not significant, $F(66,4339.45) = 1.12$, $p = .231$, meeting the assumption of equality of covariance matrices. The discriminant analysis model explained 43.96% of the variance between the conditions (Wilks' Lambda = .56, $\chi^2(11) = 18.26$, $p = .076$), which was not significant. The group classification showed that 87.2% of the original cases were correctly classified overall and 61.5% were correctly classified after cross-validation.

For comparisons between the auditory and motor conditions, critical time-frequency windows of delta and theta band IMC at -200 to 100 ms and alpha, beta, and gamma band IMC at -200 ms to 0 ms, were able to discriminate between the auditory and motor conditions. The auditory condition was characterized by right fronto-central delta, central-to-parietal alpha, and fronto-temporal beta and gamma IMC. The motor condition was characterized by left frontal delta, fronto-central theta, and parieto-occipital alpha and beta IMC. While there were some visual differences in alpha, beta, and gamma band IMC at 0 to 200 ms, the discriminant analysis was not significant. Band-channel pair maps of the standardized IMC averaged within each

critical time-frequency window (with a standardized IMC of less than ±0.6 in the rest condition) and the location of band-channel pair predictors to discriminate between the auditory and motor conditions are shown in Figure 2.9.

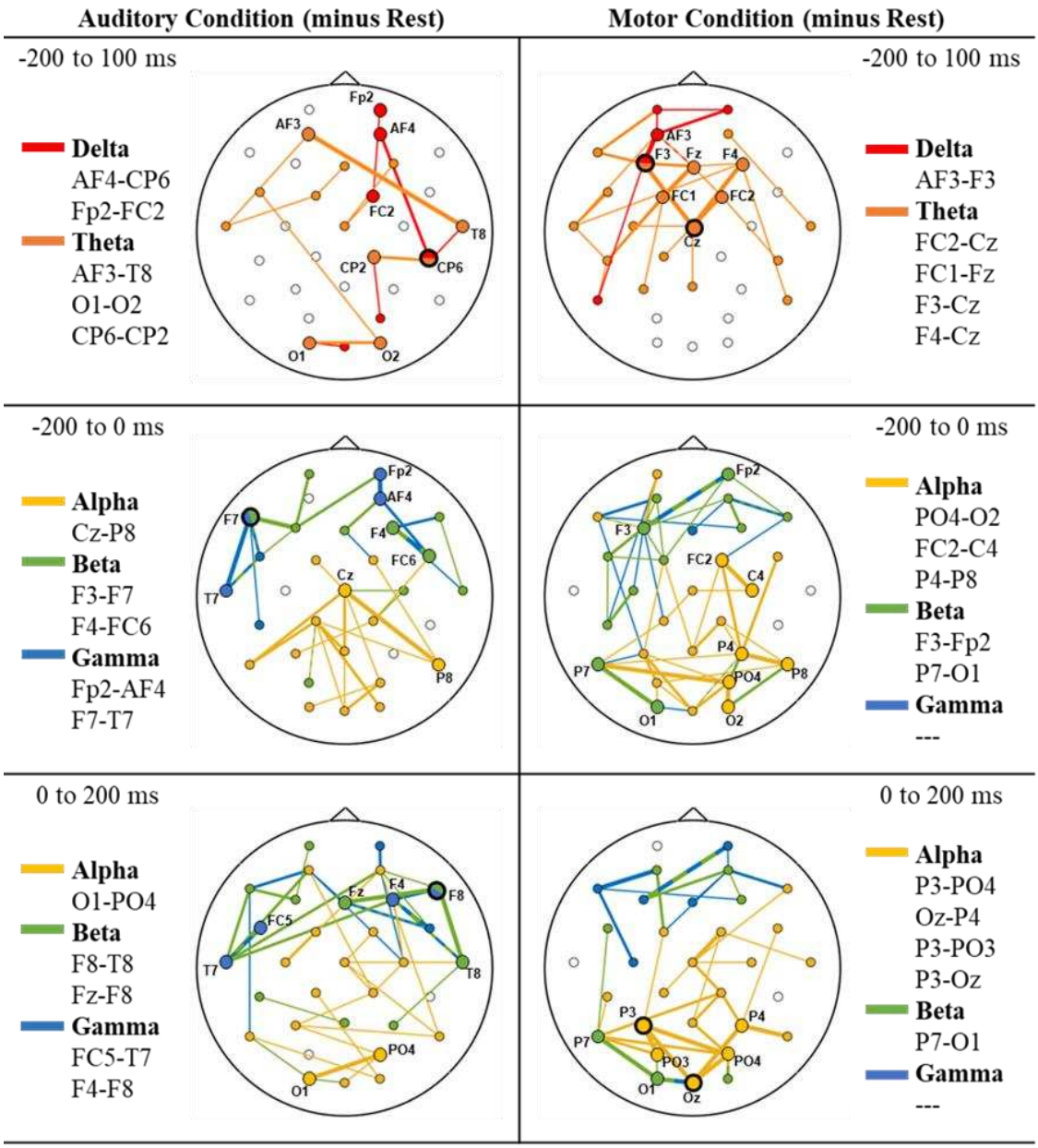

Figure 2.9. Band-channel pair maps comparing the auditory and motor conditions withing the auditory group for standardized IMC at a threshold of ± 0.6 averaged within four critical time-frequency windows: 1) delta and theta band IMC at -200 to 100 ms 2) alpha, beta, and gamma band IMC at -200 ms to 0 ms, and 3) alpha, beta, and gamma band IMC at 0 to 200 ms. For each critical time-frequency window, the top 5 unique channel pairs for each condition (those included in the discriminant analysis) are listed, with the corresponding sites labeled in the band-channel pair map. Color indicates the frequency band (red = delta, orange = theta, yellow = alpha, green = beta, and blue = gamma). Thicker lines indicate greater standardized IMC values.

Discussion

This exploratory study examined a previously existing EEG dataset collected with two groups who participated in one of two task conditions: a passive rhythmic auditory task (auditory condition) or a self-paced rhythmic motor task (motor condition). The first research question was aimed examining how functional connectivity during each task condition differed from a rest condition. The second research question involved comparing the auditory and motor conditions. Overall, results showed hypotheses about qualitative differences were partly supported by band-channel pair map comparisons. Quantitative differences, as hypothesized, were able to discriminate between conditions in at least one critical time-frequency window.

Qualitative and Quantitative Differences between Task and Rest Conditions

The first research question involved examining qualitative and quantitative differences between the auditory and rest conditions and between the motor and rest condition within each group. Hypothesis 1a, *the auditory condition will show more localized connectivity at higher frequencies (beta and gamma) following the stimulus compared to the rest condition,* was partly supported in that more channel pairs showed stronger standardized IMC in the beta band. However, it was slower frequencies, especially theta and alpha, which were most distinct from the rest condition. Further, the auditory condition was mostly defined by both short-distance (localized) and long-distance band-channel pairs. Hypothesis 1b, *the motor condition will show more long-range connectivity at lower frequencies (delta, theta, and alpha) following the stimulus compared to the rest condition.*, was partly supported by the qualitative findings of this study. However, the motor condition had greater long-distance and short-distance IMC in all frequency bands compared to rest. Finally, Hypothesis 1c, that inter-site coherence would *discriminate between a) the auditory condition and the rest condition and b) the motor condition*

and the rest condition, was supported by the results of the discriminant analyses for lower frequency bands (delta, theta, and alpha).

Functional Connectivity During a Passive Listening to Rhythmic Auditory Tones. When comparing the auditory and rest conditions, four critical time-frequency windows were identified which appeared qualitatively different between conditions. Of these, IMC for theta-alpha from 250 to 500 ms was both qualitatively and quantitatively different in the auditory condition compared to the rest condition, suggesting this window represented task-specific functional connectivity. Previous research has found theta and alpha oscillations to play a role in predicting auditory events and auditory gating (Kayser et al., 2015). Therefore, the alpha and theta band connectivity observed from 250 to 500 ms following the tones may represent endogenous processes related to temporal prediction. Theta IMC from 250 to 500 ms in the auditory condition was strongest in central, frontal, and temporal sites. Thus, theta connectivity may represent communication between auditory cortices (located under temporal sites) and motor brain regions (located under central and frontal sites), which has been observed during passive listening to auditory rhythm (Morillon & Baillet, 2017). One theory to explain the coupling of auditory and motor regions is that the brain uses auditory cues in the environment for motor planning. In this model, auditory beats serve as temporal markers for the movement trajectory (for review, see Zatorre et al., 2007). Theta is also associated with the perception of rhythmic patterns in speech (Haegens & Zion Golumbic, 2018), which may correspond to a proposed dorsal stream for processing speech as articulatory and motor-based representations (Hickok & Poeppel, 2004). This dorsal pathway has also been linked to spatial processing and sensorimotor integration in auditory processing (Rauschecker, 2011) and the general transformation of auditory information to motor representations (Warren et al., 2005).

Alpha band activity has also been linked to sensorimotor processing during auditory-paced finger tapping paradigms (Pollok, Gross, et al., 2005; Pollok, Südmeyer, et al., 2005). Alpha IMC from 250 to 500 ms between parietal and occipital sites in the current study suggests that passive listening to auditory rhythm may activate sensorimotor integration networks for motor planning, even in the absence of movement. However, alpha IMC which was most discriminating was stronger in the rest condition. Alpha is known to be more active when individuals are relaxed and in the absence of active cognitive processes (Stern et al., 2001). Alpha has also been associated with the Default Mode Network (DMN) (Knyazev et al., 2011), which is active during introspective thought and tends to be less active during cognitive tasks (Shulman et al., 1997). Further, frontal theta, which was stronger in the auditory condition, has been found to decrease with increase DMN activation (Scheeringa et al., 2008). Therefore, the discriminating alpha band connectivity may represent increased activation of the DMN and decreased DMN activation during the auditory condition.

In this sample, the discriminant analysis for delta and theta oscillations from -200 to 100 ms was not distinguishable from the rest condition. However, the phase of endogenous delta and theta oscillations in the auditory cortex have been shown to align with auditory stimuli (Kayser et al., 2015; Riecke et al., 2015). Further research is needed to determine how the synchronization of low-frequency brain oscillations to auditory rhythms affects brain connectivity. The critical time-frequency windows for high frequency bands, alpha and beta IMC from 50 to 250 ms and beta and gamma IMC from -200 to 200 ms, were also not distinguishable between the auditory and rest conditions in this study. Previous studies have linked beta and gamma evoked and induced power to processing rhythmic auditory stimuli (Fujioka et al., 2009, 2012; Snyder & Large, 2005). However, higher frequency bands also tend to be prominent at

rest. For example, Pfurtscheller & Lopes da Silva (1999) demonstrated a high coherence of alpha band activity between C3-Cz at rest. Beta activity is also positively correlated with increased activity in brain regions which form the DMN (Hlinka et al., 2010). Therefore, the overall lack of distinguishing connectivity between the auditory and rest condition for alpha, beta, and gamma support that the auditory task was passive.

Functional Connectivity During a Self-Paced Rhythmic Motor Task. When comparing the motor and rest conditions, three critical time-frequency windows were identified which appeared qualitatively different between conditions. Of these, delta, theta, and alpha from -150 to 150 ms was able to distinguish between the motor and rest conditions. Delta activity in central brain areas contralateral to the moving hand has been associated with repetitive finger movements (Paek et al., 2014), which was also observed in this study using IMC, but mostly at frontal sites. Alpha power tends to decrease before movement and increase after movement (Hari & Salmelin, 1997; Pfurtscheller & Lopes da Silva, 1999). In the current study, increased alpha IMC at the back of the head following the tap may correspond to this alpha power synchronization. Together, delta and alpha connectivity from -150 to 150 ms in this sample may correspond to networks coordinating the timing and spatial organization of movement, which is characterized by connections between the parietal cortex and prefrontal cortex, premotor cortex, and the medial temporal lobe (Kravitz et al., 2011).

Delta and alpha band activity have also been associated with interactions between left and right regions of the dorsal attention network (DAN) (Marzetti et al., 2013), which is the most prominent “task positive” network, thought to represent top-down and goal-directed cognitive processing. The DAN includes gyri adjacent in intraparietal sulcus, cortex near the middle temporal cortex, and both frontal and secondary eye fields (Seitzman et al., 2019). However,

increased global field power of alpha (10–12 Hz) has also been shown to negatively correlate with the DAN and positively correlate with increased activity in a cingulo-insular-thalamic network associated with tonic alertness (Sadaghiani et al., 2010). Additionally, theta oscillations in frontomedial regions have been linked to attention monitoring (Clayton et al., 2015). Therefore, frontal delta and theta and parietal alpha connectivity in the -150 to 150 ms window during the motor task could be driven by cognitive processes necessary to sustain attention and monitor performance during a self-directed task. As in the auditory group, frontal alpha was characteristic of the rest condition in the motor group as well, which may represent activation of the DMN (Knyazev et al., 2011). Additionally, theta and alpha band connectivity from -350 to -100 ms prior to the tap was not distinguishable from rest, suggesting motor processes were most task-relevant immediately before and after the motor response, rather than throughout the task.

In motor tasks such as tapping, beta band activity typical decreases before movement and increases after movement (Hari & Salmelin 1997; Pfurtscheller & Lopes da Silva, 1999). This pattern was not observed for beta IMC in this sample. Beta-band activity is also correlated with a blood oxygen level-dependent signal in somato-motor areas (Hipp & Siegel, 2015; van Ede & Maris, 2013), but beta IMC was relatively low compared to other frequency bands during the motor condition in this study. Gamma activity tends to spike before movement onset and have high coherence between C3-Cz during movement (Pfurtscheller & Lopes da Silva, 1999). This could be seen, in part, as increased fronto-central gamma connectivity from -50 to 0 ms (see Appendix C). However, beta and gamma IMC from -300 to 0 ms during the motor condition was not distinguishable from rest in this sample. Therefore, more research is needed to clarify the role of high-frequency connectivity during self-paced rhythmic motor performance.

Differences in Functional Connectivity between Rhythmic Auditory and Motor Processes

The second research question involved examining qualitative and quantitative differences between the auditory and motor conditions. Hypothesis 2a, *the auditory condition will show more localized connectivity at higher frequencies (beta and gamma) compared to the motor condition.*, was largely supported by stronger beta and gamma in the auditory condition at short-distance fronto-temporal sites, especially from -200 to 0 ms). However, from 200 to 0 ms the auditory condition had more long-distance beta connectivity compared to the motor condition. In line with the hypothesis, the auditory condition also had greater beta and gamma IMC overall compared to the motor condition which had greater alpha IMC. Hypothesis 2b, *the motor condition will show more long-range connectivity at lower frequencies (delta, theta, and alpha) compared to the auditory condition*, was partly supported in that the motor condition had more long-distance theta IMC pairs at threshold from -200 to 100 ms compared to the auditory condition. However, there was not a noticeable difference in the number or distance of band-channel pairs for delta or alpha IMC between the auditory and motor conditions. Hypothesis 2c, that inter-site coherence would *discriminate between the auditory condition and the motor condition*, was supported by significant discriminant analysis results for two out of the three critical time-frequency windows.

Crasta et al. (2018) found that evoked power and phase locking factor measured at site C3 for 4-20 Hz (theta, alpha, and low beta) 60-250 ms, representing sensorimotor processes, was significantly greater in the auditory condition compared to the motor condition. The current study found that delta and theta IMC from -200 to 100 ms was able to distinguish between the auditory and motor condition, but with more central theta connectivity in the motor condition. Therefore, the finding in Crasta et al. (2018) of increased neural resources during the auditory

condition may not represent increased connectivity. Crasta et al. (2018) also found that evoked power and phase locking factor measured at site C3 for 20-45 Hz (high beta and low gamma) from 10-60 ms, representing motor processing, was significantly lower during the auditory condition compared to the motor condition. Instead, this study found that alpha, beta, and gamma connectivity from 0 to 200 ms was not distinguishable between the auditory and motor conditions. Crasta et al. (2018) also found that total power from 1–16 Hz (low beta) from 50–150 ms, representing anticipation and predictive timing, was not significantly different between the auditory and motor conditions. This is consistent with the finding in this study of no distinguishable connectivity for beta and gamma from 0 to 200 ms between the auditory and motor conditions. However, in the current study, alpha, beta, and gamma from -200 to 0 ms was able to distinguish between the auditory and motor conditions. Therefore, the auditory and motor condition may have distinct anticipatory processes, but may share some networks for post-event processing, possibly related to motor processing, as the processing of rhythmic auditory stimuli is known to activate motor networks (for review, see Zatorre et al., 2007). Additionally, participants in the motor group may have received auditory feedback from the button press, activating auditory brain regions.

Differences in functional connectivity between the auditory and motor conditions may be related, in part, to differences in attentional requirements. Clayton et al. (2015) have proposed four primary mechanisms by which brain oscillations promote sustained attention: 1) theta (4–8 Hz) in frontomedial regions, i.e., the posterior medial frontal cortex (pMFC) for monitoring and control of attention, 2) low-frequency (< 14 Hz) phase synchronization for long-range communication between brain regions which 3) promotes gamma oscillations in task-relevant areas for the excitation of cognitive processing and 4) promotes alpha oscillations in task-

irrelevant areas for the inhibition of cognitive processing (Clayton et al., 2015). When positioning the results within Clayton et al.'s (2015) model for sustained attention, the critical time-frequency window for delta and theta band IMC -200 to 100 ms around the event (tone or tap) may represent the differences in performance monitoring during the auditory and motor conditions.

In the auditory condition, delta and theta band IMC between frontal and temporal sites could represent communication between functionally distinct neural sources, such as between auditory brain regions and premotor and prefrontal brain regions (Morillon & Baillet, 2017). There was also greater fronto-temporal beta and gamma IMC in the auditory condition compared to the motor condition, possibly representing a more consistent pattern of connectivity required for the excitation of task-relevant (e.g., auditory and motor) brain regions during the auditory task. In the motor condition, theta was localized over frontomedial sites, which could represent increased performance monitoring in the motor condition compared to the auditory condition. More channel pairs with strong theta IMC between frontal and parietal sites in the motor condition could represent increased overall connectivity required to maintain long-range communication between brain regions. Greater right-localized parieto-occipital alpha IMC in the motor condition also suggests the motor condition may have required more suppression of task irrelevant brain regions than the auditory condition.

Overall, the auditory task may be characterized by greater gamma excitation in task-relevant brain regions and by functional connectivity between functionally distinct, underlying sources, e.g., between auditory and premotor regions. The motor task may be characterized more by alpha suppression of task-irrelevant brain regions, facilitated by more global low-frequency connectivity between brain regions necessary to sustain attention (Clayton et al., 2015). As the

model for the beta and gamma from 0 to 200 ms after the event was not able to distinguish between the auditory and motor conditions, both conditions evoke some of the same underlying functional connectivity related to motor or auditory processes. However, more research is needed to determine distinct and shared mechanisms of rhythmic auditory and motor processes and their effect on functional connectivity.

Limitations and Future Directions

There are some potential limitations in the methodology of this study. The selection of critical time-frequency windows based on visual inspection of band-channel pair maps involved some subjectivity. Future studies using data-driven approaches such as network-based statistics (Zalesky et al., 2010) for selecting thresholds may be a next step. Additionally, functional connectivity methods, while appropriate for exploratory analyses, do not provide information about the direction of connectivity or causation. Further, the discriminant analyses included only a small portion of the total number of band-channel pairs. Future research may use measures of directed or effective connectivity methods such as Granger Causality or Dynamic Causal Modeling (Friston et al., 2013) to provide insight into underlying cognitive processes and greater complexity in the representation of networks. Source localization methods in combination with coherence measures (Hoechstetter et al., 2004; Pascual-Marqui et al., 2011) could also provide more precise information about which brain regions are involved in the patterns of connectivity observed in this study.

Due to the exploratory nature of the current study, future research is warranted to confirm findings and examine more specific research questions. Based on the findings of this study, future studies may more closely examine functional or effective connectivity with time-frequency windows selected *a priori*. The critical time windows of this study ranged from 200 to

400 ms in duration, but future studies may more closely examine changes across smaller windows of time, especially for faster frequencies. A larger sample size may also be necessary to detect more significant effects for faster frequencies. Finally, future research may use the findings from this study to better interpret connectivity during auditory-motor entrainment tasks.

Conclusion

The results of this study demonstrate that functional connectivity, as measured using EEG, is qualitatively and quantitatively different during 1) a passive auditory rhythmic task compared to a rest condition, 2) a self-paced rhythmic motor task compared to a rest condition, and 3) an auditory rhythmic task compared to a motor rhythmic task. Differences in connectivity between the task and rest conditions were especially prominent in lower frequency bands (delta and theta), as measured using the imaginary part of coherency, which may represent attentional demands of the tasks. For example, low frequency connectivity during the auditory task may represent automatic communication between auditory and motor regions, while the motor condition may require increased sustained attention and the suppression of task-irrelevant activity. Connectivity patterns for alpha, beta, and gamma showed differences between auditory and motor conditions in the anticipatory stage of processing, which may represent connections for the anticipation of auditory stimuli and the spatial organization of movement, respectively. Overall, findings from this study help lay the foundation for future studies examining immediate and lasting changes in functional connectivity as a target for rhythm-based interventions.

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Chapter 3: Study 2

Introduction

A previous study conducted by Crasta et al. (2018) found evidence of an auditory priming effect. Participants listened to auditory rhythmic stimuli prior to performing an auditory-paced rhythmic finger tapping task, i.e., a rhythmic entrainment task. These participants used fewer neural resources during rhythmic entrainment compared to those who first participated in a motor priming task. Based on these findings, Crasta et al. (2018) suggested auditory priming may be beneficial for interventions using rhythmic auditory stimulation. As the previous study had no control group (Crasta et al., 2018), the current study sought to replicate the finding of a priming effect and compare findings to a control group with no auditory priming. Additionally, the previous study used a duration of auditory priming of approximately five minutes. In clinical practice where therapists often have limited time and patients may have attention deficits, this duration of auditory priming may be impractical. Therefore, the current study included two additional groups to determine if a priming effect is still achieved, and to what degree, with shorter durations of approximately one and two minutes. Results have implications for the use of auditory rhythmic priming and rhythmic auditory stimulation in rehabilitation interventions.

Rhythmic Entrainment

Music and movement are inextricably linked. Movement in time to music often occurs spontaneously (Lesaffre et al., 2008) and is strongly tied to rhythmic patterns (Burger et al., 2014). Movement to music is one example of *entrainment*, which is the voluntary or involuntary synchronization of the brain and body to the environment (for review, see Ross & Balasubramaniam, 2014). Humans can entrain to any sensory environmental stimuli (e.g.,

auditory, visual, tactile); however, entrainment to rhythmic auditory stimuli tends to be more precise (Hove et al., 2013). Therefore, auditory *rhythmic* entrainment, entrainment to auditory rhythmic stimuli, is used in rehabilitation and music therapy interventions to improve motor function in clinical populations (Thaut et al., 1999; Thaut et al., 2015). Whole-body entrainment to music is physically and rhythmically complex (Burger et al., 2014). Therefore, researchers studying the underlying motor and neural mechanisms of rhythmic entrainment often use auditory-paced finger tapping paradigms (Repp, 2005).

In finger tapping paradigms, rhythmic entrainment is often measured behaviorally by the *period*, the length of time between the taps, and the *phase*, the time between the tap and the auditory stimulus presentation. Rhythmic entrainment typically results in a negative mean asynchrony, with the tap occurring slighting before the tone, which is well-documented in the literature (Repp, 2005). However, musicians tend to have smaller negative mean asynchronies than non-musicians (see reviews: Aschersleben, 2002; Repp & Su, 2013), Evidence from neuroimaging studies suggests rhythmic entrainment occurs through innate auditory-motor connections in the brain (Cameron & Grahn, 2016; Zatorre et al., 2007) as well as the synchronization of rhythmic electrical impulses in the brain, i.e., neural oscillations, to the external auditory rhythmic stimuli i.e., *neural* entrainment (Haegens & Zion Golumbic, 2018). However, continued research is needed to understand the relationship between the auditory-motor coupling during rhythmic entrainment and neural oscillations.

Priming

Prior exposure to rhythmic stimuli e.g., rhythmic auditory tones, may influence the efficiency of subsequent behavioral and neural performance by providing anticipatory cues (for review, see Nobre & van Ede, 2018). For example, electrophysiological recordings from monkey

auditory cortex demonstrated that neural entrainment persisted even after the rhythmic stimuli ended i.e., the timing of brain oscillation peaks coincided with when the stimuli *would* have occurred if it had continued (Lakatos et al., 2013). In humans, a similar effect has been demonstrated with the timing of high frequency (about 30 Hz) brain oscillations continuing to follow a rhythmic pattern even when tones are omitted (Fujioka et al., 2009). Further, neural entrainment may be enhanced in musicians (Celma-Miralles & Toro, 2019; Doelling & Poeppel, 2015). The effects of priming on behavioral performance have mostly been studied in the context of memory tasks, with priming improving memory task performance (Richardson-Klavehn & Bjork, 1988). Studies using fMRI to study neurological underpinnings of improvements in memory show faster and more efficient neural processing as demonstrated by a decreased hemodynamic response to primed auditory stimuli (Henson, 2003).

In rehabilitation, priming is used to augment the physical and neurological effects of therapeutic interventions and can include motor priming (Stoykov et al., 2017; Stoykov & Madhavan, 2015) and auditory priming (Janzen et al., 2019). Using time-frequency measures, Crasta et al. (2018) demonstrated a more significant priming effect, or greater reduction in the recruitment of neural resources, following a rhythmic auditory priming task compared to a rhythmic motor priming task. Time-frequency measures allow EEG researchers to extract information about the intensity and timing of specific frequencies, measured in Hertz (Hz), across time (Cohen & Grafman, 2014). Intensity is measured as power, or amplitude squared. Timing is measured by extracting phase information. Time-frequency measures in the Crasta et al. (2018) study included evoked power (power time locked to the event), total power (power regardless of the timing of the signal relative to the event; Cohen & Grafman, 2014), and phase

locking factor (PLF), which measures the consistency of brain oscillations across segments. Greater power and phase locking represent greater recruitment of neural resources.

In the Crasta et al. (2018) study, half of participants engaged in an auditory priming task, which consisted of listening to 400 presentations of rhythmic tones presented every 800 ms. The other half of participants engaged in a motor priming task, which consisted of self-paced finger tapping 400 times at a rhythmic pace of 800 ms briefly demonstrated by the experimenter. All participants then completed a rhythmic entrainment task in which participants tapped along to 400 rhythmic tones identical to those in the auditory priming task.

These researchers identified five frequency ranges within specific time windows i.e., time-frequency regions of interest (ROIs), which were compared across groups and conditions. The five ROIs included 1) evoked power and 2) PLF at 20-45 Hz 10-60 ms following the event (i.e., auditory stimulus or finger tap) representing motor processing, 3) evoked power and 4) PLF at 4-20 Hz 60-250 ms following the event representing sensorimotor processing and 5) total power at 13-16 Hz 50-150 ms following the event representing anticipation and predictive timing (see Figure 3.1). Overall, the rhythmic entrainment task following the auditory priming task elicited reduced evoked power and PLF in the ROI associated with sensorimotor processing and reduced total power in the ROI associated with anticipation and predictive timing compared to the rhythmic entrainment task following motor priming.

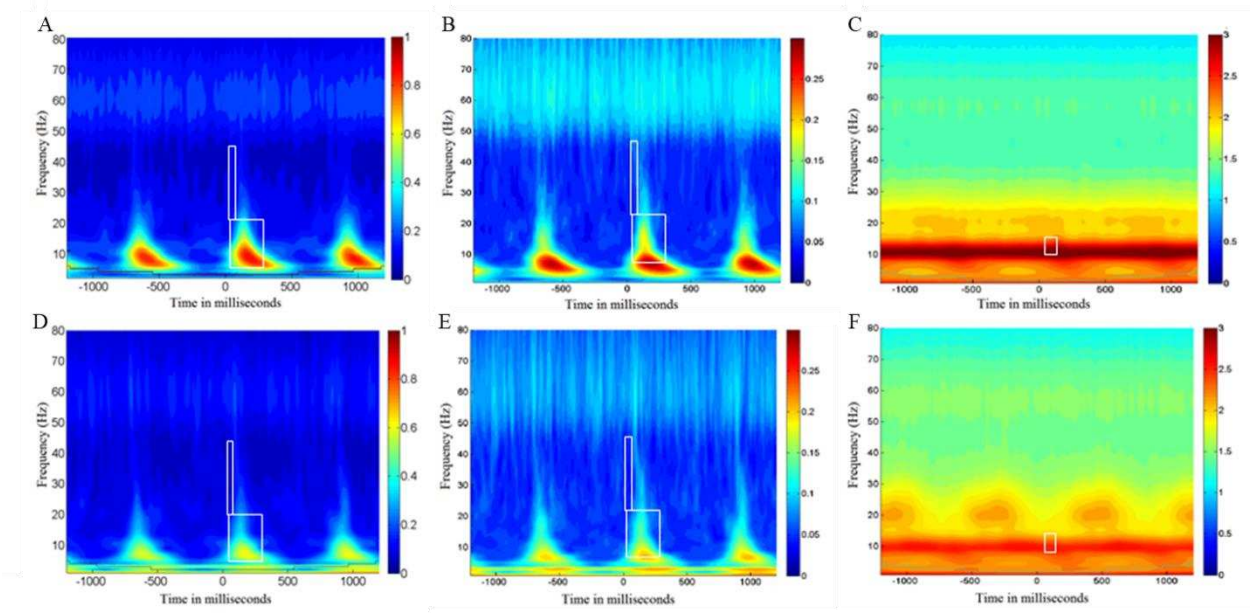

Figure 3.1. *Regions of interest from Crasta et al. (2018).* **A.** Evoked power for the auditory priming condition. **B.** PLF for the auditory priming condition. **C.** Total power for the auditory priming condition. **D.** Evoked power for the rhythmic entrainment condition. **E.** PLF for the rhythmic entrainment. **F.** Total power for the rhythmic entrainment. The boxes outlined in white represent 1) the motor ROI, 20–45 Hz from 10 to 60 ms for evoked power and PLF, and 2) the sensorimotor ROI, 4–20 Hz from 60 to 250 ms for evoked power and PLF, 3) the anticipation and predictive timing ROI, 13-16 Hz 50-150 ms for total power.

Purpose of Study

Results from the Crasta et al. (2018) study demonstrated that the auditory priming task resulted in reduced neural resources needed during rhythmic entrainment. However, the auditory priming task in the Crasta study used 400 tone presentations and had a duration of approximately five minutes (i.e., 5.32 minutes). In clinical interventions where time is limited and patients may have reduced attention, providing auditory priming for over five minutes prior to a task may not be practical. Additionally, the minimum duration of auditory presentation to achieve neural priming effects is unknown. Therefore, the first aim of this study is to compare the effect of different numbers of tone presentations, representing different durations of rhythmic auditory priming, on neural resources during auditory priming and rhythmic entrainment. In the current study, three auditory priming groups of neurotypical adults were presented with a different

duration of auditory priming (100, 200 or 400 tone presentations) followed by a rhythmic entrainment task. A fourth group, a control group, completed only the rhythmic entrainment task (no auditory priming). To ensure results are comparable to previous findings, the current study compared time-frequency measures (evoked power, total power, and PLF) within and between groups using the five ROIs identified during the Crasta et al., 2018 study. Finally, little is known of the effects of auditory priming on motor performance. Therefore, a secondary aim of this study was to determine the effect of different durations of auditory priming on motor performance in a neurotypical adult population. To measure this effect, behavioral responses during the rhythmic entrainment task were compared across all four groups.

Research Questions

Research Question 1: Is the brain's response to auditory tones influenced by prior exposure to auditory tones?

> *Hypothesis 1:* Between the three groups that receive auditory priming, there will be a significant effect of prior tone exposure on the power and phase locking factor during the last 100 tone presentations of the auditory priming condition.

Research Question 2: Is there a significant difference in time-frequency measures during the end of the auditory priming condition and the beginning of the rhythmic entrainment condition within each of the three auditory priming groups?

> *Hypothesis 2:* In all three auditory priming groups, there will be significantly less power and phase locking factor during the first 100 tone presentations of the rhythmic entrainment condition compared to the last 100 tone presentations of auditory priming condition.

Research Question 3: How does the number of tones, representing duration of auditory priming, affect changes in time-frequency measures during the rhythmic entrainment condition?

Hypothesis 3: There will be a significant main effect of the number of tone presentations during auditory priming (0, 100, 200, or 400) on power and phase locking factor during the entrainment condition with the control group (no priming) having the highest values and the 400-group having the lowest values. A possibility exists that the effect may reach a plateau earlier in the rhythmic entrainment condition.

Research Question 4: How does rhythmic auditory priming affect behavioral performance during the rhythmic entrainment task, and will this effect vary based on the number of tone presentations representing duration of priming?

Hypothesis 4: There will be a main effect of number of tones presented during the rhythmic auditory priming (i.e., duration) on behavioral performance with the control group having the highest inter-response interval and asynchrony means and variabilities and the 400-group having the lowest. A possibility exists that the effect may reach a plateau sooner than 400 tone presentations.

Method

Participants

A total of 92 adults participated in the research study. Participants were recruited via word of mouth, recruitment emails to university students, and flyers on university campus and in the surrounding community. Of the participants who came to the lab, a total of 12 participants were excluded: 2 outside the age range, 1 auditory processing difficulties, 2 learning disability, 1 motor disability, 4 ADD/ADHD, 2 taking medication for anxiety/depression. Final data analysis was conducted on 80 participants who met the inclusion criteria: 18–39 years old with normal or

corrected vision and normal hearing and no history of or current significant brain injury, disability (e.g., learning disabilities, ADHD, speech or language impairments, hearing impairments, or motor/physical disability), or neurological or psychiatric conditions (e.g., epilepsy, schizophrenia, bipolar), and not taking medication for other mental health conditions (e.g., anxiety, depression). Participants included 23 males and 57 females ages 18-39 (M = 24.82, SD = 5.7). Participants' self-reported race included 1 (1.3%) Native American, 7 (8.8 %) Asian, 4 (2.5%) Black, 63 (78.8% White), and 2 (2.5%) of participants selected multiple races (1 Native American and White, 1 Asian and White). In total, 7 participants (8.8%) self-reported as Hispanic or Latino/a.

Participants were assigned to one of four groups. Of the 80 participants included in final data analysis, 60 participants were assigned to one of three auditory priming groups and heard 100, 200, or 400 presentations of auditory rhythmic tones (auditory priming condition) prior to tapping a finger along to 400 auditory rhythmic tones (rhythmic entrainment condition): the 100-auditory group (n = 20, M = 23.72 years, SD = 5.87, 4 males, 16 females) the 200-auditory group (n = 20, M = 24.87 years, SD = 5.25, 4 males, 16 females) and the 400-auditory group (n = 20, M = 24.78 years, SD = 5.94, 8 males, 12 females). Twenty participants were assigned to the control group, i.e., 0-auditory group, (n = 20, M = 25.90 years, SD = 5.97, 7 males, 13 females) and received 0 priming tones prior to rhythmic entrainment. Groups were assigned based on the order in which the participants came to the lab with all four group assignments were distributed across the data collection period. Participants were not significantly different in age between the four groups, $F(3,76) = 0.479$, $p = .689$. Participants self-reported their level of music expertise and dance expertise on a Likert scale from 0 to 3 (0 = None, 1 = Novice, 2 = Moderate, and 3 = Expert). The average level of music expertise was 1.44 (SD = 1.004) and the average level of

dance expertise was 0.66 (*SD* = 0.80). Participants were not significantly different in music expertise, $F(3,76) = 0.69$, $p = .556$, or dance expertise, $F(3,76) = 0.86$, $p = .466$, between the four groups. The recruitment and data collection protocol for this study was approved by the Colorado State University Institutional Review Board (IRB number 2206).

Procedure

Participants completed a self-report demographic questionnaire (see Figure D1) and a musical expertise and experience questionnaire (see Figures D2a and D2b), which took about 5–15 minutes. The music questionnaire included two questions which asked participants to select their overall level of music expertise and dance expertise as "none," "novice," "moderate," or "expert" which were then coded on Likert scale from 0 to 3. EEG data collection took place in an electrically shielded and sound-attenuating booth in the Brainwaves Research Laboratory on the CSU campus. Participants were seated in a high-back comfortable chair facing a computer monitor. Cap application took approximately 20–30 minutes and was completed by one of the lead researchers and at least one trained research assistant. The EEG recording and paradigms took about 15–20 minutes. Cap removal and debriefing with the participant took about 5–10 minutes. In total, data collection with each participant took about 1 hour.

Paradigm and Stimuli

During the EEG data collection, all participants first completed an eyes-open rest condition which consisted of the participant staring at a fixation point for three minutes. In all auditory priming conditions (100, 200, or 400) and the rhythmic entrainment condition, the tones were generated using a 1kHz sinusoidal wave set to approximately a 70 decibels sound pressure level, when sustained, with a 50 ms duration and 10 ms rise/fall time. Tones were presented electronically every 800 ms through ER-3A binaural ear buds (Etymotic Research) using E-

Prime 3.0 software (Psychology Software Tools, 2016). The control group did not complete a priming condition. During the priming condition, the three priming groups were instructed to listen to the tone presentations while keeping their eyes on a fixation point. The group with 400 presentations took a short break (approximately 30–60 seconds) half-way through to allow participants to stretch and rest their eyes. Including time for instructions, the 100-auditory priming task took approximately 1–2 minutes, the 200-auditory priming task took 2–3 minutes, and the 400-auditory priming task (including the break) took 5–6 minutes. All participants completed a rhythmic entrainment condition in which they heard 400 presentations of tones identical to the priming condition but were instructed to push a button with their right index finger every time they heard a tone. The rhythmic entrainment condition, including a break for participants half-way through for all participants, took about 5-6 minutes.

Data Acquisition

EEG data were collected using a BioSemi ActiveTwo (BioSemi, 2016) EEG Acquisition System with 64 pin-type Ag/AgCl sintered active-electrodes which recorded the brain's electrical activity at the scalp. A Common Mode Sense (CMS) active electrode and a Driven Right Leg (DRL) passive electrode served as online reference and ground (https://www.biosemi.com/faq/cms&drl.htm). Pins were inserted into an Active Two Lycra head cap based on a modified 10-20 system according to American Electroencephalographic Society nomenclature guidelines (American Electroencephalography Society, 1994). Four flat electrodes recorded vertical and horizontal eye movements (EOGs) and two flat electrodes placed on the left and right earlobes recorded environmental noise for later use in offline referencing. Data were sampled at a rate of 2048 Hz with a bandwidth of 0-417 Hz.

Data Reduction

BrainVision Analyzer, Version 2.2.0 software (Brain Products GmbH, 2019) was used for preprocessing of EEG data. First, the four eye channels were converted into vertical and horizontal bipolar eye movement channels. Using the bilateral ears channels as the offline reference, data were filtered from the continuous EEG with a bandpass setting of 0.1–80 Hz. Following filtering, data were segmented 1800 ms before and 1800 ms after the auditory stimulus. Data were baseline corrected relative to a baseline of −200 to 0 ms. Next, a regression method which removed eye movement from trials was conducted via a custom script in MATLAB (Segalowitz, 1996). Following the eye regression, a baseline correction was performed again relative to a baseline of −200 to 0 ms for all remaining segments. Finally, an artifact rejection step removed segments with voltage deviations greater than ±200 microvolts (μV) on any EEG channel. Artifact rejection at ±200 μV ensured at least 90% of segments were maintained for data analysis (Im, 2018). For the auditory condition, at least two trials were always excluded due to the large size of the segmentation window. Therefore, the last 98 trials were averaged in the 200-auditory and 400-auditory groups, for a total 98 trials analyzed in each priming group. For the entrainment condition, the data were divided into four equal blocks of trails before averaging for each group. Each block was analyzed separately.

Data Analysis

Behavioral Measures. Behavioral measures for the entrainment task included inter-response interval (IRI) mean and variability and asynchrony mean and variability (Thaut et al., 1998), measured in milliseconds. The IRI mean provides a measure of the average rate of tapping. The IRI variability was calculated as the standard deviation of the mean IRI for each participant which provided a measure of consistency in the time between taps across trials. The

asynchrony mean provides a measure of the how closely the participant's tap aligned with the tone. Asynchrony variability was calculated as the standard deviation of the mean asynchrony for each participant which provided a measure of how much their behavioral performance aligned with the tones across trials, i.e., their behavioral entrainment.

Behavioral measures were calculated using a MATLAB script modified from that used by Crasta et al. (2018) by S.M. The IRI was calculated as the time between each tap. The IRIs for missed taps and double taps were removed. IRIs of greater than 1200 ms were considered missed taps and IRIs of less than 200 ms were considered double taps. The IRI mean and standard deviation were then calculated for each participant. To calculate asynchrony, the response within 400 ms before or after the tone was identified. Next, the time of the response was subtracted from the time of the tone presentation to calculate the asynchrony measure. Finally, the asynchrony mean and standard deviation were calculated for each participant.

EEG Time-Frequency Analysis. Custom MATLAB scripts (Brainwaves Research Lab, 2018, 2020), used equations outlined by Roach and Mathalon (2008) to visualize and analyze the EEG time-frequency data. Following the preprocessing steps, a continuous Morlet wavelet transformation was performed in MATLAB to convert the data into the time-frequency domain. The wavelet transformation converts the data from a two-dimension matrix containing intensity at each time point to a three-dimensional matrix containing the intensity of each frequency at each time point in a segment. The frequency range and a constant (number of cycles) determines the length of each wavelet. A frequency range of 1-80 Hz and a constant of 5 was selected to provide a good balance of temporal and frequency resolution (Cohen & Grafman, 2014). The number of frequency steps, which determines the number of wavelets, was set to 80, with frequency steps set to a linear scale (1 layer for each whole number frequency).

Following the wavelet transformation, time-frequency measures of total power (amplitude squared), evoked power (power time-locked to the stimulus/response), and phase locking factor (PLF; the consistency of the phase of the signal across time) were calculated in MATLAB at EEG site C3 (see Figure 3.2). Site C3 was selected *a priori* for its proximity to auditory and motor brain regions and to increase comparability of results to the Crasta 2018 study. For visual inspection of a priori ROIs, time-frequency plots of evoked power, PLF, and total power were mapped from -400 ms to 400 ms around the auditory stimulus for the 98 trials, i.e., "last 100 trials," of the auditory priming condition, and each block of the four blocks of the rhythmic entrainment condition, i.e., "block 1," "block 2," "block 3," and "block 4" in each group (see Appendix E).

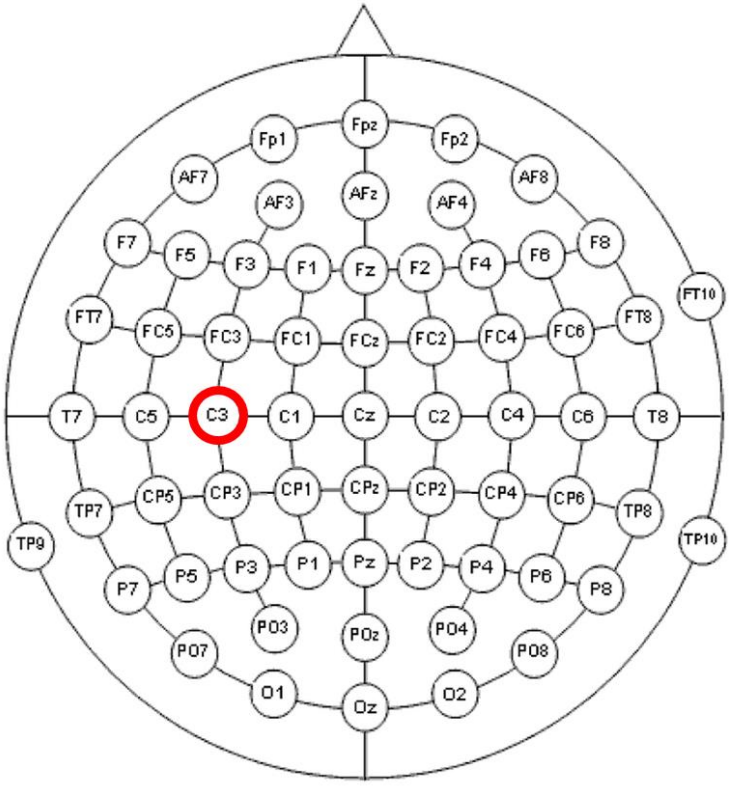

Figure 3.2. Location of EEG site C3 (outlined in red), within the modified 10 – 20 system, used in time-frequency analysis in the Crasta et al. (2018) study and in the current study. Image adapted from https://www.researchgate.net/figure/Positions-of-the-64-electrodes-including-their-number-and-their-designations-The_fig1_308182406

Statistical Analyses. For statistical analysis, the five regions of interest (ROIs) as defined by Crasta et al (2018) were selected *a priori*: 1) evoked power and 2) PLF of 20-45 Hz from 10-60 ms representing motor processing, 3) evoked power and 4) PLF of 4-20 Hz from 60-250 ms representing sensorimotor processing, and 5) total power of 13-16 Hz from 50-150 ms representing anticipation and predictive timing (see Figure 3.1). The averages within in the ROIs for each participant were used for statistical analyses. For the first three research questions, a MANCOVA was conducted with the five ROIs as the dependent variables. The final MANCOVAs included music expertise as a covariate. Dance expertise was not included as a covariate in the final analyses as it was nonsignificant. For MANCOVAs, an alpha level of .05 was used to indicate significance.

To answer the first research question and determine if the brain's response to auditory stimuli is influenced by prior experience, a MANCOVA was used to compare time-frequency measures during the end (last 100 trials) of the auditory priming condition for each ROI between the three auditory priming groups. The dependent variables were the five ROIs. The between-subject factor was priming group (100, 200, or 400 tone presentations). Music expertise was the covariate.

To answer the second research question and see if there was significant difference in time-frequency measures during the end of the auditory priming condition compared to the beginning of the rhythmic entrainment condition within each of the three auditory priming groups, a MANCOVA was used to compare time-frequency measures during the last 100 trials of the auditory priming condition to the first block of the rhythmic entrainment condition. The dependent variables were the five ROIs. The within-group factor was condition (auditory priming versus rhythmic entrainment). The between-group factor was priming group (100, 200, or 400 tones). Music expertise was the covariate.

To answer the third research question and measure the effect of the number of tones during the auditory priming condition on the brain response during rhythmic entrainment condition, a third MANCOVA was conducted. The dependent variables were the five ROIs. The within-subject factor was the block (1^{st}, 2^{nd}, 3^{rd}, or 4^{th}) of the rhythmic entrainment condition. The between-subject factor was group: 0, 100, 200, or 400 tone presentations prior to entrainment. Music expertise was the covariate.

To answer the fourth research question about the effect of auditory priming on motor performance, four ANCOVAs were conducted, each with a different DV: mean inter-response interval (IRI), IRI variability, mean asynchrony, and asynchrony variability. In each ANCOVA,

group was the between-subject factor and music expertise was the covariate. A Bonferroni corrected alpha level of .0125 (.05/4) was used to correct for multiple comparisons.

For significant main effects and interactions of each analysis, post-hoc tests were conducted to identify significant differences between all levels of within- and between-subjects factors, as described in Kirk (1968). For post-hoc comparison an alpha level of .5 was used to indicate significance. For significant covariate effects, data visualizations were examined to characterize the nature of the findings.

Results

Behavioral Results

Behavioral results for the rhythmic entrainment condition included the IRI mean and variability and the asynchrony mean and variability. The mean IRI for all participants was 799.97 ms (*SD* = 2.68), suggesting that, on average, participants tapped only 0.03 ms faster than the inter-stimulus interval (ISI) of the tones (800 ms). The mean IRI variability for all participants was 53.31 ms (*SD* = 15.28), suggesting participants varied the interval between their taps by about 50 ms on average. The mean asynchrony across all participants was -32.15 ms (*SD* = 88.51), suggesting an overall negative mean asynchrony. However, the minimum mean asynchrony was -174.26 ms and the maximum was 281.18 ms, suggesting participants varied in whether their tap preceded the tone (negative mean asynchrony) or followed the tone (positive mean asynchrony). The average asynchrony variability for all participants was 70.86 ms (*SD* = 37.12), suggesting participants varied the time between their tap and the tone by about 71 ms, on average.

Differences between Auditory Priming Groups within the Auditory Priming Condition

Means and standard deviations are reported in Table 3.1. The results of the MANCOVA to test the first research question and compare the last block of the auditory-only condition between groups did not show a significant multivariate effect of group for all five ROIs collectively in relation to the duration of priming, $F(10,106) = 1.56$, $p = .129$, $\eta^2 = .128$. As a Box's M of 92.02 was significant, $F(30,10295.12) = 2.28$, $p < .001$, Pillai's Trace is reported above which is robust against violations of the assumption of homogeneity of variances (Field, 2012a). Univariate tests showed a significant between-subject effects in the motor ROI for evoked power, $F(2,57) = 3.47$, $p = .038$, $\eta^2 = .110$ and PLF, $F(2,57) = 3.89$, $p = .026$, $\eta^2 = .122$. The auditory-100 group had the greatest mean evoked power ($M = 0.35$, $SD = 0.22$) and PLF ($M = 0.15$, $SD = 0.06$). The auditory-200 group had the second greatest mean evoked power ($M = 0.27$, $SD = 0.11$) and PLF ($M = 0.15$, $SD = 0.08$). The auditory-400 group had the least mean evoked power ($M = 0.24$, $SD = 0.12$) and PLF ($M = 0.11$, $SD = 0.03$). Post hoc comparisons using the Tukey HSD test found no significant differences between groups, although the difference in evoked power in the motor ROI between the auditory-100 and auditory-400 groups approached significance ($p = .051$). There was not a significant main effect of group for either evoked power in the sensorimotor ROI or total power in the anticipation and predictive timing ROI (see Table 3.2).

Table 3.1. Means and standard deviations for each ROI for the last 100 trials of the auditory priming condition, and each of the four blocks of the rhythmic entrainment condition for each group (0-Aud = 0-auditory group, 100-Aud = 100-auditory group, 200-Aud = 200-auditory group, 400-Aud = 400-auditory group) and the total mean and standard deviation. Abbreviations: M = mean, PLF = phase locking factor, SD = standard deviation.

		Auditory Priming		Rhythmic Entrainment							
				Block 1		Block 2		Block 3		Block 4	
Sensorimotor ROI		M	SD	M	SD	M	SD	M	SD	M	SD
Evoked Power	0-Aud			0.46	0.18	0.46	0.31	0.48	0.35	0.44	0.29
	100-Aud	0.43	0.15	0.38	0.13	0.40	0.12	0.41	0.11	0.50	0.19
	200-Aud	0.46	0.21	0.41	0.16	0.43	0.13	0.42	0.21	0.44	0.21
	400-Aud	0.43	0.20	0.45	0.30	0.44	0.21	0.46	0.39	0.45	0.30
	Total	0.44	0.18	0.42	0.20	0.43	0.20	0.44	0.28	0.46	0.25
PLF	0-Aud			0.14	0.03	0.14	0.04	0.13	0.05	0.13	0.03
	100-Aud	0.14	0.03	0.13	0.04	0.12	0.03	0.13	0.02	0.14	0.04
	200-Aud	0.16	0.08	0.14	0.04	0.14	0.02	0.13	0.03	0.14	0.04
	400-Aud	0.13	0.04	0.14	0.04	0.13	0.04	0.12	0.05	0.13	0.03
	Total	0.14	0.05	0.13	0.04	0.13	0.04	0.13	0.04	0.13	0.03
Motor ROI											
Evoked Power	0-Aud			0.29	0.13	0.25	0.11	0.29	0.18	0.25	0.14
	100-Aud	0.35	0.22	0.28	0.13	0.26	0.12	0.28	0.15	0.25	0.10
	200-Aud	0.27	0.11	0.21	0.07	0.26	0.13	0.29	0.20	0.23	0.08
	400-Aud	0.24	0.12	0.24	0.12	0.25	0.16	0.24	0.20	0.21	0.10
	Total	0.29	0.16	0.25	0.12	0.26	0.13	0.27	0.18	0.23	0.11
PLF	0-Aud			0.12	0.02	0.12	0.03	0.13	0.05	0.11	0.04
	100-Aud	0.15	0.06	0.13	0.05	0.13	0.05	0.13	0.05	0.12	0.04
	200-Aud	0.15	0.08	0.11	0.04	0.13	0.04	0.13	0.05	0.13	0.05
	400-Aud	0.11	0.03	0.12	0.04	0.12	0.05	0.13	0.08	0.12	0.05
	Total	0.14	0.06	0.12	0.04	0.12	0.04	0.13	0.06	0.12	0.04
Anticipation and Timing ROI											
Total Power	0-Aud			3.02	1.23	3.20	1.27	3.20	1.47	3.35	1.62
	100-Aud	2.84	0.95	2.82	0.84	3.03	0.93	2.95	0.94	3.12	0.99
	200-Aud	3.06	1.54	2.89	1.30	3.02	1.40	3.02	1.68	3.03	1.33
	400-Aud	3.24	1.54	2.83	1.27	3.12	1.60	3.05	1.49	3.05	1.48
	Total	3.05	1.36	2.89	1.16	3.09	1.30	3.06	1.40	3.14	1.35

Table 3.2. Results of one-way MANCOVA comparing time-frequency measures in five regions of interest between the three auditory priming groups. Abbreviations: DV = dependent variable, IV = independent variable, η^2 = partial eta squared.

IV	DV	*F*	*p*	η^2
Group (between-group effect)				
Multivariate		1.56[a]	.129	0.128
Univariate	sensorimotor evoked power	0.34	.715	.012
	sensorimotor PLF	1.48	.236	.050
	motor evoked power	3.47	.038	.110
	motor PLF	3.89	.026	.122
	anticipation and timing total power	0.39	.680	.014
Music Expertise (covariate)				
Multivariate		1.38[b]	.248	.117
Univariate	sensorimotor evoked power	1.16	.285	.020
	sensorimotor PLF	0.74	.395	.013
	motor evoked power	5.47	.023	.089
	motor PLF	5.40	.024	.088
	anticipation and timing total power	0.37	.548	.006

a. Pillai's Trace
b. Exact statistic

A lack of significant post hoc comparisons for the motor ROI, which cannot include covariate effects, suggest that music expertise may have substantially moderated differences between groups. In fact, there was a significant effect of music expertise in the motor ROI for evoked power, $F(1,57) = 5.469$, $p = .023$, $\eta^2 = .089$ and PLF, $F(1,57) = 5.402$, $p = .024$, $\eta^2 = .088$. Follow-up bivariate Spearman's rank correlations showed music expertise was significantly negatively correlated with evoked power in the motor ROI, $r = -.37$, $p = .003$, and PLF in the motor ROI, $r = -.27$, $p = .035$, with participants with the most musical expertise having the least evoked power and PLF. The scatter plots in Figures 3.3 and 3.4 show that evoked power and PLF decreases with increased music experience for the auditory-100 and auditory-400 groups, but less so for the auditory-200 group.

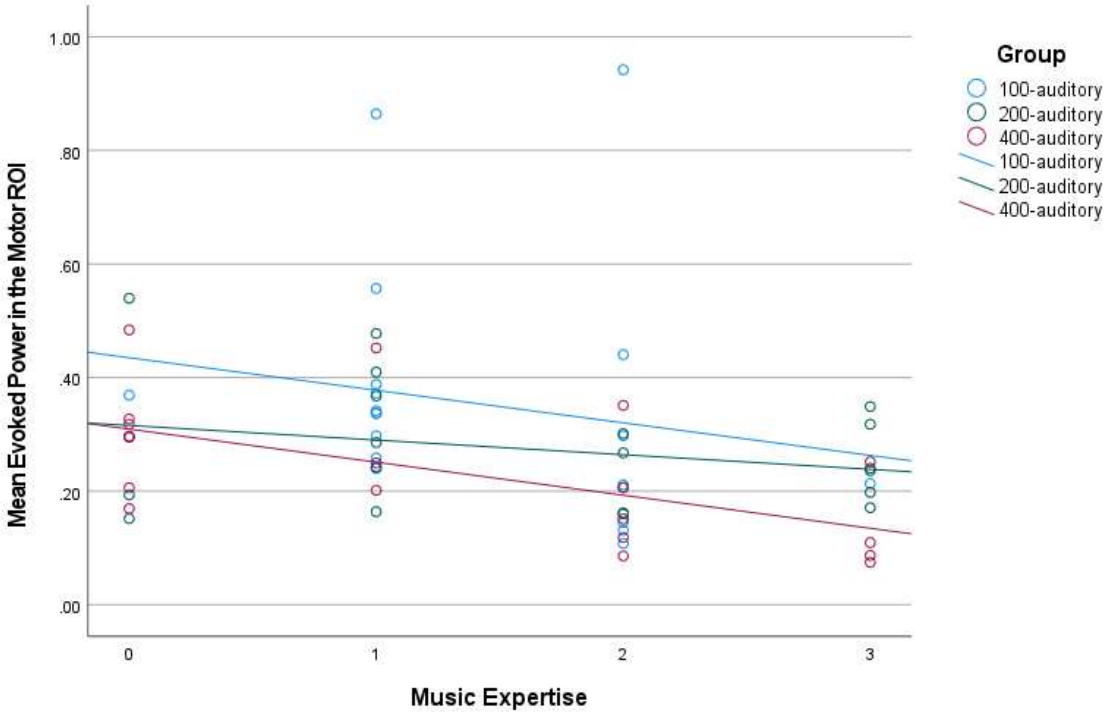

Figure 3.3. Scatter plot of evoked power in the ROI representing motor processes, 20–45 Hz from 10 to 60 ms (x-axis) for each level of self-reported music expertise (y-axis), with different colors indicating the auditory group: 100-auditory, 200-auditory, or 400-auditory. Music expertise was coded on a Likert scale from 0–3: 0 = "none," 1 = "novice," 2 = "moderate," and 3 = "expert."

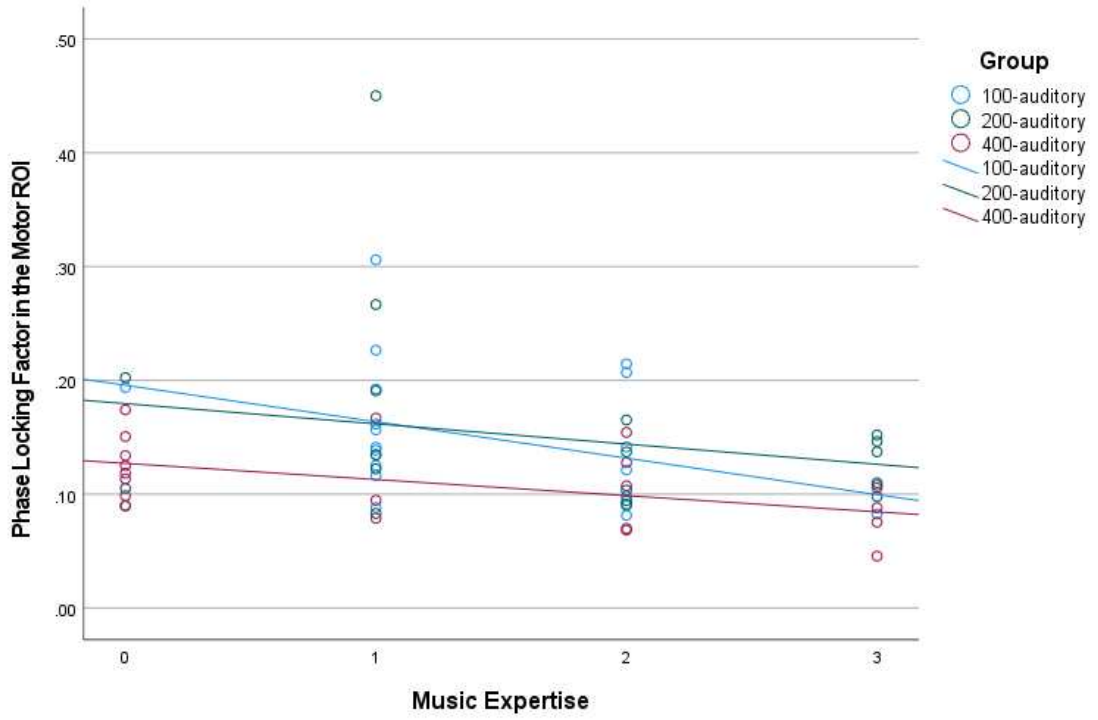

Figure 3.4. Scatter plot of PLF in the ROI representing motor processes, 20–45 Hz from 10 to 60 ms (x-axis) for each level of self-reported music expertise (y-axis), with different colors indicating the auditory group: 100-auditory, 200-auditory, or 400-auditory. Music expertise was coded on a Likert scale from 0–3: 0 = "none," 1 = "novice," 2 = "moderate," and 3 = "expert."

Differences between the Auditory Priming and Rhythmic Entrainment Conditions

The results of the 2x3 MANCOVA to test the second research question and compare the last 100 trials of the auditory-only condition to the first block of entrainment condition within and between three auditory priming groups (100, 200, and 400) showed a significant within-subjects multivariate effect of condition (auditory or entrainment) for all five ROIs collectively, $F(5,52) = 3.615$, $p = .007$, $\eta^2 = .258$. The between-subjects multivariate effect of group was not significant, $F(10,106) = 1.681$, $p = .095$, $\eta^2 = .137$. As Box's M was significant, Box's M = 246.15, $F(110,8793.97) = 1.67$, $p < .001$, the F statistic reported above is Pillai's Trace which accounts for the violation of assumption of homogeneity of variances (Field, 2012b). Univariate tests of within-subjects contrasts showed a significant effect of condition for PLF in the

sensorimotor ROI, $F(2,57) = 4.20$, $p = .045$, $\eta^2 = .070$, evoked power in the motor ROI, $F(2,57) = 9.85$, $p = .003$, $\eta^2 = .150$, PLF in the motor ROI, $F(2,57) = 8.04$, $p = .006$, $\eta^2 = .126$, and total power in the anticipation and predictive timing ROI, $F(2,57) = 6.59$, $p = .01$, $\eta^2 = .105$. There was not a significant effect of condition for evoked power in the sensorimotor ROI (see Table 3.3).

Table 3.3. Results of 2x3 MANCOVA comparing time-frequency measures in five regions of interest within groups between the auditory priming and rhythmic entrainment conditions and between the three auditory priming groups. Abbreviations: DV = dependent variable, IV = independent variable, η^2 = partial eta squared.

IV		DV	*F*	*p*	η^2
Condition (within-group effect)					
	Multivariate		3.62[b]	.007	.258
	Univariate	sensorimotor evoked power	2.58	.114	.044
		sensorimotor PLF	4.20	.045	.070
		motor evoked power	9.85	.003	.150
		motor PLF	8.04	.006	.150
		anticipation and timing total power	6.59	.013	.105
Group (between-group effect)					
	Multivariate		1.68[a]	.095	.137
	Univariate	sensorimotor evoked power	0.30	.739	.011
		sensorimotor PLF	0.75	.476	.026
		motor evoked power	3.66	.032	.116
		motor PLF	2.70	.076	.088
		anticipation and timing total power	0.14	.869	.005
Music Expertise (covariate)					
	Multivariate		0.81[b]	.549	.072
	Univariate	sensorimotor evoked power	0.18	.669	.003
		sensorimotor PLF	0.06	.811	.001
		motor evoked power	2.51	.119	.043
		motor PLF	3.18	.080	.054
		anticipation and timing total power	0.15	.698	.003
Condition*Music Expertise					
	Multivariate		1.43[b]	.230	.121
	Univariate	sensorimotor evoked power	1.44	.235	.025
		sensorimotor PLF	2.03	.160	.035
		motor evoked power	5.24	.026	.086
		motor PLF	4.38	.041	.073
		anticipation and timing total power	1.54	.220	.027
Condition*Group		multivariate			
	Multivariate		1.59[a]	.120	.130
	Univariate	sensorimotor evoked power	0.92	.405	.032
		sensorimotor PLF	2.11	.130	.070
		motor evoked power	1.94	.154	.065
		motor PLF	3.77	.029	.119
		anticipation and timing total power	2.14	.128	.071

a. Pillai's Trace
b. Exact statistic

Post hoc a priori one-tailed t-tests (Kirk, 1968) were conducted for significant main effects to test within-group mean differences based on the hypothesis that power and PLF would decrease from the auditory priming condition to the entrainment condition. For PLF in the sensorimotor ROI, there was a significant decrease from the auditory priming and entrainment condition for the 200-auditory group, $t(57) = 3.69$, $p < .05$, but not the 100-auditory group, $t(57) = 2.71$, $p > .05$ or the 400-auditory group, $t(57) = -1.16$, $p > .05$. For evoked power in the motor ROI, there was a significant decrease from the auditory priming and rhythmic entrainment condition for the 100-auditory group, $t(57) = 3.64$, $p < 0.05$, and the 200-auditory group, $t(57) = 3.06$, $p < .05$, but not the 400-auditory group, $t(57) = -0.13$, $p > .05$. For PLF in the motor ROI, post hoc t-tests revealed a significant decrease between the auditory priming and rhythmic entrainment condition for the 200-auditory group, $t(57) = 4.72$, $p < .01$, but not the 100-auditory group $t(57) = 2.09$, $p > .05$, or the 400-auditory group, $t(57) = -1.04$, $p > .05$. Total power in the anticipation and predictive timing ROI significantly decreased from the auditory priming condition to the rhythmic entrainment condition for the 400-auditory group, $t(57) = 5.59$, $p < .01$, but not the 100-auditory group, $t(57) = 0.34$, $p > .05$ or the 200-auditory group, $t(57) = 2.28$, $p > .05$. Overall, a decrease in evoked power and PLF during the rhythmic entrainment condition was driven by the 100-auditory and 200-auditory groups, while a decrease in total power during the rhythmic entrainment condition was driven by the 400-auditory group.

In the motor ROI, there was a significant interaction between condition and music expertise for evoked power, $F(2,57) = 5.24$, $p = .026$, $\eta^2 = .086$, and PLF, $F(2,57) = 4.38$, $p = .041$, $\eta^2 = .073$. The bar graphs in Figures 3.5 and 3.6 illustrate the nature of the interaction. For musical experts, evoked power increased in the rhythmic entrainment condition compared to the auditory priming condition, while those with none to moderate expertise had decreased evoked

power in the rhythmic entrainment condition compared to the auditory priming condition. Novices had the greatest evoked power in the motor ROI for both the auditory priming (M = 0.35, SD = 0.16) and rhythmic entrainment (M = 0.29, SD = 0.15) conditions. Those with no musical training and novices had decreased PLF in the rhythmic entrainment condition compared to the auditory priming condition, but those with moderate musical training or experts had increased PLF in the rhythmic entrainment condition compared to the auditory priming condition. Novices had the greatest PLF in the motor ROI for both the auditory priming (M = 0.17, SD = 0.09) and rhythmic entrainment (M = 0.14, SD = 0.06) conditions.

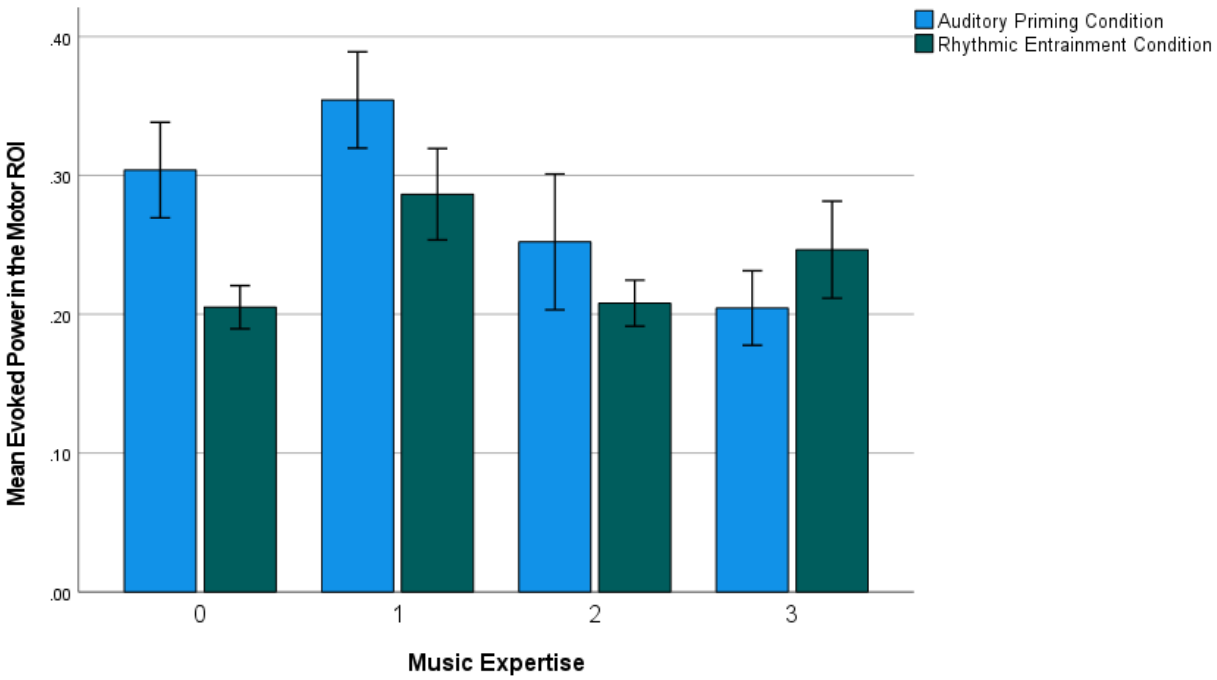

Figure 3.5. Bar plot of the average evoked power in the motor ROI, 20–45 Hz from 10 to 60 ms for each self-reported level of music expertise for the last 100 trials of the auditory priming condition and the first block of the rhythmic entrainment condition. Music expertise was coded on a 0–3 Likert scale: 0 = "none," 1 = "novice," 2 = "moderate," 3 = "expert." Error bars represent ± 1 standard error.

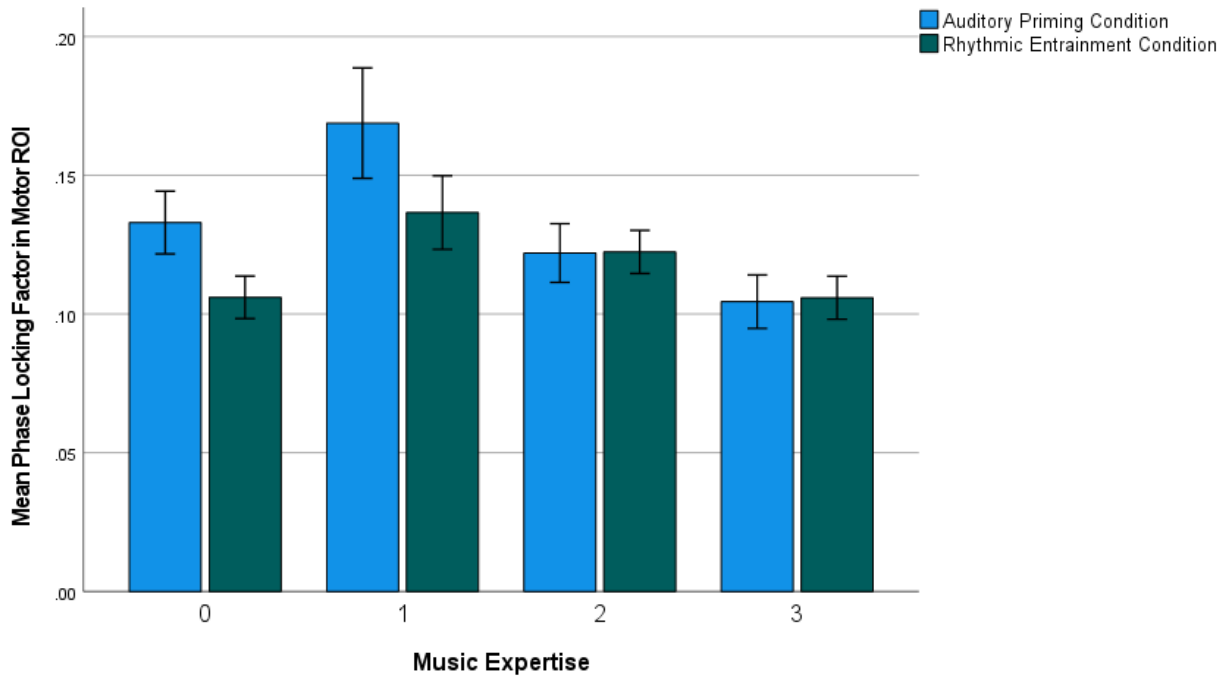

Figure 3.6. Bar plot of the average phase locking factor in the motor ROI, 20–45 Hz from 10 to 60 ms for each self-reported level of music expertise for the last 100 trials of the auditory priming condition and the first block of the rhythmic entrainment condition. Music expertise was coded on a 0–3 Likert scale: 0 = "none," 1 = "novice," 2 = "moderate," 3 = "expert." Error bars represent ± 1 standard error.

There was a significant between-subject effect of group for evoked power in the motor ROI, $F(2,57) = 3.66$, $p = .032$, $\eta^2 = .116$, with the auditory-100 group having the greatest mean evoked power in both the auditory priming ($M = 0.35$, $SD = 0.22$) and rhythmic entrainment ($M = 0.28$, $SD = 0.13$) conditions, the auditory-400 group having the least evoked power in auditory priming condition ($M = 0.24$, $SD = 0.12$), and the auditory 200-group having the least evoked power in the rhythmic entrainment condition ($M = 0.21$, $SD = 0.07$). Post hoc two-tailed Tukey tests (Kirk, 1968) found no significant differences. There were no significant between-group differences for either evoked power or PLF the sensorimotor ROI, PLF in the motor ROI, nor total power in the anticipation and predictive timing ROI (see Table 3.3).

There was a significant interaction between group and condition for PLF in the motor ROI, $F(2,57) = 3.77$, $p = .029$, $\eta^2 = .119$, suggesting the duration of auditory priming moderated the effect of condition, when accounting for music expertise. Post hoc two-tailed Tukey tests to compare between groups within each condition (Kirk, 1968) revealed significant differences between groups for the auditory condition, but not the entrainment condition. For the auditory condition, there was significantly greater PLF in the 100-auditory group compared to the 200-auditory group, $q' = 8.78$, $p < .01$, and the 400-auditory group, $q' = 4.40$, $p < .01$, and significantly great PLF in the 200-auditory group compared to the 400-auditory group, $q' = 4.24$, $p < .05$. As reported above, post hoc tests revealed significantly less PLF in the motor ROI during the rhythmic entrainment condition compared to the auditory condition only for the 200-auditory group, $t(57) = 4.72$, $p < .01$. Therefore, the interaction between group and condition for PLF in the motor ROI is characterized by a significant effect of condition in the 200-auditory group but not in the 100-auditory group or the 400-auditory group.

Differences between Auditory Priming Groups within the Rhythmic Entrainment Condition

The results of the 4x4 MANCOVA to test the third research question and compare the four blocks of the motor-only condition within and between all four groups (0, 100, 200, and 400) showed no significant multivariate main effects of block or group (see Table 3.4). Box's M was not able to be computed due to issues with the covariance matrices. Therefore follow-up Box's M were calculated for each ROI separately, revealing violations of the assumption of homogeneity for the sensorimotor evoked power motor ROI, Box's M = 105.69, $F(30, 15880.55) = 3.18$, $p < .001$, the motor evoked power ROI, Box's M = 81.45, $F(30, 15880.55) = 2.54$, $p < .001$, and the anticipation and predictive timing total power ROI, Box's M = 88.74, $F(30,15880.55) = 2.67$, $p < .001$, violating the assumption of homogeneity of variance for these

ROIs. Therefore, Pillai's Trace is reported in Table 3.4 to account for the violation of the assumption of homogeneity of variance for three out of the five ROI (Field, 2012b). Tests of univariate within-subjects contrasts showed a significant effect of block for total power in the anticipation and predictive timing ROI, $F(3,76) = 5.093$, $p = .003$, $\eta^2 = .064$. As Mauchly's test indicated a violation of the sphericity assumption, $\chi^2(5) = 26.63$, $p < .001$, $\varepsilon = 0.897$ and the Greenhouse-Geisser estimate of sphericity was greater than .75, Huynh-Feldt corrected results are reported above (Field, 2012b). When totaled across all four groups, the first block had the least total power ($M = 2.89$, $SD = 1.16$) and the fourth block ($M = 3.14$, $SD = 1.35$) had the greatest total power in the anticipation and predictive timing ROI. There was no significant effect of block for the other four ROIs. There were no significant univariate between-group effects. There were no significant interactions between block and group or between block and music expertise (see Table 3.4).

Table 3.4. Results of 4x4 MANCOVA comparing time-frequency measures in five regions of interest within groups between five blocks of the rhythmic entrainment condition and between four groups, a control group and the three auditory priming groups. Abbreviations: DV = dependent variable, IV = independent variable, η^2 = partial eta squared.

IV	DV	*F*	*p*	η^2
Block (within-group effect)				
Multivariate		1.57[b]	.109	.279
Univariate	sensorimotor evoked power	1.73	.162	.023
	sensorimotor PLF	0.03	.994	.0004
	motor evoked power	2.16[c]	.107	.028
	motor PLF	0.61	.611	.008
	anticipation and timing total power	5.09[c]	.003	.064
Group (between-group effect)				
Multivariate		0.63[a]	.849	.041
Univariate	sensorimotor evoked power	0.14	.939	
	sensorimotor PLF	0.08	.972	
	motor evoked power	0.47	.707	
	motor PLF	0.25	.865	
	anticipation and timing total power	0.11	.953	
Music Expertise (covariate)				
Multivariate		1.07[b]	.383	.070
Univariate	sensorimotor evoked power	0.06	.804	
	sensorimotor PLF	0.95	.332	
	motor evoked power	0.78	.379	
	motor PLF	0.78	.381	
	anticipation and timing total power	0.20	.657	
Block*Music Expertise				
Multivariate		1.08[b]	.391	.210
Univariate	sensorimotor evoked power	1.29	.279	.017
	sensorimotor PLF	0.53	.662	.007
	motor evoked power	2.48[c]	.075	.032
	motor PLF	0.55	.652	.007
	anticipation and timing total power	0.94[c]	.415	.012
Block*Group	multivariate			
Multivariate		0.98[a]	.508	.190
Univariate	sensorimotor evoked power	1.10	.367	.042
	sensorimotor PLF	1.75	.079	.065
	motor evoked power	1.09[c]	.370	.042
	motor PLF	0.08	.626	.031
	anticipation and timing total power	0.58[c]	.797	.023

a. Pillai's Trace
b. Exact statistic
c. Huynh-Feld corrected for significant Mauchly's test of sphericity and Greenhouse-Geisser epsilon >.75

Post hoc two-tailed Tukey tests were conducted to compare means of total power in the anticipation and predictive timing ROI between blocks within each group (Kirk, 1968). There was significantly less total power first block (M = 2.89, SD = 1.15) compared to the second block, $q(4,228) = -4.38$, $p < .01$, the third block, $q(4,228) = -4.49$, $p < .05$, and the fourth block, $q(4,228) = -6.73$, $p < .01$. There was not a significant difference between the second and the third block, $q(4,228) = 1.71$, $p > .05$, the second and the fourth block, $q(4,228) = 0.003$, $p > .05$, or between the third block and the fourth block, $q(4,228) = -1.71$, $p > .05$. Overall, total power in the anticipation and predictive timing ROI was the least during the beginning of the rhythmic entrainment task which increased by the second block, slightly decreased at the third block (following a break), then slightly increased at the fourth block. Figure 3.7 illustrates this effect in each group and averaged across all groups. T-maps comparing total power for the four blocks of the rhythmic entrainment condition within each group (see Figures E10–E13) support these findings, but also show that total power outside of the anticipation and predictive timing ROI, above 30 Hz, decreased from the first to the last block.

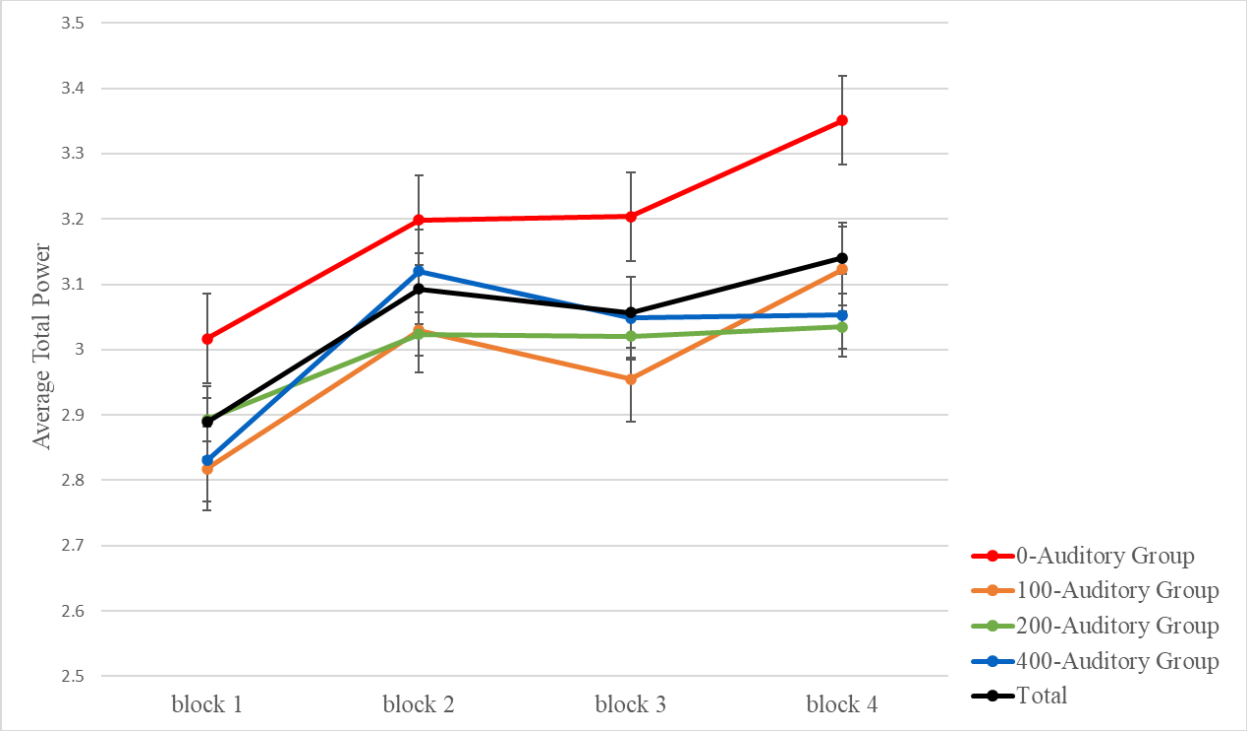

Figure 3.7. Line plot of the average total power within the anticipation and predictive timing ROI, 13–16 Hz from 50 to 150 ms at during each of the four blocks within the rhythmic entrainment condition Error bars represent ± 1 standard error.

Differences in Behavioral Performance between Groups

The results of the ANCOVAs to test the fourth research question and measure the effect of group on behavioral measures found no significant differences between groups overall. Means and standard deviations of behavioral measures in each group are listed in Table 3.5. The results of the ANCOVA for IRI variability found no significant effect of group, $F(3,75) = 0.17$, $p = 0.916$, $\eta^2 = .007$, but a significant effect of the covariate music expertise, $F(1,75) = 11.64$, $p = .001$, $\eta^2 = .134$. Participants who self-reported their musical expertise as "expert" (coded as 3 on a Likert scale from 0-3) had the least IRI variability ($M = 43.86$ ms, $SD = 7.07$). Participants who self-reported as a "novice" (coded as 1 on a Likert scale 0-3) has the highest IRI variability ($M = 58.70$ ms, $SD = 18.22$). A follow-up one-tailed Spearman correction found that IRI variability significantly decreased with increased music expertise, $r = -.43$, $p < .001$. Figure 3.8 illustrates

this trend across each group. The results of the ANCOVA for asynchrony variability found that a main effect of group approached significance and had a moderate to large effect size, $F(3,75) = 3.45$, $p = .021$, $\eta^2 = .752$, but was not significant at a Bonferroni corrected alpha level of .0125. The effect of the covariate music expertise approached significance, $F(1,75) = 4.33$, $p = .041$, $\eta^2 = .537$, but was not significant at a Bonferroni corrected alpha level of .0125. A follow-up one-tailed Spearman correlation found that asynchrony variability significantly decreased with increase music expertise, $r = -.44$, $p < .001$. Figure 3.9 illustrates this trend across each group. The results of the ANCOVA for mean IRI found no significant effect of group, $F(3,75) = 0.27$, $p = .844$, $\eta^2 = .011$. The results of the ANCOVA to measure the effect of group on mean asynchrony found no significant effect of group, $F(3,75) = 2.44$, $p = .71$, $\eta^2 = .587$.

Table 3.5. Means and standard deviations for behavioral measures in each group (0-Aud = 0-auditory group, 100-Aud = 100-auditory group, 200-Aud = 200-auditory group, 400-Aud = 400-auditory group) and the total mean and standard deviation. Abbreviations: M = mean, SD = standard deviation.

		Inter-Response Interval		Asynchrony	
		M	SD	M	SD
Mean	0-Aud	799.55	3.24	7.72	121.17
	100-Aud	800.32	2.09	-62.10	51.79
	200-Aud	800.09	3.02	-26.21	83.65
	400-Aud	799.92	2.35	-48.00	72.74
	Total	799.97	2.68	-32.15	88.51
Variability	0-Aud	52.63	15.89	92.50	48.48
	100-Aud	52.254	9.09	66.04	25.32
	200-Aud	53.52	22.29	58.31	28.77
	400-Aud	54.83	11.59	66.57	34.70
	Total	53.31	15.28	70.86	37.11

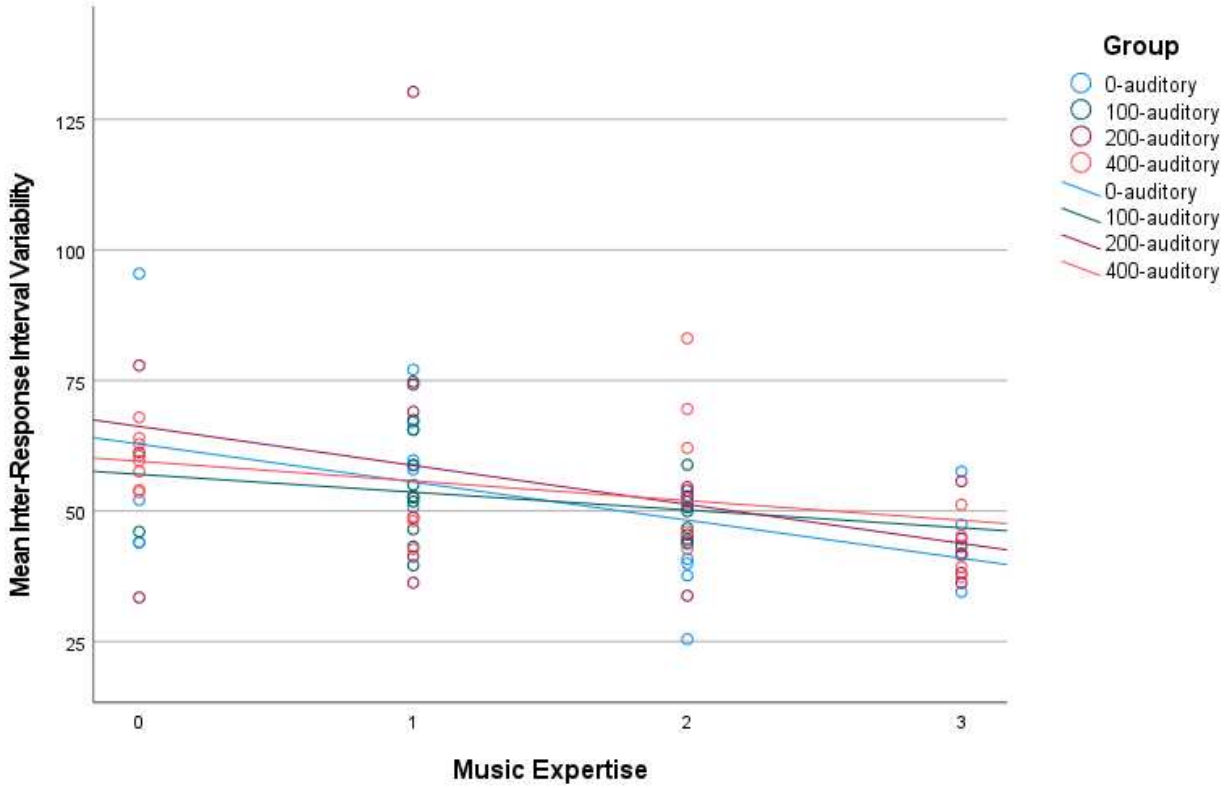

Figure 3.8. Scatter plot depicting the inter-response interval variability averaged across all trials for each level of self-reported music expertise. Music expertise was coded on a 0–3 Likert scale: 0 = "none," 1 = "novice," 2 = "moderate," 3 = "expert." Error bars represent ± 1 standard error.

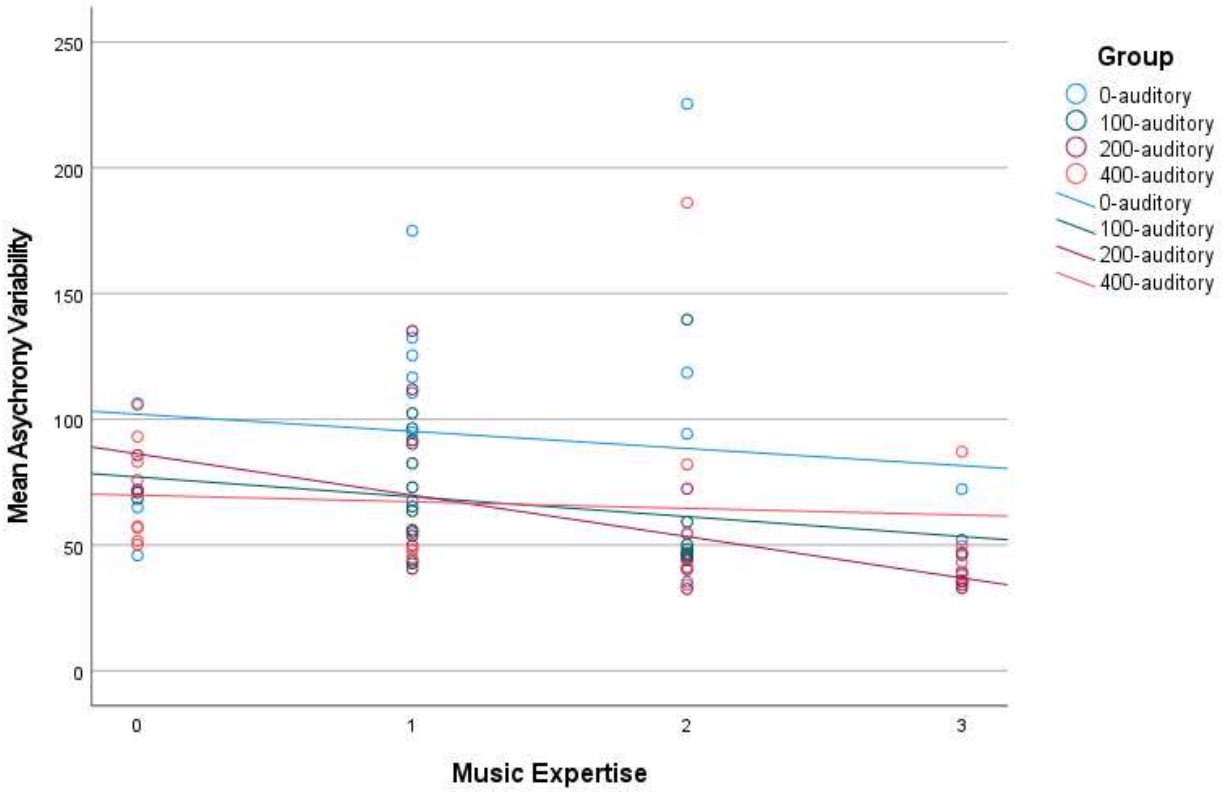

Figure 3.9. Scatter plot depicting the asynchrony variability averaged across all trials for each level of self-reported music expertise. Music expertise was coded on a 0–3 Likert scale: 0 = "none," 1 = "novice," 2 = "moderate," 3 = "expert." Error bars represent ± 1 standard error.

Discussion

The primary purpose of this study was to compare the effect of different numbers of tone presentations, representing different durations of rhythmic auditory priming, on neural resources during auditory priming and rhythmic entrainment using time-frequency measures of evoked power, PLF, and total power. For statistical analyses, ROI were selected *a priori* to ensure results were comparable to findings by Crasta et al. (2018). First, time-frequency measures from the end of the auditory priming condition compared between the three auditory priming groups showed participants with increased exposure to auditory tones had decreased evoked neural responses in an ROI associated with motor processing. Second, there were decreased neural responses at the beginning of a rhythmic entrainment condition following 100 or 200 auditory tone presentations,

but not 400 tone presentations. Third, statistical comparisons of the rhythmic entrainment condition between groups found no significant differences between groups, suggesting the duration auditory priming did not affect neural processing during rhythmic entrainment in any of the *a priori* ROIs. However, total power in an ROI associated with anticipation and predictive did significantly increase in later trials. Fourth, a secondary aim of this study was to determine the effect of different durations of auditory priming on motor performance during the rhythmic entrainment task by comparing inter-response interval mean and variability and asynchrony mean and variability between all four groups. While not statistically significant different with Bonferroni correction, participants with 200 auditory tone presentations had the least asynchrony variability. Finally, music expertise was an important factor for both neural processing and behavioral performance when listening and tapping along to auditory rhythmic stimuli. Implications for future research and clinical practice are discussed.

The Effect of Prior Exposure to Auditory Tones on Auditory Processing

When comparing the last 100 trials of the auditory priming condition between the three auditory priming groups, there was a significant effect of prior tone experience on the evoked power and PLF in the ROI associated with motor processing, 20-45 Hz from 10-60 ms, such that participants in the 400-auditory group used fewer neural resources than the 200- or 100-auditory groups. Orienting responses to novel auditory stimuli are directly tied to motor reflexes (Westman & Walters, 1981). Therefore, decreased evoked power and PLF in the motor ROI following more stimulus repetitions could reflect habituation (Sokolov, 1963), which is a decreased orienting response due to decreased novelty associated with the stimuli (Siddle & Jordan, 1993). EEG researchers have consistently demonstrated a decreased evoked response to a repeated auditory stimulus using sensory gating paradigms (e.g., Boutros & Belger, 1999;

Freedman et al., 1991) which is considered an adaptive response necessary for selective attention and filtering of task-irrelevant information (Jones et al., 2016).

The relatively short ISI of 800 ms in this study must also be taken into consideration. Compared to longer ISIs, shorter ISIs for repeated auditory stimuli may provide less time for recovery of neural generators responsible for auditory processing, which has been measured as a greater decline (attenuation) in the amplitude of the event-related potential component N1 (Budd et al., 1998). Repeated auditory stimuli with short ISIs have also shown greater reduction of event-related evoked potentials in the beta (12-20 Hz) and gamma (30-50 Hz) bands compared to longer ISIs, with the effect being especially strong in the beta band (Kisley & Cornwell, 2006). Therefore, decreased evoked power and PLF of 20-45 Hz (high beta and low gamma) in this study could reflect compounded reduced recovery for auditory processing across time. However, other researchers have found that the recovery period alone was insufficient to explain attenuation of the N1 to auditory stimuli. For example, a delayed inhibitory process 300-400 ms after the initial stimulus may contribute to decreased evoked responses to repeated stimuli with ISIs of 100-400 ms (Sable et al., 2004). Thus, future research comparing time-frequency measures across trials with different ISIs is needed to better understand the role of habitation, neural recovery, and inhibition in auditory processing of rhythmic stimuli.

The finding that prior exposure to rhythmic auditory tones may decrease neural resources required to process of rhythmic auditory tones has some implications for music therapy interventions involving music listening. In neurotypical individuals, listening to music may initially require more neural resources allocated to motor processing, as passive listening to auditory rhythm is known to activate motor brain regions (for review, see Zatorre et al., 2007). Although, continued exposure may free up neural resources for additional processing. Therefore,

patients may benefit from passive listening to allow time for habituation. The music therapist may then gradually increase the degree and complexity of active participation for the patient. In music therapy interventions where the goal is to promote neuroplasticity through repeated firing of neurons (for review, see Stegemöller, 2014), music therapists may consider providing breaks to allow time for the recovery of neural generators. However, more research is needed to understand if recovery time is necessary. Further, it is unknown how the processing of rhythmic auditory stimuli differs in clinical populations known to have decreased habituation and sensory gating e.g., schizophrenia (Arnfred & Chen, 2004; Freedman et al., 1991) or sensory processing disorders (Davies et al., 2009).

An Optimal Duration of Auditory Priming for Rhythmic Entrainment

As hypothesized, there was evidence of a "priming effect" – less power and phase locking during the beginning of the entrainment condition compared to the end of the auditory priming condition. Overall, findings of a priming effect in this study are somewhat consistent with the findings by Crasta et al. (2018) who found significantly less evoked power and PLF in the sensorimotor ROI and significantly less total power in the anticipation and predictive timing ROI in the entrainment condition compared to the auditory priming condition. The current study replicated the priming effect with the 100-auditory and 200-auditory groups, but not the 400-auditory group. In fact, for the 400-auditory group, evoked power and PLF were slightly greater at the beginning of the entrainment condition compared to the end of the auditory priming condition. However, Crasta et al. (2018) compared the average of all 400 trials in the auditory priming condition to the average of all 400 trials in the entrainment condition. Thus, findings in Crasta et al. (2018) may also include the effect of prior exposure to rhythmic tones on subsequent auditory process, rather than priming alone.

The current study was able to replicate Crasta et al.'s (2018) finding for the anticipation and predictive timing ROI, with the greatest difference in total power between the auditory priming and the rhythmic entrainment condition in the 400-auditory group. However, across all ROIs, the groups which had a significant "priming effect" also had the greatest power and PLF at the end of the auditory priming condition. Therefore, significant differences between the conditions tend to reflect more power at the end of auditory priming rather than a greater reduction (i.e., increased efficiency) in neural resources during rhythmic entrainment. Additionally, there was a lack of significant differences between groups in the rhythmic entrainment condition, suggesting different durations of auditory priming did not reduce neural resources during rhythmic entrainment more than other durations or a control. Thus, longer priming may not provide additional neural benefits for engaging rhythmic entrainment interventions compared to shorter durations of priming.

Crasta et al. (2018) did not find a significant priming effect for the motor ROI. Post hoc tests revealed that the current study partly replicated this finding for the 400-priming group. However, there was a significant decrease in evoked power and PLF in motor ROI for the 100- and 200-groups. Therefore, auditory priming may significantly reduce neural resources for motor processes during rhythmic entrainment, but only for durations less than five minutes. Additionally, less PLF in the 200-auditory group compared to the 100-auditory group could reflect fewer resources toward orienting and attending to auditory stimuli, which could free up more neural resources for other tasks. If so, 200 tone presentations (about two minutes) may promote greater neural efficiency than 100 tone presentations (about one minute) for auditory processing of rhythm. However, there were no significant differences in PLF between groups during the entrainment condition. Therefore, it is unclear if two minutes of priming was

advantageous over one minute if priming in increasing neural efficiency during rhythmic entrainment in this sample. To our knowledge, no other studies have measured the effects of duration of auditory priming on the power and PLF of brain oscillations during rhythmic entrainment. Therefore, before clinical recommendations can be drawn about the optimal duration of auditory priming, more research is needed to confirm the effects of different durations of auditory priming on neural performance in neurotypical and clinical populations.

Findings from statistical analyses suggest that different durations of auditory priming did not affect neural resources during rhythmic entrainment in the *a priori* ROIs. However, visualizations of the data showed (see Appendix E) suggested the control group used more neural resources compared to the auditory priming groups. Therefore, this study may be underpowered to detect this differences and future research with a larger sample size is warranted. Further, visual inspection (see Appendix E) showed more differences in rhythmic entrainment condition between groups for higher frequencies outside of the ROIs, including evoked power and PLF above 40 Hz and total power from 20–50 Hz. Future studies may examine ROIs within these higher frequencies to better understand the effects of duration of auditory priming on the allocation of neural resources for anticipation and predictive timing.

The current study also found significantly less total power in the anticipation and predictive timing ROI in the first block compared to later blocks of the rhythmic entrainment condition. Therefore, auditory priming may have a stronger neural effect on the beginning of a rhythmic entrainment task. Behavioral findings by Repp (2010) that participants make more adaptive adjustments during a rhythmic entrainment over time, suggests this may be due to auditory-motor coupling decreasing over time. Changes across blocks of rhythmic entrainment could explain some of the discrepancies between the current study and the Crasta et al. (2018)

study. While the current study compared the end (last 100 trials) of the auditory priming condition to the beginning (first block) of the entrainment condition, Crasta et al. (2018) compared the average of all 400 trials in both conditions. Trends in total power in the anticipation and predictive timing ROI across blocks of the rhythmic entrainment condition in each group (see Figure 3.7) suggest that auditory priming, compared to no priming, produced a more prolonged decrease in neural resources required during rhythmic entrainment. However, this effect was not significant, and more research is needed to determine if auditory priming has prolonged effects on neural resource allocation.

The Effects of Auditory Priming on Behavioral Performance

In this study, there were no significant differences in behavioral performance on the entrainment task between the auditory priming groups. This is not surprising given we found no significant neural differences in the *a priori* ROIs between groups during the rhythmic entrainment condition overall. However, the main effect of group approached significance for asynchrony variability, with the 400-group having the most variable responses and 200-auditory group having the least variable responses. Thus, 200 tone presentations, or about two minutes, may have been the most optimal duration of auditory priming in this sample for improving behavioral performance during rhythmic entrainment.

Few studies have examined the effect of auditory priming on behavioral performance during rhythmic entrainment. A study with patients with Parkinson's Disease found that participants who participated in a finger tapping training saw significant improvements in gait velocity and gait cadence compared to participants who participated in an arm swinging training and a control group (Janzen et al., 2019). The finger tapping training consisted of the participants tapping an index finger along to a metronome at a pace 20% faster than their pre-training

walking cadence for three 1-minute blocks with 30 seconds of rest in between blocks. While the authors considered the finger tapping task a rhythmic priming task, the task also involved movement, making it difficult to compare to the current study. However, findings suggest that auditory priming effects during fine motor tasks may transfer to gross motor movements, supporting the applicability of the current findings to clinical interventions. For example, the finding of reduced asynchrony variability following auditory priming in the current study may support the use of auditory priming to improve the consistency of gross motor movements during rhythm interventions. However, more research is needed to confirm this theory and understand the relationship between neural and behavioral performance following auditory priming.

Musical Expertise and Neural and Behavioral Performance during Rhythmic Entrainment

Examining differences between musicians and nonmusicians was not a primary aim of this study, but due to known functional and structural differences in the brains of musicians and non-musicians (for review, see Kraus & Chandrasekaran, 2010), this factor was tested as covariate. There was a significant covariate effect of music expertise on evoked power in the motor ROI during the auditory priming condition, with greater musical expertise associated with consistently lower evoked power. Adult musicians have less variability in prefrontal auditory evoked responses than nonmusicians, which provides evidence that those with musical training have more efficient selective auditory attention (Strait & Kraus, 2011). Due to this increased efficiency, musicians may require less time to habituate to auditory stimuli. A body of neuroimaging evidence suggests that the coupling of auditory and motor systems, while inherent to humans in general, may be especially efficient in those with musical expertise (for review, see Zatorre et al., 2007). Therefore, less evoked power in the motor ROI during the auditory priming

condition for musicians suggests those with musical expertise in this sample may have been more consistent and efficient in processing auditory rhythmic tones.

There was a significant interaction between condition (auditory priming or rhythmic entrainment) and music expertise for evoked power and PLF in motor ROI. Consistent with findings for the first research question, evoked power and PLF decreased with increased music expertise, suggesting musicians were more consistent and efficient in processing auditory rhythmic tones. In the entrainment condition, differences in evoked power and PLF based on musical expertise were less pronounced. The time-frequency measures at site C3, while closest in proximity to the primary somatosensory cortex (Koessler et al., 2009) likely reflect contributions multiple brain regions including auditory (Henshall et al., 2013) and motor brain regions (Karabanov et al., 2012). Neuroimaging studies of musicians and nonmusicians have demonstrated that, during non-rhythmic finger tapping tasks, piano players tend to show less activity in primary and secondary motor areas (Jäncke et al., 2000) and the cerebellum (Koeneke et al., 2004) than non-musicians. However, when motor tasks which are musically relevant, such as imitating auditory rhythms, engagement of motor brain regions is similar between musicians and non-musicians (Chen et al., 2008). Therefore, the lack of effect of musical training on neural processing for the entrainment condition may be due to the musical relevance of the task. The same study by Chen et al. (2008) also found that recruitment of prefrontal brain regions was greater in musicians than non-musicians during musically relevant tasks, suggesting more top-down recruitment in musicians.

Finally, those with the most musical expertise in this study had the least variable IRI and asynchrony during the rhythmic entrainment task. The mean IRI and asynchrony were not significantly different between auditory priming groups. Together, these findings suggest most

participants were able to perform the entrainment task, but musicians' performance was more consistent. Similarly, Repp (2010) found that musicians did not have significantly different mean asynchrony from nonmusicians, but musicians had significantly less variability of asynchrony than nonmusicians. Repp et al. (2013) also found significantly lower IRI variability in percussionists, i.e., "rhythm experts," compared to other musicians, suggesting performance on rhythmic entrainment tasks can be improved with training. However, Hove et al., 2010 found no significant differences in IRI or asynchrony between musicians and nonmusicians. These contradictory findings may be due to an inconsistency in calculations used for behavioral measures across studies, and future research is warranted.

Limitations and Future Directions

The design of this study had strengths and limitations. This study used *a priori* ROIs so results would be comparable to Crasta et al. (2018). However, time-frequency maps and t-maps (see Appendix E) revealed other potential ROIs which may be examined in a future study. For example, time windows which precede the stimulus may provide more information about anticipation and predictive timing. Additionally, ROIs including higher frequencies, which are associated with higher-order cognitive and attentional processes (Debener et al., 2003) and perception of auditory rhythm (Snyder & Large, 2005), may capture the effect of auditory priming on cognitive resources needed perform the rhythmic entrainment task.

The auditory stimuli used in this study likely had an impact on the outcomes. The simple rhythmic stimuli used in this study served to isolate the effect of rhythm on priming and entrainment. These findings will improve the interpretability of future studies using different tempos (IRIs), complex rhythms, or other musical elements including pitch or harmony, which are known to affect rhythmic entrainment performance (for review, see Repp, 2005). Another

consideration is the duration of the auditory priming condition. The shortest duration of auditory priming in this study, 100 auditory tone presentations, was around one minute and 20 seconds. In music therapy practice, this duration of auditory priming may still have practical limitations, especially with clinical populations with reduced attentional resources. Future studies may examine the effects of shorter durations of auditory priming (i.e., less than one minute) on neural and behavioral performance during rhythmic entrainment.

The participant sample in this study should be considered when interpreting findings. Most participants were college students, which may not be representative of a larger neurotypical adult population. There were more females than males in the study overall and a proportion which may not be representative of a larger population. Further, the proportion of males and females was not equal across groups. Therefore, sex differences could possibly contribute to significant group differences in this same. The current study should be replicated with a larger and more diverse sample to confirm current findings. There were significant covariate effects of musical expertise, suggesting musical training may decrease neural resources needed for neural processing and increase the consistency of behavioral performance on rhythmic entrainment tasks. However, musical expertise was self-reported in this sample, somewhat limiting the reliability and validity of this measure. Further, longitudinal studies or studies directly measuring the effect of musical training on neural and behavioral measures during rhythmic entrainment are needed to confirm causation.

Overall, findings suggest that about two minutes may be an ideal duration for rhythmic auditory stimulation to increase neural efficiency and produce a priming effect. Future studies could test this in the context of a music therapy intervention, which would be approximately the duration of a short song. While finger tapping paradigms are useful for examining basic

mechanisms of rhythmic entrainment, music therapy interventions are often aimed at improving more complex gross motor patterns, such as rhythmic auditory stimulation for gait training (Thaut & Hoemberg, 2014). While there were no significant differences in behavioral measures between groups in the current study, this may be due to the simplicity of the motor task. Future studies may examine the effects of auditory priming on gross motor performance or more complex motor tasks. Finally, as the aim of rhythmic entrainment interventions is to decrease motor impairments, future studies should replicate the current study with clinical populations.

Conclusion

Evidence from the current study suggests that exposure to rhythm reduces neural resources required for auditory processing of rhythm. This effect is moderated by musical expertise, with those with more musical training have more consistently reduced neural responses. A priming effect occurred for participants following 100 and 200 tone presentations, but not following 400 tone presentations, suggesting an ideal duration for auditory priming may be between two and five minutes. However, more research is needed to determine a more precise time frame and apply these findings to clinical interventions using auditory priming. The current study found limited evidence that different durations of auditory priming affected neural and behavioral performance during rhythmic entrainment. However, there were trends in the data showing that the control group with no auditory priming used more neural resources for anticipation and predictive timing overall, especially at the end of the rhythmic entrainment condition, which warrants further investigation. There was also evidence suggesting neural resources for anticipation and predictive timing may increase over time during rhythmic entrainment, regardless of priming. Therefore, rhythmic entrainment interventions may consider how the duration of the intervention affects neural resources. Overall, the current study serves as

a baseline for comparison to improve interpretation of findings in future studies aimed at improving the effectiveness of rhythmic entrainment clinical interventions.

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Chapter 4: Dissertation in Relation to Occupation and Rehabilitation Science

Occupation and Rehabilitation Science (ORS) serves as the theoretical foundation for the ORS Ph.D. program at Colorado State University. "Occupation and Rehabilitation Science focuses on the interdisciplinary study of human performance and participation in everyday occupation and contexts across the lifespan." (Ph.D. in Occupation and Rehabilitation Science, Ph.D. Student Handbook, Colorado State University, 2020-2021). Performance is defined here as discrete capacities necessary for functional behaviors and tasks, including sensory processing and motor control (Brandt & Pope, 1997). Participation is defined here as engagement in everyday activities and occupations which ideally provides a sense of order, balance, health, well-being, meaning, or purpose to life (Matuska & Christiansen, 2008; Pierce, 2000). As defined by Dickie and colleagues (2006), occupations are all activities, ordinary or special, in which humans engage through their lives as occupational beings.

Both rehabilitation science and occupational science provide unique yet overlapping perspectives of human performance and participation. Broadly, rehabilitation science is the study of the process by which performance and participation improve (Brandt & Pope, 1997). Occupational science is the study of human engagement in occupation (Wright-St. Clair & Hocking, 2014), of which human performance and participation are essential components. This dissertation project was designed primarily from a neuroscience perspective. From a neuroscience view, human performance and participation are driven by underlying neural mechanisms. Together, all three sciences provide a richer and more integrated picture of performance and participation from a cellar to occupational level. Additionally, each science offers a different perspective of the role of contextual factors in the environment and in the individual. Thus, the framework informing the rationale for this dissertation project is a modified

version of ORS, Neuroscience-Based Occupation and Rehabilitation Science (Neuro-ORS). The Neuro-ORS framework applied to the dissertation illustrates the neuroscience, occupational science, and rehabilitation science perspectives to rhythmic entrainment auditory priming and their areas of overlap (Figure 4.1).

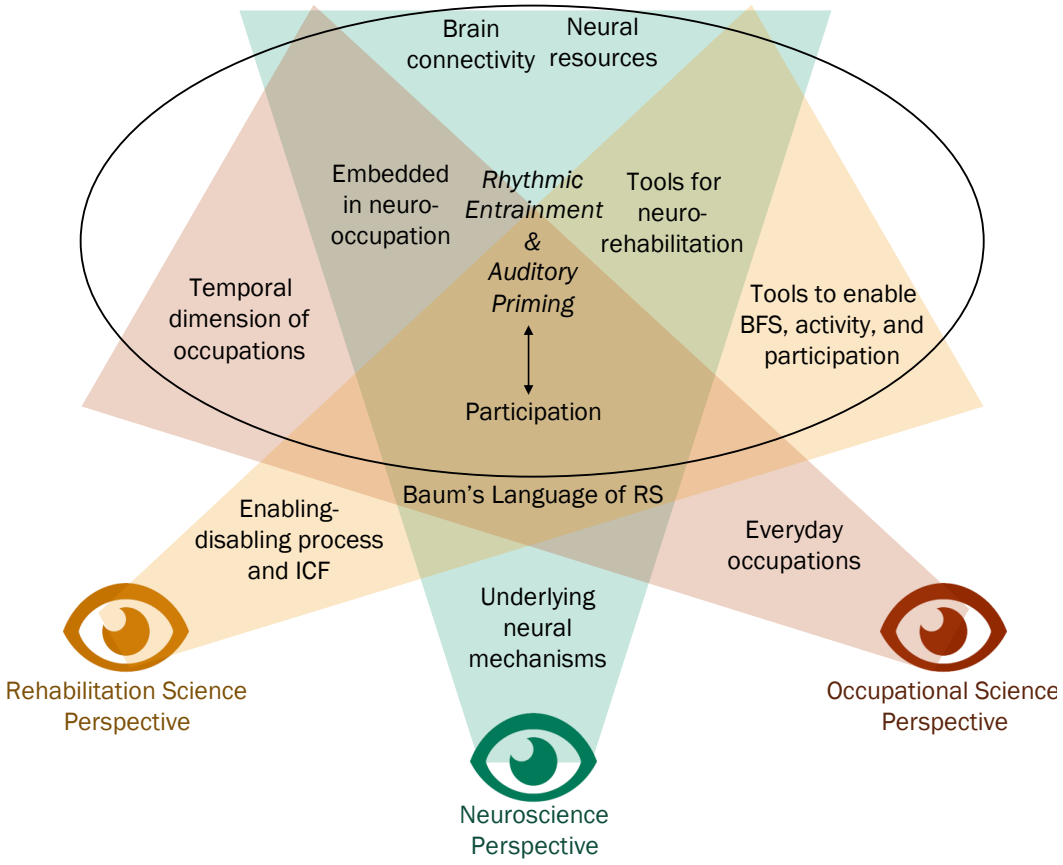

Figure 4.1. *Neuroscience-Based Occupation and Rehabilitation Science View of Dissertation.* The circle in the center represents the proposed dissertation project. Three different but overlapping sciences: neuroscience, occupational science, and rehabilitation science each provide a unique perspective of the proposed dissertation. Each perspective brings to light a different aspect or potential application of the two primary topics of the project: rhythmic entrainment and auditory priming.

Rehabilitation Science Perspective: The ICF

One of the earliest models informing rehabilitation science was developed by Saad Nagi at the end of the 1950s to describe a "disablement process," which was later refined in

collaboration with Nagi by the Institute of Medicine (IOM) in their report "Disability in America" (Pope & Tarlov, 1991). Nagi and the IOM's model was the first to recognize the role of the physical and social context on disability (Masala & Petretto, 2008). Brandt & Pope (1997) later expanded this model as to the *enabling-disabling process*. The most recent version of the Internal Classification of Functioning, Disability, and Health (IFC; Figure 4.2) released by the World Health Organization (WHO) in 2002, is a more comprehensive model based on the enabling-disabling process. Further, the ICF provides a common language for rehabilitation science and practice which allows for communication across disciplines (Stucki, 2005). The ICF is based on a biopsychosocial model (Engel, 1977), as it is designed to integrate medical and social views of disability and health. The ICF defines three levels of functioning which occur at the level of body/body part, whole person, and person in a social context—*body functions and structures*, *activity*, and *participation*, respectively. People can move along a continuum of function and disability at each level while interacting with contextual factors in the *person* and *environment*. Finally, while *health conditions*, can negatively impact any level of the ICF, improvements at any level can attenuate negative effects.

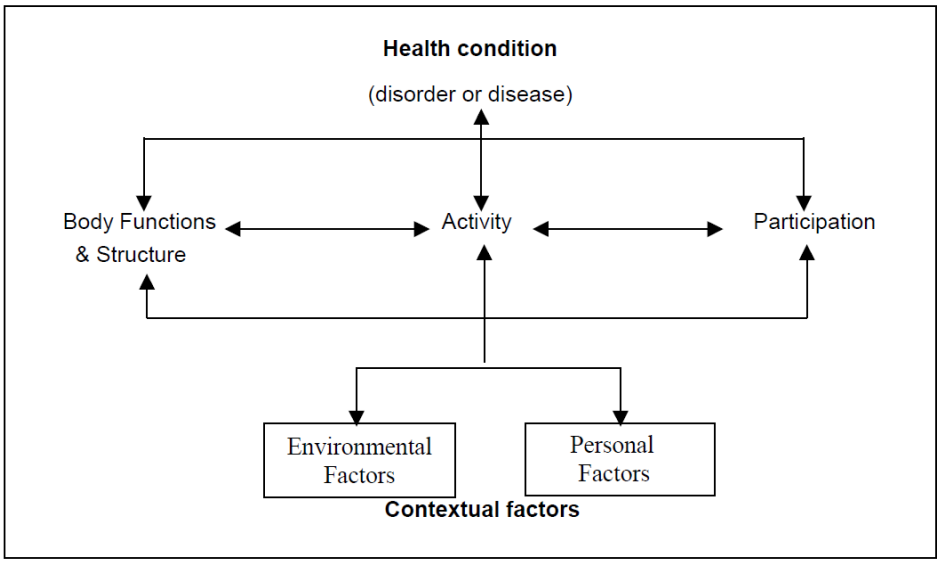

Figure 4.2. *The International Classification of Functioning, Disability, and Health (ICF).* Developed by the World Health Organization (2002), the ICF shows how body functions and structures, activity, and participation interact with each other, contextual factors, and health conditions to change the level of performance along a continuum of function.

Rhythmic Entrainment Applied to the ICF

In the literature review (see Chapter 1), a RS perspective primarily informed the sections on clinical applications. From the RS perspective, rhythmic entrainment and auditory priming may be utilized as tools to enable human performance and participation. For example, rhythmic entrainment may improve motor performance and auditory priming may improve neural efficiency. When applied to the ICF, most research on rhythmic entrainment or priming has focused either at the level of body functions and structures (e.g., Repp, 2005; Repp & Su, 2013) or activity e.g., the effects on motor performance (Thaut et al., 2015). The focus of Study 1 of this dissertation was a better understanding of rhythmic entrainment at the level of body functions and structures, specifically brain connectivity. Study 1 provides evidence that processing auditory rhythm (auditory condition) may promote a consistent pattern of connectivity between functionally distinct brain regions. Therefore, auditory rhythm may be a powerful tool for promoting neural integration necessary for complex activities. The motor

condition had more long-range connections including frontal sites compared to the auditory condition, possibly due to an increased demand for sustained attention in the motor task. Thus, populations with deficits in rhythmic motor performance may benefit from targeting improvements in attention. Further, in the pre-stimulus/response stage of processing, the auditory condition had stronger beta gamma band connections including frontal sites while the motor condition had stronger alpha band connections including parietal and occipital site. This differentiation between the faster frequency bands may represent connections for anticipation (Fujioka et al., 2009) in the auditory condition and connections for spatial organization (Kravitz et al., 2011) in the motor condition. Future research can use these findings to understand how the interaction between anticipatory processes and spatial organization during rhythmic entrainment (for reviews, see Janzen & Thaut, 2018; Nozaradan, 2014; Zatorre et al., 2007) affects functional connectivity. In the post-stimulus/response stage, there was limited evidence of differentiation in connectivity between the auditory and motor conditions, possibly due in part to some shared connectivity patterns. For example, the processing of rhythmic auditory stimuli is known to activate motor networks (for review, see Zatorre et al., 2007). Further, the button presses in the motor condition likely provided some auditory feedback to participants, which would activate auditory pathways. There is evidence suggesting the neural effects of rhythmic stimuli (body functions and structures level) may improve behavioral performance at the activity level (e.g., Haegens & Zion Golumbic, 2018), but research directly relating the neural mechanisms of rhythmic entrainment to behavior limited. Therefore, next steps include relating functional connectivity to discrete measures of rhythmic entrainment motor performance, such as the inter-trial interval and asynchrony variability. Future research may also measure the relationship

between functional connectivity during rhythmic entrainment and motor performance, such as gait variability, or with cognitive skills, such as attention or executive functioning.

Crasta et al. (2018) provided evidence that rhythmic auditory priming may enhance the effects of rhythmic entrainment at the body functions and structures level. Study 2 sought to examine how the duration of auditory priming affects the brain (body functions and structures) and behavior (activity) during rhythmic entrainment. Overall, Study 2 confirmed a neural auditory priming effect and found evidence that prior exposure to auditory rhythm decreases the neural resources required for subsequent auditory processing. Further, the auditory priming effect reached a plateau somewhere between two and five minutes. There was limited evidence that the duration of auditory priming affected discrete measures of behavioral performance during this simple rhythmic task in a neurotypical population. However, there was some evidence to suggest around two minutes of auditory priming may be ideal for improving the consistency of motor performance. Given evidence that rhythmic priming may improve walking in people with Parkinson's Disease (Janzen et al., 2019), future research examining the relationship between neural priming and performance during more complex motor tasks (the influence of body functions and structures on activity) is warranted in neurotypical and clinical populations to be able to effectively measure and target motor deficits. Results will inform the refinement of rhythm- and music-based interventions to effectively target improved neural efficiency, increased consistency in motor performance, and ultimately increased participation.

Neuroscience-Based Rehabilitation Science: Neurorehabilitation

In the context of the ICF, neuroscience primarily focuses on understanding body functions and structures, namely brain/nervous system functions and structures. An approach to rehabilitation which focuses on targeting changes in the brain to improve function at the levels of

activity and participation is *neurorehabilitation* (Khan et al., 2017). Evidence supporting neurorehabilitation is multidisciplinary and includes research in medicine, neurophysiology, physiotherapy, biomechanics, and biomedical engineering. While neurologists may prescribe interventions such as non-invasive brain stimulation, deep brain stimulation, or pharmacological treatments, neurorehabilitation therapists utilize behavioral interventions to promote adaptive neural plasticity (Cramer et al., 2011; Khan et al., 2017).

Adaptive Neural Plasticity and Experience-Dependent Learning. While the general layout of the nervous system is similar across humans, connections are adjusted and reorganized throughout life in response to the environment in a process known as *neural plasticity* (Cramer et al., 2011). At the level of the synapse, there are short-term and long-term adjustments in synaptic strength. An increase in synaptic strength is called potentiation and a decrease in synaptic strength is called depression. Long-term potentiation and long-term depression are prolonged effects on synaptic strength which are the basis of learning and memory (Vanderah et al., 2016). Neural plasticity also occurs in response to brain injury, and can be shaped through therapy (Cramer et al., 2011; Khan et al., 2017). Neural plasticity, both in development and following injury, can be either adaptive or maladaptive. Adaptive neural plasticity is associated with improvements in function. Neural plasticity is maladaptive when it results in loss of function or increased injury (Cramer et al., 2011; Khan et al., 2017; Sharp et al., 2014). While neural plasticity occurs naturally in response to internal and external influences, neurorehabilitation aims to promote adaptive neural plasticity using *experience-dependent principles* such as salience, repetition, and intensity (Kleim & Jones, 2008).

Classical conditioning research has demonstrated the positive effects of salience on learning. Pairing a stimulus with a reward results in increased representation of that stimulus in

the brain, thus improving learning and the ability to successfully and independently perform the behavior in the future (Weinberger, 2004). Kleim and Jones (2008) also argue that high intensity repetitions following a period of rest can improve neural and behavioral outcomes. The benefits of salience, repetition, and intensity are driven by the underlying mechanism of long-term potentiation (LTP), through which repeated firing between neurons results in a lasting increase to the strength of the synaptic connection (Caporale & Dan, 2008). To understand if rhythmic entrainment auditory priming can promote neuroplasticity through these mechanisms, we first need a better understanding of their basic neural mechanisms and relationship to behavior.

Rhythmic Entrainment in Neurorehabilitation. Behavioral interventions which utilize rhythmic entrainment and auditory priming may promote adaptive neural plasticity. It has been established that brain oscillations synchronize to external rhythmic tones i.e., neural entrainment (Cameron & Grahn, 2016; Nozaradan, 2014). There is also evidence that neural entrainment improves behavioral performance on attentional tasks (Haegens & Zion Golumbic, 2018). Thus, rhythmic entrainment paired with a behavior may make the behavior more salient, promoting learning or recovery after injury. Phase-based measures of brain connectivity are thought to reflect the synchrony of neural populations (Cohen & Grafman, 2014). Therefore, rhythmic entrainment may promote LTP necessary for adaptive neural plasticity (Stegemöller, 2014). Study 1, measuring the immediate effects of auditory and motor rhythmic processes on phase-based connectivity, was a necessary first step for future research studying the immediate and long-term effects of rhythmic entrainment on the brain. Evidence from Study 1 suggests both the auditory and motor conditions required synchronization between spatially separate brain regions. However, fewer low-frequency band connections in the auditory condition suggests greater efficiency, which may be ideal for promoting adaptive neuroplasticity following injury (Sharp et

al., 2014). Next steps include measuring functional connectivity when auditory processing and motor performance are combined during rhythmic entrainment. Does rhythmic entrainment increase or decrease the efficiency of motor networks? Does it increase integration between auditory and motor networks? Answers to such questions will be helpful for understanding the mechanisms underlying potential adaptive changes in brain function and behavior performance following rhythmic entrainment. Further, understanding these mechanisms will allow for improvements in rhythmic entrainment interventions.

Rhythm- and music-based interventions are inherently repetitive. In addition, movement to music may decrease perception of exertion and fatigue in neurologic patients compared to physical exercises without music (Lim et al., 2011), potentially increasing intensity of repetitions necessary for adaptive neural recovery. At a neural level, rhythmic auditory priming may reduce neural resources needed in the short-term during rhythmic entrainment compared to motor priming (Crasta et al., 2018). However, based on the findings from Study 2, it is unclear if rhythmic auditory priming significantly reduced neural resources more than no priming (control group) and future research with a larger sample size is needed. Further, more research is needed confirm the optimal duration of rhythmic auditory priming found in Study 2, between two and five minutes, and the effects on neural efficiency and behavioral performance. Finally, Study 2 showed those with more musical training had reduced neural resources needed to process rhythmic auditory stimuli, suggesting a possible training effect. However, more causal evidence is needed to confirm the role of rhythmic entrainment in promoting long-term improvements in neural efficiency and behavioral performance.

Occupational Science Perspective: Neuro-occupation

Neuroscience and occupational science may seem disparate – neuroscience is traditionally more reductionist while occupational science is more holistic. However, both perspectives are needed to fully understand the human experience. Seminal works in occupational therapy reference the link between occupation and the nervous system. For example, Dr. Adolph Meyer in his 1921 talk, "The Philosophy of Occupation Therapy," describes occupations as requiring a connection between the mind, body, and world (Meyer, 1977). Later, Mary Reilly in her 1961 Eleanor Slagle Lecture argued that occupational participation provides the "rich and varied stimuli" (p. 86) needed to support a complex human nervous system (Reilly, 1962). Soon after, A. Jean Ayres (1963) identified the critical role of sensory processing in performing occupations.

Neuro-occupation, a term coined by Padilla and Peyton (1997), describes the dynamic and interdependent relationship between the human nervous system and occupation, situated in the environment. The neuro-occupation model illustrates how healthy human nervous system function is needed to effectively engage in occupations. The nervous system receives feedback about the environment through sensory processing of stimuli. In turn, the nervous system uses this information to direct occupation within the environment. Conversely, participation in occupation allows the nervous system to develop and adapt to the environment appropriately (Padilla & Peyton, 1997). Occupations are inextricably linked with the environment and context through both "temporal and spatial dimensions" (Dickie et al., 2006, p. 88). In other words, the relationship between occupations and the environment changes across time and in different physical contexts. On the nervous system level, sensory processing also includes both spatial and temporal dimensions (Paton & Buonomano, 2018). For example, processing auditory stimuli

allows us to localize the position of objects in space perceive the passage of time. On both an occupational and neural level, temporal and spatial dimensions interact to provide the necessary context for understanding and interacting with the environment. Like neuro-occupation, movement to rhythm is a continuous process involving a cycle of interactions between the environment and brain (Zatorre et al., 2007). Within the neuro-occupation model, rhythm can be viewed as environmental stimuli which cues the brain and nervous system (neural mechanisms). Underlying neural mechanisms then direct the motor behaviors based on these cues. The brain also receives somatosensory feedback about rhythmic entrainment performance. Then, underlying neural mechanisms adjust based on this feedback which often results in more consistent and efficient motor performance during rhythmic entrainment. This iterative process continues throughout.

Rhythmic Entrainment in Neuro-occupation

Occupations have inherent "rhythms" (Meyer, 1977) which can take place in the moment, throughout the day, or over many days or years (Pierce, 2001). Generally, the "rhythm" of occupations is one way of characterizing the temporal dimension. In the moment, each occupation has a unique duration, pacing, sequencing, timing, and frequency/rate of occurrence (Zerubavel, 1985). Throughout the day, habits and routines form through repeated patterns of occupation (Christiansen & Townsend, 2009). Over year of life, patterns of daily occupations shift to help form a personal identity (Matuska & Christiansen, 2008; Pierce, 2001).

Rhythmic entrainment principles may be most directly applicable to the timing of occupations in the moment, for example, pacing. While occupational therapy research has primarily focused on the benefits of improved pacing of occupations through the day (e.g., Birkholtz et al., 2004; Katz et al., 2015; Kengen Traska et al., 2012), pacing during a single task

or activity may also be an important consideration for improving engagement in occupations. One common strategy is to use a timer. However, many occupational therapists report they do not use timers as it may feel unnatural to clients (Birkholtz et al., 2004). Further, timers only provide a cue at the beginning and end of a task. Rhythmic entrainment may be an alternative strategy to cue pacing throughout a task. Rhythmic entrainment to improve discrete motor patterns, such as using auditory rhythmic cues to train upper extremity movements (Jeong & Kim, 2007; Thaut et al., 2002) could be incorporated into more complex and contextually based activities and occupations (e.g., lifting arms to reach for objects in the kitchen).

On the timescale of occupations throughout hours or days, the pacing of individual activities can affect engagement in habits and routines (Pyatak et al., 2022). Habits are one type of behavior or occupation which is repeated, learned, and mostly automatic (Clark et al., 2007). Rhythmic entrainment, when applied to habitual behaviors, may improve performance and participation in occupations. For example, rhythmic auditory stimulation to improve gait (Thaut & Abiru, 2010; Thaut et al., 2015), a habitual motor skill, could then be intentionally transferred to activities such as hiking. Routines are sometimes considered type of habit involving a combination of several activities, or as a structure for organizing habits and other non-habitual occupations (Clark, 2000). Healthy routines synchronize occupations with biological rhythms (Matuska & Christiansen, 2008). Circadian rhythms are processed through different neural mechanism than smaller timescales (Paton & Buonomano, 2018), such as those of rhythmic entrainment. However, improving the pacing of habits and activities embedded within larger routines may ultimately contribute to improved temporal organization of occupations throughout the day. Many people already use music to increase motivation during non-musical activities, often selecting music based on tempo and rhythmicity (Kim et al., 2020). For example, using

upbeat music to encourage exercise or slow music to help with relaxation. Rhythmic entrainment principles may underly this natural inclination.

Rhythmic entrainment is obviously embedded in musical occupations such as playing musical instruments or dancing. Study 2 found evidence those with more music experience and expertise may require fewer neural resources to process rhythmic auditory stimuli and engage in rhythmic entrainment. Thus, participation in musical occupations overtime may change the brain's response to auditory stimuli in the environment. Further, musicians had more consistent behavioral performance on rhythmic entrainment, suggesting that these neural differences may also affect performance and participation in rhythmic activities. Conversely, those who require fewer neural resources to process and engage in rhythmic activities may be more drawn to musical occupations. Some longitudinal studies have confirmed a direct effect of musical training on auditory processing (Kraus et al., 2014). Yet, others have found evidence of a predisposition to improved auditory processing (Herholz et al., 2015; Vaquero et al., 2018). In line with the interactive and iterative relationship between the brain and occupation in neuro-occupation model, it is most likely a combination of training and predisposition which shapes the brain and participation in music (Olszewska et al., 2021). Study 2 did not find a significant covariate effect of dance experience on auditory processing in this sample. Given that movement to music is an important part of rhythmic entrainment interventions, this is surprising. However, the overall dance experience of participants in Study 2 was low. Future studies are needed to understand the role of rhythmic entrainment during participation in dance and how dance affects the brain. Overall, this dissertation, when viewed from a neuro-occupational perspective, provides foundational research on the neural mechanisms of rhythmic entrainment, which can be

applied to improving participation in more complex musical and nonmusical activities and occupations.

Where Occupational and Rehabilitation Science Overlap: Participation

A shared crucial concept in occupation and rehabilitation is participation in everyday contexts. Though each science views participation from different perspectives, both sciences view performance as essential component of function and occupation, with participation as a primary goal. From a rehabilitation science perspective, full participation is subjective and multidimensional, containing both individual and social components (Hammel et al., 2008). However, some argue that the ICF definition of participation is not clear and should be differentiated from social participation (Piškur et al., 2014). From an occupational science perspective, participation in occupation is essential to developing a personal identity and a meaningful life (Matuska & Christiansen, 2008; Pierce, 2000). Compared to occupation and rehabilitation science, neuroscience may appear reductionist. However, explicitly linking neuroscience to participation is necessary for communication among all sciences studying human health and well-being.

A Neuroscience Perspective to Participation

Both the ICF and neuro-occupation models recognize the interaction between brain function and participation. However, neither model clearly links nervous system mechanisms to participation. Baum (2011) proposed an expanded ICF model, called "the language of rehabilitation science" (p. 172) to explicitly connect neuroscience mechanisms to participation in occupations. Baum (2011) argues that including neuroscience language and language from the ICF in one unified spectrum supports communication across disciplines and connects objective and subjective measures of participation. Therefore, Baum's (2011) language of rehabilitation

science provides a useful framework for describing how the EEG measures in this dissertation will contribute to future research and practiced aimed at improving participation. Table 4.1 demonstrates how the EEG measures used to examine biomedical mechanisms in this dissertation connect to participation within Baum's framework. Study 2 also found evidence that participation in music may also affect underlying neural mechanisms. Together, findings from both studies support my overarching long-term goal to contribute to knowledge aimed at developing rhythmic interventions to promote adaptive neural plasticity in those with neurologic-based impairments – ultimately promoting performance and participation in everyday occupations and contexts across the lifespan. This dissertation examining the basic neural mechanisms of rhythmic entrainment and auditory priming in neurotypical individuals was a necessary first step.

Table 4.1. *Rhythmic Entrainment Applied to Baum's (2011) Language of Rehabilitation Science*

Language of Rehabilitation Science Level	EEG Measure	Biomedical Mechanisms	Body Function/Body Structure (ICF)	Functional Limitations	Activity (ICF)	Participation (ICF)
Study 1: Rhythmic Entrainment	• Synchronization of EEG oscillations across sites	• Brain connectivity	• Motor planning • Auditory anticipation	• Mobility • Cognitive skills	• Walking • Learning	• Recreation and leisure • Work or school
Study 2: Auditory Priming	• EEG power and PLF	• Neural resources	• Sensory processing	• Coordination • Attention	• Rhythmic entrainment	• Playing a musical instrument

Conclusion and Overall Connection to Dissertation

All three sciences of the Neuro-ORS model provide unique but overlapping perspectives of the overall purpose of this dissertation: investigating the underlying neural mechanisms of rhythmic entrainment and auditory priming. From a basic neuroscience perspective, this research will fill gaps in knowledge about rhythmic entrainment and priming. For a rehabilitation science perspective, findings can inform interventions aimed at improving function by targeting adaptive

changes in the brain. From an occupational science perspective, findings may inform the temporal components embedded in occupations such as habits and routines. When viewed together, this dissertation answered specific questions about complex and dynamic brain-behavior-environment interactions during rhythmic entrainment which can be applied to improving performance and participation in occupations.

The models of the ICF, neuro-occupation, and Baum's language of rehabilitation science have informed my decision making throughout my dissertation, interpretation of findings, and plans for future research. My research questions were aimed at investigating the underlying neural mechanisms of rhythmic entrainment and auditory priming to provide a piece of the puzzle necessary to understanding the bigger picture of how music-based interventions can impact performance and participation in occupations. The culmination of these models in the Neuro-ORS framework helps me consider my dissertation from multiple perspectives and share findings across multiple disciplines, expanding the reach and impact of my work. Finally, a Neuro-ORS framework will guide my future research using multidisciplinary and translational approaches to integrate knowledge across perspectives and connect findings along a continuum of human function, performance, and participation.

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Appendix A

Adult Screening Questionnaire

Today's Date: _____ Age: _____ Date of birth: _____

Please check your gender: _____ Male _____ Female

Your current educational level _____

The following questions provide us with some information on your learning abilities.
Please answer YES (Y) or NO (N) or Don't Know (D) to the questions.

1. Have you ever been diagnosed by a professional (doctor, psychologist, diagnostician) as having a problem with any of the following?
   a) Reading Disability _____
   b) Learning Problem _____
   c) Depression _____
   d) Delayed Speech _____
   e) Stuttering _____
   f) Other Speech and Language Impairments _____
   g) Attention Deficit Disorder or Hyperactivity _____
   h) Sensory Processing Difficulties _____
   i) Autism _____

2. Have you ever experienced a head injury? _____
   If yes, were you unconscious at the time? _____
   If yes, for how long approximately? _____
   Were you hospitalized at the time for the injury? _____

3. Have you ever had a fainting episode? _____
   If yes, please explain. _____

4. Have you ever been diagnosed with a neurological or psychiatric disorder such as seizures, epilepsy, or depression? _____ Or family history of any of these? _____
   If yes, please explain. _____

5. Are you on any prescription medication? _____
   If so, please write the type of medication that you take. _____

Please answer the following questions about hand preference.
6. Are you right or left handed? _____
7. Which hand do you write with? _____
8. Do you use one hand for some activities and the other of other activities? _____

What is your ethnic and racial background? Please check the all that apply.
Note: This information is required for reporting to our funding agencies.

9. Ethnicity: _____ Hispanic or Latino _____ Not Hispanic or Latino

10. Race: _____ American Indian/Alaska Native _____ Asian
    _____ Native Hawaiian/other Pacific Islander _____ Black/African American
    _____ White _____ Other, please specify _____

_____
Participant Code: **To be filled in by project staff**

Figure A1. Demographic and screening questionnaire used in Study 1.

Participant Code:_____

Auditory-Motor Entrainment Study

Additional questions:

1. Please circle your musical expertise:
   None Novice Moderate Expert
   Please describe:

2. Do you play any music instrument: Yes No
   If yes: please provide name of the instrument/s:

   Number of years you have been playing the instrument:

3. Please circle your expertise at dance
   None Novice Moderate Expert
   Please describe:

   Number of years of training:

4. Languages known:

Figure A2. Music experience and engagement questionnaire used in Study 1.

Appendix B

List of Scripts Written by Susan Mingils for Study 1 Data Analysis

a. Aggregate_CoherenceFiles_from_GenericExport_final.m

Location: V:\Susan Mingils\Coherence Analysis Scripts\Final scripts

Description: Script to aggregate 3 generic data files exported from BrainVision Analyzer, Version 2.2.0 by concatenating the data and saving as a new .mat file. Variations of the script are listed below with differences from original script bolded. Differences from the original script include:

- Changing the filter to select files to aggregate based on analysis type

Aggregate_CoherenceFiles_from_GenericExport_IMC_final.m
Line 40: `[Filenames, Pathname, Filterindex] = uigetfile('*IMC.dat', 'Select data files for the same participant', 'MultiSelect', 'on');`
Aggregate_CoherenceFiles_from_GenericExport_PLV_final.m
Line 40: `[Filenames, Pathname, Filterindex] = uigetfile('*PLV.dat', 'Select data files for the same participant', 'MultiSelect', 'on');`
Aggregate_CoherenceFiles_from_GenericExport_PLG_final.m
Line 40: `[Filenames, Pathname, Filterindex] = uigetfile('*PLG.dat', 'Select data files for the same participant', 'MultiSelect', 'on');`

- Version for eyes-open rest condition with different paths to select and save data

Aggregate_CoherenceFiles_from_GenericExport_EOP_final.m
Line 37: `cd 'U:\U - Entrainment\Export Files - EOP_Coherence'`
Line 40: Manually changed filter for each type of analysis (MSC, IMC, PLV, or PLG)
Line 106: `cd 'U:\U - Entrainment\Export Files - EOP_Coherence\Aggregated Data Files'`

b. Create_Coherence_DataTables_from_AggFile_final_short.m

Location: V:\Susan Mingils\Coherence Analysis Scripts\Final scripts

Description: The script serves three main functions: 1) to put the data into a table format, 2) average the data into 50 millisecond bins within 5 different frequency bands, and 3) export the data averaged into bin to the Access database for the study. Variations of the script are listed below with differences from original script in red. Differences from the original script include:

- A version which looks through current records in Access database and deletes duplicates before adding new records.

Create_Coherence_DataTables_from_AggFile_final.m
Lines 284-304 (commented out in "short" version to reduce processing time)

- Changing the filter to select files to average and store

Create_Coherence_DataTables_from_AggFile_final_short_MSC.m
Line 59: `[Filenames, Pathname, Filterindex] = uigetfile('*MSC.mat', 'Select aggregated data files to process', 'MultiSelect', 'on');`

Create_Coherence_DataTables_from_AggFile_final_short_IMC.m
Line 59: `[Filenames, Pathname, Filterindex] = uigetfile('*IMC.mat', 'Select aggregated data files to process', 'MultiSelect', 'on');`
Create_Coherence_DataTables_from_AggFile_final_short_PLV.m
Line 59: `[Filenames, Pathname, Filterindex] = uigetfile('*PLV.mat', 'Select aggregated data files to process', 'MultiSelect', 'on');`
Create_Coherence_DataTables_from_AggFile_final_short_PLG.m
Line 59: `[Filenames, Pathname, Filterindex] = uigetfile('*PLG.mat', 'Select aggregated data files to process', 'MultiSelect', 'on');`

- Version for eyes-open rest condition with different path to select data

Create_Coherence_DataTables_from_AggFile_final_Rest_short.m
Line 47: `cd 'U:\U - Entrainment\Export Files - EOP_Coherence\Aggregated Data Files'`
Line 58: Manually changed filter for each type of analysis (MSC, IMC, PLV, or PLG)

c. Z_scores_calculatemeans_bandchannelmaps_fromdatabase_final.m

Location: V:\Susan Mingils\Coherence Analysis Scripts\Coherence Map Drawing

Description: Retrieve data from Access database to calculate z scores from coherence or phase locking data within 50 ms bins and draw band-channel pair maps based on a selected threshold. Variations are listed below.

- Version to calculate z-scores and draw band-channel pair maps for one frequency band from data base

Z_scores_calculatemeans_bandchannelmaps_fromdatabase_ROIs_final.m

- Version to draw band-channel pair maps for multiple frequency bands in one map withing ROIs using the saved mean data files.

ROIs_bandchannelmaps_final.m

- Version to draw band-channel pair maps for multiple frequency bands in one map withing ROIs using the saved mean data files with thresholds for both phase locking value and phase lag index.

ROIs_bandchannelmaps_PLVandPLG_final.m

d. Motor_only_IRI_final_SM.m

Location: V:\Susan Mingils\Coherence Analysis Scripts\Final scripts

Description: Script to calculate the inter-response interval mean and variability from the behavioral data for the motor condition in Study 1.

Appendix C

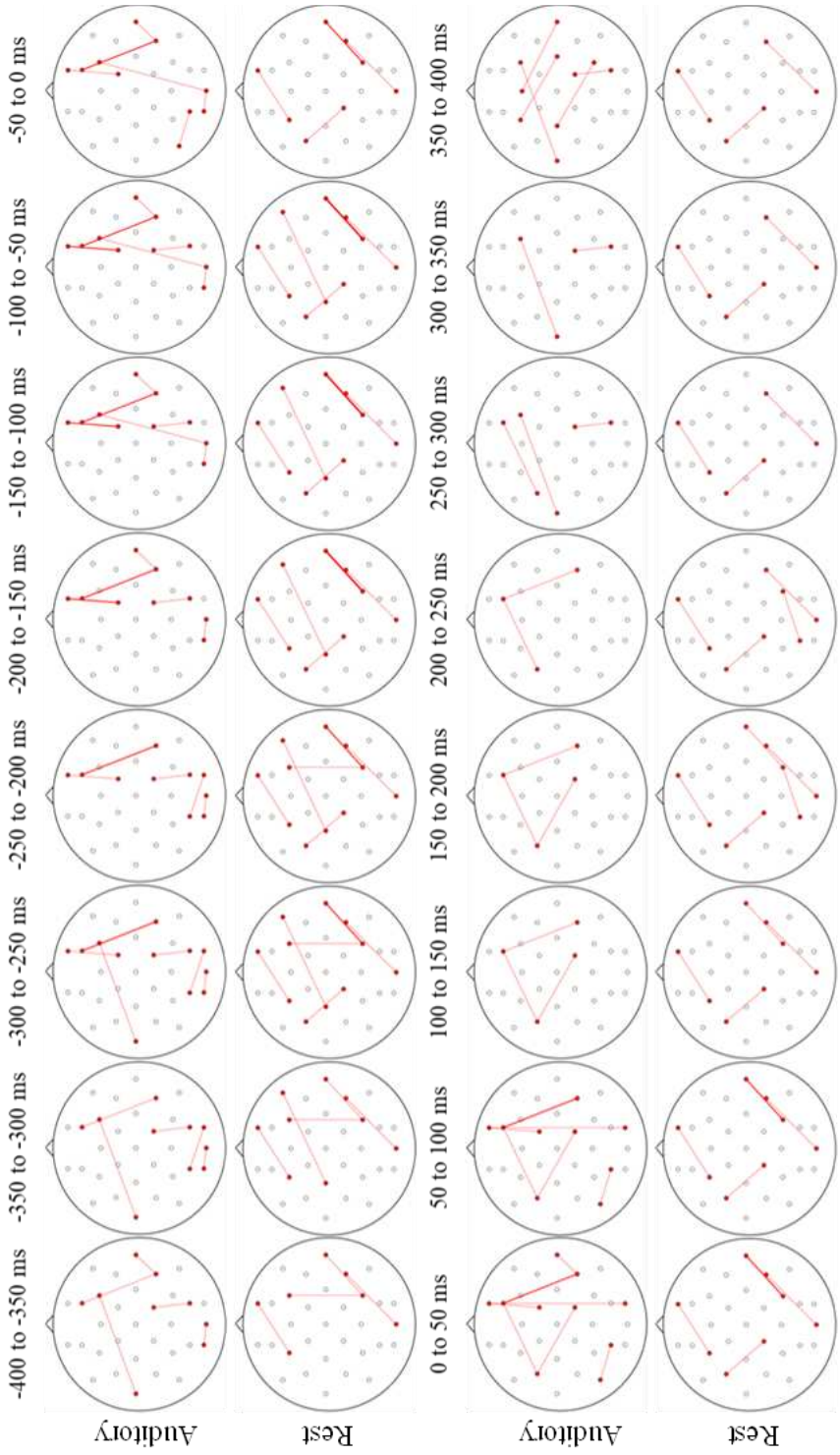

Figure C1. 50 ms bins from -400 to 400 ms for standardized imaginary part of coherency with threshold of ±0.6 for the delta band in the auditory and rest conditions in Study 1.

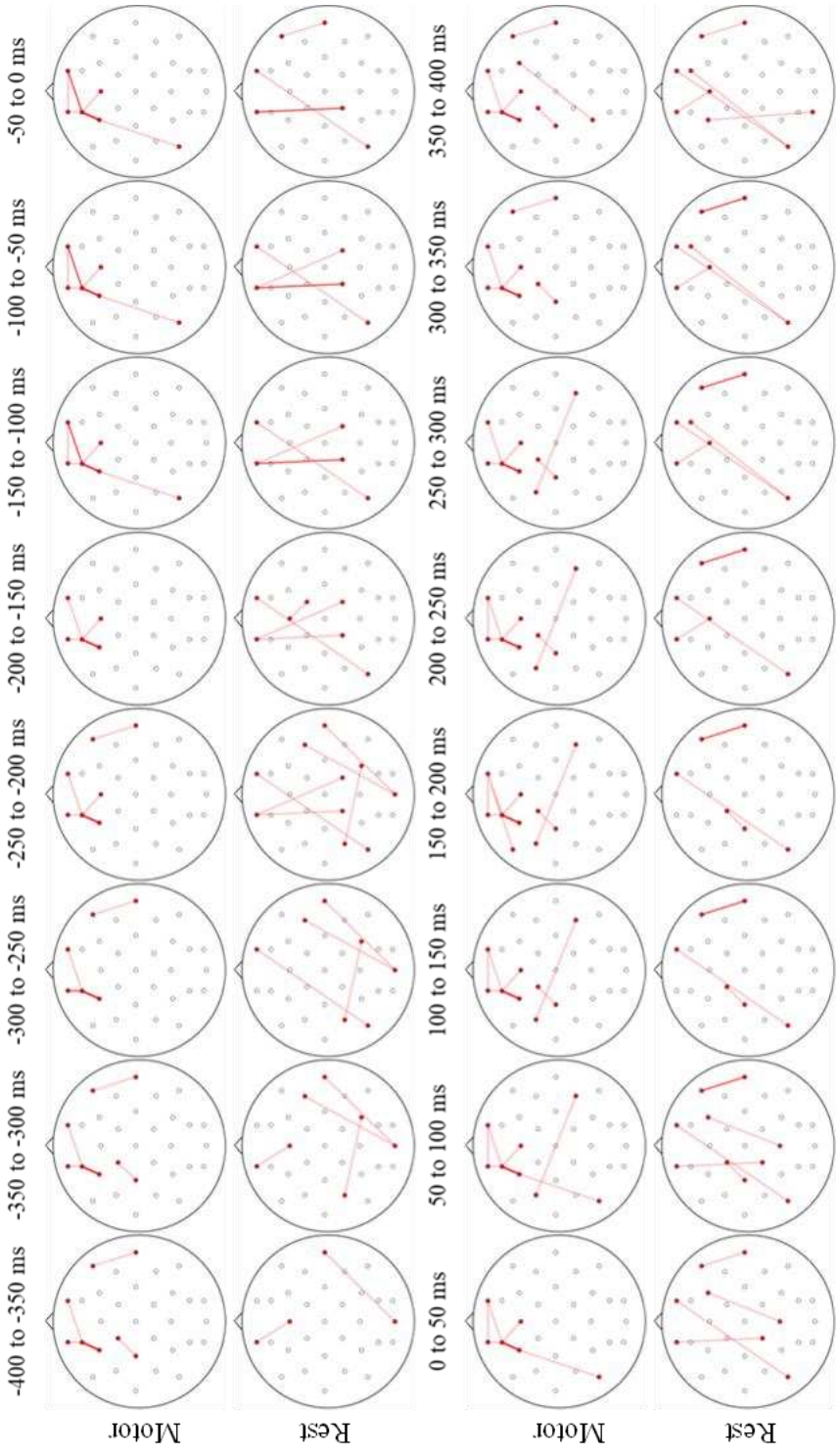

Figure C2. 50 ms bins from -400 to 400 ms for standardized imaginary part of coherency with threshold of ±0.6 for the delta band in the motor and rest conditions in Study 1.

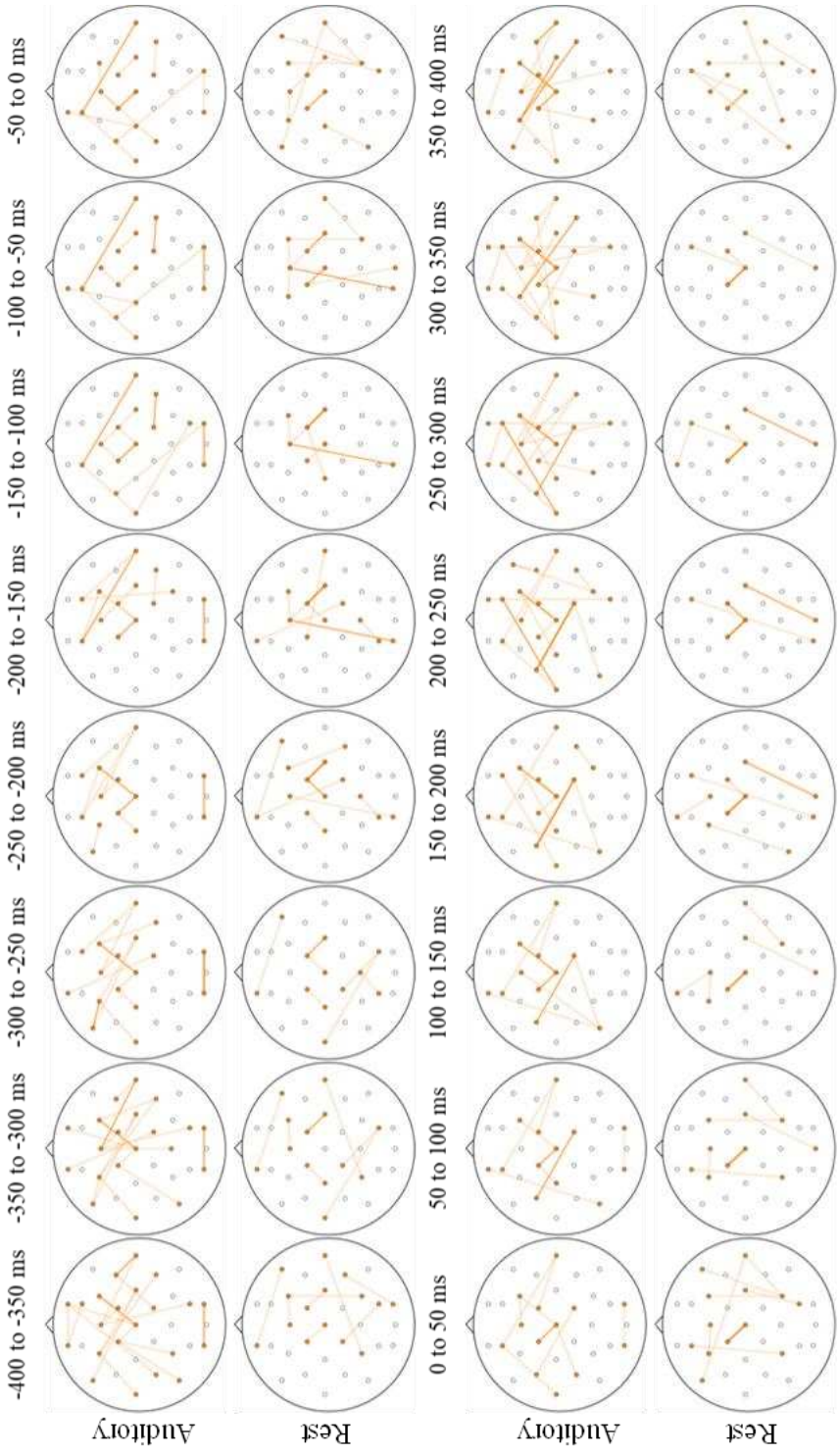

Figure C3. 50 ms bins from -400 to 400 ms for standardized imaginary part of coherency with threshold of ±0.6 for the theta band in the auditory and rest conditions in Study 1.

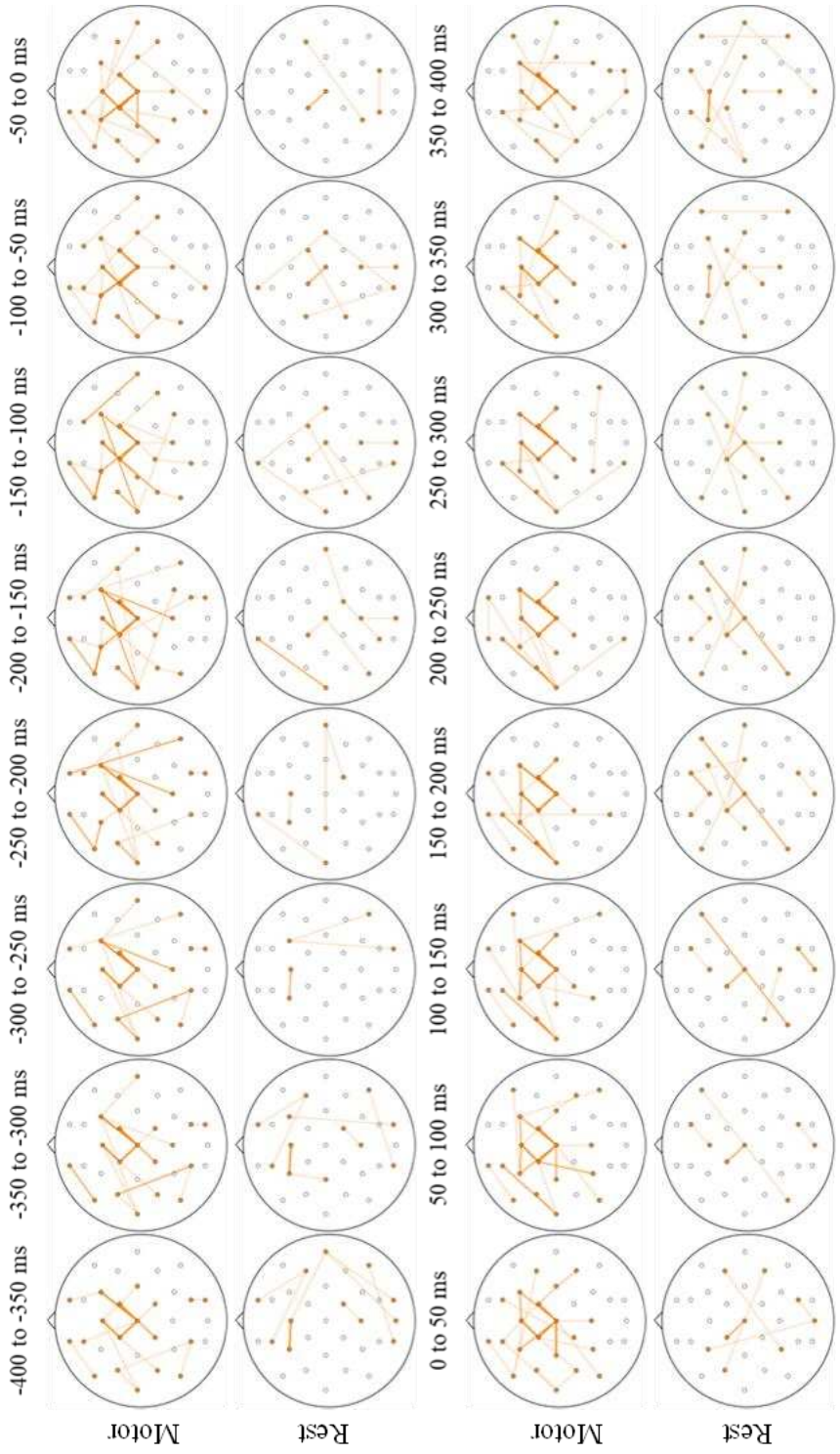

Figure C4. 50 ms bins from -400 to 400 ms for standardized imaginary part of coherency with threshold of ±0.6 for the theta band in the motor and rest conditions in Study 1.

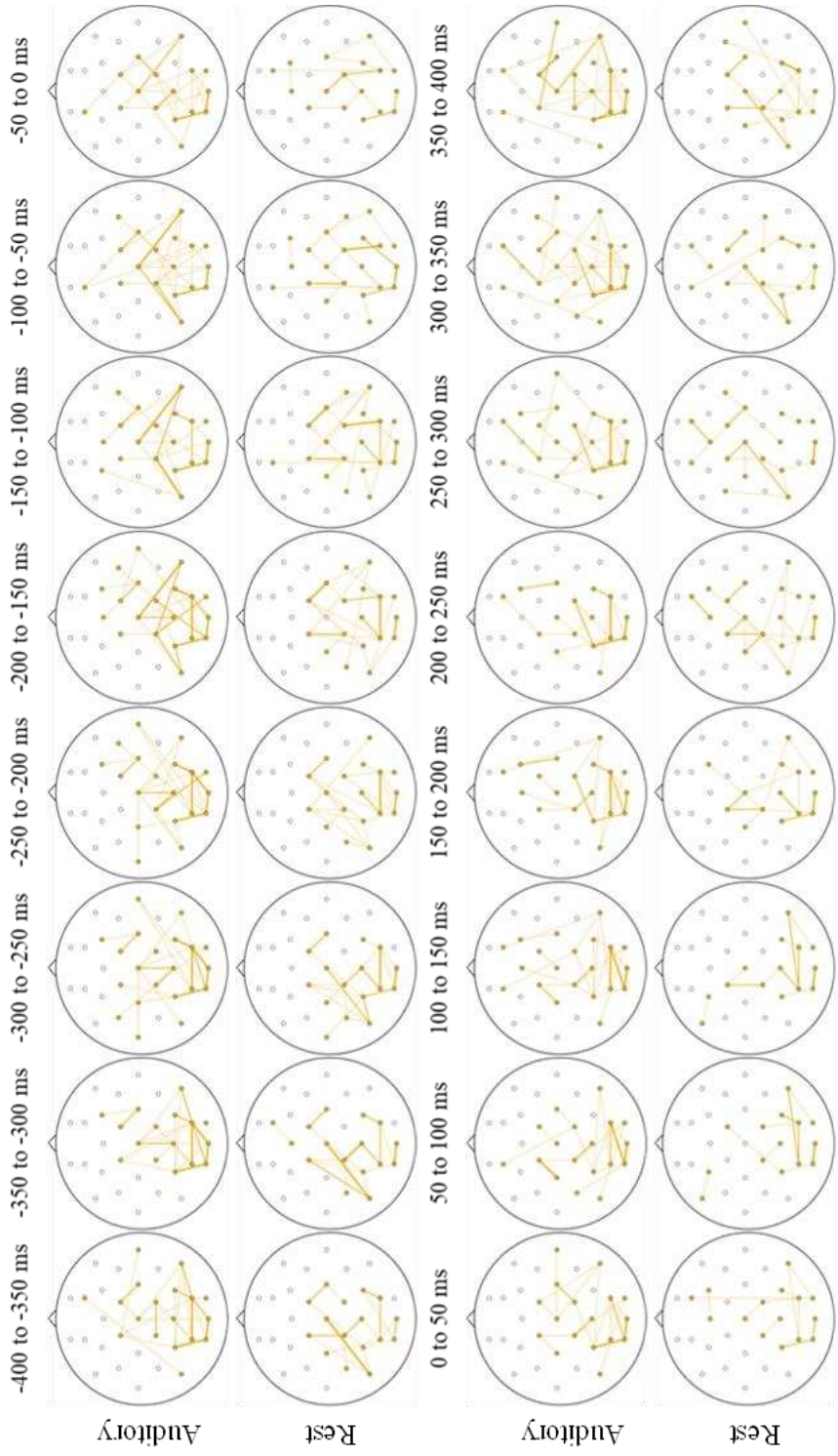

Figure C5. 50 ms bins from -400 to 400 ms for standardized imaginary part of coherency with threshold of ±0.6 for the alpha band in the auditory and rest conditions in Study 1.

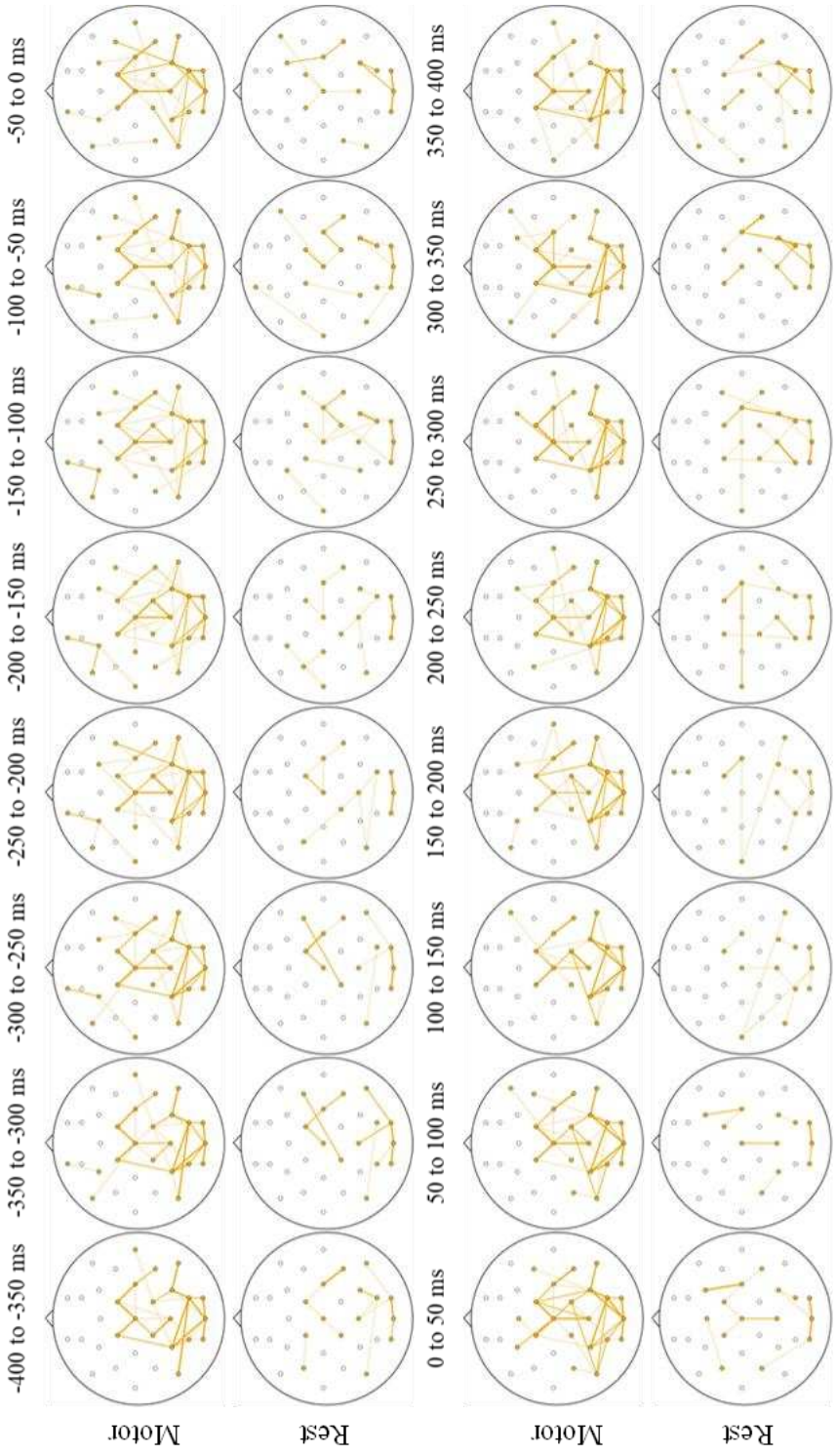

Figure C6. 50 ms bins from -400 to 400 ms for standardized imaginary part of coherency with threshold of ±0.6 for the alpha band in the motor and rest conditions in Study 1.

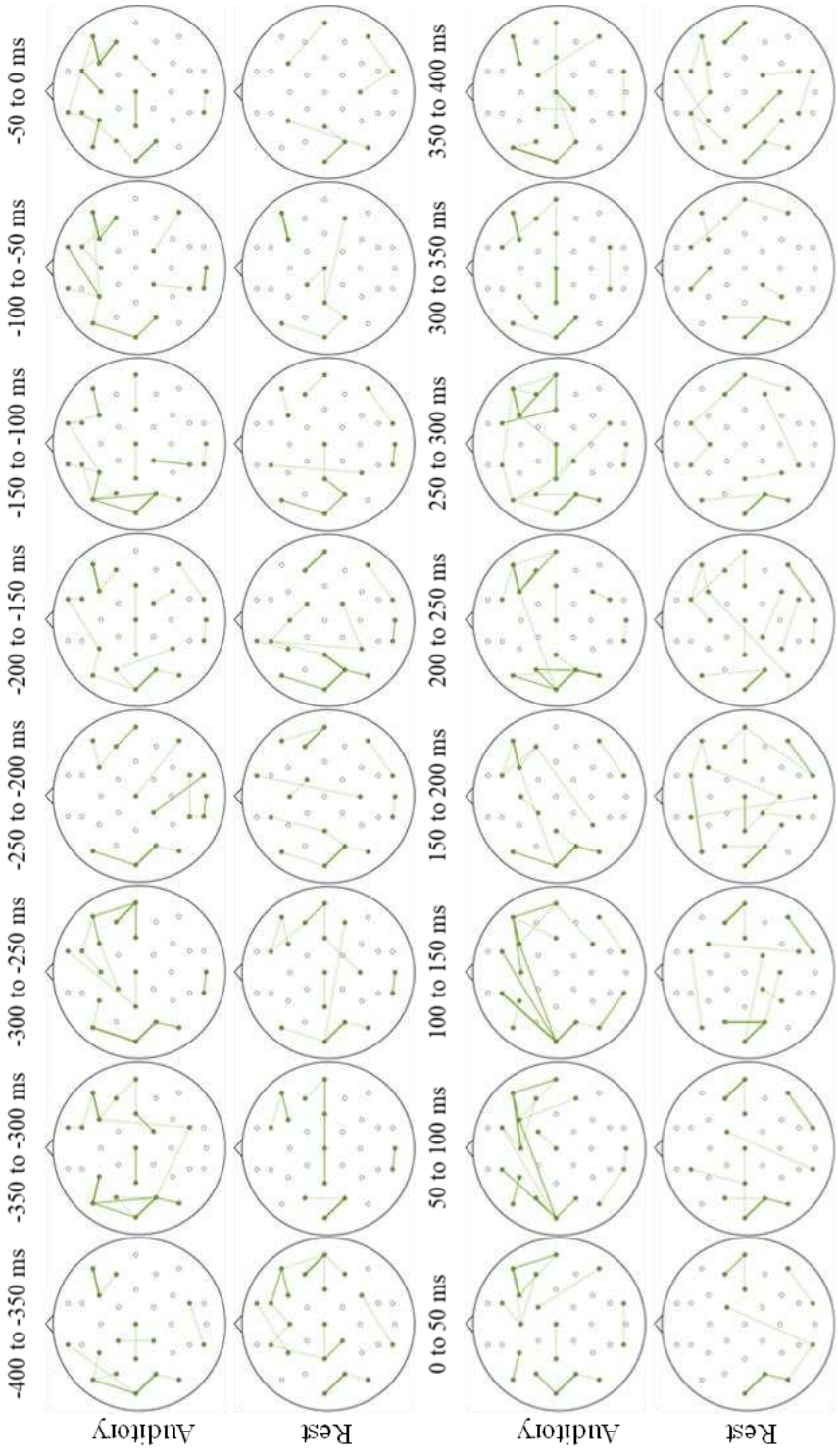

Figure C7. 50 ms bins from -400 to 400 ms for standardized imaginary part of coherency with threshold of ±0.6 for the beta band in the auditory and rest conditions in Study 1.

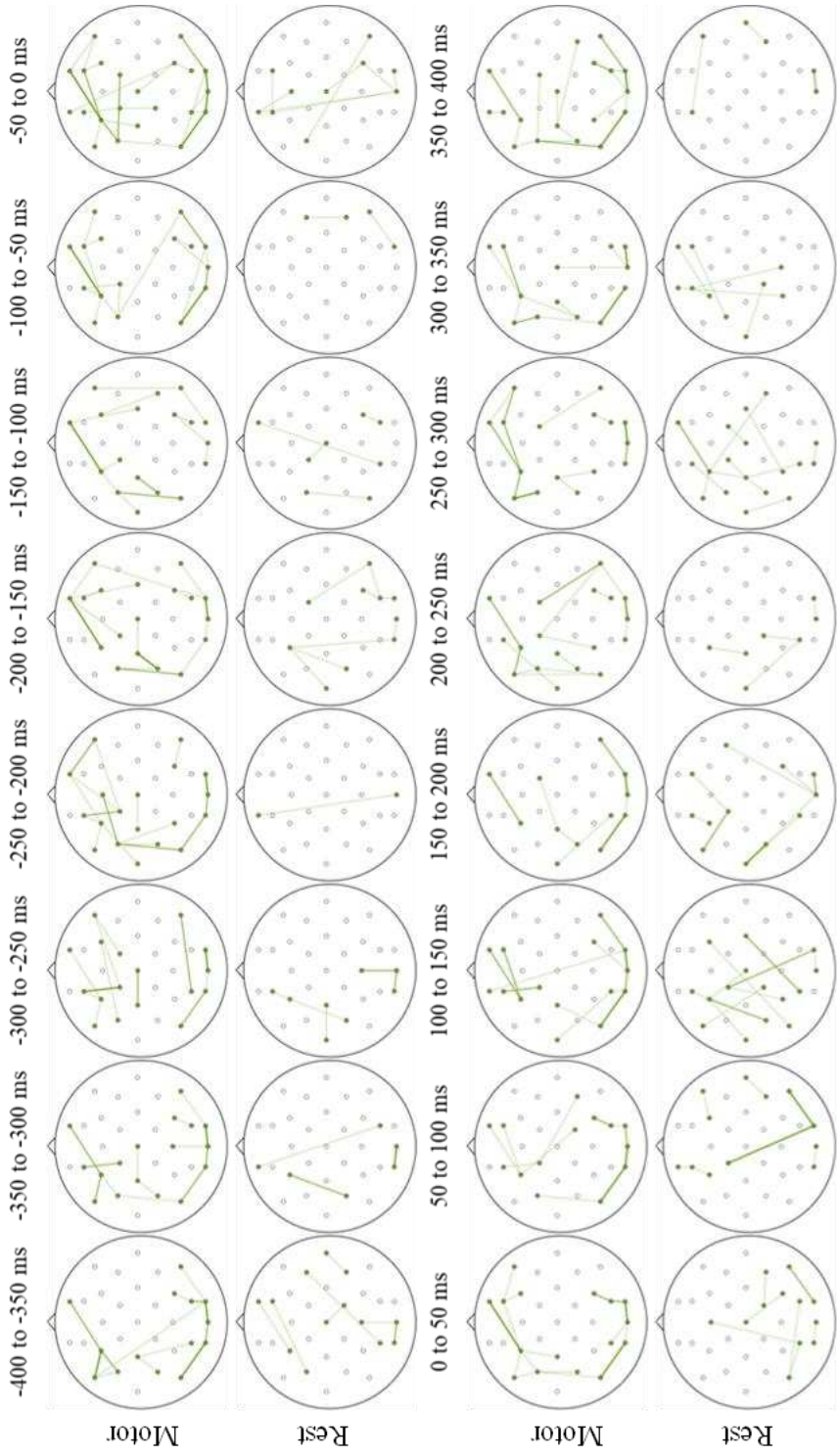

Figure C8. 50 ms bins from -400 to 400 ms for standardized imaginary part of coherency with threshold of ±0.6 for the beta band in the auditory and rest conditions in Study 1.

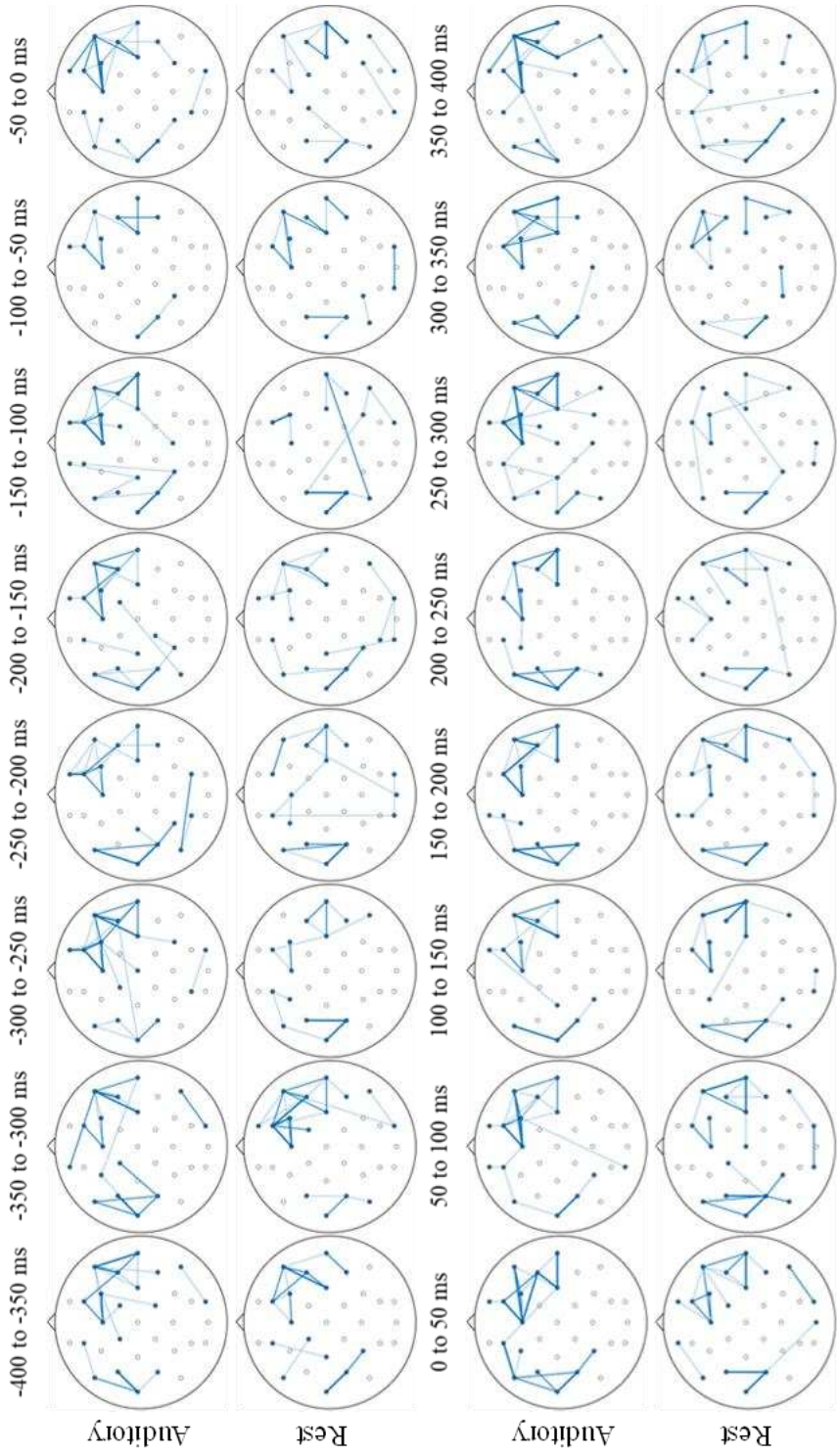

Figure C9. 50 ms bins from -400 to 400 ms for standardized imaginary part of coherency with threshold of ±0.6 for the beta band in the auditory and rest conditions in Study 1.

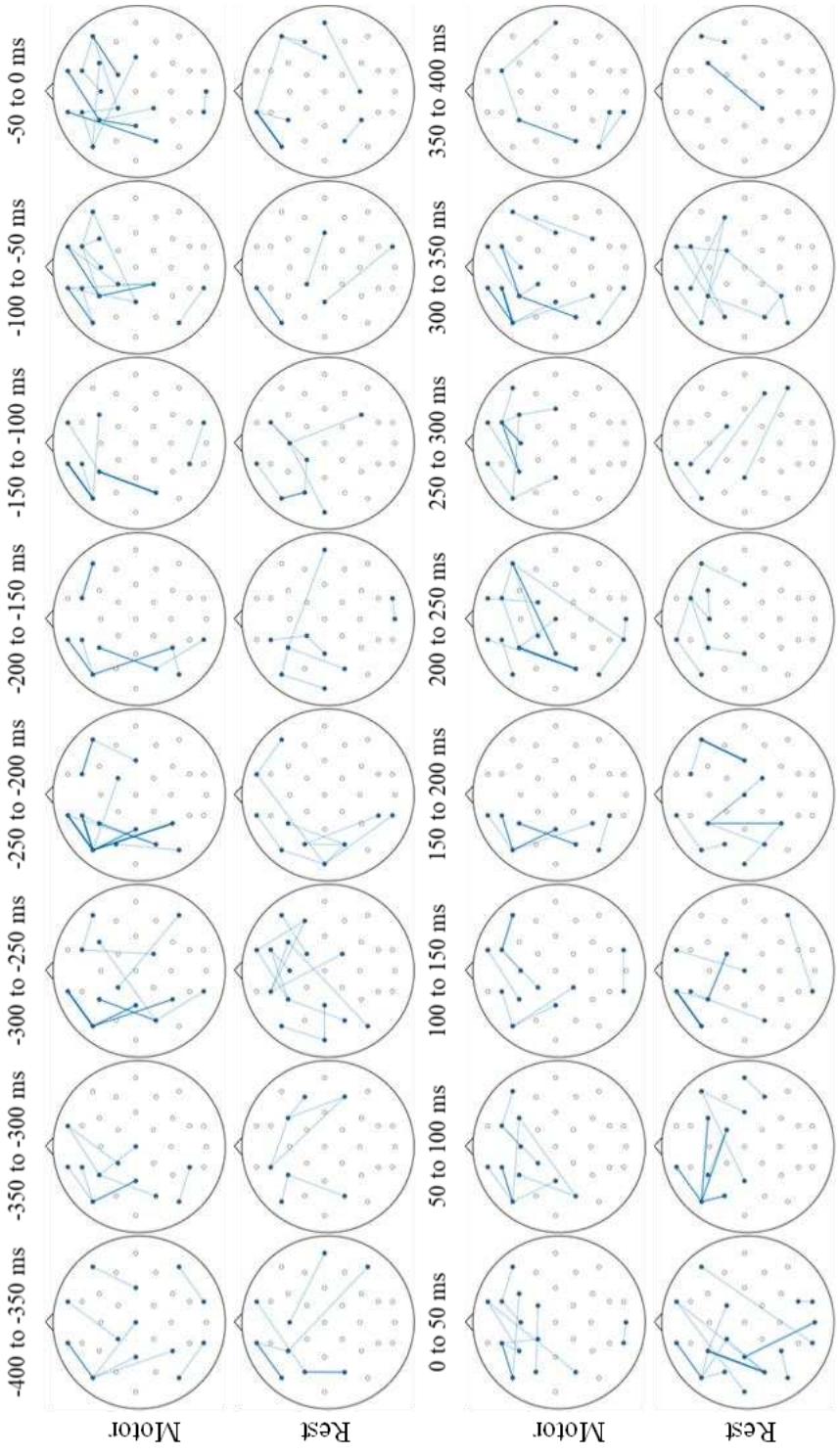

Figure C10. 50 ms bins from -400 to 400 ms for standardized imaginary part of coherency with threshold of ±0.6 for the beta band in the auditory and rest conditions in Study 1.

Appendix D

Adult Screening Questionnaire

Today's Date: _____ Age: _____ Date of birth: _____

Please check your sex at birth: _____ Male _____ Female

Your current educational level _____

The following questions provide us with some information on your learning abilities.
Please answer YES (Y) or NO (N) or Don't Know (D) to the questions.

1. Have you ever been diagnosed by a professional (doctor, psychologist, diagnostician) as having a problem with any of the following?
   a) Reading Disability _____
   b) Learning Problem _____
   c) Depression _____
   d) Delayed Speech _____
   e) Stuttering _____
   f) Other Speech and Language Impairments _____
   g) Attention Deficit Disorder or Hyperactivity _____
   h) Sensory Processing Difficulties _____
   i) Autism _____

2. Have you ever experienced a head injury? _____
   If yes, were you unconscious at the time? _____
   If yes, for how long approximately? _____
   Were you hospitalized at the time for the injury? _____

3. Have you ever had a fainting episode? _____
   If yes, please explain. _____

4. Have you ever been diagnosed with a neurological or psychiatric disorder such as seizures, epilepsy, or depression? _____ Or family history of any of these? _____
   If yes, please explain. _____

5. Are you on any prescription medication? _____
   If so, please write the type of medication that you take. _____

Please answer the following questions about hand preference.
6. Are you right or left handed? _____
7. Which hand do you write with? _____
8. Do you use one hand for some activities and the other of other activities? _____

What is your ethnic and racial background? Please check the all that apply.
Note: This information is required for reporting to our funding agencies.

9. Ethnicity: _____ Hispanic or Latino _____ Not Hispanic or Latino

10. Race: _____ American Indian/Alaska Native _____ Asian
    _____ Native Hawaiian/other Pacific Islander _____ Black/African American
    _____ White _____ Other, please specify _____

_____
Participant Code: **To be filled in by project staff**

Figure D1. Demographic and screening questionnaire used in Study 2.

Participant Number:_____

Music Engagement Questionnaire

1. Please circle your musical expertise:

None Novice Moderate Expert

Please describe:

2. Please circle your expertise at dance

None Novice Moderate Expert

Please describe:

3. How important is music in your life? (circle one)

not at all of little importance somewhat important very important

4. List all the languages in which you are proficient:

Which of the following activities have you participated in?

5. Play in a band Yes_____ No_____
If you answered yes, for how long did you participate in this activity (check one)?

____0-6 months
____6 months-1 year
____1 to 2 years
____2 to 3 years
____3 to 4 years
____5+ years

At what age were you when started this activity? _____

6. Play in an orchestra Yes_____ No_____
If you answered yes, for how long did you participate in this activity (check one)?

____0-6 months
____6 months-1 year
____1 to 2 years
____2 to 3 years
____3 to 4 years
____5+ years

At what age were you when started this activity? _____

Continued on back

Figure D2a. Music experience and engagement questionnaire used in Study 2.

7. Sing in a chorus or choir Yes_____ No_____
   If you answered yes, for how long did you participate in this activity (check one)?
   ____0-6 months
   ____6 months-1 year
   ____1 to 2 years
   ____2 to 3 years
   ____3 to 4 years
   ____5+ years

   At what age were you when started this activity? _____

8. Take private singing lessons Yes_____ No_____
   If you answered yes, for how long did you participate in this activity (check one)?
   ____0-6 months
   ____6 months-1 year
   ____1 to 2 years
   ____2 to 3 years
   ____3 to 4 years
   ____5+ years

   At what age were you when started this activity? _____

9. Take private lessons on an instrument Yes_____ No_____
   If you answered yes, for how long did you participate in this activity (check one)?
   ____0-6 months
   ____6 months-1 year
   ____1 to 2 years
   ____2 to 3 years
   ____3 to 4 years
   ____5+ years

   At what age were you when started this activity? _____

10. Formal training (lessons or class instruction) in dance Yes_____ No_____
    If you answered yes, for how long did you participate in this activity (check one)?
    ____0-6 months
    ____6 months-1 year
    ____1 to 2 years
    ____2 to 3 years
    ____3 to 4 years
    ____5+ years

    At what age were you when started this activity? _____

Figure D2b. Music experience and engagement questionnaire used in Study 2, continued.

Appendix E

Visual Inspection of Time-Frequency Data in Study 2

For visual inspection of the data, time-frequency plots of evoked power, PLF, and total power were mapped from -400 ms to 400 ms around the auditory stimulus for the last 100 trials of the auditory priming condition and each of the four blocks of the rhythmic entrainment condition for each group. T-maps were created in MATLAB by testing for significant differences ($p < 0.05$) at each data point within and between groups. Results were mapped if at least 5 consecutive data points were significantly different. To answer the first research question and determine if the brain's response to auditory stimuli is influenced by prior experience, the last 100 trials of the auditory between the three auditory priming groups were compared using t-maps. To answer the second research question, t-maps were created to see if there was a significant difference in time-frequency measures during the last 100 trials of auditory priming condition compared to the first block of the rhythmic entrainment condition within each of the three auditory priming groups. To answer the third research question and see if the number of tones, representing duration of auditory priming, affects changes in time-frequency measures during the rhythmic entrainment condition, the first block of the rhythmic entrainment condition between groups using t-maps.

Visual Inspection – First Research Question

To see how prior exposure to auditory tones affected auditory processing (first research question), time-frequency plots for last 100 trials of the auditory priming condition between the three auditory priming groups were visually inspected and compared using t-maps. For evoked power (Figure E1), t-maps showed no significant differences between the auditory-100 and auditory-200 group. The t-map comparing the auditory-200 and auditory-400 groups showed significant differences around -400 and -300 ms, with more evoked power in the 200-auditory

group between 15–20 Hz and 25–40 Hz. The t-map comparing the auditory-100 and auditory-400 groups confirmed an *a priori* ROI of 20-45 Hz 10-60 ms, corresponding to motor processes. For PLF (Figure E2), t-maps showed two small time-frequency regions around 0 and 100 ms and 40–50 Hz with less PLF in the 200-auditory group compared to the 100-auditory group. T-maps also showed significantly less PLF in the 400-auditory group overall compared to the 100-auditory group and the 200-auditory group and confirmed the *a priori* ROI of 20–45 Hz 10–60 ms, corresponding to motor processes. For total power (Figure E3), t-maps showed significant differences between the 100-auditory and 200-auditory groups from approximately 30–45 Hz in 50 to 100 ms windows across time, but not between the 100-auditory and 400-auditory group, nor between the 200-auditory and 400-auditory groups.

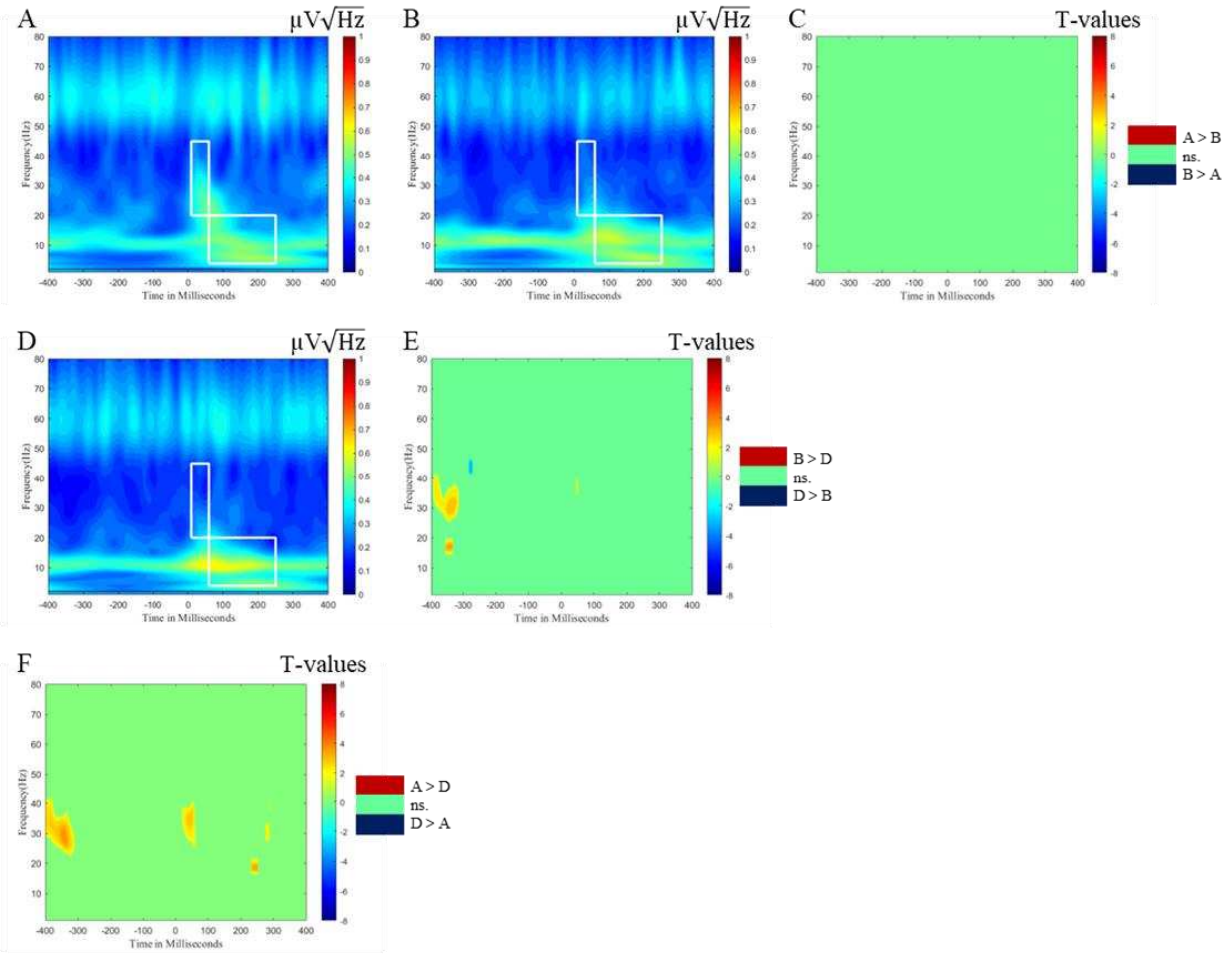

Figure E1. Evoked power time-frequency plots and t-maps of the last 100 trials of the auditory condition between each auditory priming group at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, & D, represents evoked power with warmer colors indicating greater intensity. The color bar for plots C, E, & F represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Auditory-100 group. **B.** Auditory-200 group. **C.** T map comparing the auditory-100 group to the auditory-200 group. **D.** Auditory-400 group. **E.** T map comparing the auditory-200 group to the auditory-400 group. **F.** T map comparing the auditory-100 group to the auditory-400 group. The white outlined boxes represent 1) the motor ROI, 20–45 Hz from 10 to 60 ms, and 2) the sensorimotor ROI, 4–20 Hz from 60 to 250 ms.

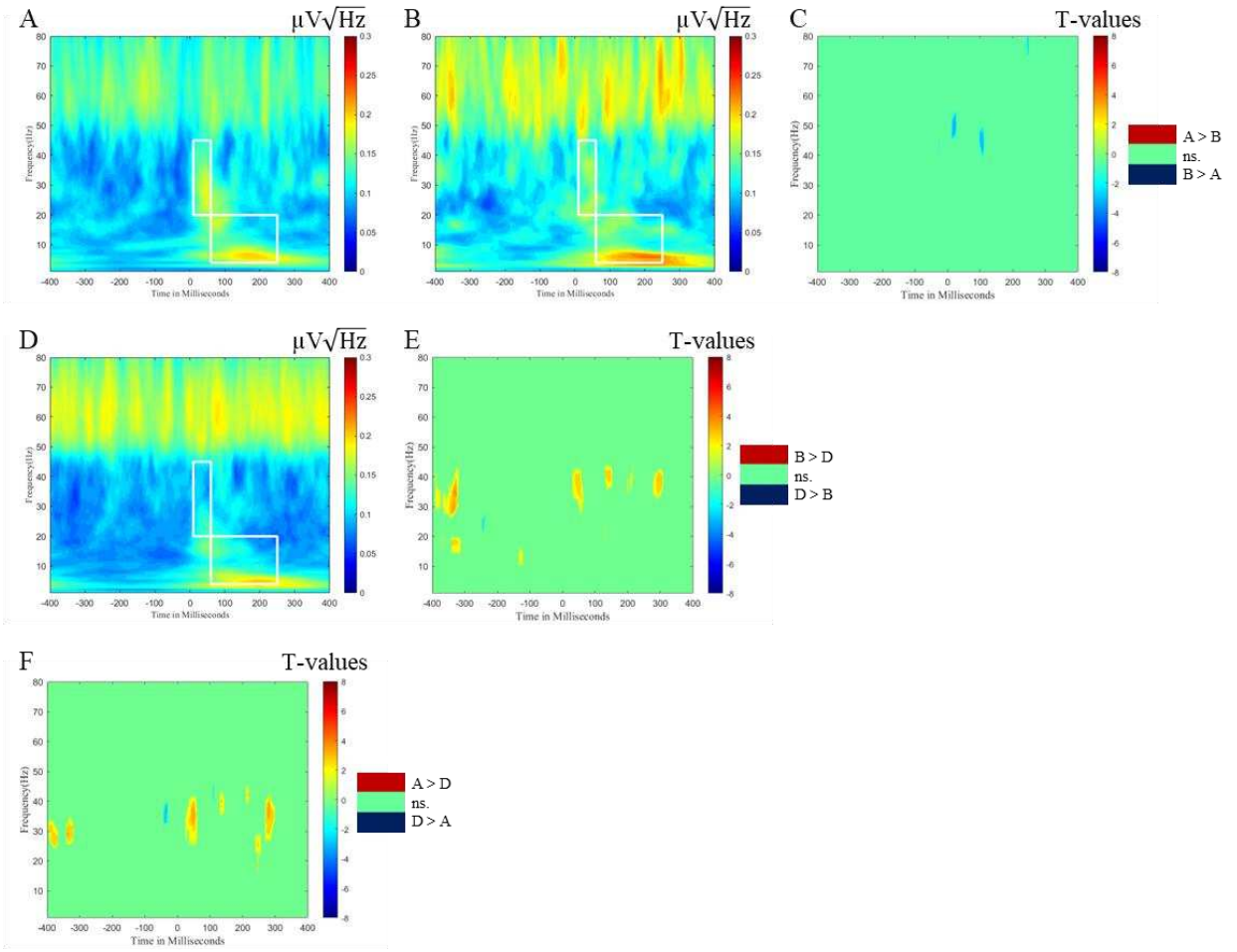

Figure E2. Phase locking factor time-frequency plots and t-maps of the last 100 trials of the auditory condition between each auditory priming group at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, & D, represents phase locking factor with warmer colors indicating greater consistency across trials. The color bar for plots C, E, & F represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Auditory-100 group. **B.** Auditory-200 group. **C.** T map comparing the auditory-100 group to the auditory-200 group. **D.** Auditory-400 group. **E.** T map comparing the auditory-200 group to the auditory-400 group. **F.** T map comparing the auditory-100 group to the auditory-400 group. The white outlined boxes represent 1) the motor ROI, 20–45 Hz from 10 to 60 ms, and 2) the sensorimotor ROI, 4–20 Hz from 60 to 250 ms.

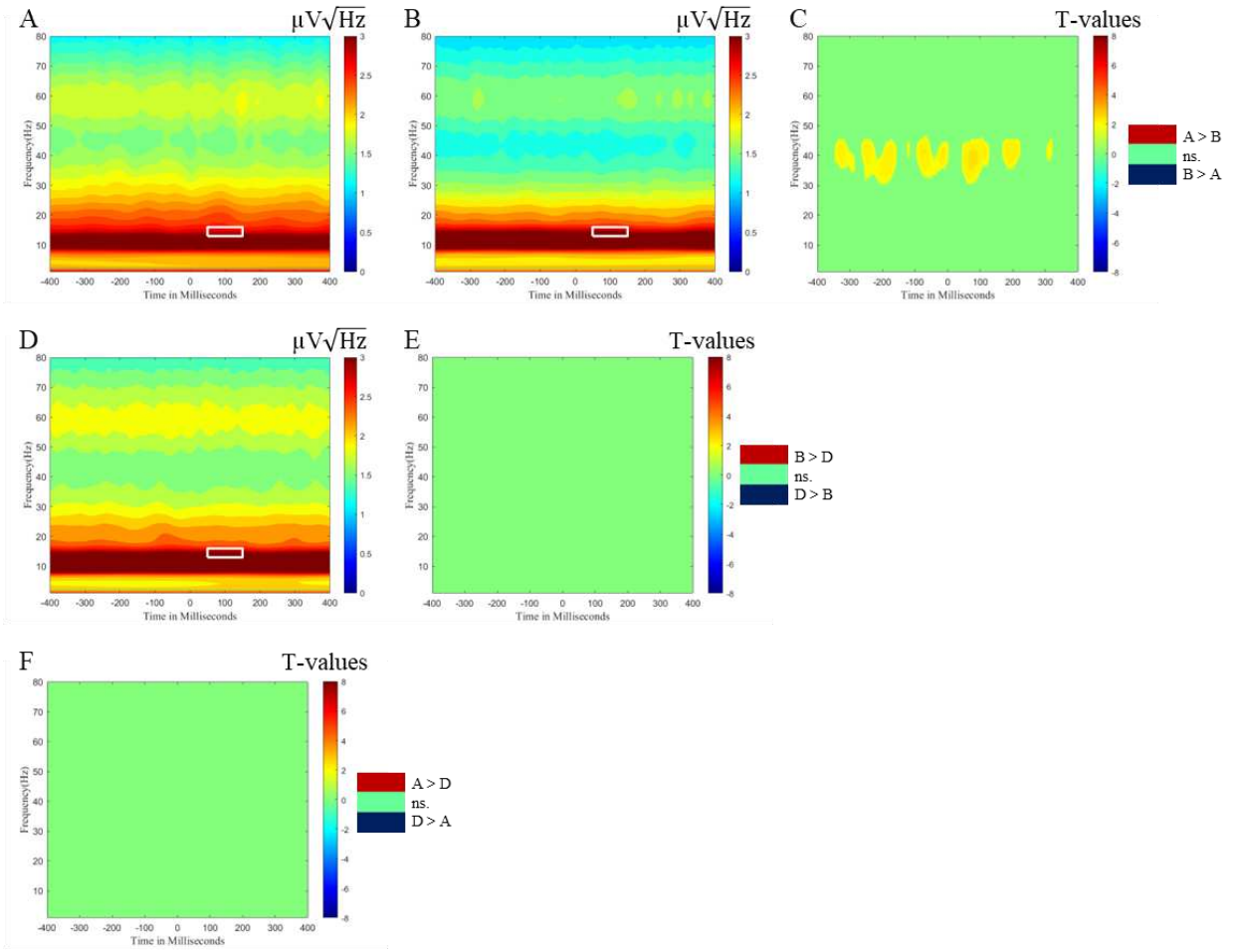

Figure E3. Total power factor time-frequency plots and t-maps of the last 100 trials of the auditory condition between each auditory priming group at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, & D, represents total with warmer colors indicating greater intensity. The color bar for plots C, E, & F represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Auditory-100 group. **B.** Auditory-200 group. **C.** T map comparing the auditory-100 group to the auditory-200 group. **D.** Auditory-400 group. **E.** T map comparing the auditory-200 group to the auditory-400 group. **F.** T map comparing the auditory-100 group to the auditory-400 group. The white outlined box represents the anticipation and predictive timing ROI, 13–16 Hz from 50 to 150 ms.

Visual Inspection – Second Research Question

To test for a "priming effect" and see if participants used fewer neural resources at the beginning of the rhythmic entrainment condition compared to the end of auditory priming condition (second research question), time-frequency plots for last 100 trials of the auditory priming condition and the first block of the rhythmic entrainment condition were visually inspected and compared using t-maps. For evoked power (Figure E4) t-maps showed a priming effect for the 100-audiory and 200-auditory groups with significantly greater evoked power in the auditory priming condition compared to the rhythmic entrainment condition in a time-frequency region corresponding to the motor ROI as well as other time-frequency windows from 40–50 Hz before and after the stimulus, including the beginning of the sensorimotor ROI, 4–20 Hz from 60 to 250 ms. However, for the 400-priming group, there was significantly less evoked power in the auditory priming condition compared to the rhythmic entrainment condition suggesting a priming effect did not occur for evoked power in this group. For PLF (Figure E5) the t-maps showed a priming effect for the 100- and 200-auditory groups. The 100-auditory group had several time-frequency regions with significantly greater PLF in the auditory priming condition, especially in the higher frequencies (>30 Hz) and some small time-frequency regions with greater PLF in the rhythmic entrainment condition around -300 ms, -200 ms, and 100 ms, which includes the beginning of the sensorimotor ROI, 4–20 Hz from 60 to 250 ms. The auditory-200 group t-map showed the greatest decrease in PLF in the rhythmic entrainment condition a time-frequency region corresponding to the motor ROI. The 400-auditory group showed less PLF in the auditory priming condition overall compared to the rhythmic entrainment condition. For total power (Figure E6), t-maps showed evidence of a priming effect for all three auditory priming groups, with greater total power in least one time-frequency region during the

auditory priming condition compared to the rhythmic entrainment condition. However, there was one region in the t-map for the 100-auditory group from -400 to -300 ms around 15–25 Hz which had less total power in the auditory priming condition (i.e., greater total power in the rhythmic entrainment condition). The priming effect for total power was most prominent for the 400-auditory group, with decreased total from approximately 10-20 Hz across time.

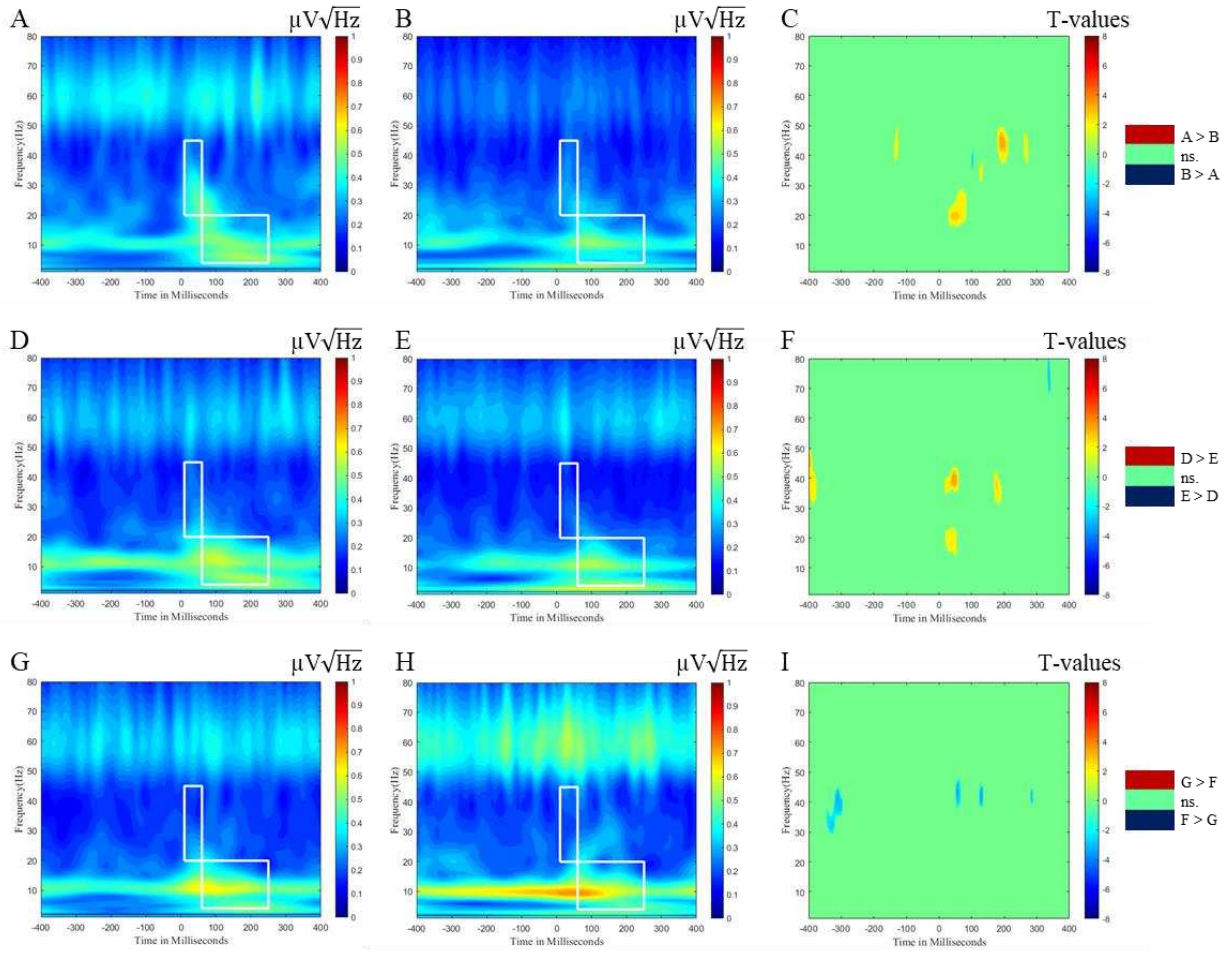

Figure E4. Evoked power time-frequency plots and t-maps between the last 100 trials of the auditory condition and the first block of the rhythmic entrainment condition within each auditory priming group at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, D, E, G, & H represents evoked power with warmer colors indicating greater intensity. The color bar for plots C, F, & I represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Auditory condition for the auditory-100 group. **B.** Entrainment condition for the auditory-100 group. **C.** T map comparing the auditory condition to the entrainment condition for the auditory-100 group. **D.** Auditory condition for the auditory-200 group. **E.** Entrainment condition for the auditory-200 group. **F.** T map comparing the auditory condition to the entrainment condition for the auditory-200 group. **G.** Auditory condition for the auditory-400 group. **H.** Entrainment condition for the auditory-400 group. **I.** T map comparing the auditory condition to the entrainment condition for the auditory-400 group. The white outlined boxes represent 1) the motor ROI, 20–45 Hz from 10 to 60 ms, and 2) the sensorimotor ROI, 4–20 Hz from 60 to 250 ms.

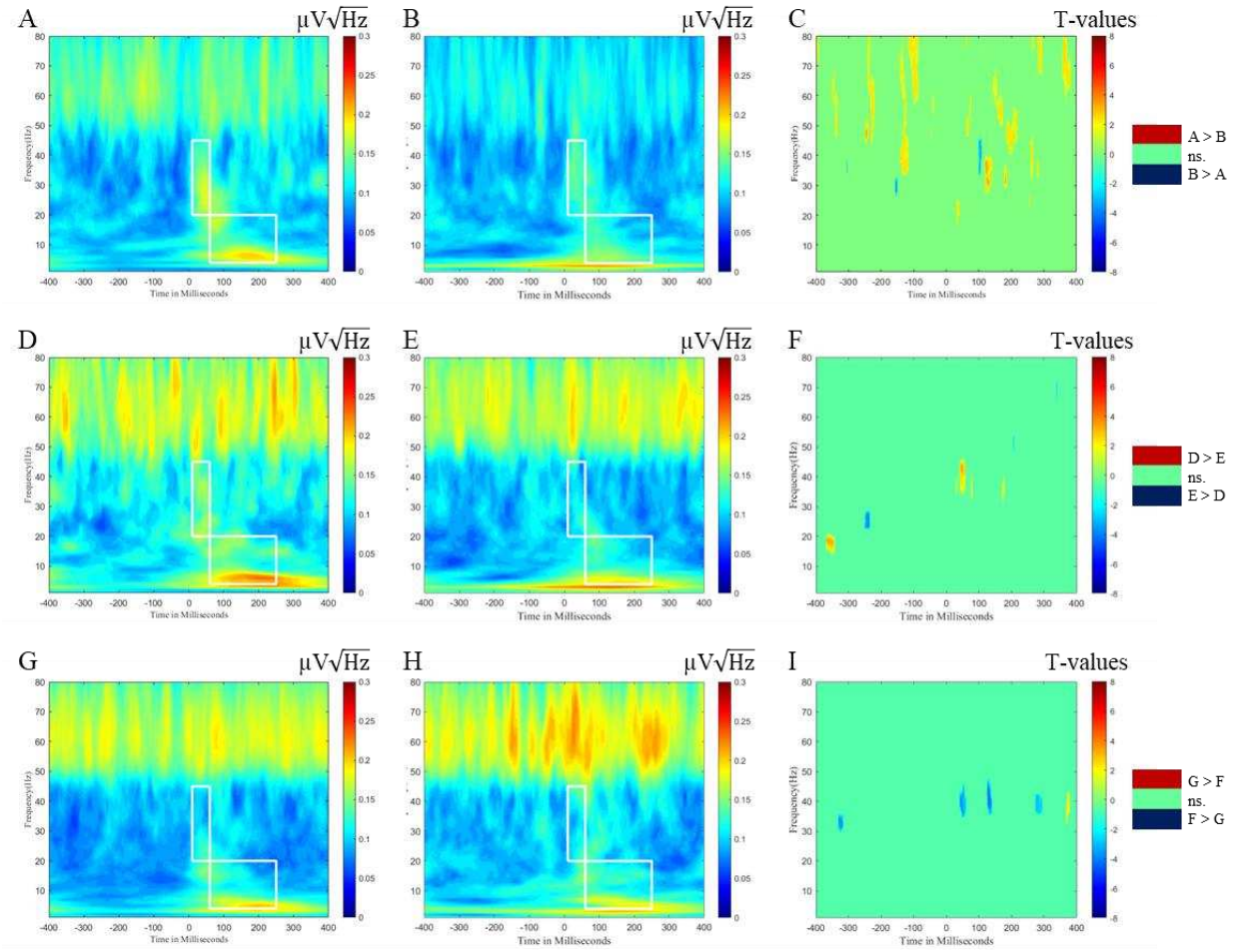

Figure E5. Phase locking factor time-frequency plots and t-maps between the last 100 trials of the auditory condition and the first block of the rhythmic entrainment condition within each auditory priming group at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, D, E, G, & H represents phase locking factor with warmer colors indicating greater consistency across trials. The color bar for plots C, F, & I represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Auditory condition for the auditory-100 group. **B.** Entrainment condition for the auditory-100 group. **C.** T map comparing the auditory condition to the entrainment condition for the auditory-100 group. **D.** Auditory condition for the auditory-200 group. **E.** Entrainment condition for the auditory-200 group. **F.** T map comparing the auditory condition to the entrainment condition for the auditory-200 group. **G.** Auditory condition for the auditory-400 group. **H.** Entrainment condition for the auditory-400 group. **I.** T map comparing the auditory condition to the entrainment condition for the auditory-400 group. The white outlined boxes represent 1) the motor ROI, 20–45 Hz from 10 to 60 ms, and 2) the sensorimotor ROI, 4–20 Hz from 60 to 250 ms.

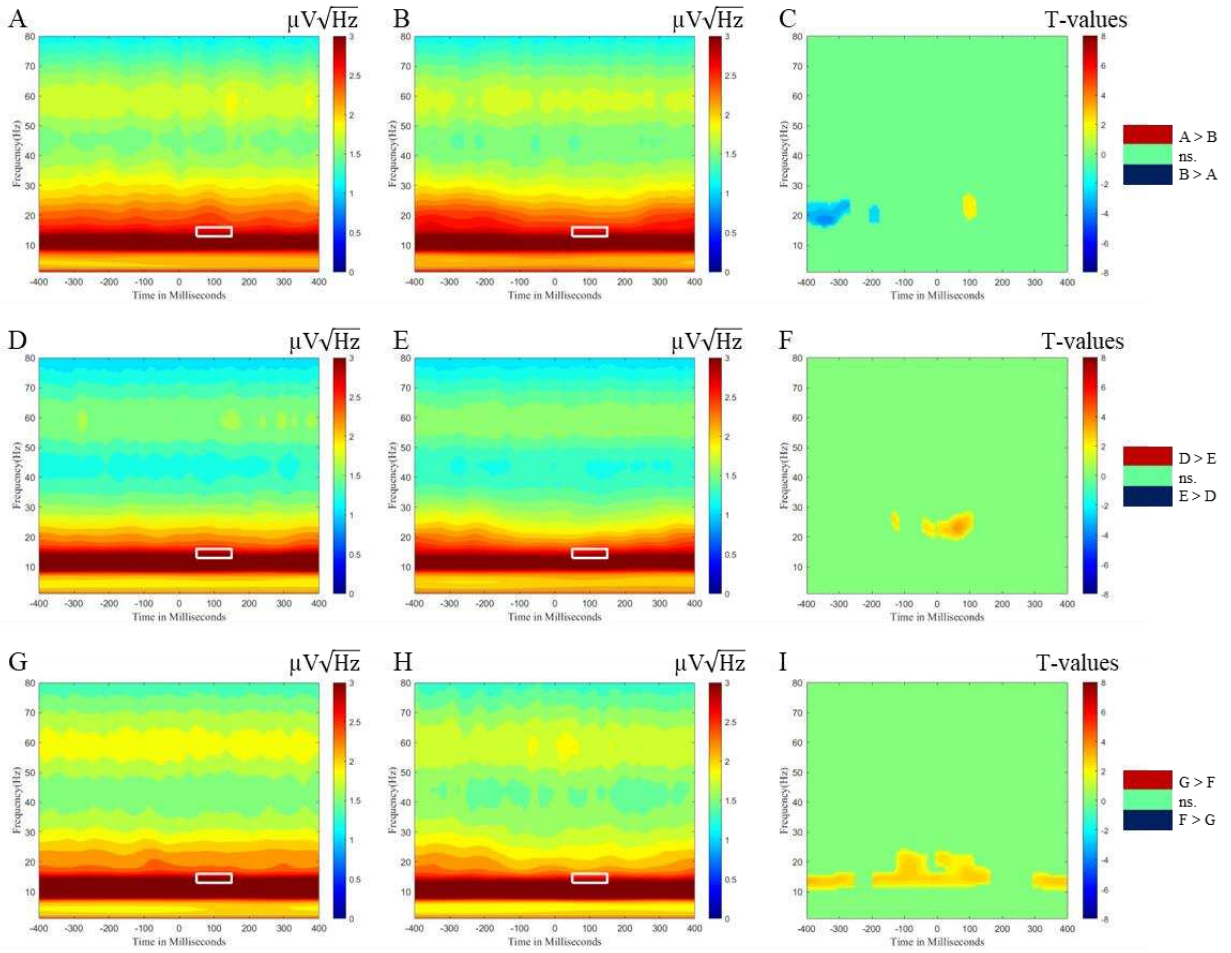

Figure E6. Total factor time-frequency plots and t-maps between the last 100 trials of the auditory condition and the first block of the rhythmic entrainment condition within each auditory priming group at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, D, E, G, & H represents total power with warmer colors indicating greater intensity. The color bar for plots C, F, & I represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Auditory condition for the auditory-100 group. **B.** Entrainment condition for the auditory-100 group. **C.** T map comparing the auditory condition to the entrainment condition for the auditory-100 group. **D.** Auditory condition for the auditory-200 group. **E.** Entrainment condition for the auditory-200 group. **F.** T map comparing the auditory condition to the entrainment condition for the auditory-200 group. **G.** Auditory condition for the auditory-400 group. **H.** Entrainment condition for the auditory-400 group. **I.** T map comparing the auditory condition to the entrainment condition for the auditory-400 group. The white outlined box represents the anticipation and predictive timing ROI, 13–16 Hz from 50 to 150 ms.

Visual Inspection – Third Research Question

To determine if the number of tones, representing duration of auditory priming, affects changes in time-frequency measures during the rhythmic entrainment condition, time-frequency plots of the average of the first block of the rhythmic entrainment condition for all four groups (control group and three auditory priming groups) was visually inspected using and t-maps were used to compare between groups. For evoked power (Figure E7), there was significantly greater evoked power in the lower frequencies (<30 Hz) in the 0-auditory group and the 100-auditory group compared to the 200-auditory group. The 400-auditory group showed significantly greater high frequency (>30 Hz) evoked power, including parts of the motor ROI, compared to all other groups. For PLF (Figure E8), there was greater lower frequency (<30 Hz) PLF in the 0-auditory compared to the 200-auditory group. The 400-auditory group had significantly more PLF in the higher-frequencies (>30Hz), including the motor ROI, especially compared to the 0-auditory and 100-auditory groups. For total power (Figure E9) time frequency maps show no differences between the 0-auditory and 100-auditory group, and the least total power in the 200-auditory group compared to the 100-auditory group and the 400-auditory group around 20-50 Hz across time. Overall, evoked power, PLF, and total power at the beginning of the rhythmic entrainment condition decreased with increased duration of auditory priming up to 200 tone presentations but increased after 400 tone presentations.

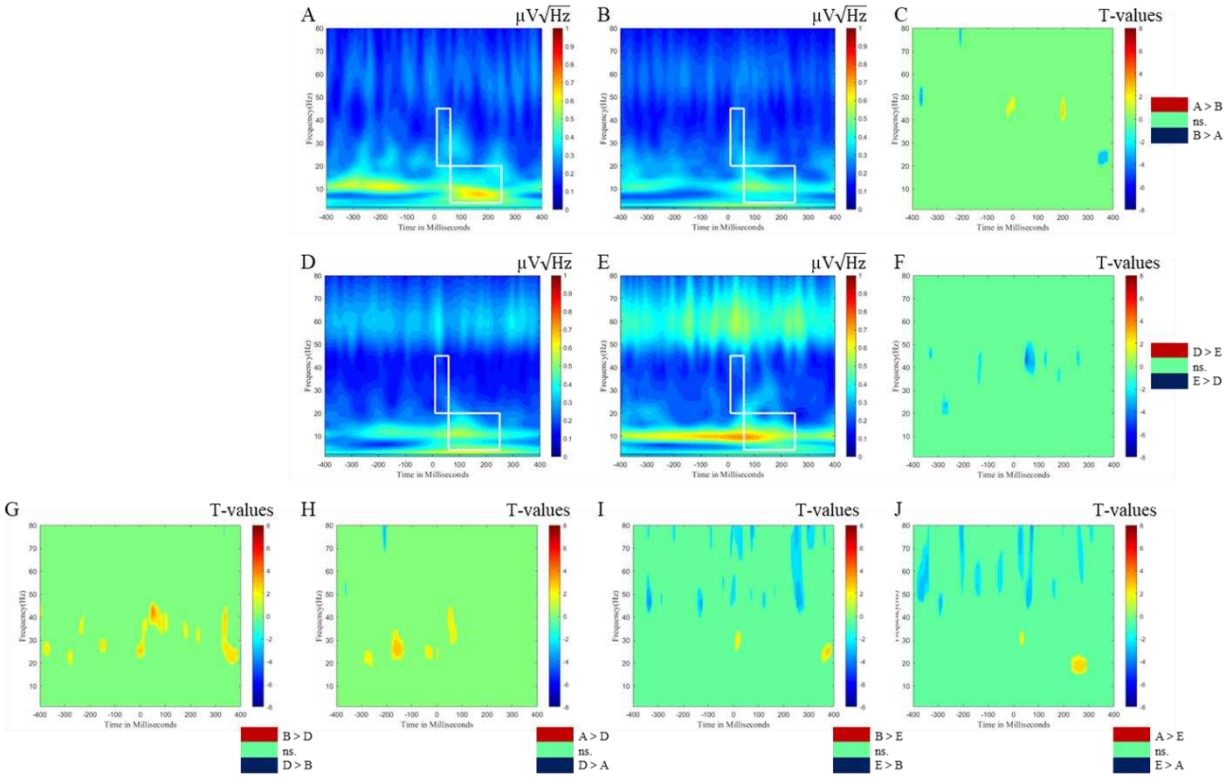

Figure E7. Evoked power time-frequency plots and t-maps of the first block of the rhythmic entrainment condition between each group at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, D, & E represents evoked power with warmer colors indicating greater intensity. The color bar for plots C, F, G, H, I, & J represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Auditory-0 (control) group. **B.** Auditory-100 group. **C.** T map comparing the auditory-0 group to the auditory-100 group. **D.** Auditory-200 group. **E.** Auditory-400 group. **F.** T map comparing the auditory-200 group to the auditory-400 group. **G.** T map comparing the auditory-100 group to the auditory-200 group. **H.** T map comparing the auditory-0 group to the auditory-200 group. **I.** T map comparing the auditory-100 group to the auditory-400 group. **J.** T map comparing the auditory-0 group to the auditory-400 group. The white outlined boxes outlined in white represent 1) the motor ROI, 20–45 Hz from 10 to 60 ms, and 2) the sensorimotor ROI, 4–20 Hz from 60 to 250 ms.

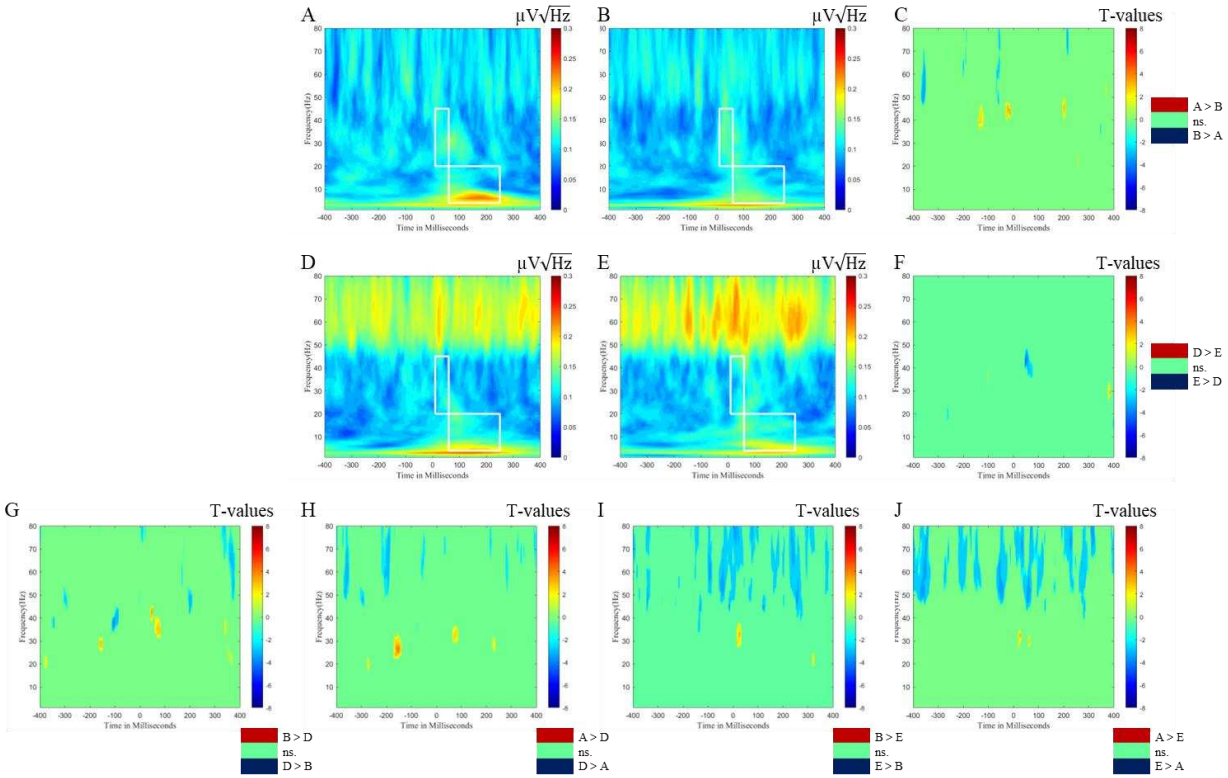

Figure E8. Phase locking factor time-frequency plots and t-maps of the first block of the rhythmic entrainment condition between each group at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, D, & E represents phase locking factor with warmer colors indicating greater consistency across trials. The color bar for plots C, F, G, H, I, & J represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Auditory-0 (control) group. **B.** Auditory-100 group. **C.** T map comparing the auditory-0 group to the auditory-100 group. **D.** Auditory-200 group. **E.** Auditory-400 group. **F.** T map comparing the auditory-200 group to the auditory-400 group. **G.** T map comparing the auditory-100 group to the auditory-200 group. **H.** T map comparing the auditory-0 group to the auditory-200 group. **I.** T map comparing the auditory-100 group to the auditory-400 group. **J.** T map comparing the auditory-0 group to the auditory-400 group. The white outlined boxes represent 1) the motor ROI, 20–45 Hz from 10 to 60 ms, and 2) the sensorimotor ROI, 4–20 Hz from 60 to 250 ms.

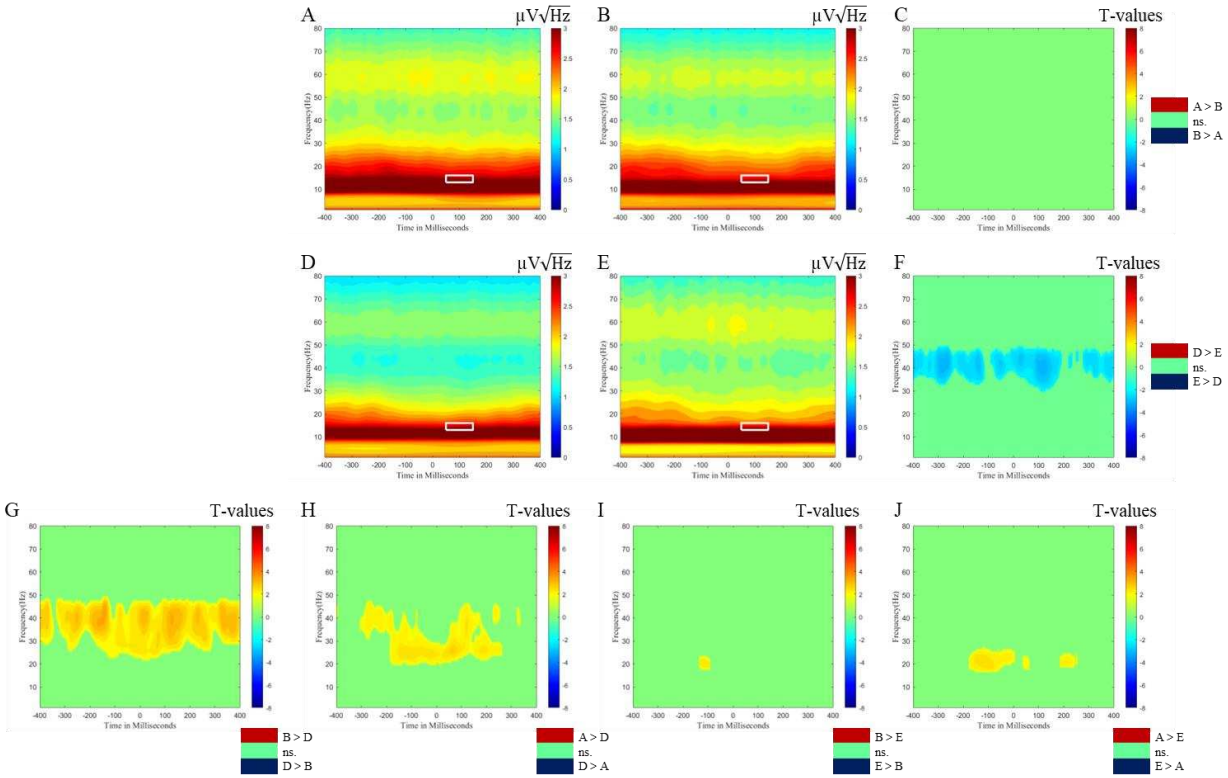

Figure E9. Total power time-frequency plots and t-maps of the first block of the rhythmic entrainment condition between each group at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, D, & E represents total power with warmer colors indicating greater intensity. The color bar for plots C, F, G, H, I, & J represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Auditory-0 (control) group. **B.** Auditory-100 group. **C.** T map comparing the auditory-0 group to the auditory-100 group. **D.** Auditory-200 group. **E.** Auditory-400 group. **F.** T map comparing the auditory-200 group to the auditory-400 group. **G.** T map comparing the auditory-100 group to the auditory-200 group. **H.** T map comparing the auditory-0 group to the auditory-200 group. **I.** T map comparing the auditory-100 group to the auditory-400 group. **J.** T map comparing the auditory-0 group to the auditory-400 group. The white outlined box represents the anticipation and predictive timing ROI, 13–16 Hz from 50 to 150 ms.

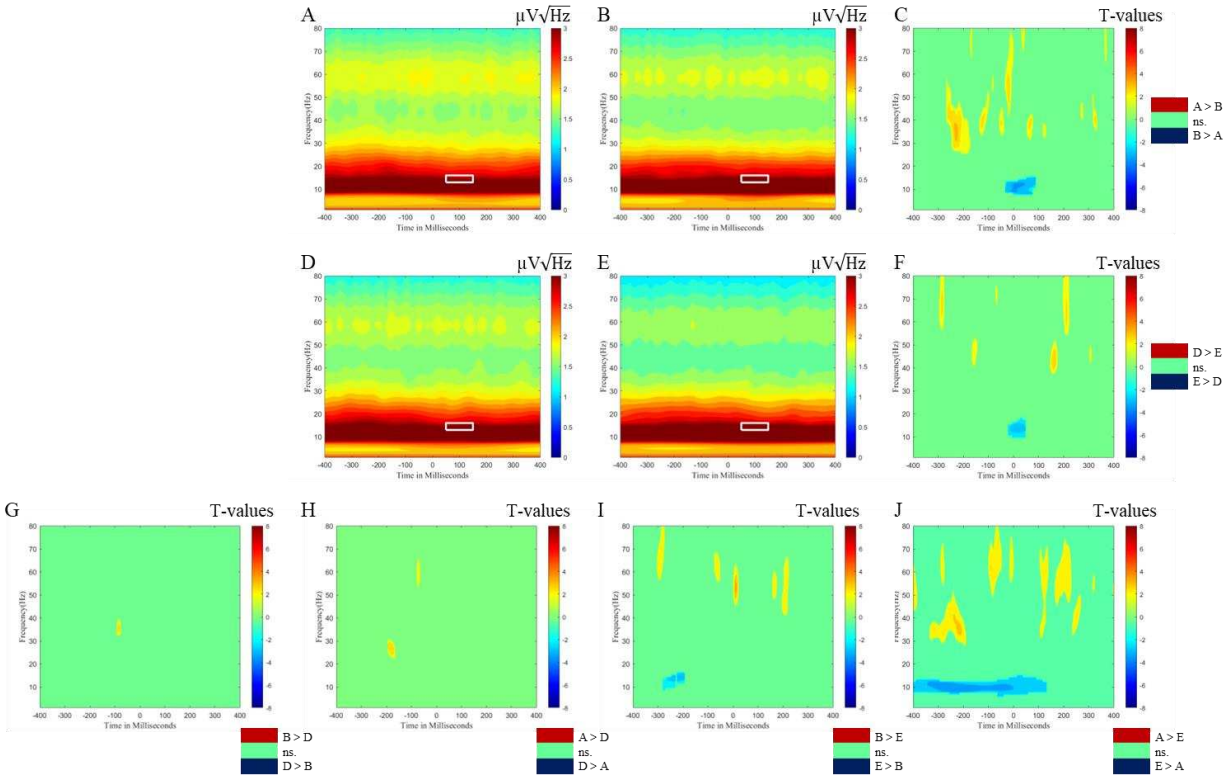

Figure E10. Total power time-frequency plots and t-maps of the four blocks of the rhythmic entrainment condition within the auditory-0 (control group) at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, D, & E represents total power with warmer colors indicating greater intensity. The color bar for plots C, F, G, H, I, & J represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Block 1 of the rhythmic entrainment condition. **B.** Block 2 of the rhythmic entrainment condition. **C.** T map comparing block 1 to block 2 of the rhythmic entrainment condition within the auditory-0 group. **D.** Block 3 of the rhythmic entrainment condition. **E.** Block 4 of the rhythmic entrainment condition. **F.** T map comparing block 3 to block 4 of the rhythmic entrainment condition within the auditory-0 group. **G.** T map comparing block 2 to block 3 of the rhythmic entrainment condition within the auditory-0 group. **H.** T map comparing block 1 to block 3 of the rhythmic entrainment condition within the auditory-0 group. **I.** T map comparing block 2 to block 4 of the rhythmic entrainment condition within the auditory-0 group. **J.** T map comparing block 1 to block 4 of the rhythmic entrainment condition within the auditory-0 group. The white outlined box represents the anticipation and predictive timing ROI, 13–16 Hz from 50 to 150 ms.

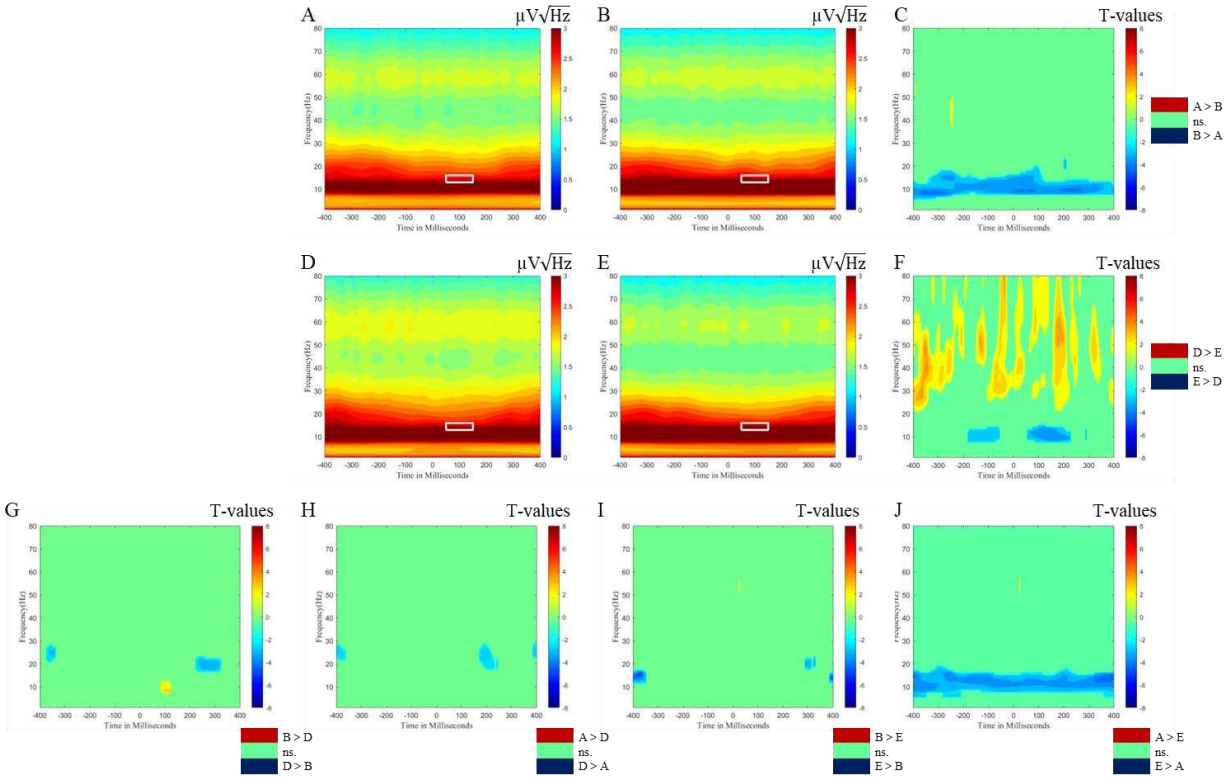

Figure E11. Total power time-frequency plots and t-maps of the four blocks of the rhythmic entrainment condition within the auditory-100 (control group) at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, D, & E represents total power with warmer colors indicating greater intensity. The color bar for plots C, F, G, H, I, & J represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Block 1 of the rhythmic entrainment condition. **B.** Block 2 of the rhythmic entrainment condition. **C.** T map comparing block 1 to block 2 of the rhythmic entrainment condition within the auditory-100 group. **D.** Block 3 of the rhythmic entrainment condition. **E.** Block 4 of the rhythmic entrainment condition. **F.** T map comparing block 3 to block 4 of the rhythmic entrainment condition within the auditory-100 group. **G.** T map comparing block 2 to block 3 of the rhythmic entrainment condition within the auditory-100 group. **H.** T map comparing block 1 to block 3 of the rhythmic entrainment condition within the auditory-100 group. **I.** T map comparing block 2 to block 4 of the rhythmic entrainment condition within the auditory-100 group. **J.** T map comparing block 1 to block 4 of the rhythmic entrainment condition within the auditory-100 group. The white outlined box represents the anticipation and predictive timing ROI, 13–16 Hz from 50 to 150 ms.

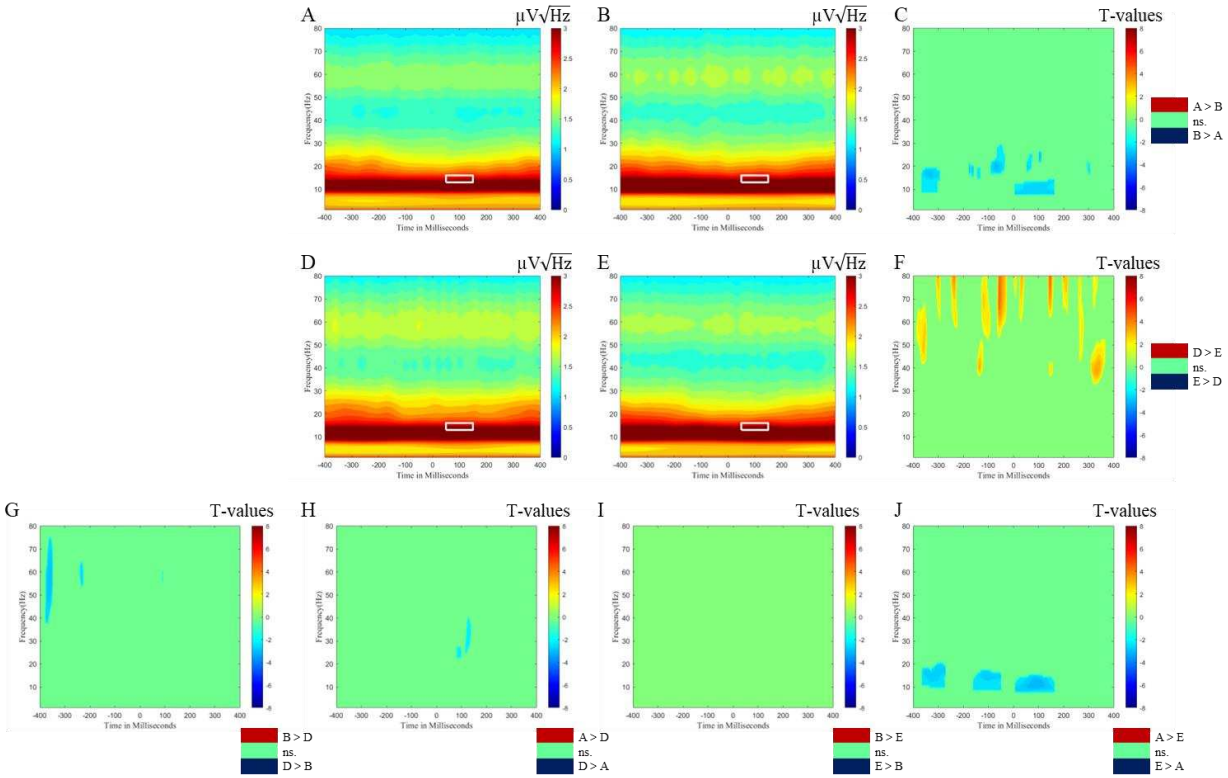

Figure E12. Total power time-frequency plots and t-maps of the four blocks of the rhythmic entrainment condition within the auditory-200 (control group) at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, D, & E represents total power with warmer colors indicating greater intensity. The color bar for plots C, F, G, H, I, & J represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Block 1 of the rhythmic entrainment condition. **B.** Block 2 of the rhythmic entrainment condition. **C.** T map comparing block 1 to block 2 of the rhythmic entrainment condition within the auditory-200 group. **D.** Block 3 of the rhythmic entrainment condition. **E.** Block 4 of the rhythmic entrainment condition. **F.** T map comparing block 3 to block 4 of the rhythmic entrainment condition within the auditory-200 group. **G.** T map comparing block 2 to block 3 of the rhythmic entrainment condition within the auditory-200 group. **H.** T map comparing block 1 to block 3 of the rhythmic entrainment condition within the auditory-200 group. **I.** T map comparing block 2 to block 4 of the rhythmic entrainment condition within the auditory-200 group. **J.** T map comparing block 1 to block 4 of the rhythmic entrainment condition within the auditory-200 group. The white outlined box represents the anticipation and predictive timing ROI, 13–16 Hz from 50 to 150 ms.

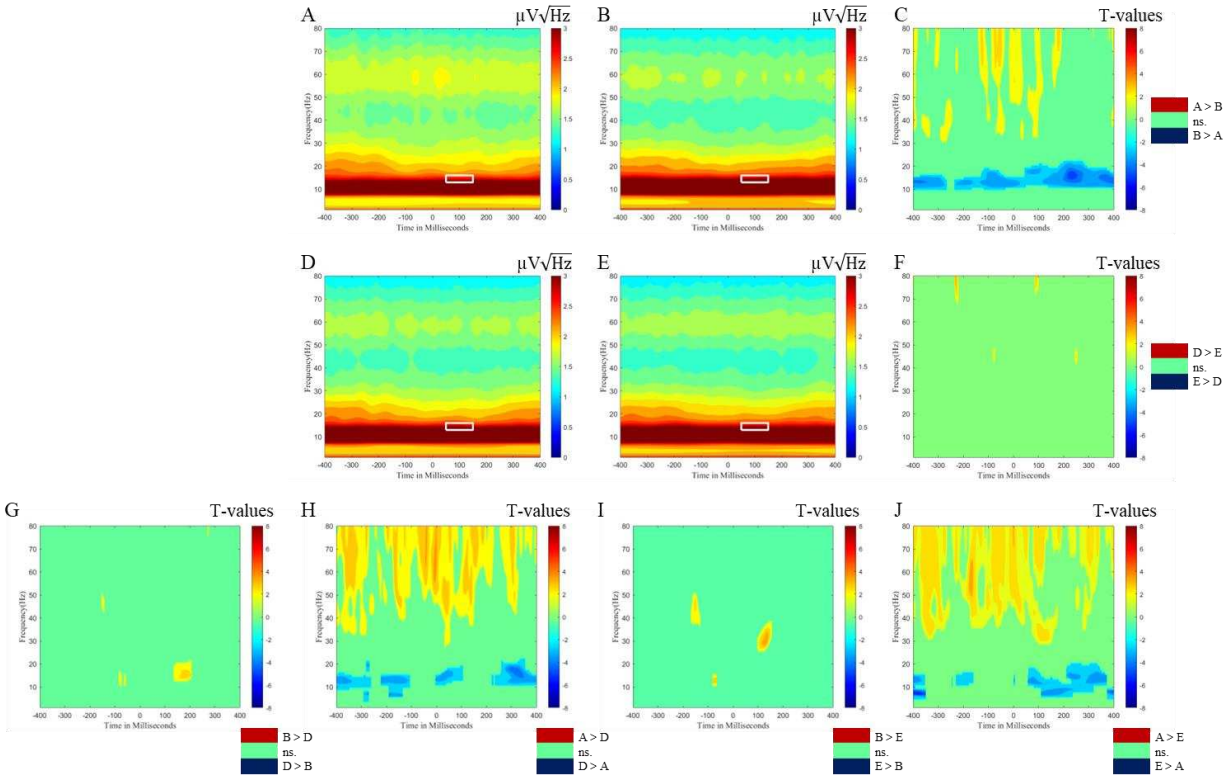

Figure E13. Total power time-frequency plots and t-maps of the four blocks of the rhythmic entrainment condition within the auditory-400 (control group) at site C3. The x-axis represents time in milliseconds from -400 to 400 ms with 0 representing the time of the auditory tone presentation. The y-axis represents frequency ranges from 0 to 80 Hz. The color bar for plots A, B, D, & E represents total power with warmer colors indicating greater intensity. The color bar for plots C, F, G, H, I, & J represents the T values with green indicating no significant (ns.) difference between conditions. **A.** Block 1 of the rhythmic entrainment condition. **B.** Block 2 of the rhythmic entrainment condition. **C.** T map comparing block 1 to block 2 of the rhythmic entrainment condition within the auditory-400 group. **D.** Block 3 of the rhythmic entrainment condition. **E.** Block 4 of the rhythmic entrainment condition. **F.** T map comparing block 3 to block 4 of the rhythmic entrainment condition within the auditory-400 group. **G.** T map comparing block 2 to block 3 of the rhythmic entrainment condition within the auditory-400 group. **H.** T map comparing block 1 to block 3 of the rhythmic entrainment condition within the auditory-400 group. **I.** T map comparing block 2 to block 4 of the rhythmic entrainment condition within the auditory-400 group. **J.** T map comparing block 1 to block 4 of the rhythmic entrainment condition within the auditory-400 group. The white outlined box represents the anticipation and predictive timing ROI, 13–16 Hz from 50 to 150 ms.

Glossary

Term	Definition
amplitude (of EEG signal)	The voltage of the EEG, typically relative to a baseline and measured in microvolts.
auditory-motor entrainment	When rhythmic motor patterns automatically synchronize to external auditory rhythmic cues (Thaut et al., 2015).
brain connectivity	Communication between brain regions
brain oscillation	Rhythmic patterns of electrical activity in the brain (Herrmann et al., 2005).
connectivity analyses	Any analysis where more than one signal is considered at a time. In EEG, the similarity of signals from two different electrodes (Cohen & Grafman, 2014).
connectivity, effective	The direct influence of one brain region on another (Friston, 2011).
connectivity, functional	Co-dependency between brain activity from spatially separate brain regions (Friston, 2011).
connectivity, structural	The physical connections of white matter tracts, groups of neurons in specific brain regions, and connections between individual neurons at the level of the synapse (Friston, 2011).
continuous wavelet transform	Converts the EEG signal into a matrix containing frequency, power, and phase at each time point within a segment.
current source density (CSD) transformation	Where changes in electrical activity at each electrode are typically compared to a common reference signal, CSD creates “reference-free” signal which attenuates the effects of volume conduction (Tenke & Kayser, 2012).
depression (of synapses)	A decrease in synaptic strength (Vanderah et al., 2016).
dynamic attention theory (DAT)	A model of how external and internal rhythms interaction to direct attention (Jones, 1976; Jones, 1987, 1990; Large & Jones, 1999; McAuley & Jones, 2003).
EEG oscillation	A brain oscillation measured using EEG. EEG oscillations are generally grouped into frequency bands: delta (0–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (15–30 Hz), lower gamma (30–80 Hz), and upper gamma (80–150 Hz) (Cohen & Grafman, 2014; Herrmann et al., 2005).
electroencephalography (EEG)	A technique where electrical activity of the brain is recorded noninvasively by electrodes places on the scalp (Polich, 1993; Stern et al., 2001).
entrainment	In physics: When two oscillating systems synchronize, such as when the pendulums of two clocks mounted on the same wall swing together in time (Pantaleone, 2002).

event-related potential (ERP)	The brain unique response to a stimulus or event created by averaged segmented EEG data time-locked to the stimulus/event (Polich, 1993; Stern et al., 2001).
excitatory activity	Synaptic activity which "excites" a neuron and increases its chance of firing (Vanderah et al., 2016).
experience-dependent principles	Principles to promote neural plasticity and learning in neurorehabilitation (Kleim and Jones, 2016).
Fourier transform	Converts the time-based EEG signal in a frequency-based signal; provides a measure of the average power or phase of each frequency band within a specific time window (Cohen & Grafman, 2014; Im, 2018; Zhang, 2019).
frequency (of the EEG signal)	Frequency is how fast the signal cycles and is measured in hertz (Hz) (Cohen & Grafman, 2014).
functional magnetic resonance imaging (fMRI)	A neuroimaging technique developed for research which measure the function of brain areas and circuits by using magnetic pulse sequences to detect the ratio between oxyhemoglobin and deoxyhemoglobin as a measure of areas of brain activation; fMRI has good spatial resolution (Camprodon & Stern, 2013).
imaginary part of coherency	A phase-based connectivity method using only the time-lagged "imaginary" component of the coherence value, to control for volume conduction (Nolte et al., 2004).
information processing theory	Treats sensorimotor synchronization as discrete events (Repp, 2005).
inhibitory activity	Synaptic activity which "inhibits" a neuron and decreases its chance of firing (Vanderah et al., 2016).
Long-term potentiation (LTP)	When repeated firing between neurons results in a lasting increase to the strength of the synaptic connection (Caporale & Dan, 2008).
magnetoencephalography (MEG)	Measures changes in the electromagnetic activity of the brain at the scalp (Cohen & Grafman, 2014).
Melodic Intonation Therapy (MIT)	NMT and speech therapy technique for expressive aphasia which utilizes a patient's unimpaired ability to sing to facilitate speech through sung and chanted melodies resembling natural speech intonation patterns (Devlin et al., 2019; Thaut & Hoemberg, 2014).
Morlet wavelet	The combination of a sine wave for a specific frequency band and a Gaussian wave used as a template in a continuous wavelet transformation (Cohen & Grafman, 2014).
music therapy	The clinical & evidence-based use of music interventions to accomplish individualized goals within a therapeutic relationship by a credentialed professional who has completed an approved music therapy program (American Music Therapy Association, 2013).

negative mean asynchrony	This anticipation tendency in sensorimotor synchronization in which the tap occurs slightly before the stimulus/beat (Aschersleben, 2002; Repp, 2005; Repp & Su 2013)
neural entrainment	The synchronization of brain oscillations to the external auditory rhythm (Haegens & Zion Golumbic, 2018; Large & Jones, 1999).
neural plasticity	When connections in the brain are adjusted and reorganized throughout development or in response to the environment or injury (Cramer et al., 2011).
Neurologic Music Therapy (NMT)	A system of standardized music techniques based on neuroscience principles. The Academy of Neurologic Music Therapy provides a training for music therapists and other rehabilitation therapists (Devlin et al., 2019; Thaut & Hoemberg, 2014).
neuro-occupation	Models the relationship between the human nervous system and occupation as a dynamic and interdependent relationship situated in the environment (Padilla & Peyton, 1997)
neurorehabilitation	An approach to rehabilitation which focuses on targeting changes in the brain i.e., neural plasticity (Cramer et al., 2011; Khan et al., 2017).
occupational science	The study of everyday occupation and its relation to health and well-being (Wright-St. Clair & Hocking, 2014).
occupations	Regular repeated patterns or periodic event.
oscillation or oscillatory system	Any regular repeated patterns or periodic event including external rhythmic stimuli (e.g., auditory rhythm), internal processes (e.g., brain oscillations), or behaviors (e.g., walking, tapping a finger).
Patterned Sensory Enhancement (PSE)	NMT technique; the application of musical elements of provide temporal, spatial, and force cues for non-rhythmic movements (Thaut; Devlin).
period (in sensorimotor synchronization)	The interval between two stimuli or two taps (Repp, 2005).
period correction	In the dual-process model of error correction: When the rate/tempo of tapping increases or decreases to match the external rhythmic period (Mates, 1994a, 1994b).
phase (of EEG signal)	The position of the oscillation in time and is measures in radians (0-2 π) or degrees (Cohen & Grafman, 2014).
phase-based connectivity analyses	EEG connectivity methods measuring the similar of the phase of neural oscillations across EEG sites (Cohen & Grafman, 2014).
phase correction	In the dual-process model of error correction: When the interval between taps does not change, but the taps shift in time (Mates, 1994a, 1994b).

phase locking factor (PLF)	The consistency of the phase of EEG oscillations relative to the stimulus/event can be measured across trials independently of power (Roach & Mathalon, 2008).
phase locking value (PLV)	Also called Inter-site Phase Consistency (ISPC) measures the similarity of phase between sites regardless of the power of the signal (Lachaux et al., 1999).
phase synchronization error	The difference between the time the tap occurs (the moment the finger contacts the surface) and the time the beat occurs (the moment the stimulus is presented) (Repp, 2005).
positron emission tomography (PET)	A neuroimaging technique which requires the injection of a radioactive substance or radiopharmaceutical to measure regional blood flow, metabolic changes, and neurotransmitter dynamics (Camprodon & Stern, 2013).
potentiation (of synapses)	An increase in synaptic strength (Vanderah et al., 2016).
power (of EEG signal)	Power is the amount of energy or intensity contained in the signal and is the amplitude of the signal squared (Cohen & Grafman, 2014).
power, evoked	Changes in EEG power which are correlated and phase-locked the stimulus/event and thought to reflect brain processing which is directly related to the stimulus/event (Roach & Mathalon, 2008).
power, induced	Stimulus/event related changes in EEG power which are time-locked, but not phase-locked across trials thought to reflect brain processes which are related to but not directly evoked by the stimulus/event (Roach & Mathalon, 2008).
power, total	Contains both phase-locked and non-phase locked EEG power across trials (Roach & Mathalon, 2008).
priming	When prior experience changes the processing of a stimulus e.g., reduces neural resources, and often improves subsequent performance e.g., faster reaction times or improved accuracy (Henson, 2003).
rehabilitation science	The study of how functional capacities improve and disabilities develop along a continuum, i.e., an enabling-disabling process (Brandt & Pope, 1997).
rhythmic auditory priming	Priming through rhythmic auditory stimuli.
Rhythmic Auditory Stimulation (RAS)	NMT technique; the application of rhythmic auditory stimuli to intrinsically rhythmic movements, such as gait, to achieve more functional movement patterns (Devlin et al., 2019; Thaut & Hoemberg, 2014).
rhythmic entrainment	The synchronization of internal rhythm processes (e.g., brain oscillations) or behavior (e.g., talking, walking) to external periodic events (e.g., betas in a rhythm) (Cameron & Grahn, 2016).
Rhythmic Speech Cueing (RSC)	NMT technique; the application of rhythmic cueing via metronome, drum, or moving the client's hand to prime and control initiation and rate of speech (Thaut, Devlin).

salience	An experience-dependent principle in which pairing a stimulus with a reward results in increased representation of that stimulus in the brain and improving learning (Kleim and Jones, 2016).
segment (in EEG data)	A slice of the EEG signal, typically with some time before the stimulus or event onset and some time after the stimulus or event onset.
sensorimotor synchronization	In information processing theory, the synchronization of movement to external rhythmic stimuli (Repp, 2005).
time-frequency measures	The methods for measuring the frequency, power, and phase of EEG oscillations across time (Cohen & Grafman, 2014).
volume conduction	When the similarity between two EEG electrodes reflects brain activity from the same underlying source. Results due to volume conduction do not reflect true connectivity (Cohen & Grafman, 2014).