Title

Cortical Motor Rhythms, Auditory Processing, and Plasticity

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Publication Date

2014

UNIVERSITY OF CALIFORNIA, SAN DIEGO

Cortical Motor Rhythms, Auditory Processing, and Plasticity

A dissertation submitted in partial satisfaction of the
requirements for the degree
Doctor of Philosophy

in

Cognitive Science

by

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2014

The dissertation of Matt Schalles is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2014

DEDICATION

For my guides, fellow travelers, and Teil.

EPIGRAPH

Any sufficiently advanced form of Magick should appear indistinguishable from Science.

—Stokastiko's Law (obverse form of Arthur C. Clarke's second law.)

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ACKNOWLEDGEMENTS

Thanks to my ever growing list of mentors: Jaime Pineda, Seana Coulson, Irina Gorodnitsky, Cynthia Gibson, Mark Reedy, the first Dr. Schalles, Perere, Kenny Beaumont, and Paul Horn.

Many thanks for all the support I received from the following organizations: The Cognitive Neuroscience Lab at UCSD, The Geyer Lab Group, and The Olmeca Roots Orchestra.

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ABSTRACT OF THE DISSERTATION

Cortical Motor Rhythms, Auditory Processing, and Plasticity

by

Matt Schalles

Doctor of Philosophy in Cognitive Science

University of California, San Diego, 2014

Professor Jaime Pineda, Chair

Synchronizing our movements to rhythmic sounds is a complex behavior, but easy for many humans, whether in the form of playing an instrument, dancing, or simply nodding/tapping along to a musical beat. How is this feat accomplished? A Hebbian hypothesis would argue that when sounds and movements co-occur, the systems become strongly associated, however many children exhibit a rhythmic sensitivity and do not seem to require training to move in time with music. An alternate explanation is that the motor system provides top down constraints to auditory processing (e.g. prediction and sequencing), such that the movement centers are already synchronized to external auditory cues prior to movement. In this dissertation I introduce three different electro-encephalography (EEG) studies that compare listening to, and moving along with rhythmic sounds, and explore the sensitivities of cortical motor rhythms to newly acquired action-sound pairings. In the first study I taught piano naive subjects to play a piano melody by ear and observed their motor rhythms showing preferential engagement when listening to the learned melodic sequence compared to unlearned melodies. In the second experiment, I compared the brainwave responses before and after subjects tapped or heard a tone and observed differences in motor rhythms in the time window before the events, but similarities in motor rhythm responses after sounds and after movements. In the third study, I introduce a novel EEG task - rhythmic hand drumming. I found that experienced drummers show greater engagement of motor rhythms while drumming than novice drummers, but across all subjects, motor rhythms were observed to modulate in time with drum rhythms regardless of whether subjects were just listening, or drumming themselves. Taken together, these three studies indicate that the motor system is sensitive to both rhythmic timing effects, and sequential effects of pitch order, and support a role for the motor system in auditory processing, when not otherwise engaged by movement.

Chapter 1

Introduction

1.1 Setting the Stage

There is an intimate connection between movements and sounds. In nature, sounds cannot exist without movement, and in our brains our motor system may play a role in the perception of sounds. Humans have an easier time synchronizing rhythmic movements with auditory rather than with visual stimuli, and this is exemplified by an inability to synchronize to intervals shorter than 460 ms in the visual domain (Repp, 2005). Musical rhythms often contain time intervals twice as fast as our fastest visual synchronization. The auditory and motor systems are also more functionally connected in terms of their neurophysiology. For instance, tapping along with increasingly difficult rhythms simultaneously increases recruitment of premotor and para-belt auditory cortices (Chen et al., 2009). Pianists who listen to songs they know how to play, exhibit activity in their premotor cortices, and furthermore exhibit activity in their auditory cortices when playing a digital keyboard with sound output disabled (Baumann et al., 2005). Pianists also have greater auditory and motor activations when they listen to, and play piano passages, compared with piano naive controls (Bangert et al., 2006). A picture is painted by the extant literature of the auditory and motor systems coactivating during the production and perception of music, but the obvious question is why? What does the motor system contribute to perception? What does the auditory system contribute to movements? There is a straightforward Hebbian learning explanation that accounts for the coactivation of the auditory and motor systems while playing a musical instrument or dancing that associates the activity of the two and strengthens synaptic connections between them. The strengthened connections could lead to extrinsic activity in just one of the systems to coactivate the other system. An alternative hypothesis is called the 'action simulation for auditory prediction' (ASAP) hypothesis (Patel and Iversen, 2014). Patel and Iversen argue that because of the predictive nature of the relationship between movement and sound, the motor system implements a form of simulation of auditory perception of rhythmic sounds.

Prediction is at the heart of moving in time with rhythmic sounds. Hitting a drum, strumming a guitar, or stomping on the ground requires movement preparation, such as moving the hand up before bringing it down onto a drum head. But how does the brain take an auditory input such that it can precisely match timing with a motor output? If we assume that computational resources are constrained in the brain, then a shared network of audiomotor processing may subserve both prediction of auditory events and preparation for coordinated movement. At the cortical level, tertiary auditory and premotor systems share direct fiber connections (Romanski et al., 1999; Frey et al., 2008), and both participate in a network with connections to the inferior parietal association cortex (Petrides and Pandya, 2006, 2001). This parallels the human mirror neuron system for visuomotor processing (Rizzolatti and Craighero, 2004), and suggests an integrated network of bottom-up and top-down processing of sounds.

Functional connectivity analysis implicates the audio-motor network as sensitive to changes in rhythmic and metrical complexity for both listening and tapping (Chen et al., 2009). We also see auditory system activity when an experienced pianists plays a piano keyboard sans sound (Bangert et al., 2006; Baumann et al., 2005), and likewise see motor activity when subjects listen to songs they know how to play (Lahav et al., 2007). The amount of information processed in these respective systems during professional piano playing, as measured by scalp electrical current density, varies over time, and the granger causal estimate of direction of influence implicates a feed-forward network driven more often by auditory cortex stimulating premotor cortex (Jäncke, 2012). Feed forward connections in the audiomotor system are already described (Frey et al., 2008), as auditory spatial localization pathways project to motor planning areas controlling the frontal eye fields. But what about top down influences from the motor system to the auditory domain? If there is a predictive element generated by the motor system, then there would need to be information flowing in the reverse direction. A rodent model reveals the potential for direct connections from secondary motor cortices to auditory cortex that exhibit excitatory and inhibitory effects (Nelson et al., 2013). Human evidence shows top down modulation of perceived beat position (Iversen et al., 2009) and is attributed to motor system influence of early auditory responses. In the connectivity models discussed above, both premotor and auditory cortices project to the inferior parietal cortex. If the direct connections between auditory and premotor cortex are based on feedforward activity, then the inferior parietal cortex may be part of a top down pathway performing an action-perception matching function. The IPL is part of a network, also including the superior temporal gyrus, medial prefrontal area, broca's area, and the precentral gyrus, that shows selective enhancement of responses when listening to music played by one's own instrument of expertise Margulis et al. (2009). The listening biography based on expertise in a specific instrument will be sensitive to not only auditory feature differences, such as timbre, but also sensorimotor patterns built on musculature, somatosensory, and proprioceptive integration. This area also serves as an integrative center for musical sequence processing for transposing musical passages (Foster et al., 2013).

Given a plausible neuroanatomical network for the integration of auditory and motor systems, there are still unanswered questions about how the integration works and in what ways the motor system makes contributions to the perception of sound, and how these might change as a function of experience. This dissertation seeks to address some of these questions and to test logical extensions of the ASAP hypothesis. The first study tests whether the motor system, which excels at sequencing muscles in very tight temporal order, is also sensitive to the sequential effects of auditory streams associated with movement. The second and third studies examine synchronizing behavior in the form of rhythmic tapping and drumming to test if similar motor preparatory activity is detected prior to both movements and sounds. Given the amount of interest in hypotheses linking motor systems and simulation during audition, there is a lack of controlled studies directly comparing the activity in cortical motor systems during both movement and auditory perception with the temporal precision that playing music requires. This dissertation makes a unique contribution to a body of literature on synchronizing movement that is primarily based on functional magnetic resonance imaging (fMRI) findings by using the temporal precision of electroencephalography (EEG).

1.2 Review of Sensorimotor neuroanatomy and neurophysiology

Animal Models

To date, motor contributions of visual perception have received more attention than that of audiomotor interactions. A cursory Google Scholar search for 'visuomotor' returns approximately 45,700 results, whereas a search for 'audiomotor' returns only 1830 (as of summer 2014), and on PubMed, the same searches return 3219 and 48, respectively. From electrophysiological recordings of neurons in the macaque ventral premotor cortex, we know that the motor system is involved in observation of object directed actions (Gallese et al., 1996), predicting the goal of observed actions, (Rizzolatti and Craighero, 2004) even when the goal is occluded from sight (Umiltà et al., 2001), and responds to the sight of tools (Ferrari et al., 2005). These properties seem to be somatotopically organized such that neurons representing hand actions are engaged during the perception of those actions. The motor system also seems to play a role in higher level visual perception, whose input requires interaction with objects. While responses for these neurons are similar between a monkey performing an action and observing the same action, they differ in frequency of neuron firing rate and latency of firing onset. Observed actions often elicit reduced firing rates, yet have an earlier onset of firing than self actions. This firing onset could relate to the relatively earlier presence of visual information, such as an arm extension, which precedes a grasping action that might be the goal of an outstretched arm. If the motor system is indeed predicting the future states of ongoing observed movements, could it also have a similar role for predicting auditory events?

Sounds are fundamentally different than sights in that they do not persist in time. Stationary objects, even moving objects, have visual properties that suggest continuity from one moment to the next. Since sounds are vibrations in the air, persistence is only a function of environmental effects, such as reverberation indoors, or echoes off of a canyon wall. Given sounds' transient nature, prediction of sound requires either visual information, or an auditory expectancy built on previously heard rhythmic sounds. Responses to sounds are reported in a subset of mirror neurons, called audiovisual and audiomotor mirror neurons, in the macaque premotor cortex (Kohler et al., 2002). With regard to firing onset, neurons receiving visual information alone, or visual information plus sound were seen to exhibit activity prior to the onset of sound. When deprived of visual input, these same neurons would have a delayed response to the sound, on the order of 100 msecs. This places the auditory mirroring response on the same level as an incidence detector and not a predictor of action. However, action related sounds, such as ripping paper or breaking peanuts, used by Kohler et al. (Kohler et al., 2002) may not be indicative of motor responses to musical or rhythmic sounds, which typically occur in a context embedded with prior associations and expectancies. Prediction of non-musical action sounds is often contingent upon visual information, such as the grasping of a peanut or paper between two hands. Musical or rhythmic action sounds can be predicted by past auditory events, and therefore do not require visual input. This mismatch in sensory input to the system may create differential responses, which could explain the difference in latency between auditory plus visual and auditory information alone in the macaque findings.

When looking to animal models to explain human auditory motor synchronization, we should keep in mind that musical behaviors are relatively unique to humans. The vocal mimicry hypothesis (Patel et al., 2009; Schachner et al., 2009) posits that only species which possess the ability to learn or mimic vocalizations posses the ability to synchronize to movements. Of the handful of species that could meet the criteria (e.g. parrots, cetaceans, pachyderms), only a small fraction of animals seem to exhibit sound-synchronizing behavior. In addition to vocal mimicry, Schachner et al. point out that all of the documented cases of motor entrainment were all highly enculturated around humans (Schachner et al., 2009). Given the above, caution should be applied to overgeneralizing monkey recordings to explaining human musical behavior. To date there is only one published example of a non-human primate synchronizing movements to sounds (Hattori et al., 2013), though this could partially be a reflection of a novel direction in the field.

In studying human motor responses to sounds, looking at mirroring literature is nonetheless a good place to start. Since single unit recordings are not a commonly viable method in humans, the mirroring response has been studied at the systems level. Biological motion is processed in the superior temporal sulcus (STS) and projects to the inferior parietal sensory integration center, and then on to the premotor cortex (Rizzolatti and Craighero, 2004). This pathway parallels the dorsal auditory pathway originating in posterior superior temporal gyrus, then projecting to inferior parietal, and premotor cortex in macaque histology (Petrides and Pandya, 2001; Romanski et al., 1999) and in human diffusion imaging (Frey et al., 2008).

Romanski et al. (1999) propose an auditory processing stream partitioned into dual dorsal/ventral projections from tertiary auditory cortices to premotor and inferior frontal regions, respectively, in an analogous fashion to visual processing streams. These auditory streams are functionally distinct in that the dorsal stream processes temporal and spatial aspects of sound, whereas the ventral stream more likely plays a role in identifying the source of a sound based on frequency profiles. Of the two pathways, the dorsal pathway likely plays a more direct role in predicting the occurrence of auditory events based on its temporal sensitivities. Other cortical structures, such as primary motor and somatosensory systems likely play a role in auditory-motor integration (Pineda, 2008), as evidenced by mu rhythm oscillations (discussed later). Additionally, subcortical structures like the basal ganglia and cerebellum likely play a role in audiomotor transformations, but are beyond the scope of the present study (see (Zatorre et al., 2007) for a review).

In Vivo Human Observations

Two main bodies of literature comprise what is known about the human mirror neuron system, drawing from functional imaging and electro or magnetoenecephalography. Functional MRI findings indicate that a homologous system of mirror neurons, split between the premotor cortex and inferior parietal cortex, are found in humans as to those initially reported in monkeys (Rizzolatti and Craighero, 2004). In addition to the classic properties of responding to movement and observation of that movement, the mirror system in humans is: sensitive to contextual effects of object interactions (Iacoboni et al., 2005), somatotopically organized (Buccino et al., 2001), and relies on familiarity of movements (Calvo-Merino et al., 2005).

We also see these brain regions, in addition to the superior temporal gyrus, active during the production and perception of sounds. Hand and mouth sounds, such as crushing a soda can, or crunching on potato crisps, activate the premotor, inferior parietal, and superior temporal cortices (Gazzola et al., 2006). In both the premotor and inferior parietal regions, hand sounds and mouth sounds are somatotopically distinct during both production and perception, whereas activity in the superior temporal gyrus is influenced by the presence of a sound, not the body part that produced it (Gazzola et al., 2006). This indicates a level of specificity for discriminating between different muscles used to create specific sounds in high level auditory perception, and a lack of specificity at lower levels. Familiarity of movements not only leads to increased recruitment of motor systems for visual perception (Calvo-Merino et al., 2005), but also has effects on auditory perception in the premotor, inferior parietal, and superior temporal cortex as well. Margulis et al. (2009) report that expert violinists and flautists show significantly larger BOLD activation in the classic mirror system regions when listening to a song melody that is played by their own instrument, as opposed to the same melody played by the alternate instrument. The effects of motor specificity for sounds may also be a quickly acquired effect too. Lahav et al. (2007) trained non musicians to play a simple piano melody over five days and when subjects listened back to clips from the learned song, they exhibited increased activation in the premotor and inferior parietal cortex compared with clips from similarly composed, yet non-learned songs. Taken together, these studies point to a sensorimotor circuit for auditory perception that is dynamic, adaptable, and parallels the visual mirroring system. Transmodal sensory activation is also possible through this network as just the visual observation of someone playing the piano sans sound can elicit auditory cortex responses in the expert pianist, but not in piano naive controls (Haslinger et al., 2005).

EEG and MEG oscillatory work

EEG correlates of mirroring activity predate the discussion of mirror neurons by several decades. Reports from the late 1940s through the late 1970s describe mu power (8-13 Hz) over sensorimotor cortex as decreasing from a resting state during both actions, and observation of actions, as discussed in (Pineda, 2005; Neuper et al., 2006; Oberman et al., 2008). The mu rhythm suppresses during movement observation (Cochin et al., 1998), performance of an action (Pineda et al., 2000), and observation of object directed actions (Muthukumaraswamy et al., 2004). In addition to observation and movement, the mu rhythm also suppresses during motor imagery (Pfurtscheller et al., 2006). The mu rhythm itself shares frequency properties with other brain rhythms, such as occipital alpha, but its intrinsic activity is functionally distinct, and source estimates localize it to the sensorimotor cortex surrounding the central sulcus (Salmelin and Hari, 1994). While the mu rhythm is not likely generated by the same premotor-inferior parietal cortices as revealed in human functional imaging and macaque single unit recordings, the primary somatosensory and motor cortices are direct targets for the premotor and inferior parietal circuits (Luppino et al., 1999), and M1 and S1 have been proposed as part of the extended mirror neuron system in humans (Pineda, 2008). The mu rhythm may be a good index of audiomotor processing as its suppression is associated with movement sounds, and combined sight and sound of actions suppresses mu greater than either sensory input alone (McGarry et al., 2012). Mu rhythms, as well as beta rhythms (15-30 Hz.), desynchronize prior to a sound action (such as tapping on a drum), and exhibit rebound synchronization after performing, listening and observing the action (Caetano et al., 2007). The synthesis of these studies indicates a similar neural process that is active during movement and listening, which is recorded most strongly over the sensorimotor cortex. Additionally, sounds that have no clear movement association exhibit higher amounts of mu desynchronization after watching a video that associates that sound with a clear movement (Li et al., 2011). Over a longer time scale, the mu rhythm becomes associated with visual input leading to paired auditory and motor output in the form of sheet music that desynchronizes mu when read by pianists but not controls (Behmer and Jantzen, 2011).

Brain responses to rhythmic stimuli have been reported in terms of slow responses such as event related potentials (ERPs) and in the form of oscillatory activity, such as changes in gamma frequency bands. Both of these responses can be detected simultaneously in response to rhythmic sounds, though the faster the tempo, the greater the attenuation of longer latency responses (Snyder and Large, 2004). The evoked gamma band does not appear to show these attenuation effects as a result of decreased intervals between stimuli. These gamma band oscillations occur approximately 50 ms post stimulus onset (Snyder and Large, 2005) and even occur in the absence of tones that are expected due to previous rhythmic periodicity (Zanto et al., 2006). In these experiments, the gamma band is defined as 20-60 Hz, which overlaps considerably with what is defined by others as the high beta band (20-30 Hz (Iversen et al., 2009), 15-30 Hz (Caetano et al., 2007)). In these studies beta has been associated with post movement and sound perception rebound (Caetano et al., 2007; Boonstra et al., 2006) and is modulated when beat structure is imagined over rhythmic sounds (Iversen and Patel, 2008). There is clearly a role for these higher frequency components in auditory and beat perception, however due to inhomogeneity in frequency band definitions, these bands may be functionally the same. Research by Fuijoka et al. (2009) revealed that beta (15-20 Hz) signals did not respond with discrete fluctuations to missing expected sounds, whereas those in the gamma range (28-48 Hz) do. The gamma band exhibits a short burst following both sounds and missing sounds. The beta responses, in contrast, show positive deflections which increase in amplitude until just post sound onset when they return to a negative trajectory. In the case of a missing sound this negative deflection does not occur. In summary, it would appear that possibly two distinct neural oscillations, one centered in the 15-30 Hz range, and another in the 30-60 Hz range respond to rhythmic sounds, even in their absence for higher frequencies, and can be modulated by imaging beat structure (emphasis) in the lower frequencies. The lower frequencies in this range tend to decrease in power prior to stimulus onset, and increase in power either immediately before (Fujioka et al., 2009), or just after (Boonstra et al., 2006) the onset of a stimulus, whereas the higher frequencies in this range show a rapid increase and then return to baseline after stimulus onset (Fujioka et al., 2009; Zanto et al., 2006; Snyder and Large, 2004; Iversen et al., 2009).

Lower frequency responses, such as ERPs, occupying a frequency range of approximate 1-10 Hz, and theta (4-8 Hz) oscillations also respond to sounds of rhythmic periodicity. As previously mentioned, these longer latency and slower frequency responses are attenuated when periodic intervals between stimuli decrease. One reason this attenuation occurs can be explain in terms of inter-trial coherence (ITC) measures, which report the phase synchrony of responses from trial to trial. The ITC decreases significantly as inter stimulus intervals decrease from 1000 ms to 250 ms, with almost total loss of theta band activity to each stimulus as the period decreases past 500 ms (Will and Berg, 2007). It is perhaps not surprising that longer latency responses cannot account for periods of activity shorter than the their response intervals. If slow wave potentials, such as the auditory N100 or N1 are reliant on phase synchrony of faster oscillations, then it might explain why the auditory N1 as a significant deviation from baseline voltage is reduced or disappears around inter stimulus intervals of approximately 400 ms and faster (Carver et al., 2002). Boonstra et al. (2006) report a theta component that loses power prior to stimulus onset and gains power just after, in a similar way to the beta band. While this is observed over auditory cortex, this is confounded by simultaneous tapping and listening behaviors, so it might be an effect of motor activity. Overall, it would appear, even at slower tempos, that the beta and gamma bands offer relatively precise temporal activity time-locked to auditory perception.

From studies examining synchronization of movements and sounds, there is a proposed role for beta oscillations in the simulation of movement during sound perception (Iversen et al., 2009; Patel and Iversen, 2014). This frequency band is associated with movement of auditorily paced movements in humans (Boonstra et al., 2006; Caetano et al., 2007; Pollok et al., 2005), and also with movements in intercranial macaque recordings (Brovelli et al., 2004; Bartolo et al., 2014). The beta band is also implicated in top-down inhibitory control, with an increase in signaling just prior to an increase in inhibitory alpha from the pre-frontal cortex (Hwang et al., 2014). This is part of a larger body of literature that contributes to the hypothesis that beta oscillations may maintain current sensorimotor or cognitive states (Engel and Fries, 2010). However, given the proposed role for this frequency band in simulation and top down control of movement and perception, no study to date has directly compared the role of beta oscillations in rhythmic listening without moving and overt movement with and without sound for rhythmic stimuli. If the simulation theories are true, then one would hypothesize a similar level, or at least similar temporal pattern of beta activity for all of these conditions. In this dissertation I propose to test this hypothesis using both tapping and drumming experiments where subjects alternately listen to rhythmic sounds, move along with them, and move without the sound exemplars. Theories about mirror neuron activity posit similar claims about the role of the motor system during action observation and simulation, and provide a framework for experimental design in which to compare movement and listening to test theories about listening involving simulated movement.

Chapter 2

Study 1 - Motor Learning and Sequential Auditory Processing

2.1 Abstract

Listening to sounds can easily stimulate the motor system to action in the form of head nodding, foot tapping, and dancing. Does the motor system play an active role in auditory perception? I hypothesized that the motor system might contribute to sequential processing of auditory information. Over five days I trained subjects to play a simple piano melody by ear with their right hand. Post-training electrical scalp recordings indicated sensorimotor engagement when listening to musical phrases that are associated with a known motor repertoire. Songs similar to learned songs, such as a transposed melody that preserves the sequential relationship between musical phrases, partially engaged the sensorimotor system compared to the learned sequence. This finding implies a potential role for the motor system in sequencing series of sounds.

2.2 Introduction

The audiomotor system is adaptable and responds to novel action sounds on short (Li et al., 2011) and intermediate (Lahav et al., 2007) time scales. What exactly the motor system contributes to perception is still unclear. It is partially sensitive to sound frequency profile in terms of note pitch (Lahav et al., 2007), as well as timbre (Margulis et al., 2009). It is also reportedly sensitive to musical timing and changes in metrical complexity (Chen et al., 2008, 2009). At the intersection of musical notes and timing is the notion of sequencing proper notes at the correct time. The motor system arranges complex sequences of muscles, it could conceivably sequence passages of sounds. Motor trajectories planned by the premotor, and implemented by the primary cortices follow hierarchical relationships between antagonistic muscle pairings. Music follows grammatical rules like language (Patel, 2003), and can be explained as a series of sounds related to each other on different time spans in a hierarchically organized fashion (Molnar-Szakacs and Overy, 2006; Overy and Molnar-Szakacs, 2009). It is not unreasonable to ask whether the motor system could fit incoming auditory stimuli into a hierarchical order that allows prediction of future sounds.

A good example of the importance of sequential relationships in music is a melodic transposition. The absolute pitch of a musical phrase is altered, such as a shift up or down, yet the relationship between all of the notes remains in tact. If one moves a whole semi-tone from A to B for the first note in a phrase, the rest of the phrase would follow, such that a D becomes an E. If the motor system can be trained to respond to a specific melodic sequence, then shifting the absolute pitch of the passage shouldn't significantly affect the motor response.

Lahav et al. (2007) report that the premotor and inferior parietal cortices respond preferentially when listening to a melodic passage that a listener knows how to play on the piano, and exhibit little to no response when listening to a song unrelated to the one they learned how to play. Additionally, if subjects listen to a novel song that is composed from the same note set as the melody they learned to play, they report reduced activation of the premotor and inferior parietal regions relative to listening to the learned song. The similarity was explained as a pitch-motion matching system, such that a single key press elicits a single sound, and hearing the sound could trigger the association with the single motor act. An alternative explanation could describe the difference between learned song and novel song with learned notes as a difference in sequential information leading to reduced activity in motor planning areas.

In the present study, I asked whether the motor system is sensitive to changes in pitch when the sequential ordering of auditory information is preserved. We used the piano ear-learning task developed by Lahav et al. (2005; 2007) and tested pitch-recognition-production matching before and after training. For the post-training motor system engagement, I used EEG rather than previously reported fMRI measures. As discussed earlier, mu rhythms exhibit properties consistent with action execution and observation matching and show promise as an index of audiomotor processing (Pineda, 2005). Mu is generated by the sensorimotor cortex, which shares reciprocal connections with the brain regions responding to sounds of the learned song (Pineda, 2008). Additionally, beta rhythms exhibit similar suppression patterns during movement as mu rhythms. The beta band is shown to cycle similarly to mu for both performed actions and heard actions (Caetano et al., 2007). If EEG is a good measure for audiomotor processing over the course of a musical phrase, it could encourage future study building on models of responses to discrete notes (Haueisen and Knösche, 2001). We predicted that the mu and beta rhythms would suppress maximally when a subject listens to a melody s/he knows how to play, partially suppress when listening to a transposed version of the song, and fail to suppress, or even show enhancement when listening to a melody unrelated to the learned song. Given the novel implementation of this behavioral task with EEG measures, it seemed prudent to explore other frequency bands outside of the mu and beta rhythms, such as theta and gamma.

2.3 Methods

Subjects

16 Undergraduate students (nine female, 19.9 years mean age, 15 right handed) from the University of California San Diego completed the experiment in exchange for a combination of monetary compensation and course credit. Three other students began the experiment but failed to complete five consecutive days of training and/or the subsequent EEG session. Subjects were screened for head trauma and use of psychiatric medication, as well as for experience playing piano or other instruments. All subjects were able to detect pure tones ranging between 250 Hz and 8 kHz at 30 db in both their right and left ears.

Song Stimuli

The same training song as described in Lahav et. al.(Lahav et al., 2005, 2007) was implemented for the current study. For all the songs, synthesized backing instruments, guitar, bass and drums were composed following the score provided in (Lahav et al., 2005). The songs were each eight measures long, and had a duration of 24 seconds at 80 beats per minute. The melodic line for each song was voiced by synthesized piano. The melody for each song was 15 notes long, and comprised from a set of five notes, one for each finger on the playing hand. The transposed melody preserved the relative intervals between the notes in the learned song, but shifts them into a set of notes that does not overlap with the learned song. The control song was comprised of the same note set as the transposed song. The notes in the control song were arranged in a different sequence from the trained and transposed melodies, but still preserved the same length of note durations.

Musical Training

For five consecutive days subjects practiced playing the melody line on a midi piano controller. On the first day, subjects were shown which five keys corresponded to the five notes used in the melody. One finger on the right hand was assigned to each of the five keys. Subjects were minimally supervised while figuring out the melody line by ear with the assistance of a computerized training environment. The song was introduced incrementally, starting with the first two measures. The subject was allowed to listen to, and play along with exemplar piano lead over the two measures as many times as s/he desired. When ready, the subject would play the melody line over the backing instruments minus the exemplar piano lead. If the correct sequence of notes were played within 1/16th note of the correct time, the computer informed the subject they could move on to the next two measures. After a subject completed an additional two measures in the same fashion, the next training step was to play all of the previously learned measures in sequence. Thus they would first practice measures one and two, then measures three and four, then play measures one through four, until they could play the complete eight measure melody. A training session was finished for the day when the subject could play the entire song with no mistakes. Time to completion was recorded for each training session. The training environment was coded in Max/MSP 4.5.5. A training session also involved listening to the transposed and control melodies before and after working through the piano sequence to control for familiarity effects.

Pitch-recognition-production Task

Before the first training session and after the last, subjects listened to a series of 30 notes, randomly selected from the 5 note set (F-G-A-Bb-C) of the training melody. After each note, subjects were asked to press the corresponding key on the keyboard. Auditory feedback from the keyboard was disabled to prevent subjects from self correcting their key presses as they progressed. This test was conducted to measure if subjects created behaviorally significant associations between sounds and discrete motor acts based on the one-note-one-finger training paradigm.

EEG Task

After completion of training and the pitch-recognition-production task, subjects completed an EEG session where they listened to six-second long clips (two measures) from the three songs. A pair of probe tones followed each song clip and subjects were asked to respond if the two tones were present in the previous song clip. Ten clips were created from each song, totaling 30 trials across the three conditions. A resting period of two seconds preceded the onset of song stimuli. A moving baseline for mu ratio calculations was collected from this prestimulus window, across all three conditions. Thirty bins of two second baselines equaled the same number of time points as ten bins of six-second long stimuli per experimental condition. Stimuli were presented pseudo-randomly by Neuro-behavioral Systems Presentation v. 13 software. Twenty-one channels of EEG were recorded using a Neuroscan Synamps system, according to the 10-20 standard for electrode placement (F3, Fz, F4, F7, F8, Fp1, Fp2, C3, Cz, C4, P3, Pz, P4, T5, T6, O1, O2, T3, T4, VEOG). Recordings were referenced to a digitally linked pair of mastoid electrodes and grounded at Fpz. Recordings were online bandpass filtered between 0.3-100 Hz, and amplified by a gain factor of 1000.

Analysis

Behavioral

Length of time to complete training was recorded each day, and a training slope variable was calculated by a linear fit of the difference between the first and second day of training. The time to complete training on the first day, and the training slope were correlated with years of previous musical experience, and pitch-recognition-production scores. Differences were calculated between pitch-recognition-production scores from the post-test and the pretest sessions. Correlations and analysis of variance were computed with MATLAB v 7.10.

EEG

Pre-Processing Offline data were processed in EEGLAB (Makeig et al., 2004). Data were bandpassed between 3 and 40 Hz using a finite impulse response filter. Epochs centered around onset of song stimuli were extracted to include the two second baseline window before sound onset, and then the six seconds of duration of song stimulus. Independent component analysis (ICA) was performed (Infomax algorithm) on the scalp channels, resulting in 19 components. Artifactual components, such as those representing eyeblinks or other head muscles, were visually identified and removed if they met the following three criteria: 1. irregular occurrence throughout the session, 2. scalp location indicating facial muscles, and 3.

presence of abnormal spectrogram, such as extremely high power low frequencies (eyeblinks) or disproportionately large power from 20-30 Hz (muscle contamination). After component rejection, data were rerun through ICA to further unmix any artifactual components from brain sources, and dipole positions estimated with the Dipfit 2.x toolbox using a boundary element head model and Montreal Neurological Institute (MNI) coordinate system.

Frequency Measures All experimental conditions and baseline were converted to frequency spectra using a Fast-Fourier Transform with 0.5 Hz resolution. Frequency bands were summed with a trapezoid function for theta (4-8 Hz), mu (8-13 Hz), beta (20-30 Hz), and gamma (30-40 Hz). Frequency band suppression was calculated as the log ratio of condition divided by baseline. This accounted for normalizing the differences inherent in spectral power due to interpersonal differences in scalp condition. Pairwise comparisons, correlations, and one way ANOVAs were calculated in MATLAB v 7.10, and repeated measure ANOVAs were computed in SPSS v 20.0.

2.4 Results

Behavioral

The amount of time it took subjects to learn the melodic sequence on the first day was highly variable (mean, 30.53 minutes; SD, 22.88). A significant effect of training day (F(4,80)=12.02,p=1.07e-7) revealed a decrease in time to error-free performance, and reduction in variability across all subjects over the five days of training (see fig 2.1). This followed the same trend previously reported (Lahav et al., 2007) and was interpreted to show learning of the musical motor

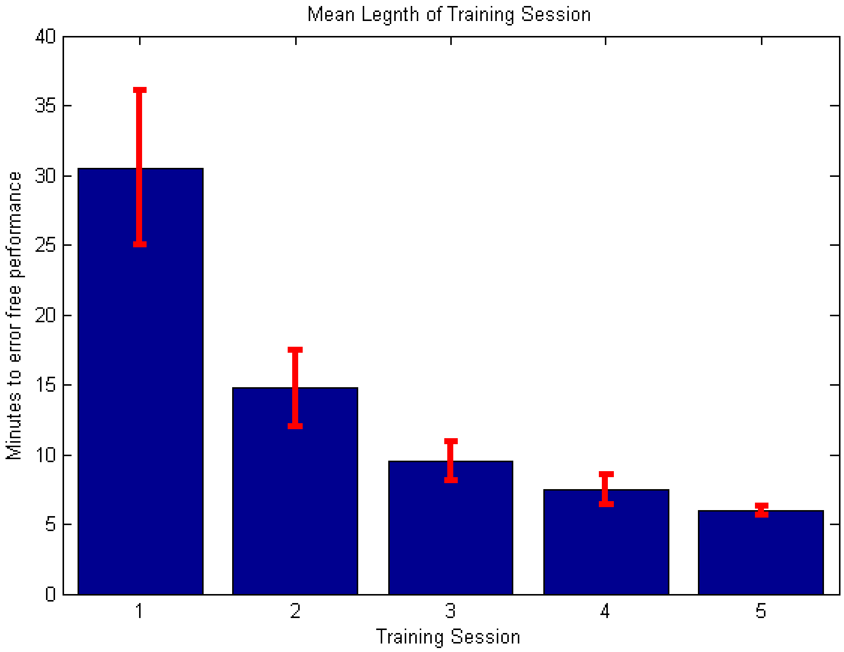


Figure 2.1: Mean amount of time subjects took each day to complete training. Error bars (red)represent the standard error of the mean.

sequence. One important difference is the floor effect for minimum length of training time. The current study approached six minutes, whereas the Lahav study approached twelve minutes. The other difference to note in the present involved the use of musically experienced, but piano naive subjects in addition to musically naive subjects. Previous musical experience may have had an effect on length of time of subjects to learn acquire the melodic sequence. Pearson Correlation of length of time to error-free performance on the first day and years playing music shows a significant, negative slope, r(15)=-0.58, p=0.01, but the relationship loses significance by the second day of training, r(15)=-0.39, p=0.12. Previous musical experience was not correlated with pitch-recognition-production pre-training scores, post-training scores, or the difference between them (see appendix for table of behavioral correlation scores).

The pitch-recognition-production matching test showed little improvement from the pre-training percent correct (mean, 38.63; SD, 5.54) to the post-training score (mean, 46.27; SD, 5.51). A paired sample, two tailed T-test shows a lack of significant difference between the pre-test and post-test scores t(16)=-1.32, p=0.21. Figure 2.2 reveals a slight increase in performance across the subject pool, with variance staying the same (SD=5.53 pre-training and SD=5.52 post-training). This finding is in contrast to that previously reported (Lahav et al., 2007) which showed an increase from 24 percent accuracy, to 77 percent after five days of training, and an increase from 30 percent pre-training, to 60 percent after a single training session (Lahav et al., 2005). The differences are not likely due to inclusion of subjects with previous musical experience, as there was no correlation between years spent playing and scores on the pitch-recognition-production test for this subject pool. The musically naive subject group showed a greater improvement in mean score, from 37.4 (SD = 5.9) percent correct to 48.5 (SD = 3.6) correct after training, compared with the musically experienced group who modestly improved from 40 (SD = 5.4)to 43.8 (SD = 7.3) percent. A mixed two-way ANOVA of within subject factor of test (pre,post) and between subject factor of musical experience corroborates this lack of significant difference between subject groups on the p-r-p test (F(1,15)=0.38, p=0.55). Extrapolation from these group results should be done cautiously as the sample size is small and not necessarily a representative sample of the populations. The nonmusician p-r-p scores more closely approximate the earlier reports of p-r-p scores from single training day sessions (Lahav et al., 2005). The difference in presently reported post-training scores is likely the result of different implementations of ear training protocol, since the presently reported minimum time to daily completion (6 minutes) was approximately half as long as the previously reported studies (12 minutes). Differences in pre-training scores might be explained by differences in task instructions to subjects. Recall that

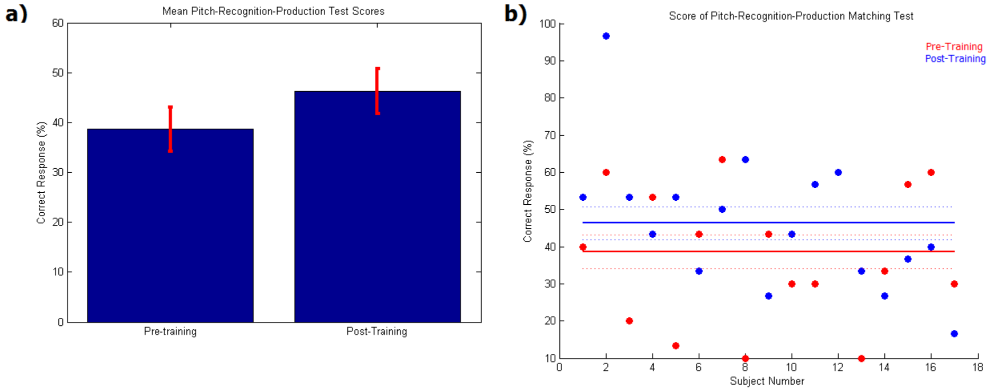


Figure 2.2: a) Mean performance on p-r-p test. Error bars (red)represent the standard error of the mean. b) Individual performance: solid lines represent the mean score, and standard error of the mean in dashed lines.

subjects heard a piano note, then had to press the corresponding key on the piano controller with the sound output disabled so s/he could not hear if s/he had chosen correctly. During the pre-test, subjects were confused about how to make a decision about a note when they had never played a piano before.

EEG

Brain rhythm suppression was calculated at electrodes C3 and C4 following reports of mu activity at these recording sites (Oberman et al., 2008; Ulloa and Pineda, 2007) and scalp projections of mu components are centered under these electrodes (Moore et al., 2011). A repeated measures ANOVA with factors of electrode (C3, C4), condition (control, learned, and transposed songs) and frequency (theta, mu, beta, and gamma) revealed a main effect of frequency F(3,13)=2988.37, p<0.0001, and a marginally significant interaction between frequency*electrode F(3,13)=2.65, p=0.09. The theta and mu bands revealed consistent enhancement of power relative to baseline across all the conditions, whereas beta and gamma were generally suppressed relative to baseline. Across theta, beta, and gamma

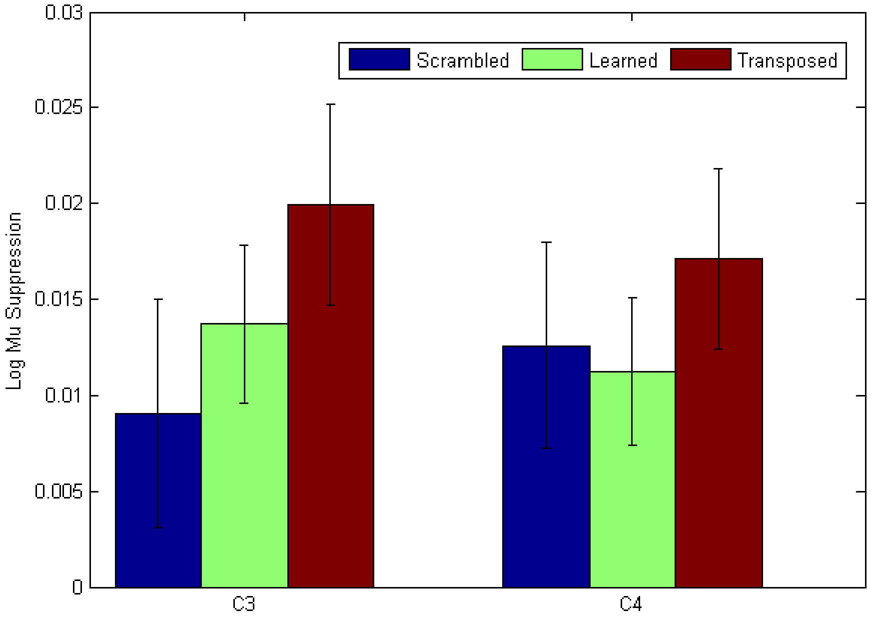


Figure 2.3: Mu suppression at electrodes C3 and C4.

frequencies at these electrodes, the relative power was lowest for the learned song, followed next by control, and then by transposed. Mu was the only frequency that exhibited higher power during the learned melody relative to the scrambled melody at C3. While I hypothesized the learned song would show greatest suppression, I did not expect the transposed song to elicit the least amount of suppression, even enhancement in some cases (see table 6.4 in Appendix A). Within subjects comparisons revealed a significant main effect for frequency F(3,45)=6247.88, p=1.0e-4, and interaction between frequency*electrode F(3,45)=2.91, p=0.05. Theta, mu and beta bands were fairly homogeneous between the electrodes, but gamma showed greater suppression over the right sensorimotor strip. A marginally significant effect was observed for condition F(2,30)=2.57, p=0.09, as well as a marginally significant interaction for frequency*electrode*condition F(6,90)=2.13, p=0.06.

The only frequency band that demonstrated suppression for all musical

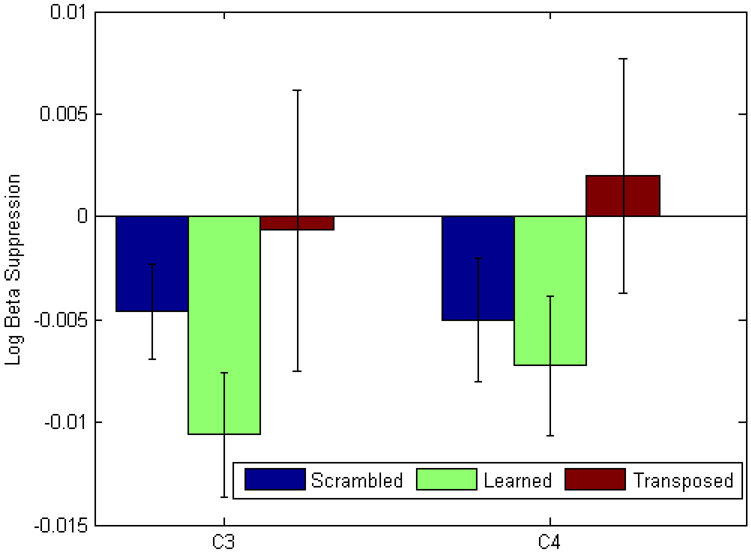


Figure 2.4: Beta suppression at electrodes C3 and C4.

conditions was the Beta band at electrode C3 (see Fig. 2.4). Again, beta shows the same pattern of lowest log ratio power for the learned song, followed by control song, and then transposed song. The pattern of relative power holds consistent for all three frequency bands at C3 and C4. The predicted results were not observed at electrodes C3 or C4 in the mu band (see figure 2.3).

Four additional repeated measure ANOVAs were calculated, one each for the theta, mu, beta, and gamma frequency bands, with electrode (19) and condition (3) factors. Within subject effects revealed a main effect of electrode for the mu F(18,270)=1.7, p=0.04, and theta bands F(18,270)=3.508, p=1.0e-3. No main effect was observed for condition, however the theta (F(36,540)=1.59, p=0.2), beta (F(36,540)=1.59, p=0.02), and gamma (F(36,540)=1.656, p=0.01) bands all revealed a significant interaction between electrodes and conditions. As seen in the supplementary material in chapter six (Fig. 6.1) the activity across all frequency bands was centered over the midline electrodes. Examining these electrodes, both

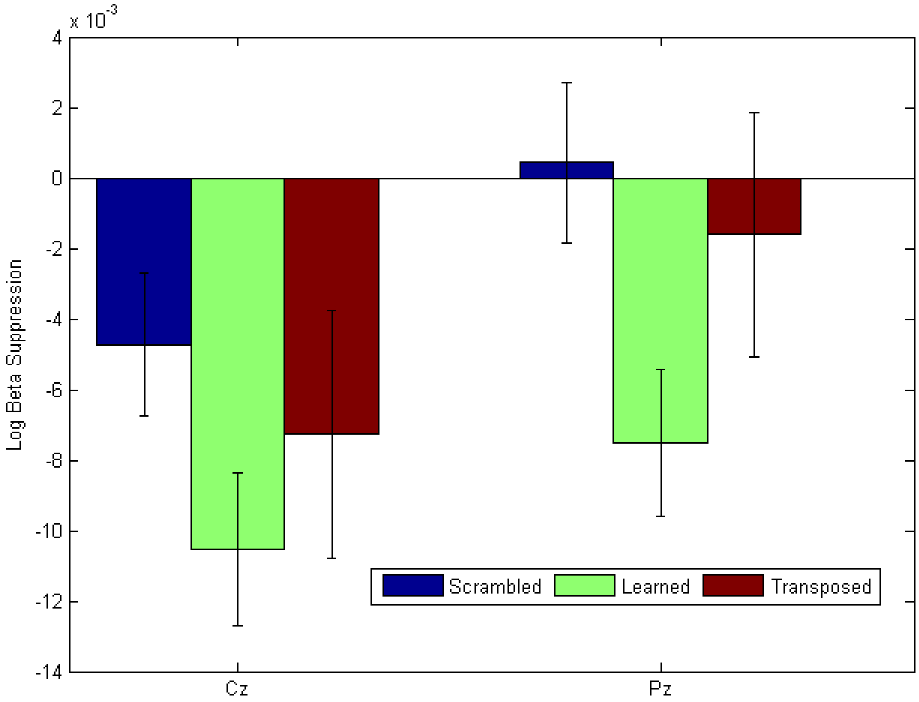


Figure 2.5: Beta suppression at electrodes Cz and Pz

Cz and Pz revealed a trend in the predicted direction across conditions in the beta band, with learned melody exhibiting greatest suppression, followed next by transposed, and lastly by the scrambled control melody. A significant main effect is observed for condition at these two recording sites $F(2,14)=7.12$, $p=0.007$. All three musical conditions exhibit suppression with regards to the baseline at Cz, and at Pz the scrambled melody control shows a slight enhancement (figure 2.5). Overall Cz reveals greater suppression than Pz for all three conditions, though the difference between learned and scrambled is larger at Pz. As the beta band has been shown to play a role in perception of sounds (Caetano et al., 2007; Iversen et al., 2009), and the effect is only observed over sensorimotor cortex, this finding supports the hypothesis that the motor system may be involved in perception of musical sequences. No significant correlations were found between beta suppression at these sites and years of musical training, pitch-recognition-production difference scores, or length of time to reach error-free performance on the first day of training. Lack of correlation between brain responses and these behavioral measures indicates that prior musical experience or aptitude is not likely influencing the neural physiological responses.

2.5 Discussion

The present study reports a novel finding that cortical motor system activity is sensitive to the effects of auditory sequences when the sounds are associated movement. When subjects hear both a melody they learned to play, and a transposed version of that melody, they exhibit suppression of the beta band relative to baseline and relative to a scrambled melody control. The level of motor system engagement indexed by beta suppression is greater in response to listening to

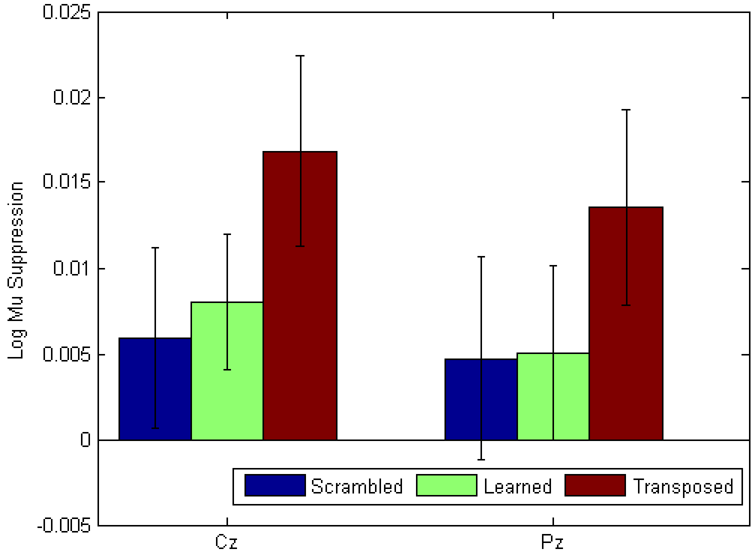


Figure 2.6: Mu suppression at electrodes Cz and Pz

learned melodies than listening to the transposed version of these melodies. Suppression of the beta rhythm while listening to transposed versions of the learned melody indicates a role for motor system associations with the sequential aspects of an auditory stimulus. The present study builds on previous work by Lahav et al. (2007) who reported motor system activity in the form of a blood oxygen level dependent (BOLD) signal when listening to the same learned melody. Lahav et al. further demonstrated partial motor system activation when subjects heard a novel melody composed of notes from the learned melody. They interpreted the partial activation as evidence that the motor system was sensitive to associations formed between single notes and single finger movements (recall one note per finger on the right hand). I hypothesized the difference between motor system engagement levels for learned melodies and scrambled melodies of the same note set could be explained by a motor system sensitivity to sequences of sounds. The evidence currently reported supports this hypothesis. A logical extension of the work would compare the levels of motor system engagement while listening to the transposed melody and scrambled melody (same notes). If the motor system is sensitive to both single note (pitch) and sequence information, then the sum of motor activation between these two conditions should approximate the level observed when subjects listen to the melody they learned to play.

Caetano et al. (2007) report that the beta frequency band desynchronizes in anticipation of actions, and hearing and seeing that same action, followed by rebound synchronization after completion of the event. They also reported the mu rhythm followed a similar time course of desynchronization and rebound synchronization, with slight delays in rebound compared to the beta rhythm. During sound only, mu and beta responses don't desychronize as much in the anticipatory phase, perhaps as no visual cues predict the onset of sound, though they both rebound at the same latency as visual based stimuli. Boonstra et al. (2006) also report a similar beta desynchronization during auditory perception and a rebound synchronization while subjects tapped along with a steady, rhythmic sound. Beta, as well as mu frequency bands, are seen as the two most active bands in terms of phase coherence between a cerebral network engaged during rhythmic sound tap synchronizing (Pollok et al., 2005). Further evidence to support the relevance of beta band in musical sequencing or rhythmic processing comes from reports of activity centered around 25 Hz in response to missing (expected) rhythmic sounds (Zanto, 2005; Snyder and Large, 2005) and from its proposed role in modulating perceived beat structure (Iversen et al., 2009).

Rather than mu suppression, mu enhancement was observed across all conditions. The trend was similar across electrodes in the sensori-motor scalp region. Scrambled and learned song conditions had similar low levels of enhancement, while the transposed song enhanced mu significantly greater than the other two conditions. Mu suppression was predicted based on past work identifying mu rhythms as having high power during rest and suppressing during visual, auditory, and audiovisual input sans movement (McGarry et al., 2012). However, these stimuli were not musical in nature, and the action was a discrete goal of tearing a sheet of paper. As discussed in the introduction, prediction of sounds in the absence of visual input is difficult. Music and language, conforming to grammatical rules can build predictions of future sounds based on relationships and sequential effects of past sounds. To assume the same neural system predicts visual and auditory movement related stimuli may be an error, even though auditory information can facilitate visual processing. While the mu rhythm is sensitive to auditory information (McGarry et al., 2012), and plays a role in visual to motor and audio transformations in terms of reading sheet music (Behmer and Jantzen, 2011), it may not play a direct role in audio and motor processing by itself. Caetano et al. (2007) report the mu rhythm responding more robustly to tapping on a drum when there is somatosensory feedback. Performing the same tapping action in the absence of any surface to tap on, fails to desynchronize the mu rhythm in the same way as a tap with tactile feedback. Listening to a melodic sequence that has motor associations may not suppress mu rhythms as the experience does not include the sensation, or perhaps even simulation of a tactile response. However one should draw comparisons cautiously as previously reported mu responses to tapping indicates a response to a discrete movement, whereas in the present study neural responses were averaged over several discrete sound-action pairings.

Mu enhancement, greatest while listening to the transposed song, may reflect an inhibitory response. The inhibition timing hypothesis (Klimesch et al., 2007; Klimesch, 2012) interprets event related increases of mu as an inhibition response during activity in other cortical rhythms. For instance, mu may signify the inhibition of motor output, such that changes in beta rhythms sequencing motor commands remain a simulation, unable to affect actual muscles. The hypothesis further proposes a role of mu enhancement as a main source of synchronization in cortical rhythms to synchronize neuronal timing. Given the strong temporal structure of musical sounds, it may be reasonable to expect mu to increase during more complex sound that require additional sequencing resources. It is possible that listening to a transposition requires more cortical resources such that greater demands are placed on the timing mechanisms critical to sound sequencing. If mu enhancement reflects increased difficulty of auditory sequencing, then listening to complex rhythmic patterns may elicit greater enhancement of mu rhythms than simple rhythmic patterns.

The changes in length of time to complete training across sessions, suggest subjects learned the melodic sequence. The data follow an exponential decay curve showing a collapse of variance across all the subjects approaching a minimum training time of six minutes. Overall, subjects showed a modest improvement in pitch-recognition-perception matching scores after training. Our novel inclusion of subjects with previous musical experience had an effect on the length of time to learn the song on the first day of training, but after five days of ear training and piano playing, differences between subjects groups were negligible. The two population groups, both piano naive, did not have significantly different p-r-p test scores before or after training. As previous reports from Lahav et al. (2005) were performed with only musically naive subjects, the present work extends this task as a viable training with little differences for both the musically naive and musically experienced, but piano naive subjects.

Of interest is the lack of replication of significant increases in the pitch-recognition-production test scores as a result of training. Two key differences stand out between the present study and those reported by Lahav et al (2005; 2007). The first was inclusion of participants with prior musical experience, with the exclusion of piano training. Years of previous musical training did not correlate with any measure except for the length of time it took to learn the sequence on the first training day. The 30 minutes it took to complete training the first day was approximately the same between the present study and that reported by Lahav et al. (2007), though the present study had increased variance. This suggests that the more important difference between studies is the implementation of the training software. With Lahav's software, a subject was reported to take at least twelve minutes to complete training, whereas with the present study's software, there was no programmed minimum time constraint. Subjects working through the incremental pieces of the song with virtually no mistakes could complete it in approximately six minutes. While minimum time to completion is the measure that indicates a difference in software protocol, the reasons behind this could be important. In my software, subjects received feedback based on their performance at the level of multiple measures. For instance, a subject learning measures 3-4 would be informed after attempting to play the 3 notes if they played the whole sequence correctly or incorrectly, and were asked to repeat the attempts until they played it correctly. If subjects would have received feedback about individual correct notes it could result in a different approach to ear learning adopted by participants, which could have impacted scores on the pitch-recognition-production task.

Taken in light of previous findings, enhanced mu and suppressed beta might indicate greater cortical demands in response to sounds associated with a motor action. As previous authors (Lahav et al., 2007) hypothesized a trained association between discrete musical pitches and discrete finger movements, a follow-up experiment could make use of the temporal resolution of EEG and design the post training assessment to focus on reactions to discrete musical notes, or a sequence of multiple notes, to test whether cortical oscillations are recruited according to the time intervals related to sequence complexity. Relevant work from functional imaging suggests increases in auditory and premotor cortical activity proportional to difficulty of tapped rhythms (Chen et al., 2009). If the motor system contributes to offline processing of sequential or rhythmic sounds at the level of discrete sounds, then one could predict beta desynchronization or mu synchronization in response to heard sounds without movement.

Chapter 3

Study 2 - Synchronizing Moving and Listening via Tapping

3.1 Abstract

If simulation accounts of motor system activity during auditory perception are true, then similar neural activity should be seen in response to single movements and single sound. As moving in time with sound involves simultaneous sounds and movements, it begs the question, how would a neural response hypothesized to be the same for a single movement or a single sound, respond when movement and sounds co-occur? I recorded the EEG of subjects engaged in a task that combined listening to rhythmic tone sequences, tapping along with those tones, and tapping in the absence of sounds. Results indicate a beta band (20-30 Hz) response that differs in the time window prior to finger movements and tap onset from the pure listening condition, but shows a similar positive deflection after all three conditions. Furthermore, when sounds and taps occured close together in time but shifted to occur not at the same moment (e.g. syncopated) the motor beta response inter-

feres with the auditory response. These findings support a simulation account of auditory perception with a cortical motor rhythm. Analysis of additional brain rhythms showed sensitivity of mu (8-13 Hz) and gamma (30-50 Hz) to both sound and movement events, but without showing similar responses across all three conditions. While the beta band may account for movement and auditory processing in similar ways, mu and gamma bands may play a more complex role in integrating these different information streams.

3.2 Introduction

Humans are one of a few select species able to synchronize movements with sounds (Schachner et al., 2009; Schachner, 2010). Simulation hypothesis (Patel and Iversen, 2014) predicts this ability as a function of the motor system simulating movement, to predict the occurrence of rhythmic or expected sounds. Of the studies supporting cortical motor rhythm contributions to the perception of sounds, none to date have compared brain responses of subjects listening to, and moving along with, rhythmic sounds, controlling for the effects of simultaneous listening and moving. In the present work I asked whether the anticipatory brain responses to rhythmic movements are also present while listening to rhythmic sounds sans movement. Tapping is a model behavior for rhythmic brain recording because it is easy to quantify with minimal equipment, temporally precise, has been well studied (for reviews see (Repp, 2005; Repp and Su, 2013)), and is a reasonable task for subjects wearing EEG sensors to do while remaining relatively still. To test whether motor systems simulate activity during auditory perception and anticipation, I asked whether power decreases observed in motor rhythms (mu (8-13 Hz) and beta(20-30 Hz)) preceded both taps and auditory pacing cues. These bands were chosen based on previous reports showing that 1. power in the 8-13 Hz band is sensitive to sound and motor actions (McGarry et al., 2012), 2. 10Hz and 20Hz centered brain responses stabilize similarly after listening to a drum tap, and executing a tap on a drum (Caetano et al., 2007), and 3. top-down perceptual effects elicit changes in 20-30 Hz responses to rhythmic sounds (Iversen et al., 2009) To isolate the influence of auditory and motor processes from simultaneous listening and moving, I tested conditions where subjects 1. listened to a rhythmic tone without moving (auditory only), 2. tapped along with the tone, and tapped 180 degrees out of phase with the tone (motor and auditory), and 3. tapped without any rhythmic tones (motor only).

Tapping is a well suited task for behavioral and perceptual research, and demonstrates transference of skills or experience from other domains. Not many musical instruments are played with index finger taps, but many musicians transfer skills learned on an instrument to this more abstract behavior. Experienced musicians are more sensitive in detecting perturbed pacing cues, and resynchronize taps more quickly after phase shifts in pacing cues, than musically inexperienced controls (Repp, 2010). Overall, musicians show decreased variability in inter-tap-intervals greater than 1000 ms, compared to nonmusicians, and exhibit less variability when asked to continue tapping after a pacing cue is removed (Repp and Doggett, 2007). As musical training affects the variability of responses in motor timing, it may also affect the brain rhythms associated with movement preparation. If motor rhythms in the brain correspond to the discrete movements, I predicted that variability in inter-tap-intervals would be inversely proportional to the summed power of the beta band. To this end, I recruited subjects on a continuum of experience from musically naive, to those with greater than 10 years of playing instruments, as this sample set should include high and low variability tapping performance.

Tapping does not always produce a sound, making it possible to measure rhythmic motor output while minimizing acoustic input to the hypothesized audiomotor system. Acoustic feedback is integral to the musician playing an instrument synchronized with other musicians, but not to the dancer who does not generate auditory feedback with most movements. Without direct auditory feedback, there is an increased reliance on predicted future states of the motor system. The motor system, in order to stay synchronized to auditory events that have yet to happen, must already be in motion prior to the onset of a sound. The time window before an auditory event is therefore an ideal time to look for similarity in responses. Boonstra et al. (2006) describe a drop in beta band power prior to a tap that happens every 500 ms in synchrony with a tone. The second place to ask if motor and auditory events induce similar brain responses is in the time window after an event. Caetano et al. (2007) demonstrated increases in both the beta and mu rhythms after a subject tapped a drum, or heard a sound of the drum. The present study will extend these findings by combing the rhythmic nature of the former study with the comparison of dissociated moving and listening described in the latter study.

An association between movement and auditory perception may provide a mechanism for experience dependent changes in perception. Past reports describe sensorimotor associations that influence perception of ambiguous pitch intervals. An ambiguous pitch interval is described previously by Deutsch (1986), and a trained pіansts can be primed to hear an ambiguous interval as either rising or falling. Pianists associate rising pitch with a movement from left to right across the piano keyboard. Hence, pressing an arbitrary key, and then pressing a key to the right of it, will influence the pianist, but not an inexperienced control, to perceive an increase in pitch over an ambiguous pitch interval (Repp and Knoblich, 2007). In another example of a top down effect on perception, Iversen et al. (2009) presented subjects with a rapid pair of tones followed by a rest. Subjects were asked to alternately imagine a musical beat on the first or second tone. The beta rhythm was increased in power when subjects heard the tone corresponding to the imagined beat. In the first study in this dissertation, beta rhythms were suppressed while subjects listened to a piano melody they could play, but not when listening to a piano melody that the subject could not play. Beta suppression indicates simulation of a motoric response to the familiar piano melody. Beta likely plays a top down role in perception of melodic sequences because it also suppresses when subjects listen to the same relative piano melody they learned, even when played relative to a different starting pitch. This sensitivity to sequences, even despite changes in pitch/frequency, is an abstract level feature that is tied to relative pitch distance associated with discrete movements.

Synchronizing movements with sounds requires temporally precise motor planning. For most sound inducing movements, a preparatory movement, such as lifting an arm for a drummer, occur tens to hundreds of msecs prior to the act of bring the hand down on the drum head. This same pre-stimulus time window is a region of interest for isolating auditory prediction. I recorded electrical activity of the extensor muscle in participants' tapping finger to identify when movement starts, to constrain the motor planning or anticipation phase during analysis. I hypothesized that similar patterns of brain rhythm suppression in terms of latency or power would occur in the mu and beta bands for both movements and rhythmic sounds.

A similarity in brain response for both movement and listening conditions would support a simulation account for the perception of sounds, and while beta is a good candidate, it is not the only brain rhythm capable of simultaneously representing auditory and motor information. Previous work indicates a role for mu rhythm suppression (8-13 Hz) associated with sound producing actions (McGarry et al., 2012; Caetano et al., 2007). Additionally, alpha (5-12 Hz) power increases when subjects are asked to make harmonic judgments about tone sequences (van Dijk et al., 2010). Increases in alpha (7-15 Hz) phase synchrony is also observed for rhythmic tones (Ghuman et al., 2011). The mu rhythm is also hypothesized to come from sources in the sensorimotor cortex (Pineda, 2008). Mu, alongside beta, is associated with increased phase coherence between motor and auditory brain sources involved in rhythmic tapping (Pollok et al., 2005). Given these observations, I predicted that the mu and beta rhythm will show similar responses to rhythmic sounds and movements in the form of decreased power during both conditions relative to baseline.

The synchronize-continue tapping task is well designed to compare listening, moving while listening, and movement without auditory cues. The subject first entrains to a rhythmic sound, then starts tapping along with it, and after a predefined period, the sound disappears while the subject continues to tap. This experiment has been used extensively, and has been validated with a wide age range of population, from children of four to adults into their seventies (McAuley et al., 2006). To address the issue previously mentioned regarding the interaction of simultaneous motor and auditory processes, I also included a syncopated tapping condition where subjects would tap in the interval between tones. For instance if a sound is presented every 750 ms, then the taps would occur 375 ms before/after the tones. An inter-trial-interval this short should still elicit discrete beta band responses for movements and tones given the previous work of Fujioka et al. (2012). In addition to providing conditions to separate movement from sounds, the syncopated condition provides an opportunity to ask whether implicit auditory images would be continue in the absence of syncopated pacing cues. I predicted that an auditory image would be visible in the beta band during the continued phase of the syncopated trials.

3.3 Methods

Subjects

Fifteen neurotypical students from the University of California, San Diego, participated in the experiment. All signed written consent for a protocol approved by the local IRB. The mean age of the subjects was 23.2 years old (SD = 5.1), three were female, and all self identified as right handed, with one also identifying as ambidextrous. All reported having normal hearing, no history of psychiatric illness or neurotrauma, and no psychotropic drug use in the 24 hours prior to participation.

Task

Subjects performed a synchronize-continue tapping task with their right hand while wearing an EEG cap. Each trial in this task is split into three phases: entrainment, synchronized tapping, and continued tapping. During the entrainment phase, a metronome triggered a 440 Hz pure tone for 50 ms duration at fixed intervals while the subject listened. After feeling adequately entrained, a subject would begin tapping along with the metronome. After twenty seconds of synchronizing, the metronome stops and subjects continue tapping at the same pace as best as they can for another twenty seconds.

Two different experiments were tested using this task, set up in an orthogonal design. The first experiment, designed to test differences in tempo, pseudorandomly presented subjects with different metronome tempos. Four speeds were chosen from the logarithmic scale reported in McAuley et al. (2006): 225, 506, 759, and 1139 msec intervals. As the different metronome speeds would affect the number of taps in each trial, I decided to control for number of tap intervals, and balanced by including more trials of longer interval taps, resulting in approximately 100 tap intervals per condition.

The second experiment, reported presently, was designed to test moving synchronously with sounds, versus tapping at the same interval, but decoupling the movement from co-occurring sounds. Instead of synchronizing their taps with sounds, subjects syncopated their taps. For this experiment I chose the 759 interval as pilot subjects showed the most easy time syncopating taps at this interval. This experiment utilized three conditions: listening to the metronome, tapping along with the metronome, and tapping counter to the metronome (syncopated). All subjects were presented trials in this order as behvioral pilot data showed an increased difficulty in correctly performing the syncopated tap condition amongst those without musical training. Even despite this, one subject had to be removed from analysis as the task was not performed correctly. Direct comparisons were made between the syncopated condition and the regular synchronizing condition at the same interval.

Data Collection

EEG data were collected on a Biosemi ActiveTwo system with 128 channels in 10-20 coordinate space. Five additional electrodes were used: two at the mastoids for offline re-referencing, one horizontal to the eye for blink and sac-

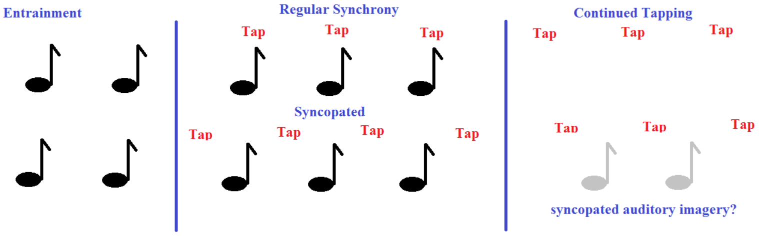


Figure 3.1: Regular synchronized tapping with sounds and movements occurring together in time, contrasted with syncopated tapping, where taps and sounds occur 180 degrees out of phase with each other.

cade detection, and two on the flexor and extensor muscles controlling the right index finger. Recordings were made with a .1-100 Hz online bandpass filter and sampled at 512 Hz and gain setting of 1000. Metronome sounds were presented via MaxMSP 4.5 and played through speakers in the EEG chamber that subjects turned to a comfortable listening level. Taps were recorded from a piezo element mounted on a board held in the subject's lap and converted to EEG triggers using MaxMSP. As piezo elements can generate current on both a tap, or an enthusiastic rebound tap release (extension of finger following tap flexion), a refractory window was coded into the MaxMSP program in which no additional triggers could be generated for 100 msec post tap detection.

Analysis

Behavioral

Taps were extracted from the EEG data file as event codes after preprocessing of EEG data (described below). Performing tap extraction post-EEG cleaning allowed for analysis and reporting of only behavioral data corresponding to the trials reported for EEG analysis. Data were converted from samples to seconds, and the mean interval and standard deviation were calculated between taps for each condition (synchronized tapping, continued tapping, syncopated tapping, and continued syncopated tapping). Occasionally subjects would tap too soft, or too far away from the piezo element to generate current. These missed taps were usually identified as an inter-tap-interval that was a multiple of the expected tap interval (759 msec), and were removed from further analysis. Statistical tests were computed in Matlabd and SPSS, with a False Discovery Rate correction for multiple comparisons (Genovese et al., 2002).

EEG

Data were analyzed using the EEGLAB toolbox for Matlab (Delorme and Makeig, 2004). Bad channels were identified via absolute voltage fluctuations and visually verified. Electrode channels were re-referenced to digitally linked mastoids, bandpass filtered from 0.1-50 Hz. Epochs were extracted for both sound and tap events, with the time window encompassing two complete inter-tap/sound intervals. For instance, the 759 msec tempo condition would have epochs from -1 to 1 second after the event marker. The baseline for each epoch was estimated as the mean of each time window, and was subtracted from the time series. Bad epochs were marked by extreme absolute voltage and visually verified. Remaining data were run through the infomax ICA algorithm to extract artifactual components used to identify non brain sources of electrical activity, such as eyeblinks, and remove them from subsequent analysis. Channel space measures used data at this stage of processing, whereas component space measures included additional spatial filtering. Dipole source estimates were calculated for independent components via the Dipfit 2.x EEGLAB plugin. Components were then clustered into 20 clusters using K-means based on scalp projections and dipole source estimates, the latter of which were weighted an order of magnitude heavier in the model. Outlier components of 3 of more standard deviations from the mean of any cluster were excluded.

Event related potentials were calculated across subjects over a 2000 ms window, with the window centered on the tone or tap event. Spectral power was computed over the same time window, performed by an FFT with the edges of the time window trimmed down 250 ms on each side to reduce tapering effects and resulted in capturing only one tap or tone in each epoch. Time-frequency decompositions were computed with wavelets using a Morlet taper across the 2000 ms time windows. Using a minimum of three cycles per wavelet, I was able to calculate down to 3 Hz, which allowed study of the theta band (4-8 Hz). Band power was estimated for both spectral and time-frequency data by integrating the power within a predefined band (theta = 4-8 Hz, mu = 8-13 Hz, beta = 20-30 Hz and gamma = 30-50 Hz) using the trapezoid rule, with a sliding integration over time for time-frequency reporting. Statistical comparisons were made using the Matlab Statistics Toolbox and permutation statistics included in EEGLAB. Permutation tests were chosen due to the small number of subjects included in the sample set, to control for the possibility than any one subject might unduly influence the overall mean. Multiple comparisons were corrected with the False Discovery Rate threshold function (Genovese et al., 2002).

3.4 Results

Behavioral

Two tailed, paired samples tests revealed significant differences in accuracy between synchronized and continued trials for standard synchronization ($t(14)=-5.01$, $p<0.001$) and syncopated trials ($t(14)=-4.17$, $p=0.001$). Accuracy was defined as the difference between mean observed inter-tap-interval and the metronome value. For both trial types, the paced tapping showed accuracy an order of magnitude greater than continued tapping (synchronized M=2 msec, SD = 1.66 msec, continued M=19 msec, SD=14 msec; syncopated M=2.5 msec, SD=2.19 msec, continued M=21.9 msec, SD=17.8 msec). There was no significant differences between synchronized and syncopated paced tapping (t(14)=-0.789, p=0.44) or continued tapping (t(14)=-0.471, p=0.65). In terms of tapping stability, defined as the standard deviation of inter-trial-tap intervals for each subject, there were no differences within trial blocks (synchronized: t(14)=-1.392, p=0.19, syncopated: t(14)=-1.86, p=0.08), or between trials (paced: t(14)=0.315, p=0.76, continued: t(14)=-0.4, p=0.7). There were no correlations between accuracy or stability measures and years spent playing instruments (see supplementary tables for Pearson values in Appendix B).

EEG - Channel Space

To simplify the analysis and reporting of channel space measures, all of the following results were calculated at recording site C3. The choice of this electrode was based on its proximity to the left sensorimotor cortex that controls the contralateral right hand used in tapping. This recording site is in close proximity to sites previously discussed in the dissertation.

Spectral Analysis

Pairwise comparisons between synchronized taps and continued taps can hypothetically reveal which frequency bands contain auditory information, as both conditions should contain the same motor information, but only the synchronized trials have sound. The difference between synchronized taps and continued taps was greatest in the gamma band (t(14)=2.18, p=0.047). The synchronized (auditory information present) trials had a greater summed power (M=1902.9, SD=154.3) than the continued (M=1875.9, SD=141.8) tapping. Past observations (Fujioka et al., 2009; Iversen et al., 2009; Snyder and Large, 2004), also credit this frequency range (30-50 Hz) with auditory dependent activity. Analysis of the gamma band across time could test this interpretation. The beta band also appeared to be modulated by condition and presence of auditory information, though not at a significant level (t(14)=1.87, p=0.083). If auditory and motor systems easily form associations (Lahav et al., 2007; Repp and Knoblich, 2007), then a relatively small effect might still be detectable in a small sample set (n=15). Additional trials per subject could also help improve the signal to noise ratio, or locking time windows to onset of motor activity rather than just tap registration. The theta (t(14)=1.66, p=0.19) and mu (14)=-0.33, p=0.74) bands did not show condition dependent differences, and this may indicate a common role in motor processing for both.

Syncopated taps and continued taps should have a similar relationship as synchronized taps with their respective continued taps. The same information is still present for both synchronized and syncopated tapping, but the occurrence of the sound and movement are 180 degrees out of phase in the latter. Gamma (t(14)=-0.053, p=0.96), and beta (t(14)=-0.93, p=0.37) bands showed smaller differences between trials when balanced for auditory information, than in the previous comparison of synchronized and continued tapping. Perhaps the phase shift is important for describing why a significant difference between tapping with sound and without sound disappears when syncopating. Direct comparison of tapping with sounds, both in phase and out of phase is necessary for further clarification (described below). Theta (t(14)=1.63, p=0.12) and mu (t(14)=-1.66, p=0.12) showed insignificant differences as well between syncopated and continued taps,

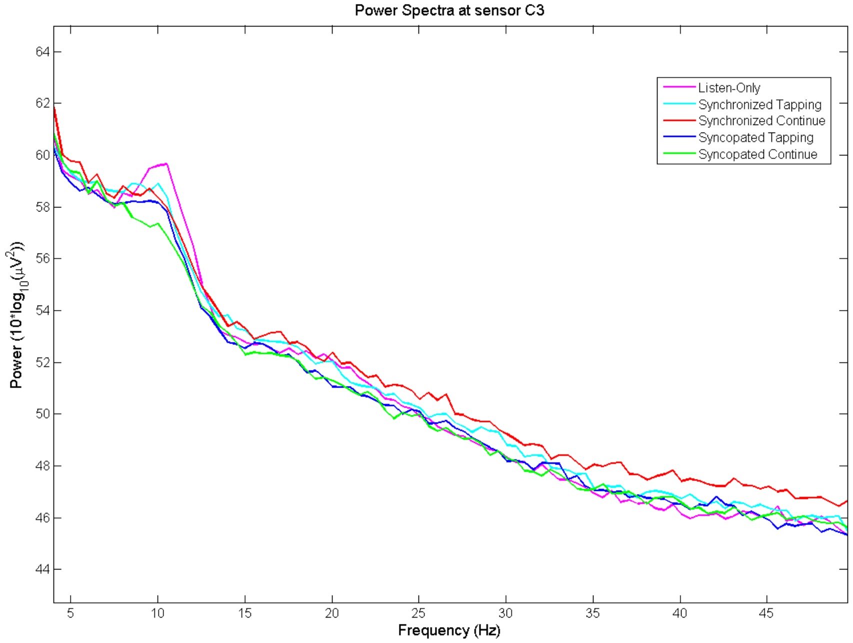


Figure 3.2: Spectral power for all conditions from electrode over left sensorimotor cortex (C3).

which supports the role of these frequency bands in performing motor related processes.

Direct comparison of synchronized tapping with syncopated tapping in the gamma band showed a lack of significant difference (t(14)=-1.47, p=0.17), however the effect is larger than comparisons of syncopated with continued trials. Beta band activity showed a significant difference between synchronized and syncopated tapping trials (t(14)=2.19, p=0.0480. The mu band also showed a significant difference in power (t(14)=2.24, p=0.042) between these conditions. Taken together, this indicates that syncopation might influence how auditory and motor information are integrated at the spectral level for at least the mu and beta bands. The theta band showed a similar difference between conditions (t(14)=1.41, p=0.18) as gamma, and likely does not reflect sensorimotor integration modulated by the task.

A last set of pairwise comparisons in an attempt to draw out which frequency bands contain motor information relative to auditory relies on the listening alone control condition. Contrasting listening-only with to synchronized tap trials showed a significant difference in the theta band power (t(14)=-3.11, p=0.008) with greater power during the tap synchronized condition (M=475, SD=19.8) than listening alone (M=470.6, 20). The mu band shows a marginally significant difference (t(14)=1.85, p=0.086). In this comparison, greater mu power was observed for listen-only (M=580, SD=36.7) over the synchronized tap (M=573.2, SD=33.7), which is consistent with past observations of mu suppression during movement. The beta band showed a marginally significant effect (t(14)=14, p=0.07) with increased power during the tap condition (M=1013, SD=67) over listen only (M=1001, SD=60). The gamma band showed a significant difference (t(14)=-2.44, p=0.03)with the greater power during tap synchronized condition (M=1901, SD=152) than listening (M=1861, SD=132.6).

Neuro-Behavioral Spectral Comparisons

I predicted that tapping stability would be proportional to the summed power in the beta or mu band, as more consistent taps could indicate more greater alignment of brain oscillation responses over trials. Correlations of tapping accuracy and stability measures (as previously discussed) showed no correlation with mu or beta band activity discussed in the previous section on spectral analysis for listening only, and tap-locked conditions. Likewise, neither tapping stability or accuracy is correlated with mu or beta suppression, calculated as the log ratio of synchronized tapping divided by listening-only power (see appendix B for tables of correlation values). The lack of similarity between variability in these two measures may be explained by the temporally imprecise nature of spectral analysis averaged over a whole tap or sound trial, or even over multiple trials. Tapping intervals may need to be compared to the spectral density of the time window centered over movement registration, or movement preparation, which may require analysis at the single trial level.

Time-Frequency Analysis

Mu Band The mu band (Fig. 3.3) revealed a rising power oscillation starting prior to tone onset for the sound only condition. A second, smaller amplitude oscillation occured in the span of time between the negative component of the post tone rise, and the start of the next tone locked rise. During the tapping conditions, this tone locked response had a similar post tone rise to peak around 130 ms, but the peak between mu reset and the next tone was absent. In both the synchronized and syncopated conditions, the continued tap-locked curve (no auditory information) showed a negative deflection corresponding to the onset of finger movement, at approximately -175 ms prior to tap registration. This suppression of mu lasted until approximately 175 ms post tap, and was followed by a rebound increase in power. This follows a similar pattern of activity as reported for mu desynchronization and post tap rebound reports in Caetano et al. (2007), however in the previous report, the inter stimulus interval was approximately four times as long as in the present study such that the window of suppression and rebound enhancement is drawn out. During the synchronized tap locked condition, suppression was not observed time-locked to the tap. In the syncopated condition, the tap-locked mu oscillation had the same temporal pattern of suppression as the continued tap (correlation coefficient $r=0.78$, $p<0.0001$), but with even greater power change. A one way ANOVA comparing syncopated and continued tap power at $T=0$ with listen only control showed a marginally significant difference ($F(2,42)=)=2.44$, $p=0.09$).

A similar test comparing synchronized and continued taps with listen-only control showed no significant effect of condition (F(2,42)=1.11, p=0.34). When the tap co-occurs with the tone, we see enhancement of mu. When the tap occurs between tones, we see suppression. The difference in oscillation between synchronized and syncopated taps, despite the presence of similar movement and sound in both conditions, indicated that the mu band likely represents activity linked to both auditory and motor processes.

Beta Band The beta band showed a low power, positive deflection (Fig. 3.4) peaking approximately 200 ms post tone onset in the listen-only condition. This is consistent with previous observations of post movement and sound rebound (Caetano et al., 2007). There was virtually no correlation between tone-locked listen-only and listen during synchronized tapping conditions (r=0.09, p=0.23). Correlation of the syncopated tone locked curve with the listen-only showed a slightly higher correlation (r=0.2, p=0.004), but still not strong. Both of the tap conditions in synchronized and syncopated trials showed a similar suppression prior to finger muscle activity, approximately -175 ms prior to tap. During synchronized tapping, a beta oscillation followed the same time course of suppression just prior to movement and continued until a post event rebound. In this band, the synchronized tap was highly correlated (r=0.93, p<0.0001) with the syncopated tap. In the syncopated condition, the tone-locked response was close to 180 degrees out of phase with the tap locked oscillations. Correlation of tone-locked and continue tap-locked is a strong negative correlation (r=-0.94, p<0.0001), indicating an almost perfect phase shift. This suggests that beta is responsive to movement information, more so than to auditory given the relationship between synchronized and syncopated tapping.

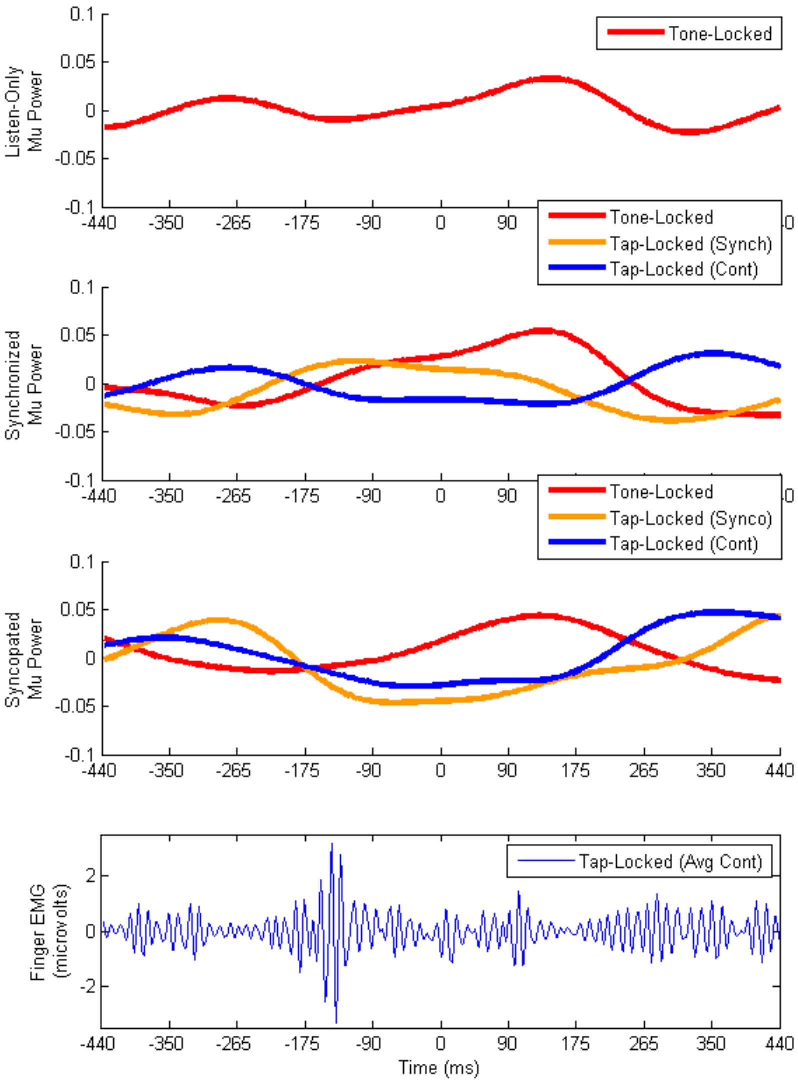


Figure 3.3: Mu bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

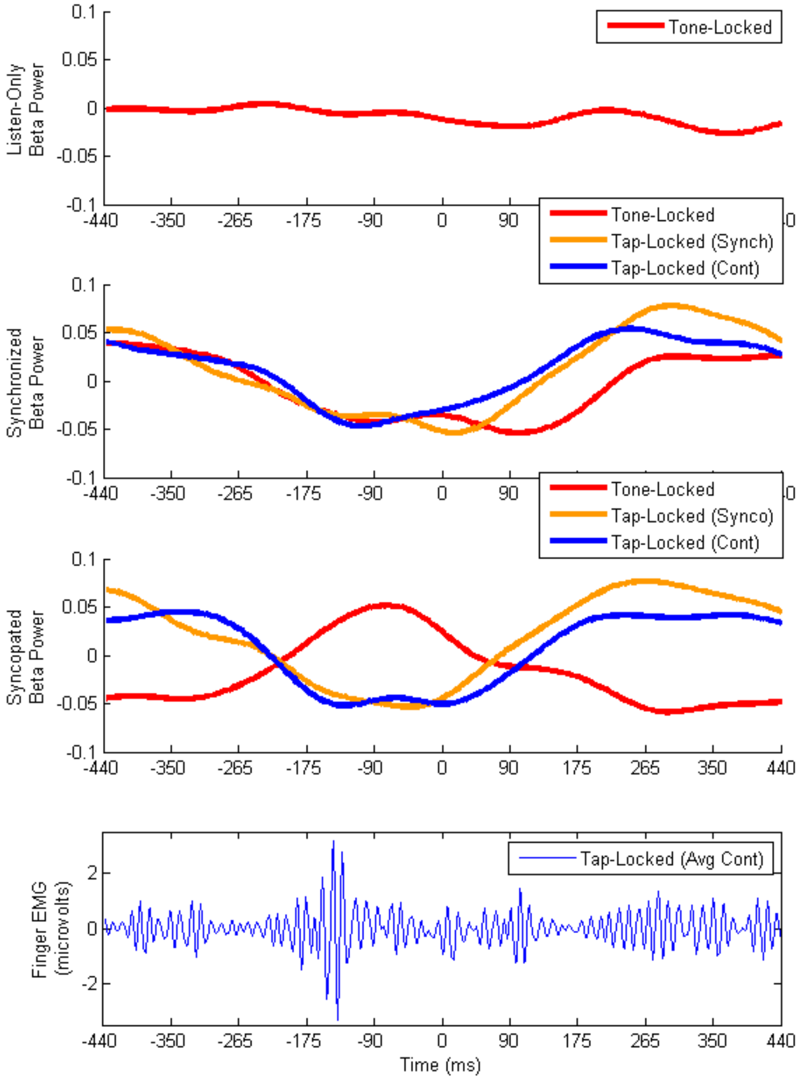


Figure 3.4: Beta bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

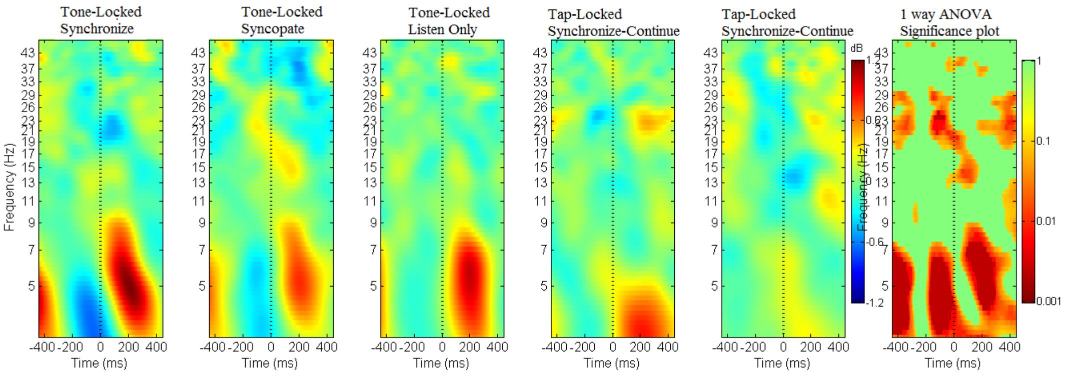


Figure 3.5: Event related spectral perturbations for brain data across conditions at electrode C3. A significance plot showing FDR corrected probabilities for significant differences across conditions is featured on the right.)

Multivariate Time-Frequency Analysis Event related spectral perturbations (ERSPs) were calculated to explore power changes in frequency over time. A one-way ANOVA was performed to compare the time-frequency responses across conditions. A separate F test was computed for each frequency bin at each time point, and a false discovery rate correction (Nichols, 2004) was applied to control for multiple comparisons. The most pronounced differences occurred in the theta and beta frequency bands over time (see Fig. 3.5). There was a significant difference in theta power 400 ms prior to event onset (F(4,56)=8.3, p<0.0001), 100ms prior to event onset (F(4,56)=11.12, p<0.0001), and again 200 ms post event (F(4,56)=7.05, p=0.0001). At the same pre-event latencies there was a significant difference in the beta band (F(4,56)=5.12, p=00.14 at T=-440ms, and F(4,56)=5.02, p=0.002). The post event rebound window was not significantly different between tone and tap-locked events in the beta band, corroborating previous observations for integrated bandpower (Caetano et al., 2007), and potentially supporting simulation hypothesis. Similar to previous results, theta and beta oscillations are tightly locked in time for tap aligned responses, but shifted in time for tone-aligned responses (Boonstra et al., 2006).

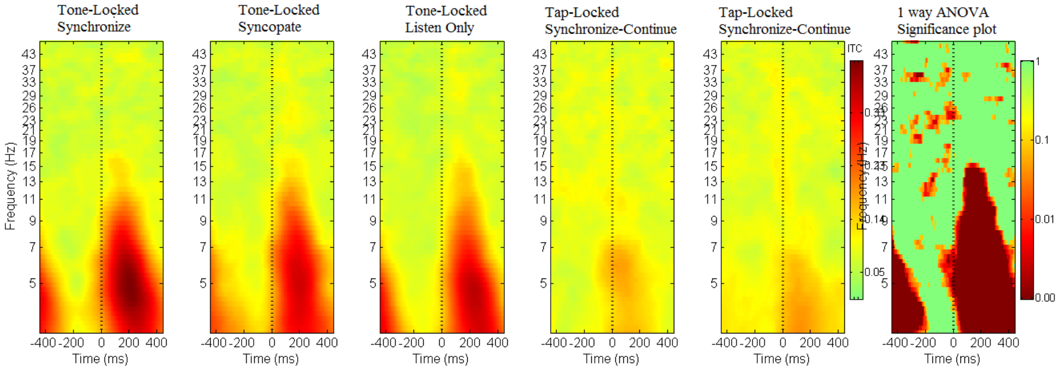


Figure 3.6: Inter-trial Coherence measures for brain data across conditions at electrode C3. A significance plot showing FDR corrected probabilities for significant differences across conditions is featured on the right.)

Inter-trial coherence (ITC) measures indicated a strong phase synchrony centered in the theta frequencies, and extended into the mu band for tone-locked conditions (see Fig. 3.6). The mu coherence was stronger in the listening-aligned trials than for tap-aligned trials post event onset (F(4,56)=24.01, p<0.0001 at t=200 ms). If mu plays an active role in auditory processing, then the stronger coherence during listening aligned trials could be explained by a consistent mu response to sounds at very precise intervals. Tap-aligned trials exhibited greater variability, which could be explained as muscle movements taking different amount of time prior to event onset if kinematics or trajectory of movement are subject to alteration over the course of the experiment. The beta band showed a significant difference just prior to event onset, with greater phase alignment between tap-locked trials than tone-locked (F(4,56)=6.51, p=0.0002). Even though predictive information is available for rhythmic tones, evoked responses prior to event are greater for motor related events than auditory. Similar calculations were made for both ERSPs and ITC at the corresponding right hemisphere electrode (C4) over sensorimotor cortex for hemispheric comparisons (see supplementary results in Appendix B).

EEG - Source Space

A total of four dipole source clusters were identified that fell within predefined regions of interest including motor and auditory cortices. The mean of cluster 11 fell on Talairach coordinates 50, -39, -7, which places it on the right medial temporal gyrus (rMTG), with components in this cluster extending to encompass other auditory processing areas in the superior temporal gyrus (STG). The scalp distribution for cluster 11 showed a dipolar pattern falling over the right anterior scalp. The mean of cluster 13 fell on the left MTG, (Talairach: -38, -60, 8). the lMTG cluster is more superior than the right hemisphere counterpart, and encompasses more of the STG and neighboring tertiary auditory processing cortices. Scalp projection of this cluster were less dipolar, showing a sink centered in R occipital-temporal cortex. Cluster 16 (Talairach: -31, -17, 34) was centered on the left pre-central gyrus (PreCG), which contains the primary motor cortex (M1). The scalp projection showed a dipolar pattern centered just posterior to the vertex, over the sensorimotor strip. The last cluster, 22, had a mean Talairach 7, -19, 55 on the medial frontal gyrus (MFG) with component estimates stretching from the cingulate gyrus to the supplementary motor area (SMA). Scalp projections were centered just anterior to the vertex, over the sensorimotor strip. For brevity's sake, only the mu and beta bands for clusters 11 and 22 are discussed in the present chapter, clusters 13 and 16 and additional frequency bands can be found in Appendix B.

Cluster 11 - right Medial Temporal Gyrus

The mu band showed a similar pattern of activity, as recorded over left sensorimotor cortex, for the listen-only tone-locked response, however the latency of peaks is shifted later in time, offset by about 90 ms. The pattern of mu suppres-

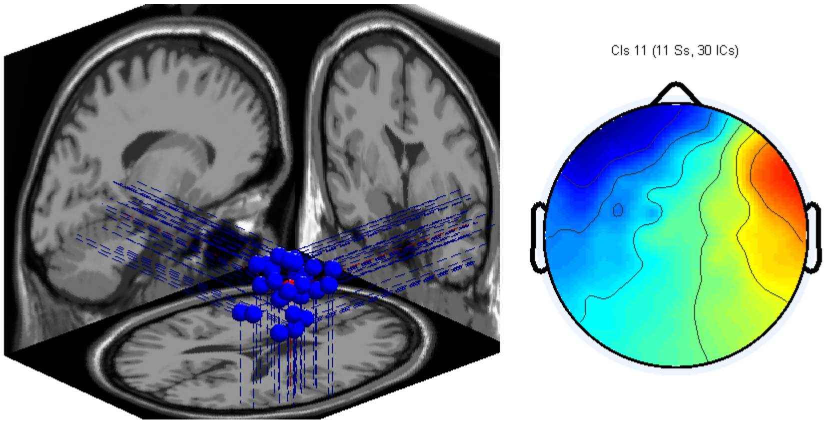


Figure 3.7: Dipole source estimate (L) and scalp projection (R) for right medial temporal gyrus cluster.)

sion in the channel space tap-locked conditions was not apparent in this cluster. The lack of suppression in temporal cortex corroborates the interpretation that the previously observed tap locked mu suppression is generated by the senori-motor strip (Pineda, 2008). Across the three conditions (listen-only, tone-locked synchronize, tone-locked syncopated) a similar suppression of mu was observed starting prior to tone onset and continued until rebounding approximately 90 ms post tone. Listen-only and syncopated conditions were strongly correlated in the time window of -175 to 90 ms) ($r=0.98$, $p<0.0001$), and only marginally less between listen-only and synchronized ($r=0.92$, $p<0.0001$). This could be evidence of the auditory alpha suppression identified in temporal cortex source space previously (Ghuman et al., 2011).

Similarly, a pattern of beta suppression occurred for tone and tap locked responses. A slight increase in power was observed for tone-locked waveforms in both the listen-only and synchronized tapping conditions. In the time window of -175 to 90 ms a significant correlation is seen between these conditions ($r=0.9$, $p<0.0001$), but the correlation is negative and less strong between listen-only and synchronized tapping ($r=-0.8$, $p<0.0001$). There is a stronger correlation between

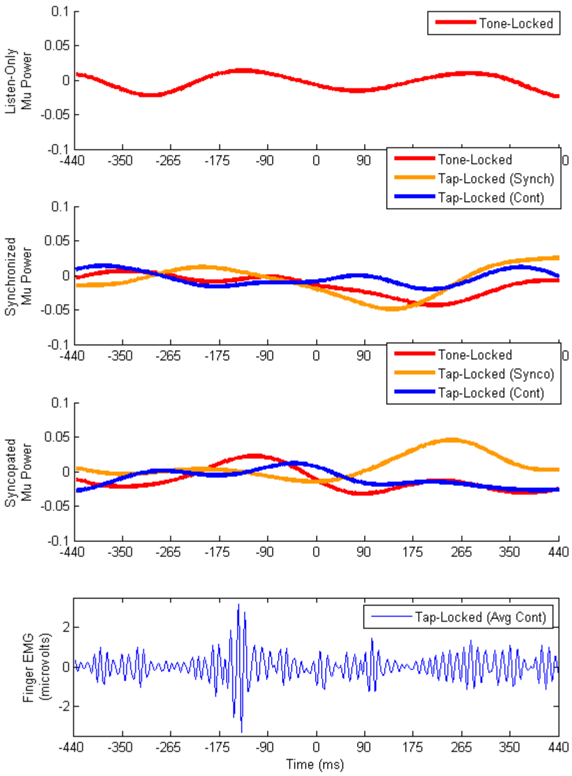


Figure 3.8: Mu bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

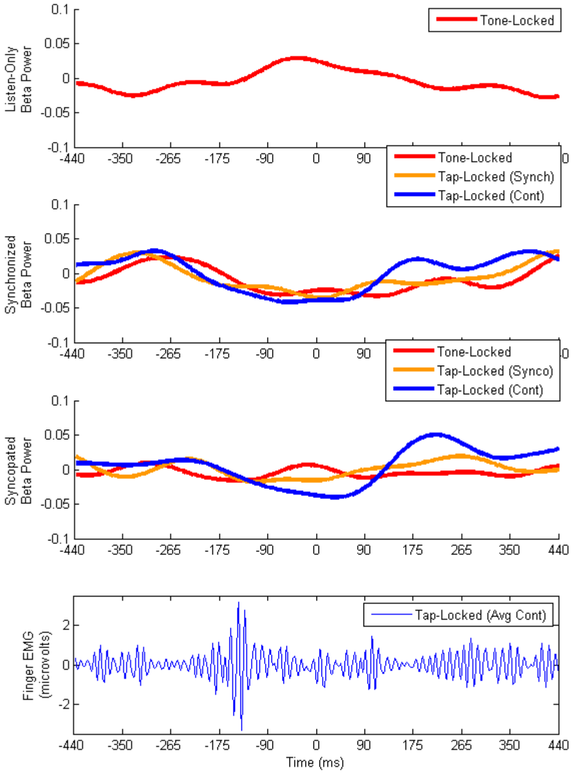


Figure 3.9: Beta bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

continued taps across these conditions (r=0.83, p<0.0001) compared to synchronized and syncopated taps (r=0.19, p=0.007), which indicates effect of auditory processing in this cluster in the beta band. This is consistent with past reports that beta is involved in auditory processing in temporal cortex Iversen et al. (2009).

Cluster 22 - Medial Frontal Gyrus Mu band responses for tap-locked trials showed slight suppression during movement preparation and execution (r=0.9, p<0.0001) in the synchronized condition, however, they revealed larger divergence in the syncopated condition (r=0.39, p=0.005). The listen-only response showed

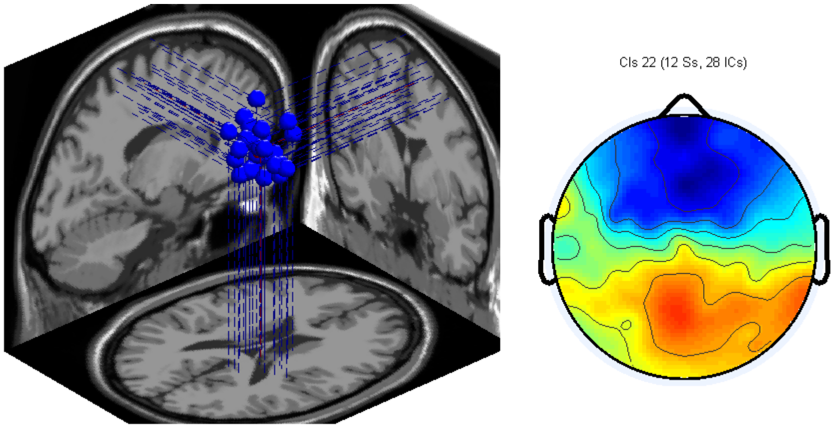


Figure 3.10: Dipole source estimate (L) and scalp projection (R) for medial frontal gyrus cluster.)

a small positive deflection peaking around tone onset, which was also observed in both the synchronized syncopated tone-locked curves, however the syncopated condition was far less correlated with the listen-only response over whole time window (r=0.04, p=0.55) than synchronized (r=-0.51, p<0.001). Responses were more similar between synchronized taps (r=0.4, p<0.001) than continued taps (r=-0.1, p=0.18) across conditions. Decreased variability in sound-locked trials could be the result of tighter inter-tap-intervals, as discussed earlier, when pacing is externally generated, despite the phase differences between conditions. This suggests a role for mu in movement, and is potentially modulated by auditory information, if only constrained.

The beta band suppressed in the tap-locked oscillations for both syncopated and synchronzied conditions. Similar to sensor space, the beta response for the tone-locked oscillations in both syncopated and synchronized conditions followed suppression that appeared locked to movement. In the absence of movement, the listen-only response was more similar to the response during syncopated tapping (r=0.63, p<0.0001), than synchronized tapping (r=-0.47, p<0.0001). This

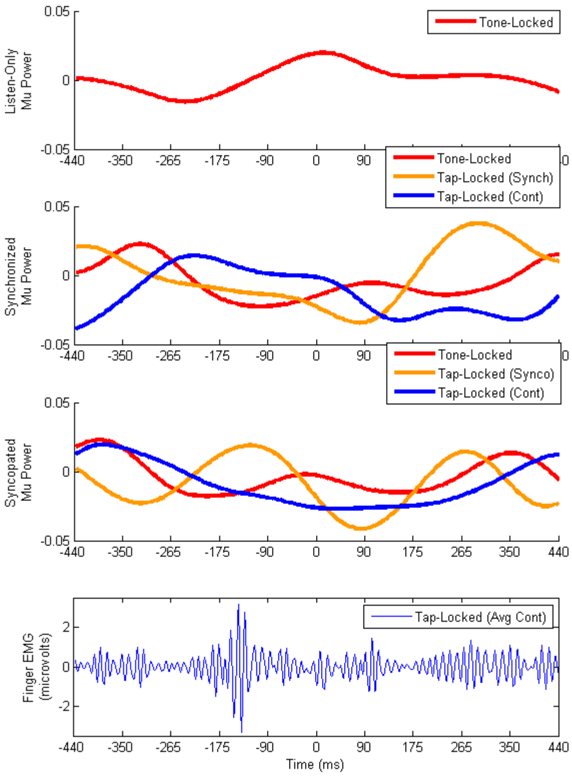


Figure 3.11: Mu bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

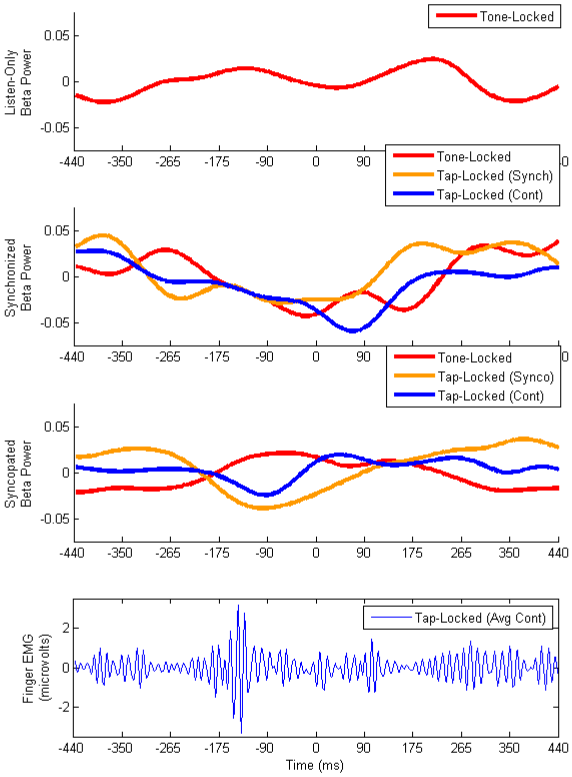


Figure 3.12: Beta bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

indicates that during synchronized tapping, the motor information influences the direction of the tone-locked oscillation in ways that the absence of movement, or the syncopation of movement does not.

3.5 Discussion

As predicted, suppression of mu and beta bands during tap-locked time windows was observed over left sensorimotor cortex. Tone-locked responses correlated strongly with motor activity in the beta band, but showed a more consistent response to auditory events across conditions in the mu band. This indicates that while both mu and beta bands show motoric processing effects, the beta band is less sensitive to perturbations from co-occurring auditory events when locked to motor actions. Comparing across tone and tap-locked responses for all conditions, the theta and beta bands showed the greatest differences in time frequency space. Based on band power calculations in time-frequency space, the theta band was most similar across conditions when tone-locked, and the beta band was most similar when tap-locked. These results are consistent with Boonstra et al. (2006) report of theta oscillations locked to sound onset when taps were synchronized with sounds. The present study also reports an increase in inter-trial coherence for tone-locked responses in the theta band. Phase locked brain responses to events is termed an evoked response. Evoked responses are thought to represent external events by subverting an oscillatory network in the brain with a phase reset, as opposed to induced responses, which are thought to vary in phase across trials and represent the modulation of an endogenously aligned brain rhythm. I observed differences in the theta and beta levels of phase locking across trials, with lower phase coherence in the beta band, and greater coherence for theta. This is consistent with reports from Boonstra et al. (2006), indicating an induced response that is time locked to tap onsets. The induced beta response is reported to have shorter latencies than evoked beta (Zanto, 2005). While the permutation tests over time frequency space showed significant differences between conditions in the beta band before and after both tone and tap events, the period immediately after (1-50 ms) tone and tap registration in all conditions is not significantly different. An induced beta band response occurring just after tone and tap events could show this pattern of activity. Beta power increased post stimulus peaks around 200 ms post tap or tone for all the conditions but tone-locked syncopated tapping. The failure

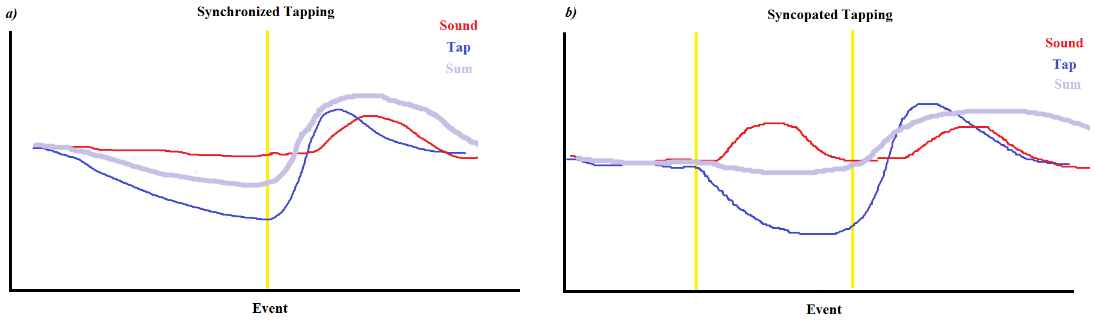


Figure 3.13: A model of interactions showing summed activity for two independent auditory and motor oscillations in the beta band for a) synchronized tapping, and b) syncopated tapping.)

of the tone-locked syncopated response to show this positive deflection can be explained by co-opting of the band for motor preparation. The negative deflections indicative of motor preparation start approximately 250 ms prior to taps. The interaction of the positive listening deflection plus negative movement preparation negative deflection would sum to zero (see Fig 3.13). The sum wave mirrors where we find the tone-locked curve at the moment of tone registration. The beta band signals auditory events, but it is more strongly influenced by motor tasks when they occur within each others refractory and preparatory periods. Hypothetically this model relies on two different beta oscillators. If there are two beta oscillators, auditory information could be represented as an evoked response due to external event phase resetting. The motor information could be represented by an induced signal that does not reset phase to external events, though it can be influenced by external auditory activity through summation of temporal neural coding.

In terms of total power across the whole condition, the gamma band showed significant differences between synchronized and continued taps, and between synchronized tapping and listening sans movement over left sensorimotor cortex. The condition containing both movement and sound showed higher overall gamma power than either listening alone or moving alone. The additive effects of simultaneous motor and auditory increasing gamma power is strong evidence in support of the gamma band carrying both information regarding movement and auditory perception. The gamma band has been discussed as involved in rhythmic expectancy (Zanto, 2005; Zanto et al., 2006; Snyder and Large, 2004, 2005; Fujioka et al., 2009).

In time-frequency responses, the gamma band showed a tone-locked response that increased prior to tone onset and fell in the period after during the listen-only condition. This is consistent with previous reports of gamma band responses to rhythmic sounds (Fujioka et al., 2009). The gamma response is diminished in power when synchronized tapping occurs in conjunction with rhythmic sound perception. The tone-locked response was not present during the syncopated tapping condition. If the gamma band carries both auditory and motor information, then the co-occurrence of these activities might interfere with individual gamma band responses to each discrete event. In the syncopated condition, events happen at twice the frequency than other conditions, with a tap or sound occurring approximately every 350 ms. If this gamma band represents integration of auditory and motor responses, then it may not have time to reset properly between each event. As reported by Snyder and Large (2004), varying the tempo of tone intervals (from 150 to 3000 ms) did not seem to affect the presence or latency of a gamma band response, while it did affect longer latency responses, such as ERPs or theta oscillations. However, this was for a listening only task, and the reset interval for gamma perturbations due to motor engagement might take longer. Indeed there are known cases of new movements being inhibited by increases of beta (13-35 Hz) power (Gilbertson et al., 2005). If rebound or resetting effects of beta or gamma oscillations occur too close to onset of new events then this could inhibit the response of the system to incoming information. A follow up experiment could include synchronized and syncopated tapping conditions at varying speeds. If a resetting phenomenon is inhibiting subsequent gamma responses, then one could predict to see an attenuated gamma power band responses for shorter intervals compared to longer intervals. In the present study, gamma power was smaller for trials during syncopated tapping than during synchronized tapping. The same amount of motor and auditory events occur in both time windows, but the intervals between any even is short in the syncopated than the synchronized.

The mu band, while classically associated with movement and visual perception of movement, also exhibited sensitivity to auditory information, as revealed by changes in tap-locked mu responses during synchronized trials compared to continued tapping in the absence of concurrent sounds. Additionally, this band showed similar responses in time for tone-locked band power averages across conditions that included a rise in power. This is consistent with findings discussed in study 1 of this dissertation, describing mu enhancement during listening to piano melodies. It is also consistent with reports of an auditory alpha effect of changes in alpha power related to sounds Ghuman et al. (2011).

Of interest in this experiment was a relative lack of beta or gamma band decreases in power with positive rebound initiating prior to tone onset in the listen only condition at motor related sites and sources. Fujioka et al. (2009; 2012) relate responses in both frequency bands that include an initial decrease in power, followed by an increase prior to tone onset, peaking shortly thereafter. These were in response to tone sequences of alternating loud and soft tones, and included missing tones as well. Similar rising and falling power dynamics just post stimulus onset are reported by Iversen et al. (2009) in response to two rapid tones followed by a rest. Synder et al. (2004; 2005), also report a rapid rise and fall in power after tone presentation with alternating tempos, and with missing expected tones.

Perhaps it is no surprise that the motor regions in the present study did not reveal these beta band oscillations for sounds, as the previous reports identify this effect coming from temporal cortex. Present findings corroborate, as the cluster of source activity localized to the rMTG show the characteristic beta oscillation. This further supports a model of two beta oscillations of different neural sources that interact for audiomotor processing.

With regards to auditory imagery, no evidence in favor of implicit imagery in the continued-syncopate condition was observed. As subjects were never instructed to imagine the tone during the continued taps, without further analysis at the level of single subjects, it is difficult to tell whether some of the subjects imagined a continued syncopated sound while continuing to tap. A follow up experiment would do well to include a motor imagery synchronize-continue tapping task. Subjects could mentally entrain to the inter-stimulus-interval, such that identification of a continued imagined response would likely still preserve the inter-stimulus-interval for later analysis.

In conclusion, this work contributes observations of combined movement and audition conditions to audiomotor literature. The ASAP hypothesis (Patel and Iversen, 2014) predicts a role for the beta frequency band as a motor oscillation involved in the perception of rhythmic auditory events. In the present study, beta oscillations were locked to movement and auditory events with differing pre-stimulus polarity, but similar post event positive deflections peaking around the same latency. When these events occur together in time, similar brain responses occur after the sound or tap. But when auditory and motor events occur out of synch with each other, the motor response co-opts the beta band. If the beta band marks the temporal occurrence of events based on motor predictions, then the gamma and mu bands also play a role in integrating auditory and motor responses.

Whereas the beta band is subverted by motor information, the mu band remains more stable in its auditory response and shows summation effects of of movement suppression and auditory enhancement. The gamma band also shows multimodal effects with an increase in power when auditory and motor events occur together, rather than just auditory or just motor. This could represent an additive effect of neural stimulation when two different sensory modalities temporally coincide, or it could represent an effect of enhanced attention.

Chapter 4

Study 3 - Synchronizing Moving and Listening via Hand Drumming

4.1 Abstract

The ability to synchronize movements with sounds is a complex behavior dependent on predicting the occurrence of future sounds. Simulation theories predict that the motor system contributes predictive information to processing of auditory streams. I proposed to compare neural responses while subjects drummed or listened to rhythmic hand drumming. I hypothesized that if the motor system is involved in auditory perception, then I would see a similar pattern of motor system engagement via the beta band of brain oscillations for both movement and listening. I found evidence partially in support of the theory, though results are difficult to interpret. I also report significant differences due to drumming expertise in the amount of mu power subjects exhibit during drumming, with

novice drummers showing enhanced mu responses for playing, and even greater enhancement with keeping time themselves.

4.2 Introduction

How is it that we can synchronize our movements to sounds? Does the auditory system feedforward into the motor system in a way that constrains the motor variability (Jäncke, 2012)? Listening to sounds can stimulate movement, even increasing walking velocity in those with difficulties moving due to Parkinson's disease (de Dreu et al., 2012). Many concert or club goers can attest to the ease which music can stimulate rhythmic movement, from dancing to head nodding. Listening to music without movement can even stimulate activity in motor cortices when listening to familiar action-related sounds (Lahav et al., 2007; Bangert et al., 2006; Baumann et al., 2005). Given these findings, it is hypothesized that the motor system may play a role in predicting the occurrence of sounds (Iversen et al., 2009) through simulation (Patel and Iversen, 2014). Past work demonstrated that our brain waves respond when hearing rhythmic sounds, and respond even when an expected sound is omitted (Zanto et al., 2006; Fujioka et al., 2009; Snyder and Large, 2005). The brain rhythms involved in responses to expected and missing sounds occupy the same frequency range as brain rhythms involved in motor planning and execution in macaques (Brovelli et al., 2004; Bartolo et al., 2014). If the same brain rhythm is involved in the perception of rhythmic sounds and in movement, then one could expect a similar pattern of brain oscillations within subjects when they are listening to a musical rhythm sans movement, and when also moving along with it. I predicted that similar to the second study in this dissertation, beta oscillations time-locked to sounds will show an increase in power after sound, and activity linked to motor effects will show a decrease in power prior to an executed or heard drum hit. I tested this hypothesis using hand drumming as model behavior to compare listening and moving.

Hand drumming, while a relatively underutilized behavior in the laboratory, is a promising approach to studying auditory and motor integration. It increases the ecological validity of a laboratory task while also offering enhanced face validity to test the effects of expertise. With audiomotor tasks such as tapping, there may be cross over from experiences playing or performing as a musician or dancer, but drumming as a laboratory task can look at direct effects of experience. Simple drum rhythms can be taught to musically naive subjects in a short amount of time, and behavioral performance is easily quantifiable with recordings of drum surfaces. There are difficulties with this approach as well. For one, drumming is a dynamic activity that involves coordination of many muscle groups, making it difficult to study neurophysiologically while the subject is moving. As it is a complex behavior, there are many things being coordinated from different types of drum hits (center of drum, outside of drum), and coordinating both hands for some rhythms. While the use of both hands can have benefits in terms of identifying neurophysiological motor activity based on hemispheric differences, the parameter space of auditory features is more complex than traditional tapping studies that make use of simple tones. The different drum hits create different sounds, which may elicit different responses in the brain. Another difficulty resides with the selection of a proper baseline for neurophysiological comparisons of experimental conditions. Traditionally studies have a pre-stimulus or inter-stimulus window of no stimuli which can be inferred to mean a resting baseline state to compare the ensuing changes when a stimulus is presented. A continuous activity increases the difficulty of finding a valid, stable baseline.

In the present study I offer solutions to these difficulties based on inferences from the audiomotor literature and some novel adaptations. To capture the EEG of a moving subject, I employ the use of a prototype EEG system that was designed by QUASAR Biosystems, Inc. (San Diego) to be relatively insensitive to small to moderate movement artifacts. With dry electrodes there is no concern about electrolytic gel moving and breaking contact, particularly when the electrodes are held securely against the scalp by spring loaded tension on individually swiveling mounts. This introduces another confound however; that of capturing added noise in the EEG signal in the form of muscle contamination from neck and shoulder muscles. One method to deal with this problem is using independent components analysis (ICA), which can help remove some of these contaminants from the brain recordings. The baseline issue is addressed by creating a baseline value that is the mean value for a given frequency across each epoched time window. The use of a mean baseline window is previously reported in a similar task of rhythmic tapping (Boonstra et al., 2006).

Given the above considerations and observations from previously discussed experiments with rhythmic sounds and tapping, I predicted decreases in beta power(20-30 Hz) prior to drum hits with increases after the hits. In particular, I predicted that beta oscillations would decrease in power prior to subjects hitting a drum, with rebound increases in power after the drum hit. These same post drum hit increases should also occur after listening to drum sound without moving. In the listening without moving condition, based on observations from the previous study discussed in the dissertation, I did not expect to see the same pre-hit decrease in power. From those same findings I also predicted mu (8-13 Hz) and gamma (30-50 Hz) bands would show sensitivities to motor and auditory information.

4.3 Methods

Subjects

Six students from UCSD and five drummers from the San Diego area were recruited for participation (mean age 26.5 years, SD=5.9, five female, two left handed). All drummers had at least two years experience playing hand drums and were familiar with Afro-Brazilian rhythms. Each subject was shown how to play the drum rhythm after initial consent and questionnaires were filled out, and had to demonstrate ability to play the correct beats with the correct hands prior to inclusion in the rest of the study.

Stimuli

This study used a variation of a hand drum rhythm belonging to a family derived from Yoruban religious rituals called 'Ijexa.' This rhythm was chosen partially for the ease of play for novice drummers, and also because it includes right and left handed hits, which should aid in identification of motor processes versus auditory processes based on hemispheric differences in the brain responses. The notes are spaced unevenly which should allow for identification of brainwave components associated with individual drum hits. Little is written about this rhythm as it is part of an oral tradition. This oral method of transmitting the rhythm also results in multiple variations of the rhythm, all using the same name. In this particular instance, subjects would play three drum hits with the right hand, and one hit with the left hand.

The stimulus used in this experiment was a recording of the drum rhythm played on a djembe. These are traditionally a rope tuned skin-covered drum in the shape of a goblet from West Africa. The drum used for recording the stimulus

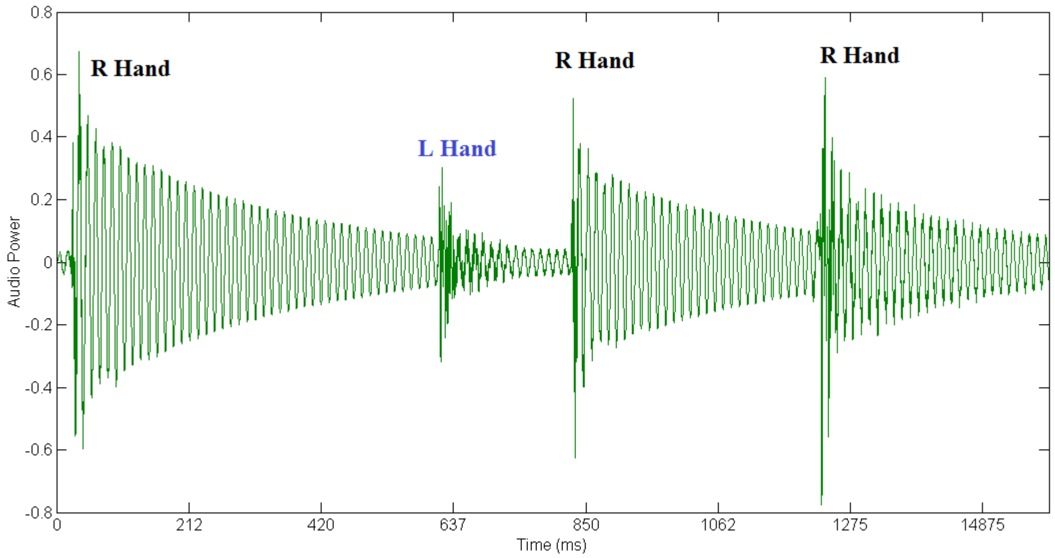


Figure 4.1: Waveform representation of drum stimulus. Note different hands used to play different drum beats. The perceptual beat occurs on the first and third drum hit

and played by experimental subjects was a synthetic head drum made by Remo. The recording was made with the drummer listening to a metronome set at 106 beats per minute. Using audio recording and editing software (Reaper v 3.92), one measure of the drum pattern was isolated and extracted to loop for the experiment. The loop was 10714 ms long, sampled at 44100 Hz. A track approximately four minutes and fifteen seconds long was created from this loop. This provided 150 repetitions of the drum pattern. Stimuli were presented via MaxMSP (v 4.5) through ambient room speakers that were adjusted to a comfortable level that could still be heard while subjects played the drum.

Task

The experiment consisted of three phases (listen, play, and solo) and took place inside of a sound attenuated Faraday cage. First subjects would listen to the looped recording of the drum track for approximately four minutes (150 trials) without moving. Then they would play along with the looped drum track (again 150 trials). The last phase required subjects to play the rhythm by themselves, without the recording, or other form of pacing. This phase lasted for approximately four minutes. After completing all three phases, subjects would repeat all three for a second block, resulting in about 300 trials per condition. Subjects sat upright and played a djembe that was held between their legs.

Data Collection

Drum hits were registered via a piezo element affixed to the drum head, and recorded using MaxMSP. This software environment filtered out drum head artifacts and sent time stamps to the EEG system. EEG data were collected with a QUASAR Biosystems active dry electrode prototype headset with 21 sensors placed according to the 10-20 system of electrodes (FP1, FP2, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, P3, Pz, P4, T5, O1, O2, T6, L/R mastoid). Each sensor was part of an array and was individually mounted within a local ground. Each array was spring loaded and mounted on swiveling arms such that they would hold tight to the scalp even when a subject moved his/her head. This significantly reduced the amount of head movement based artifacts during recording to a level that allowed drummers to not have to hold completely still for the duration of the experiment. EEG data were sampled at 300 Hz and amplified by a factor of 1000. They were recorded referenced to recording site Pz, and offline re-referenced to the mastoid. Data were recorded with QUASAR's Qstreamer software.

Analysis

Behavioral Data

Piezo voltage recorded by the stimulus machine was saved as separate output from EEG triggers. The output of the drum triggers was analyzed in Matlab to extract relevant intervals between drum hits. A more detailed description of the method can be found in Appendix C as an adaptive algorithm. Intervals between drum hits were compared between blocks (first solo drumming compared with second solo drumming) for short term practice effects. Additionally comparisons were drawn between drummers and novices for accuracy of interval stability.

EEG Data

EEG data were analyzed using the EEGLAB (Delorme and Makeig, 2004) toolbox for Matlab. Raw data were imported and re-referenced to the mean of left and right mastoid sensors. The data were then low pass filtered under 50 Hz and initially segmented into 2600 ms second long epochs. Proper identification of time windows for the solo condition relied on an adaptive algorithm designed specifically for this experiment to seek out intervals between drum hits relative to the expected pattern plus an error window based on accumulated drift (see appendix for further details). While most analyses reported here are over the 1700 ms long drum rhythm phrase, the time-frequency analysis requires longer time intervals to accurately compute low frequencies at the edges of the 1700 ms window. To assess increases or decreases in power over time, a baseline correction was performed for each epoch, deleting the mean voltage value of each time window. Epochs containing machine noise or other non-repetitive artifacts were rejected based on extreme voltage threshold detection and visual verification. Remaining data were decomposed using ICA (Infomax) to identify and remove facial and neck muscle artifacts from sensor space scalp recordings. Some neck muscle artifacts contaminated multiple components and in these cases whole epochs were removed. This cleaning procedure left approximately 200 out of 300 trials per condition per subject.

Event related potentials were calculated across subjects over the 1700 ms window, time locked to the first beat. Spectral power was also computed over the same time window, performed by an FFT. Time-frequency decompositions were computed with wavelets using a Morlet taper across the 2600 ms time windows. Using a minimum of three cycles per wavelet, I was able to calculate down to 3 Hz, which allowed study of the theta band (4-8 Hz). Bandpower was estimated for both spectral and time-frequency data by integrating the power within a predefined band (theta = 4-8 Hz, mu = 8-13 Hz, beta = 20-30 Hz and gamma = 30-50 Hz) using the trapezoid rule, with a sliding integration over time for time-frequency reporting. Statistical comparisons were made using the Matlab statistics toolbox and permutation statistics included in EEGLAB. Permutation tests were chosen due to the small number of subjects included in the sample set, to control for the possibility that any one subject might unduly influence the overall mean, particularly when comparing drummers and novices. Multiple comparisons were corrected with the False Discovery Rate threshold function (Genovese et al., 2002). Multivariate comparisons of spectral power were made with SPSS (v 20) software and multiple comparisons controlled with a Bonferoni correction.

To make a drum rhythm sample matched to the time-frequency bandpower, the envelope of the audioclip was extracted via a Hilbert transform. This was then downsampled to match the same number of samples as the EEG data, and smoothed with the default Matlab smoothing function. Since the envelope extraction into real number space lost the absolute amplitude changes in drum sample, the mean amplitude value was subtracted from the sample to normalize peaks above and below the zero point to aid in correlating to brainwaves that rise and fall above baseline.

4.4 Results

Behavioral

A total off-ness score was calculated for each subject, which was the sum of the absolute value of the difference between the recorded stimulus drum intervals, and the observed drum intervals. This provided a single score for each movement condition (play vs solo) and each trial block (first vs second). A repeated measures ANOVA with factors of condition (2) and trial (2) with between subject factor of drumming experience and Bonferoni Correction revealed a marginally significant effect of condition (F(1,8)=3.62, p=0.094), but not for trial (F(1,8)=2.35, p=0.16). Subjects drummed with greater accuracy (smaller deviations from expected intervals) during the play along condition with smaller variability (M=41.4, SD=4.2), than during the self paced solo condition (M=57.9, SD=9.2). Subjects also showed a small improvement in drumming between the first (M=52.7, SD=6.2) and the second block (M=46.6, SD=5.9). While drummers performed better in terms of off-ness than inexperienced drummers (M(drummer)=45.9 msec, SD=8.1, M(novice)=53 msec, SD=8.1), the interactions between experience and condition (F(1,8)=0.23, p=0.65), trial (F(1,8)=0.41, p=0.54), and condition*trial (F(1,8)=1.52, p=0.25) were insignificant. Since this was a novel task, the behavioral analysis confirmed basic assumptions about the task, such as performance increases across trials, increased drumming stability when pacing cue was present, and better performance for experienced drummers. Even though the differences were not pronounced enough to be statistically significant, the trend supports the aforementioned basic assumptions.

Validation with Event Related Potentials

As this was a novel task, and there is little precedent in the literature examining brainwaves to rhythmic drum sounds or actions, the first analyses were qualitative assessments of event related potentials. ERPs locked to the sound of drums revealed an auditory N1 approximately 100 ms after stimuli presentation (4.2). Unlike a standard auditory ERP experiment, there was no resting baseline window prior to stimulus onset, hence the noisy pre-stimulus period. The average sound response combines different types of drum hits, and each type of drum hit could elicit different brain responses based on differences in the kinematics or frequency profile of the drum hits. Likewise, a motor effect can be seen averaged across drum hits that shows a negative deflection, potentially similar to a readiness potential initiating about 250 ms prior to the drum hit (See figure 4.3). As the drum hit should produce a sound, the presence of a negative deflection just before 100 ms post drum hit marks the presence of an auditory response similar to what is seen in the auditory N1. I take these as evidence that auditory and motor responses to an ongoing rhythmic drumming task can be detected by the prototype EEG system.

Spectral Analysis

One of the difficulties testing simulation theories is that traditional statistical tests for behavioral and neurosciences are often focused on finding differences between conditions. Simulation theories on the other hand predict similarities be-

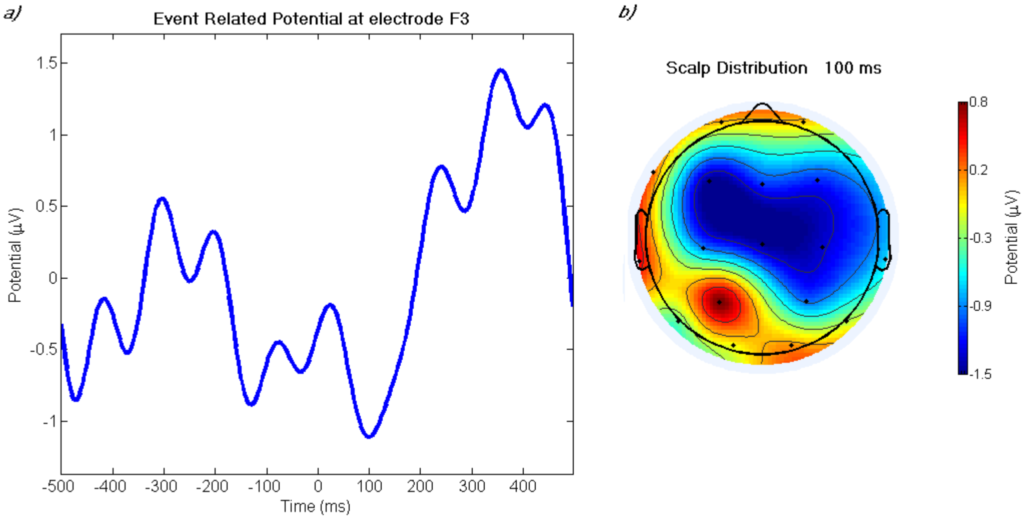


Figure 4.2: Event related brain potential at F3 time-locked to drum hit sounds in the non-movement (listen) condition. (a). Scalp distribution of potential at 100 milleseconds post drum hit shows distribution mainly over center of head (b).

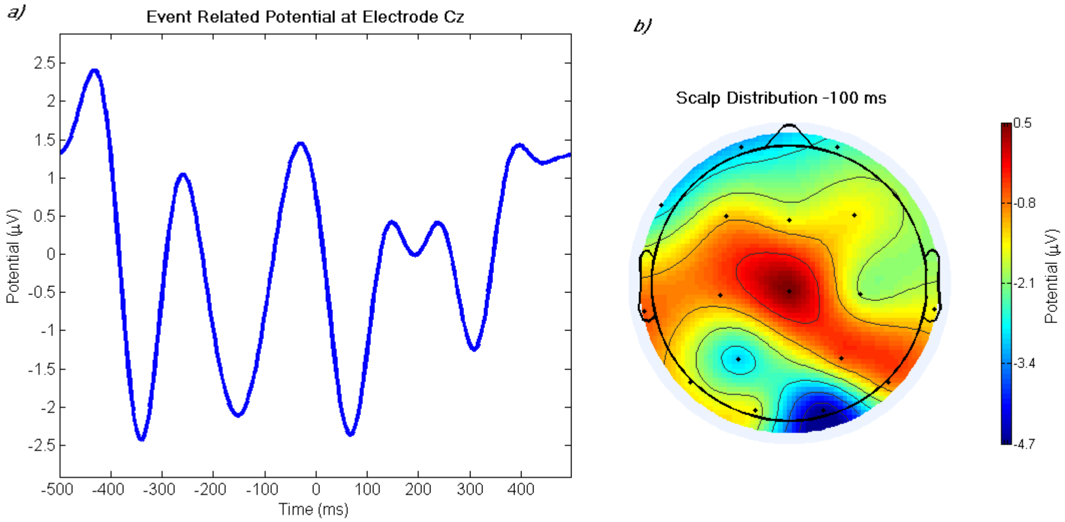


Figure 4.3: Event related brain potential time-locked to drum hit action in solo condition (a). Scalp distribution of potential at 100 milliseconds prior to drum hit shows a similar distribution to Fig 4.2(b).

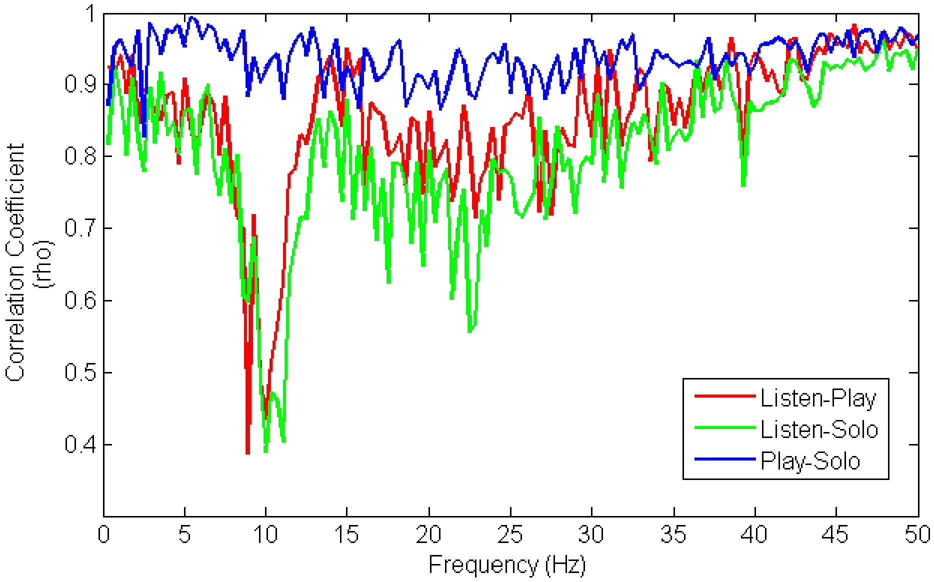


Figure 4.4: Correlation of task conditions at electrode C3

tween conditions. Correlations are one tool for assessing similarities, but these can be difficult for multivariate comparisons when there is no clear dependent variable amongst experimental conditions. For this reason I report permutations of pairwise correlations. To this extent, evidence for simulation will be conceived as significant pairwise correlation and a lack of significant difference between conditions. Correlations were performed at each frequency bin for spectral power between conditions (see Figurec3conj).

Correlations across all electrodes for the listen and play conditions revealed, on average, a high correlation in both the theta (M=0.87, SD=0.07, mean p ¡0.0001) and gamma (M=0.88, SD=0.073, mean p<0.0001) bands. The mu (M=0.75, SD=0.1, mean p = 0.0025) and beta (M=0.81, SD= 0.11, mean p ¡ 0.0001) bands showed a decrease overall, with the lowest mu correlations found over the sensorimotor strip, and lowest beta correlations over temporal sites. This is consistent with reports from literature making a connection between mu and beta power and movement, such that the amount of similarity between listening and movement conditions would expectedly differ in these frequencies. See Appendix C, supplementary tables for full list of correlations at each electrode. Overall correlations were smallest between the listen and solo conditions, which share the least amount of similarity. Once again mu frequency showed the smallest overall correlation (M=0.6420, SD=0.14, mean p=0.0041) with smallest correlations over the sensorimotor and other midline sites. Beta (M=0.76, SD=0.12, mean $p<0.0001$) and theta (M=0.79, SD=0.13, mean <0.0001) both revealed decreases when compared to the listen-play correlation, with a small increase in variance. The gamma band (M=0.86, SD=0.086, mean $p<0.0001$) showed little change, which suggests a possible role of gamma in auditory processing, since the drum sounds were the common sensory feature across all three conditions. As expected, correlations were strong across all frequencies for the play and solo conditions. Theta (M=0.9, SD=0.065, mean $p<0.0001$), mu (M=0.92, SD=0.03, mean $p<0.0001$), beta (M=0.93, SD = 0.04, mean $p<0.0001$) and gamma (M=0.95, SD=0.02, mean $p<0.0001$) were consistently high across all electrodes.

Multivariate models of frequency band effects across conditions Comparisons of all three tasks (within subjects) were made to examine the differences of condition per frequency band at each of the electrodes. A repeated measures ANOVA was calculated for each frequency band with factors of condition (3) and electrode (17). In the theta band there was a main effect of condition $F(2,8)=7.51$, $p=0.015$. As there was no baseline condition to compare bandpower and normalize within each subject for cross subject comparisons, within subject effects are reported instead. There was a main effect within subjects of condition ($F(2,18)=12.29$, $p<0.001$), electrode ($F(16,144)=5.53$, $p<0.001$), and an interaction of electrode by condition ($F(32,288)=2.449$, $p<0.001$). For the main effect of condition, across electrodes there was a trend of greatest theta power for the solo condition (M=728.59, SE=8.79), followed next by play (M=723.68, SE=8.72) and least power for listening (M=711, SE=9.46). This is consistent with previous reports of tapping that indicate theta power increases during tapping (Boonstra et al., 2006). There were 4 drum hits within a span of 1.7 seconds, which comes out to a drumming frequency of 2.35 Hz, and given that hits were unequally spaced (intervals ranging from 200 to 600 ms) we were close to seeing some contamination from the frequency of drum hits into theta oscillation range for a frequency following effect. Time-frequency space analysis might be necessary to assess whether the frequency of drum hits contaminates the theta band. Greatest theta power was observed over central recording sites with a slight left hemisphere bias (see Fig. 4.5). In the mu band there was a marginally significant effect of condition (F(2,8)=3.49, p=0.08). Within subject effects show a significant effect of electrode (F(16,144)=2.58, p=0.001) and an interaction between electrode and condition (F(32,288)=2.5, p<0.001). Overall the solo condition showed greatest amount of mu power (M=842.1, SE=9.64) followed by listen (M=836.9, SE=11.6), with the play condition showing the least (M=833.8, SE=9.9). These findings could be consistent with the previous study in this dissertation showing the highest levels of mu power during conditions requiring the most mental effort and precise timing, which is a prediction of the inhibition timing hypothesis (Klimesch et al., 2007). The beta band also shows a marginally significant effect of condition (F(2,8)=3.6, p=0.08), with the highest power seen for the solo condition (M=1679.3, SE=25.6) followed next by play (M=1666.2, SE=22.9), and then listening (M=1633.1, SE=18.8). Within subject tests show a significant interaction of condition by electrode (F(32,288)=3.23, p¡0.001), with scalp distribution showing a central to frontal bias. The gamma band also shows a significant effect of condition (F(2,8)=8.27, p=0.011), following the same trend as the beta band which has the largest power during solo condition (M=3023.9, SE=51.8) followed by play (M=20995.6, SE=49.4) and lastly listening (M=2915, SE=46.2). Within subjects there is a significant effect of condition (F(2,18)=14.2, p<0.001) and an interaction of condition by electrode (F(32,288)=2.8, p<0.001). Finding different frequency bands showing significant differences across conditions was counter to my hypothesis that simulation during listening would necessitate similar power levels of activity for both listening and moving conditions. However, these might be effects that are sensitive to levels of practice or expertise, as the previous study in this dissertation reveals that learned associations between sounds and action sequences may take more than one day to form. It is also possible that while absolute power is different between conditions, when normalized within subjects the difference may disappear. Additionally differences in absolute power may not be the import aspect for simulation hypotheses to test. Studies of mirror neurons show that it is the temporal profile of activity of multimodal neurons that matter as opposed to absolute firing rate, which would translate into spectral power density in the case of EEG.

Between groups comparisons To make comparisons between subject group spectra requires normalizing individual subject power. Since the listen condition provided the same (or at least similar) acoustical information as the two conditions where subjects drummed, this was used as a baseline for suppression. While there are likely differences in how subjects perceive the drum rhythm based on expertise, the larger domain of experience based differences is likely in playing. Suppression indices for theta, mu, beta, and gamma for a given subject were created as the log ratio of condition/baseline, in this case either play or solo condition divided

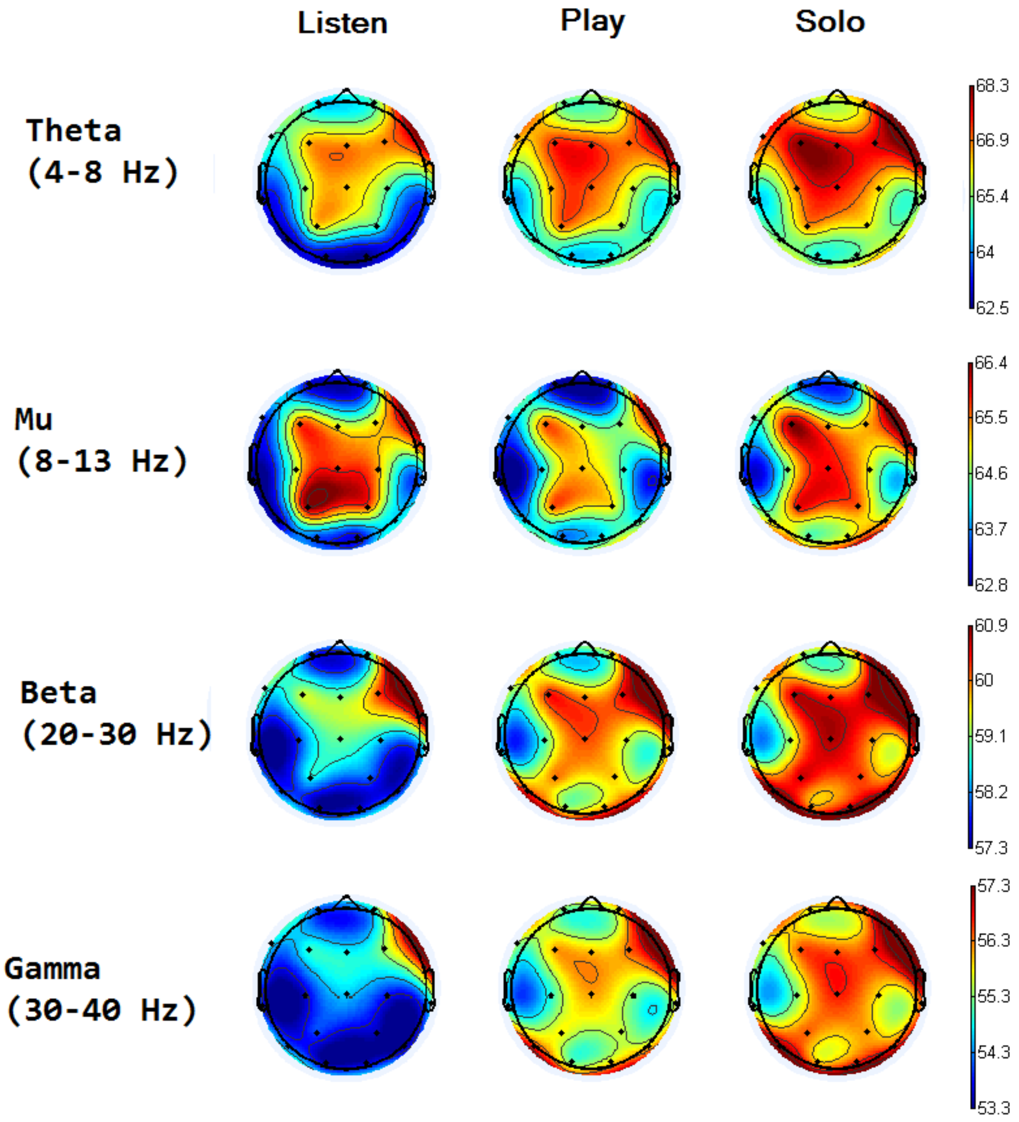


Figure 4.5: Scalp distribution of spectral power density across conditions. Frontal power on the right side centered beyond recording electrodes represents muscle contamination that was not removed through ICA.

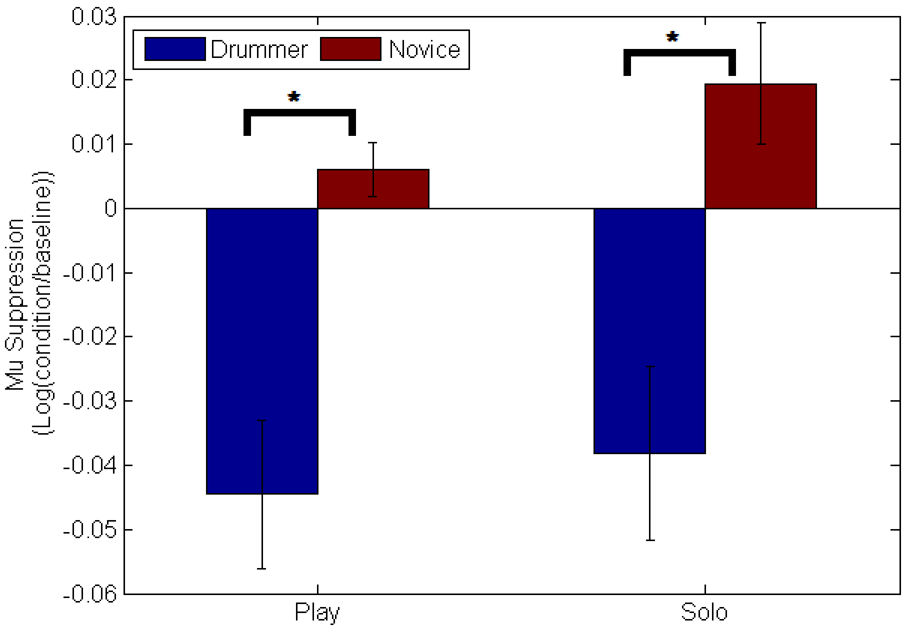


Figure 4.6: Differences in mu power suppression for drummers and novices. * denotes a significant difference, p¡=0.05.

by listen. Next a two tailed T-test compared the means of drummer and novice bandpower at each electrode, corrected for False Discovery Rate. As predicted by the conjunction analysis, the mu band showed the greatest differences between groups. In the play condition, mu was significantly suppressed for the drummers compared to novices at electrodes C4 (t(9)=-3.02, p=0.015) (see Fig. 4.6) and T4 (t(9)=-2.31, p=0.05).

Drummers exhibited mu suppression as would be expected from the literature during movement, whereas novices showed slight enhancement compared to listening (Fig. 4.7). A similar effect was observed in the mu band for the solo condition as well over the central strip, with significantly greater suppression at C3 (t(9)=-2.37, p=0.04), Cz (t(9)=-2.68, p=0.03), and C4 (t(9)=-2.49, p=0.03). This is consistent with the inhibition timing hypothesis (Klimesch et al., 2007) since novice drummers would presumably have to concentrate harder on timing

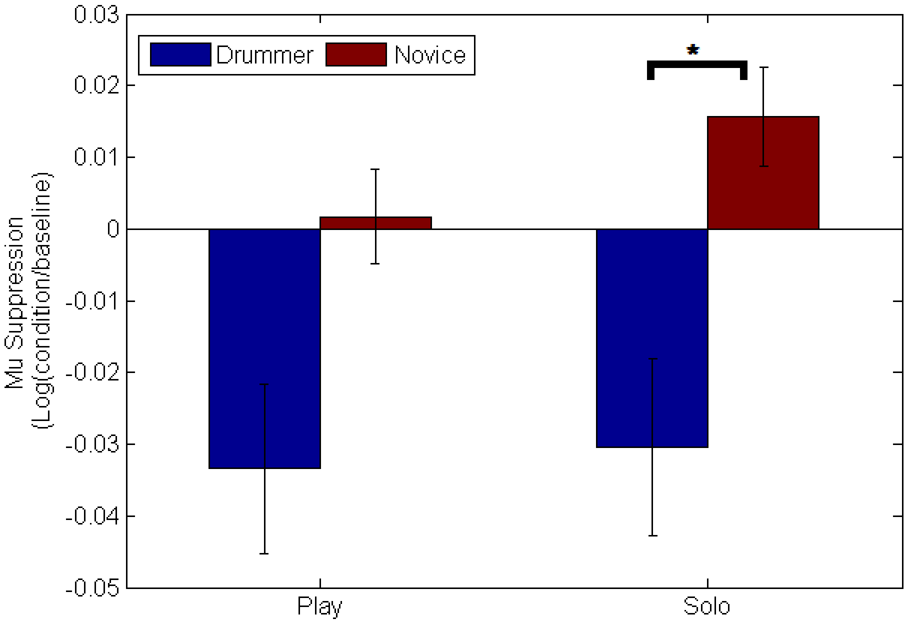


Figure 4.7: Differences in mu power suppression for drummers and novices. * denotes a significant difference, p¡=0.05.

precision with the loss of external pacing information in this condition. No significant differences between groups were observed in the theta or beta bands at any electrode. The gamma band shows a significant difference with greater suppression in drummer during the solo condition at left frontal sites F3 (t(9)=-2.3, p=0.05) and F7 (t(9)=-2.44, p=0.04). Given that the gamma band is not reported to participate in event related desynchronization, the decrease shown in drummers may also indicate an increased processing load for novices, however it cannot be ruled out that gamma is indexing attention with these responses.

Using the same log ratio normalized data, comparisons within group between conditions reveals no significant differences between play and solo conditions for the drummers in any frequency band or electrode. The novice group shows a significant difference in the mu band between play and solo at electrode Cz (t(10)=-2.43, p=0.04). Greater enhancement during the solo condition (M=0.023, SD=0.016) compared to play (M=0.005, SD=0.009) is consistent with the findings above, suggesting an increase in mu power during the solo condition is associated with greater attention demands and focus on timing.

Neuro-behavioral Comparisons A Pearson correlation between behavioral accuracy measures and mu and beta suppression indices for play and solo conditions did not reveal any significant correlations. To see a table of correlation coefficients, see Appendix C.

Time-Frequency Analysis Visual inspection can serve to describe whether a given frequency band has peaks that correspond to those seen in the drum sample, but quantifying the synchrony between the two is difficult. To that end I created a down sampled envelope of the drum recording to pair against the frequency bands in a standard correlation. The envelope of drum hits shows when drum sounds occurred and the decay of the sound in the audio recording, but the decay does not necessarily predict the sound generated by a subject in the experiment. In the theta band, electrode P3 shows the highest correlations between all three conditions and the drum sample: listen=0.52, play=0.64, and solo=0.48 (4.8). The beta oscillations likely represent an auditory response given the similarity across all three conditions. A permutation test calling a one way ANOVA on surrogate data from the EEGLAB toolbox reveals no significant differences across the 4-8 Hz band (see appendix for a significance plot).

For the mu band, electrode P3 shows the highest correlations across conditions with the drum rhythm: listen=-0.31, play=0.48, and solo=-0.43. Running another permutation test, I observed a significant difference between conditions in the mu band at site P3, (F(2,20)=10.67, p=0.05 FDR corrected), at time 1650 ms (see appendix Fig. 8.5 for a time-frequency statistical significance plot). Examina-

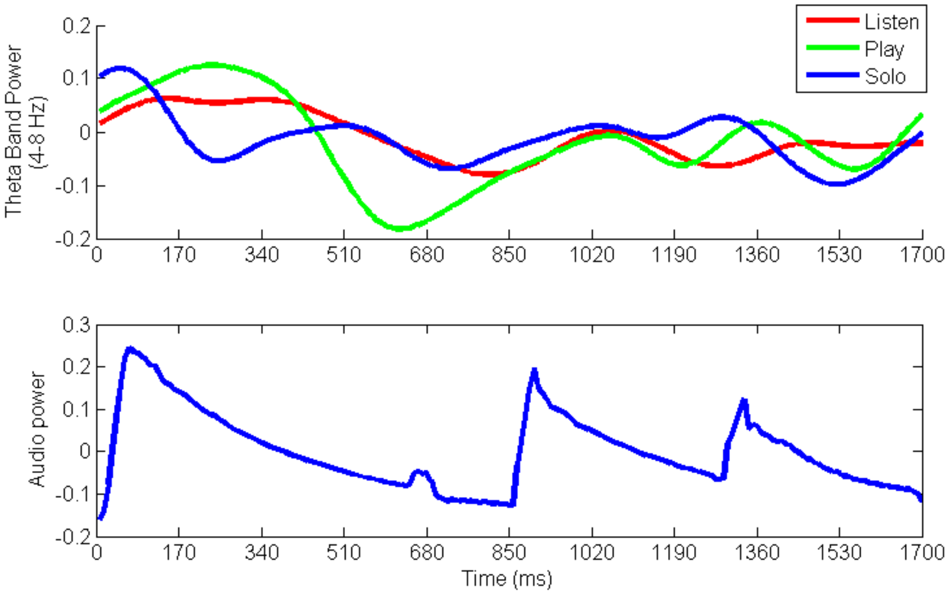


Figure 4.8: Differences in theta power over time.

tion of the plotted band power showed what might be a difference due to increase latency in the solo condition versus the play condition. This could be explained by tempo drift in the solo condition as subjects who find the pattern difficult might be inclined to slow down where they provide the tempo. If so, the group comparisons should reveal a difference for novices but not drummers (see 4.9).

However, in this case it does not appear that the difference in latency can be explained entirely by drumming experience as the peaks for the drummers during play and solo conditions do not line up as tightly as predicted.

The beta band is harder to interpret in terms of correlations between band power and drum sample. Again, the largest correlations across the three conditions can be observed at P3, (listen=-0.2, play=0.23, and solo=-0.4), but there are other sites that show correlations stronger for two conditions but not a third (see tables in appendix for full list of correlation coefficients). For instance, T4 shows a stronger correlation for solo (-0.4) and play (0.26) but not for listen (-0.07). There are no

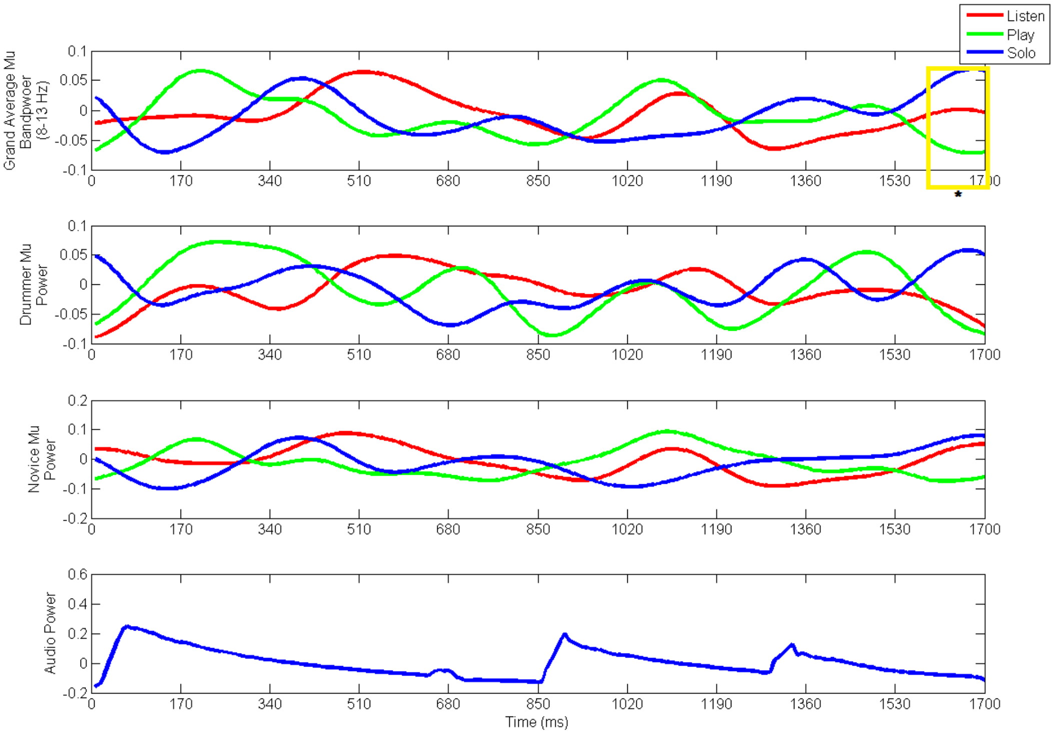


Figure 4.9: Differences in mu power over time for whole group, drummers, and novices. * denotes a significant difference, p<=0.05.

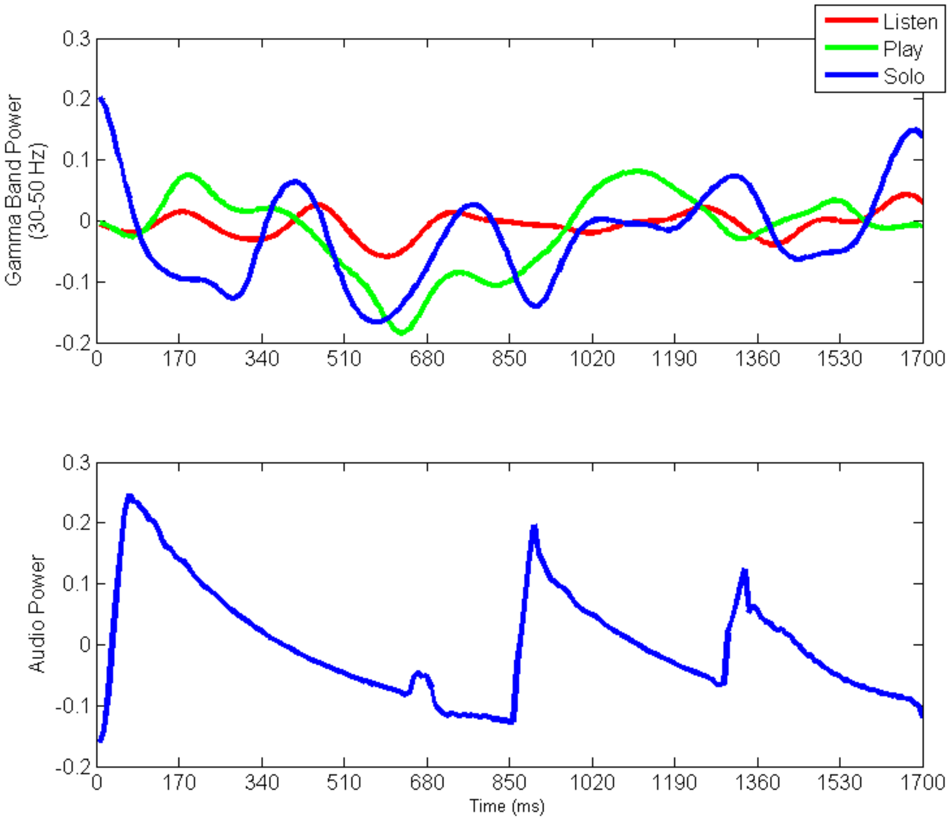


Figure 4.10: Differences in beta power over time for whole group, drummers, and novices.

significant differences across the time window in this frequency band. Correlations in the gamma band continue the trend of a strong showing at P3 with listen=-0.2

Beta bandpower shows drum-sample locking in a predicted manner for the play condition. Similar to tapping responses reported in study two, prior to the drum hit a decrease in beta power is followed by a rise after the hit peaking approximately 200 ms post drum event. Solo condition shows a similar level of pre-drum hit suppression, but the latency is not nearly as tight. The first drum hit has a negativity that overshoots the onset of the drum hit. It is possible this happens if a drummer then leaves the hand rest on the surface of the drum head. For listen-only auditory events, a similar post drum hit positivity peaks 150-200 ms

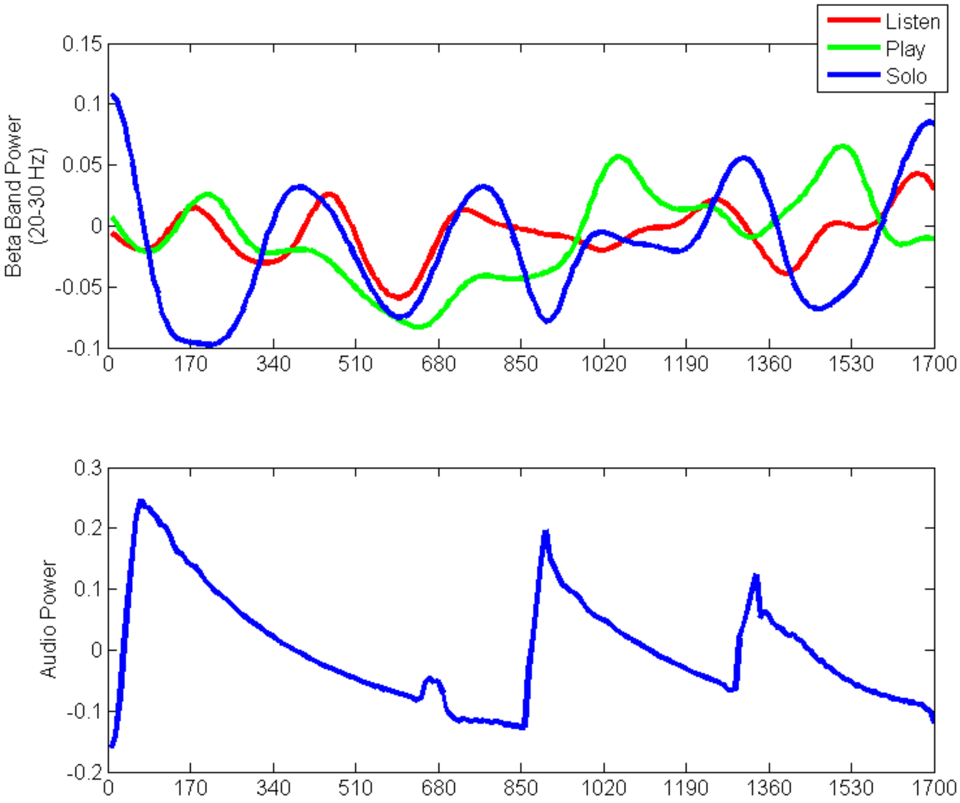


Figure 4.11: Differences in beta power over time for whole group, drummers, and novices.

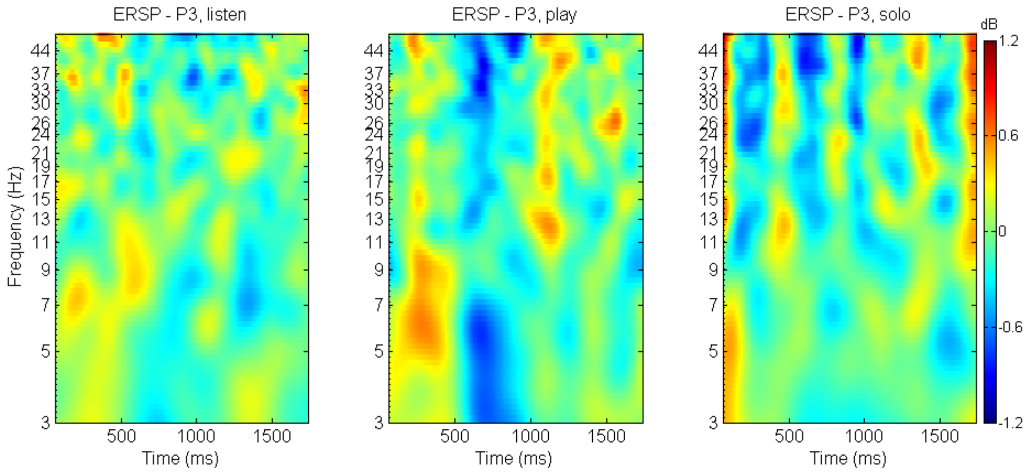


Figure 4.12: Event related spectral perturbations for 3-50 Hz These are time locked to the same drum samples displayed previously but show broad frequency responses.

post drum hit. There are additional beta oscillations present in the listen and play condition that are out of phase with the solo condition around 170 ms and again at 1400. The change in polarity of beta (see Fig. 4.11) and gamma oscillations, particularly for the solo condition are close in temporal proximity to the drum hits.

It is worth noting that many of these effects transcend the a priori defined frequency bands. Based on the broadband time-frequency plots we can see effects that transcend from the lowest frequencies to the highest frequencies displayed in fig. 4.12. Of note in the broadband display is that the mu band (8-13) is fairly attenuated compared to the other frequencies above and below it, particularly for the play and solo conditions.

4.5 Discussion

In the present study differences were found between experienced drummers and novice drummers in the mu band while drumming occurred. The level of mu suppression for drummers was not surprising as previous reports (for a review see (Pineda, 2008, 2005)) indicate normal suppression of mu at central electrode sites during action. However, that novice drummers would enhance mu during movement is unexpected. This is contrary to observations that mu is suppressed during action. However, other cognitive states and demands are known to enhance mu. For instance, during listening tasks that demand a comparison of harmonic tones (van Dijk et al., 2010) alpha power (5-12 Hz) is seen to increase in the left temporal lobes. This is interpreted as a neural mechanism to inhibit other cortical processes from interfering with working memory demands. Additionally, temporal lobe alpha (7-15 Hz) is described to participate in increased phase locking between hemisphere when subjects actively listen to pulsed sounds in frequencies that can entrain brain rhythms (Ghuman et al., 2011), which is in line with past observations of increased alpha during listening attention. Increased alpha in these reports may be similar to the increased mu (8-13 Hz) reported here. Novice drummers would have additional demands on their attention for both playing along with a drum rhythm, and subsequently trying to keep it going themselves. These reports are also consistent with the inhibition timing hypothesis that posits increased alpha (8-12 Hz) during inhibitory control over overt responses and memory recall, and these increases synchronize brain regions in a way that can inhibit other processes. Hwang et al. (2014) describe simultaneous increases in beta (18-38 Hz) and alpha (10-18 Hz) just prior to inhibition of a movement. Increased mu power in the present study may reflect an increase in vigilance or inhibition of movement at an incorrect time.

With regard to time locked features of the EEG, this novel task elicits both motor and auditory potentials in time averaged space. The auditory ERP occurs over central sites with latency of approximately 100 ms, as reported in (Hillyard et al., 1973). There is also a distinct motor ERP that shows maximal negative deflection approximately 100 ms prior to drum hit, and exhibits the pre-motion positivity in the remaining time leading up to drum hit that is described in Deecke et al. (1969) when subjects prepare to move an arm. Much of the motor preparation literature describes preparation of finger movements, but in the drumming task subjects engage whole arm movements, and the pre-motion positivity is not as evident for simple finger flexions. While more validation studies are needed with this drumming task and comparison of different drum rhythms, it shows promise as an engaging, naturalistic behavior to test in the laboratory. One undergraduate research subject said that this was the most interesting experiment she had participated in, while another one mentioned this was the least boring.

As predicted, neural oscillations were observed to move in varying degrees of time locking with drum events. These are hard to quantify but qualitative description and correlation with a down sampled audio clip provide preliminary conclusions. Particularly in the beta and gamma bands, the play condition is indicative of a neural process linked to the drum sample in the form of a motor preceding negativity that rises after drum hit as similar to that reported in (Boonstra et al., 2006; Caetano et al., 2007). A similar rise is observed in the listen-only condition following the drum hit. There are additional peaks of oscillatory activity that do not correspond to any particular drum hit.

As discussed earlier in this study, the listen and play conditions share precise timing information in that they are time locked to an external stimulus. The solo condition on the other hand relies on the intrinsic timing information generated by each subject. The play condition also has this in the sense of coordinating a pattern generator to produce the correct drum hit at the correct time, however it has the opportunity to recalibrate every iteration of the drum sample. The asynchrony between movement tasks (solo and play) in time-frequency space, when they share high correlation in frequency space, may be explained by differences in timing mechanisms. The solo condition has greater correlation with the drum sample in the beta band than the play condition. The beta rhythm may represent endogenous timing mechanisms that correspond to the drum rhythm, whereas the play condition shows higher correlation than the solo in both theta and gamma bands. Both of these have been associated with auditory and temporal processing. Gamma is already well discussed prior in this dissertation, and includes sensitivity to things such as missing expected tones (Fujioka et al., 2009; Zanto, 2005). Additionally, these theta oscillations may have effects with envelope locked gamma band activity (Lakatos et al., 2005). The lack of strong gamma or theta oscillatory activity in the solo condition is perhaps telling of a lack of reliance on auditory input. Both of the movement conditions show similar correlations of mu power over time with the drum sample.

What is a good correlation for this type of task? The highest coefficient reported is in the theta range and reaches approximately 0.6. Given the difficulty in directly matching a sound recording that emphasizes drawn out decay of a reverberating drum to a quickly oscillating brain rhythm, a liberal ceiling for declaring a good or strong correlation could be 0.2 and above. Even with False Discovery Rate correction, there is still a large amount of correlations that represent significant interactions. Relatively speaking, there is likely a better way to find important features in the behavior or drum rhythms to explain brain responses. To further identify motor output, the addition of EMG electrodes or infrared sensors to capture movement could help detect the moments when anticipatory movements occur, such as pulling the hand up before bringing it down to make contact with the drum head. Additionally, if one expects there to be one peak per frequency band per drum hit, then an adaptive algorithm as described in the appendix for use identifying epochs in the solo drumming condition could be useful. The algorithm process searches for a salient feature, such as a long or short pause between drum hits, and then counts the number of peaks before the next feature. If it conforms to the expected pattern of hits, and the total time window falls within a preset statistical tolerance (e.g. one standard deviation) based on the past time windows, then it is counted as a good example of time locking.

Initial predictions hypothesized similar beta band activity across conditions, as this follow from a simulation account of rhythmic auditory perception. The results show brain rhythms in all conditions time-locked to drum hits featured in the sample. The latency between conditions is distinct, and the movement conditions contain greater suppression prior to drum hits.

The actual results are difficult to interpret in terms of supporting a simulation account. If the assumption is that a similar brain process is engaged both during movement and during simulation of movement without overt movement, as during a listening task, then it is reasonable to assume that the differences between conditions with regard to the brain process should be negligible. While there was no statistically significant difference in the beta or gamma bands for both spectral analyses and time-frequency analyses, there was a greater than chance probability that the variance between conditions could be explained by the experimental manipulations. These present findings show a plausible application of drumming to compare listening and moving. Further work and corroboration of these findings will need to occur before we can draw strong conclusions from this work in support of simulation. A follow up with more subjects is in order. While there was a favorable signal to noise ratio from the large number of trials per subject, individual differences can account for large amounts of variability; this was why permutation tests were performed, but even still the inclusion of more subjects, and in particular a wider variety of drummers such that a continuum of experience could be built, would elucidate the effects of expertise. The inclusion of behavioral performance measures to link with electrophysiological data would further increase the signal to noise ratio and remove from analysis trials where subjects lost the beat. Additionally, the training of novice drummers followed by a retest session at a later date could answer outstanding questions related to attention or memory consolidation and demands on brain rhythms such as mu.

Chapter 5

Conclusions

5.1 Motor Rhythms are Plastic

Motor rhythms, including mu and beta oscillations, are adaptable on multiple time scales. In the first study presented in this dissertation, subjects showed increased motor rhythm activity in the form of beta suppression when listening to a piano melody they learned to play. The melody was not complicated - by day five of training, every subject was able to play the entire song without errors within six minutes of commencing training. Subjects weren't tested on the whole song sequence at the start of a training session, but it is possible most of them could have played the song from memory without practice on the final day. The motor system is rapidly adaptable, and its effects on sensory processing appear to be as well. Recall that for motor rhythms, suppression of power relative to baseline is an indicator of motor system engagement. Motor rhythms show significant engagement when subjects listened to their learned melody and not when listening to an unlearned control melody. When this learned melodic sequence was transposed into a set of different notes, subjects showed more engagement then when listening to the control melody. The motor system's adaptability extends to motor sequences based on abstract features (relative pitch distance) that aren't rooted in strictly physical phenomena (absolute pitch).

The motor system is also adaptable over longer periods of time. Drumming experience changes the amount of motor rhythm recruitment during drumming. In the third study presented in this dissertation, drummers who had at least two years experience showed a significant decrease in mu power while drumming, which was not seen in novice drummers. A decrease in mu is common during movement (Pineda, 2008). However, not only did novice drummers exhibit increased mu power relative to experienced drummers, they also increased their mu power while drumming above levels seen while listening to the same drum rhythm. An increase in mu power is typically seen in resting states (Klimesch et al., 2007), and it is also seen during inhibition of overt motor responses (Hwang et al., 2014). Novice drummers may recruit additional resources to actively suppress incorrect drum hits, or to aid in focus for precise timing, as predicted by the inhibition timing hypothesis (Klimesch et al., 2007). An extension of this study could test novice drummers after additional days of practice to test whether this effect is as quickly adaptable as beta rhythm responses to piano sequences.

Previous research details the relative adaptability of the motor system in short sensorimotor training sessions. Catmur et al. (2008) trained different groups of subjects to associate movements congruent with stimuli (moving a hand when observing a hand) or to move incongruently (moving a hand when observing a foot). Functional imaging revealed activation of associated motor area that subjects had learned to associate with hand movements (hands and feet respectively for congruent and incongruent groups) after just three days of training. In terms of lower level kinematic representations, simple digit movements can be influenced by just 30 minutes of training of transcranial magnetic stimulation. (Classen et al., 1998). For complex behaviors such as drumming, both kinematics and coordinated limb associations (right vs left hands in this case) are being trained.

The hand drumming for EEG task provides a new domain for the direct testing of real world expertise on a laboratory task. Drummers often engage in many repetitions of a given pattern, practicing with external pacing cues such as metronomes or musical recordings. Minimal adaptation is demanded of drummers to come into a laboratory setting and study a rhythm by focused listening, and playing a drum pattern many times in a row. One potential drawback of the current listen, play, and solo paradigm is the inability to say whether the motor rhythm activity during listening may be attributable to motor imagery. Imagined movements are known to desynchronize mu (Pfurtscheller and Neuper, 1997), and beta (Pfurtscheller et al., 2005), and mu effects are so robust, imagined movements can be classified to control discrete parameters of a brain-computer interface (Pfurtscheller et al., 2006). During the listening condition with the current design, there is no way to estimate what amount of motor rhythm power could be associated with imagery. Initially an imagery condition was considered, but discarded due to difficulties time locking brain recordings. Without visual cues, or auditory pacing cues it would be difficult to estimate when an imagined drum beat occurred relative to another drum beat. Single trial classification of EEG can be accomplished using spatial filters (Blankertz and Tomioka, 2008), and already show success identifying hand movements (Ramoser et al., 2000). Other methods could estimate imagery more simply by averaging in frequency space across the whole block of imagined drumming and compare spectra using something akin to correlations of spectral density with known listening and known drumming conditions.

A better understanding of motor imagery dynamics could enable testing the effects of expertise. Just as a musical audience member might tap a foot or nod along with music, drummers often will tap or mark drum beats with different body parts. This movement is a form of cognition (Kirsh, 1995), and as such, drummers may more effectively use strategies such as marking (Kirsh, 2010) when learning new rhythms compared to a novice. Cultures that practice oral histories often teach musical rhythms via mouth sounds, also called vocables, to teach a new rhythm while avoiding additional complexities of motor kinematics. Vocables, like marking, can facilitate sequencing of complex rhythms and serve as a cognitive tool which can reduce processing loads (Kirsh, 2010). If the novice drummers in this study were truly using more mental resources to increase mu power, as explained in the inhibition timing hypothesis, then use of a vocable or other marked drum rhythm might suppress mu more similarly to a drummer who is drumming. Differences between drummers and novices such as decreased mu rhythm power may indicate greater engagement of the motor system, which may correlate with faster or more accurate behavioral performance of a newly acquired rhythm.

5.2 Relation to Audiomotor Simulation Hypothesis

Overall, present findings support a simulation hypothesis describing the interaction of motor rhythms and auditory events. When both movements and sounds occur simultaneously, interactions occur in their respective brainwaves. Past reports demonstrated a similar neural response after a drum hit for subjects who either play a drum or heard a drum (Caetano et al., 2007). The present findings expand on this to describe a similar post movement and sound response that is also modulated by preparatory motor activity when sounds and movements co-occur. These interactions happen in multiple frequency bands. A more dynamic and more complex picture of the interaction between movement and sound emerges that requires more sophisticated tools to untangle the network enabling sound input to entrain motor output.

Phase coherence between different recording sites or sources of brainwaves are useful for looking at synchronizing effects. Lindenberger et al. (2009) demonstrate the feasibility of showing cross-brain coherence between dyads of guitar players. Dyads are useful tools to study the interactive nature of synchronizing behaviors, as movement synchronization is commonly a social activity. Adaptive metronomes (Repp and Keller, 2008) can simulate human performance for study of dyadic interactions for synchronizing movements within a subject. Initial reports indicate increased engagement of fronto-parietal networks when tapping along with moderately adaptive sequences, compared to nonadaptive, or overly adaptive metronomes which end up tracking the variability of each tap (Fairhurst et al., 2010, 2012). These are likely the same fronto-parietal networks that generate mu rhythms (Pineda, 2005, 2008) and contribute to motor simulation of auditory events (Patel and Iversen, 2014). Cross-frequency coupling is another approach to dealing with multiple frequency bands that show perturbations to changes in both auditory or motor information. It can examine how a frequency that primarily responds to one aspect of the task may entrain other frequencies (Canolty and Knight, 2010). If theta rhythms represent primary auditory changes, as suggested by spectral changes in tapping, then this might serve to synchronize phasic bursts of higher frequency bands. For instance recall Fig 4.3 that shows an increase in theta oscillations prior to initiation of movement in single drum hits.

A potential difficulty facing further oscillation based investigations of audiomotor coupling is disagreement in the field regarding functional distinctions of different frequency bands of interest. It may be subjective where effects appear across frequencies in broadband spectrograms. There is enough overlap in literature distinctions of frequency band boundaries to make a priori distinctions seemingly arbitrary. The definition of gamma 20-50 Hz (Zanto, 2005), 20-60 Hz (Snyder and Large, 2005), 28-48 Hz (Fujioka et al., 2009) shares overlap with what is considered the beta band, reported in the literature as 15-30 Hz (Caetano et al., 2007; Boonstra et al., 2006), 20-30 Hz (Iversen et al., 2009), 12-33 Hz (Pollok et al., 2005), and 15-20 (Fujioka et al., 2009). In the present studies 20-30 Hz was chosen as this would capture a range that included the overlap of the majority of previously cited lower gamma and upper beta ranges that seemed most prominently associated with auditory, motor, or audiomotor processing. It is possible a meta analysis of the literature could find similarities across overlapping frequencies, however other poorly controlled factors in EEG recording such as choice of reference electrode and reported location on scalp could confound cross study comparisons at this level. Additionally there are seemingly no accepted baseline conditions to compare frequency band activity. Everything from rest periods, to inter-stimulus intervals, and taking the mean of each trial have been employed, yet there is no systematic comparison of the effect these choices have on outcome of study. These are important issues to address, particularly when this field is advancing towards therapeutic use in terms of identifying biomarkers for neuropsychiatric diseases and targeting aberrant brainwaves with neurofeedback.

The role of somatosensation is often unmentioned and uncontrolled in studies of audiomotor integration, including those presented in this dissertation. When disentangling motor responses from auditory influences in brainwave frequency space, the contribution of somatosensory feedback should also be accounted for.

If a motor response can be distinguished from auditory response based on the pre-event time window (e.g. a negative power deflection in the mu or beta band prior to a tap), what distinguishes a motor response from a somatosensory response after contact is made between a finger and a tapped surface? Caetano et al. (2007) interpret an increased latency in mu band enhancement for pantomimed taps as evidence for mu participation in somatosensory feedback. Mu is thought to originate from fibers linking motor and somatosensory cortices (Pineda, 2008), and direct electrically coupled cells exist between parietal and premotor regions (Luppino et al., 1999). Somatosensory information may be a critical part of the feedback that judges the accuracy of motor synchrony, particularly for movements that do not produce sound. Adding additional control conditions for audiomotor experiments to employ movements that do not create auditory or tactile feedback will be necessary to disentangle the role of somatosensory systems in helping synchronize movements to external pacing cues.

One of the main goals of this line of research is to describe how sounds can stimulate and constrain movements. The ASAP hypothesis gives a plausible mechanism to explain how we can predict sounds and gives a foundation for how that same system would constrain the timing of movements. But it still does not explain how sounds stimulate motor function. For musical therapy and movement rehabilitation, understanding the neural pathways involved in stimulation of the motor system through sounds offers a low cost, noninvasive, drug free way to affect the quality of life for patients with difficulty otherwise moving. At the intersection of motor rehabilitation and enabling impaired individuals is the confluence of understanding perception, action, and imagery. As Lindenberger et al. (Lindenberger et al., 2009) studied the synchronization between brains at the initiation of guitar playing, future work can focus on the moment of movement initiation. Musicians count off together before initiating a song; dancers often count in to synchronize themselves. How long does one need to entrain to sounds before movement is facilitated? Can the pathway from auditory cortex activation to motor execution be mapped? An electrophysiological map of phase coupled brain regions has been described using coherence between mu and beta rhythms during rhythmic tapping to link auditory, primary somatosensory, primary motor, premotor, supplementary motor, and posterior parietal cortices with thalamic and cerebellar systems (Pollok et al., 2005). While coherence between brain regions can identify co-modulating activity, and validate similar networks proposed by functional imaging (Zatorre et al., 2007), it cannot address the directional influences of these regions on each other, as are needed to explain how we move from auditory input to motor output. Granger causal inferences have shown preliminary success in estimating the direction of influence between auditory and motor sources in EEG of subjects playing piano (Jäncke, 2012). Future work combining those causal inferences with the tight time locking of auditory entrainment and motor synchronization could map out the dynamic interaction of auditory and motor systems enabling these complex behaviors. As the experience dependent changes from the differences seen in drummers and novices suggests, the audiomotor system is adaptable, and makes plastic changes over an understudied time span.

Chapter 6

Apendix A - Motor Learning and Sequential Auditory Processing

6.1 Supplementary Results

Electrophysiological Reports

Statistical Tables

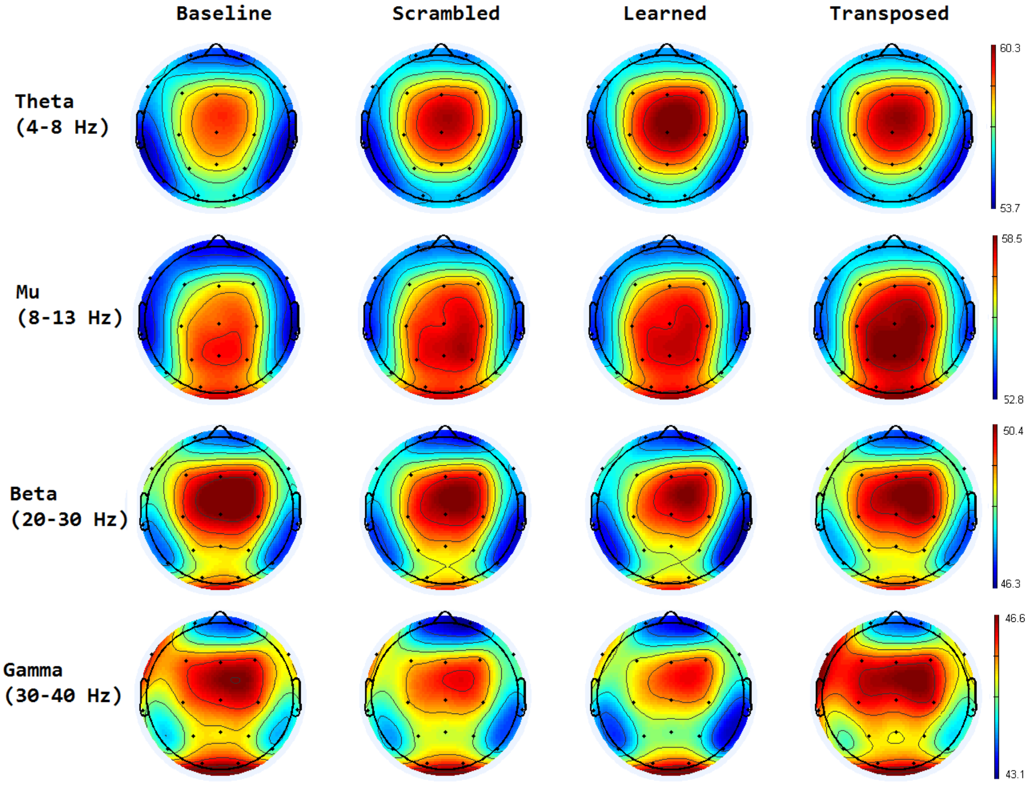


Figure 6.1: Scalp distribution of different frequency band activities

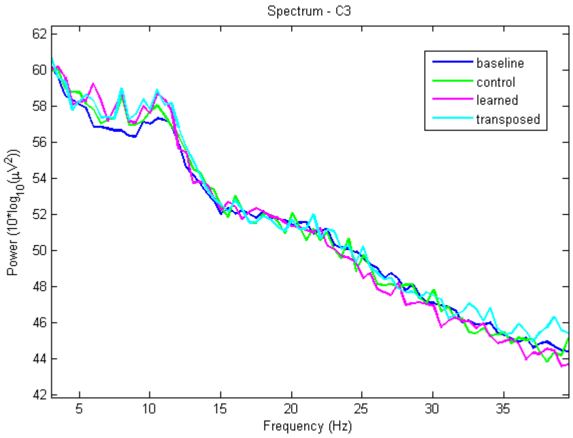


Figure 6.2: Spectral decomposition over 6 second time windows, electrode C3

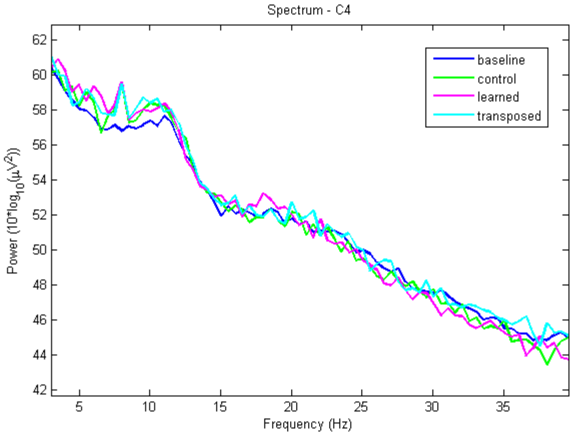


Figure 6.3: Spectral decomposition over 6 second time windows, electrode C4

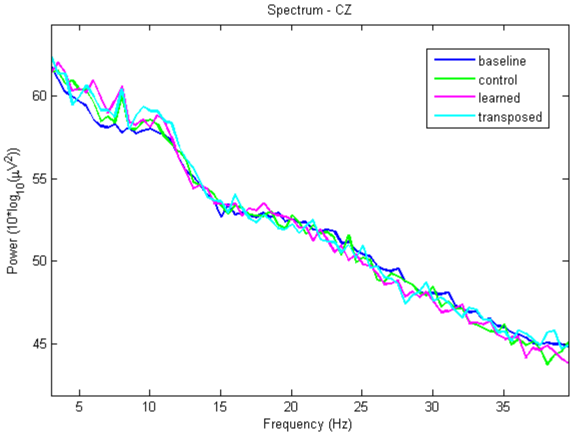


Figure 6.4: Spectral decomposition over 6 second time windows, electrode Cz

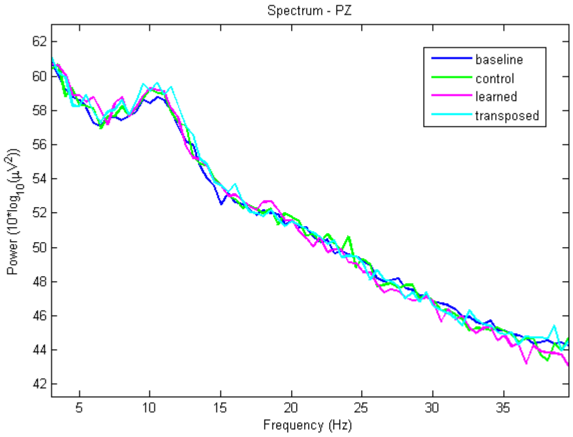
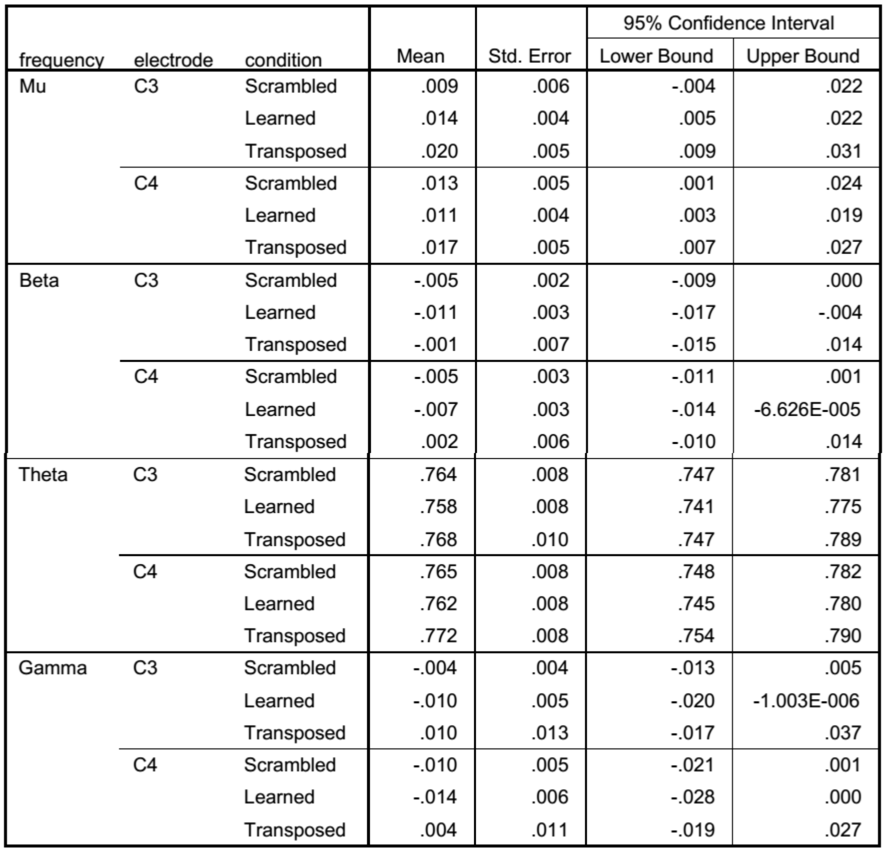


Figure 6.5: Spectral decomposition over 6 second time windows, electrode Pz

Table 6.1: Examining the effect of Frequency Band by Conditions at electrodes C3 and C4

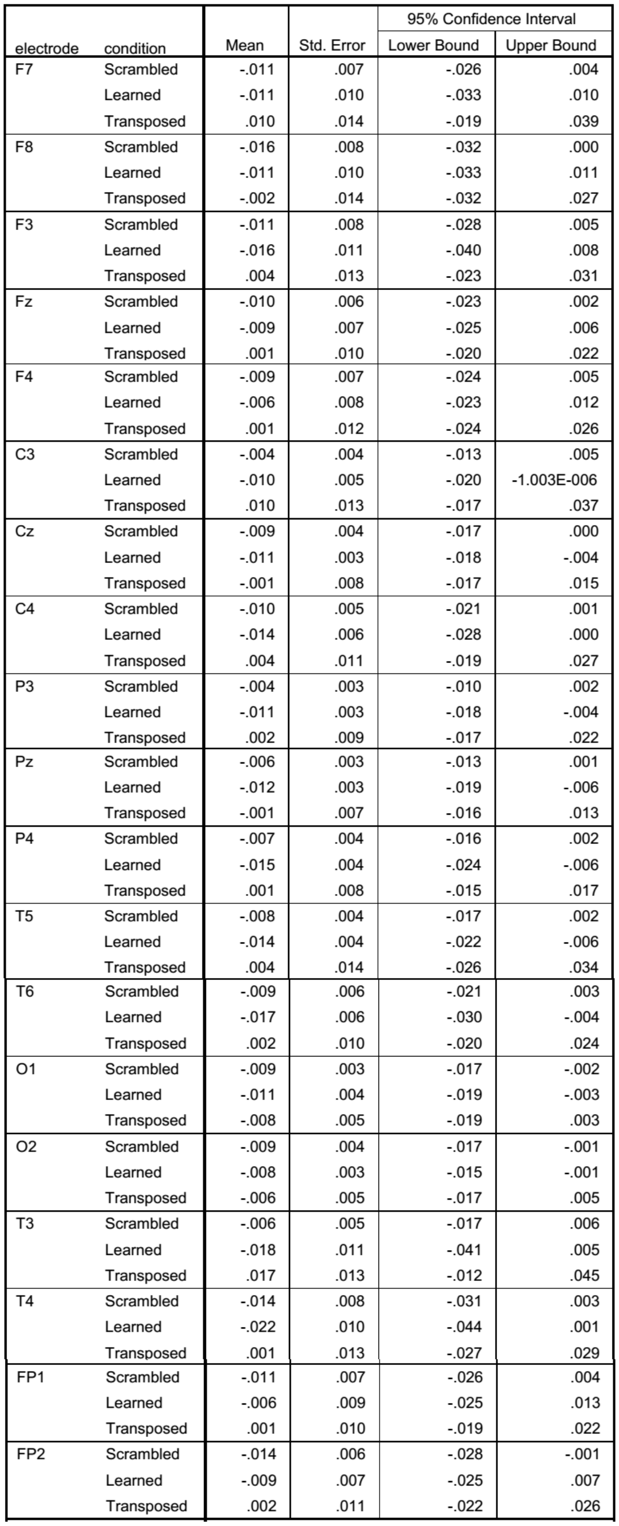


					95% Confidence Interval	
frequency	electrode	condition	Mean	Std. Error	Lower Bound	Upper Bound
Mu	C3	Scrambled	.009	.006	-.004	.022
		Learned	.014	.004	.005	.022
		Transposed	.020	.005	.009	.031
	C4	Scrambled	.013	.005	.001	.024
		Learned	.011	.004	.003	.019
		Transposed	.017	.005	.007	.027
Beta	C3	Scrambled	-.005	.002	-.009	.000
		Learned	-.011	.003	-.017	-.004
		Transposed	-.001	.007	-.015	.014
	C4	Scrambled	-.005	.003	-.011	.001
		Learned	-.007	.003	-.014	-6.626E-005
		Transposed	.002	.006	-.010	.014
Theta	C3	Scrambled	.764	.008	.747	.781
		Learned	.758	.008	.741	.775
		Transposed	.768	.010	.747	.789
	C4	Scrambled	.765	.008	.748	.782
		Learned	.762	.008	.745	.780
		Transposed	.772	.008	.754	.790
Gamma	C3	Scrambled	-.004	.004	-.013	.005
		Learned	-.010	.005	-.020	-1.003E-006
		Transposed	.010	.013	-.017	.037
	C4	Scrambled	-.010	.005	-.021	.001
		Learned	-.014	.006	-.028	.000
		Transposed	.004	.011	-.019	.027

Table 6.2: Examining the effect of Electrode by Condition in the Beta frequency band

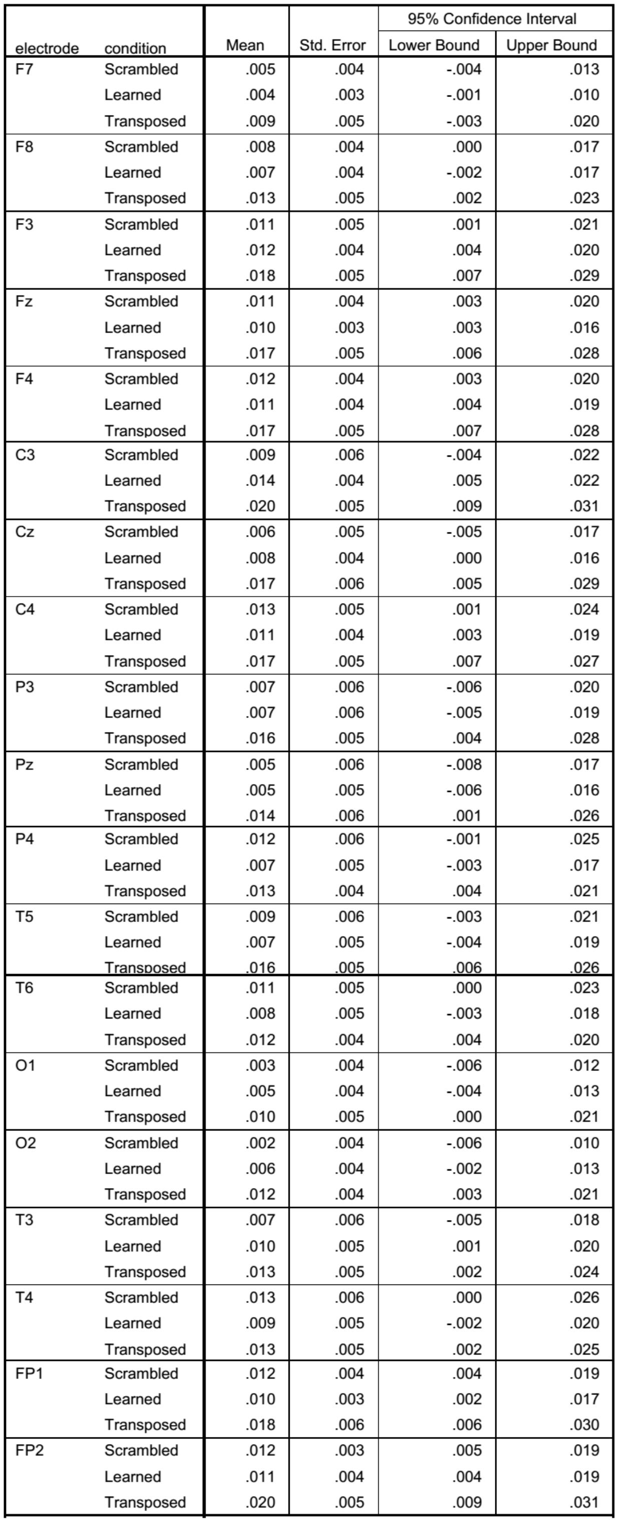
electrode	condition	Mean	Std. Error	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
F7	Scrambled	-.013	.004	-.021	-.004
	Learned	-.010	.005	-.021	.001
	Transposed	.001	.008	-.016	.017
F8	Scrambled	-.011	.004	-.019	-.002
	Learned	-.008	.005	-.017	.002
	Transposed	.000	.007	-.015	.015
F3	Scrambled	-.010	.004	-.019	-.001
	Learned	-.016	.007	-.030	-.002
	Transposed	-.002	.006	-.015	.010
Fz	Scrambled	-.007	.003	-.013	-.001
	Learned	-.008	.003	-.013	-.003
	Transposed	-.005	.004	-.013	.004
F4	Scrambled	-.007	.003	-.014	.001
	Learned	-.004	.004	-.012	.004
	Transposed	-.002	.006	-.014	.010
C3	Scrambled	-.005	.002	-.009	.000
	Learned	-.011	.003	-.017	-.004
	Transposed	-.001	.007	-.015	.014
Cz	Scrambled	-.005	.002	-.009	.000
	Learned	-.011	.002	-.015	-.006
	Transposed	-.007	.004	-.015	.000
C4	Scrambled	-.005	.003	-.011	.001
	Learned	-.007	.003	-.014	-6.626E-005
	Transposed	.002	.006	-.010	.014
P3	Scrambled	.000	.002	-.004	.004
	Learned	-.007	.002	-.012	-.002
	Transposed	9.254E-005	.005	-.010	.010
Pz	Scrambled	.000	.002	-.004	.005
	Learned	-.008	.002	-.012	-.003
	Transposed	-.002	.003	-.009	.006
P4	Scrambled	-.001	.003	-.007	.004
	Learned	-.004	.003	-.010	.001
	Transposed	.002	.004	-.005	.010
T5	Scrambled	-.002	.002	-.007	.002
	Learned	-.007	.003	-.013	.000
	Transposed	.005	.011	-.017	.028
T6	Scrambled	-.004	.003	-.011	.003
	Learned	-.008	.003	-.015	-.001
	Transposed	.005	.005	-.006	.016
O1	Scrambled	-.005	.002	-.010	.001
	Learned	-.005	.002	-.009	-.001
	Transposed	-.003	.003	-.010	.003
O2	Scrambled	-.005	.002	-.010	.000
	Learned	-.005	.002	-.008	-.001
	Transposed	-.002	.002	-.007	.003
T3	Scrambled	-.008	.003	-.013	-.002
	Learned	-.012	.007	-.028	.004
	Transposed	.003	.009	-.016	.023
T4	Scrambled	-.010	.004	-.019	-.001
	Learned	-.014	.007	-.029	.001
	Transposed	.000	.006	-.012	.013
FP1	Scrambled	-.009	.004	-.017	-.001
	Learned	-.005	.004	-.013	.003
	Transposed	-.003	.005	-.013	.007
FP2	Scrambled	-.009	.004	-.017	-.001
	Learned	-.006	.003	-.013	.001
	Transposed	-.002	.005	-.012	.009

Table 6.3: Examining the effect of Electrode by Condition in the Gamma frequency band



				95% Confidence Interval	
electrode	condition	Mean	Std. Error	Lower Bound	Upper Bound
F7	Scrambled	-.011	.007	-.026	.004
	Learned	-.011	.010	-.033	.010
	Transposed	.010	.014	-.019	.039
F8	Scrambled	-.016	.008	-.032	.000
	Learned	-.011	.010	-.033	.011
	Transposed	-.002	.014	-.032	.027
F3	Scrambled	-.011	.008	-.028	.005
	Learned	-.016	.011	-.040	.008
	Transposed	.004	.013	-.023	.031
Fz	Scrambled	-.010	.006	-.023	.002
	Learned	-.009	.007	-.025	.006
	Transposed	.001	.010	-.020	.022
F4	Scrambled	-.009	.007	-.024	.005
	Learned	-.006	.008	-.023	.012
	Transposed	.001	.012	-.024	.026
C3	Scrambled	-.004	.004	-.013	.005
	Learned	-.010	.005	-.020	-1.003E-006
	Transposed	.010	.013	-.017	.037
Cz	Scrambled	-.009	.004	-.017	.000
	Learned	-.011	.003	-.018	-.004
	Transposed	-.001	.008	-.017	.015
C4	Scrambled	-.010	.005	-.021	.001
	Learned	-.014	.006	-.028	.000
	Transposed	.004	.011	-.019	.027
P3	Scrambled	-.004	.003	-.010	.002
	Learned	-.011	.003	-.018	-.004
	Transposed	.002	.009	-.017	.022
Pz	Scrambled	-.006	.003	-.013	.001
	Learned	-.012	.003	-.019	-.006
	Transposed	-.001	.007	-.016	.013
P4	Scrambled	-.007	.004	-.016	.002
	Learned	-.015	.004	-.024	-.006
	Transposed	.001	.008	-.015	.017
T5	Scrambled	-.008	.004	-.017	.002
	Learned	-.014	.004	-.022	-.006
	Transposed	.004	.014	-.026	.034
T6	Scrambled	-.009	.006	-.021	.003
	Learned	-.017	.006	-.030	-.004
	Transposed	.002	.010	-.020	.024
O1	Scrambled	-.009	.003	-.017	-.002
	Learned	-.011	.004	-.019	-.003
	Transposed	-.008	.005	-.019	.003
O2	Scrambled	-.009	.004	-.017	-.001
	Learned	-.008	.003	-.015	-.001
	Transposed	-.006	.005	-.017	.005
T3	Scrambled	-.006	.005	-.017	.006
	Learned	-.018	.011	-.041	.005
	Transposed	.017	.013	-.012	.045
T4	Scrambled	-.014	.008	-.031	.003
	Learned	-.022	.010	-.044	.001
	Transposed	.001	.013	-.027	.029
FP1	Scrambled	-.011	.007	-.026	.004
	Learned	-.006	.009	-.025	.013
	Transposed	.001	.010	-.019	.022
FP2	Scrambled	-.014	.006	-.028	-.001
	Learned	-.009	.007	-.025	.007
	Transposed	.002	.011	-.022	.026

Table 6.4: Examining the effect of Electrode by Condition in the Mu frequency band



electrode	condition	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
F7	Scrambled	.005	.004	-.004	.013
	Learned	.004	.003	-.001	.010
	Transposed	.009	.005	-.003	.020
F8	Scrambled	.008	.004	.000	.017
	Learned	.007	.004	-.002	.017
	Transposed	.013	.005	.002	.023
F3	Scrambled	.011	.005	.001	.021
	Learned	.012	.004	.004	.020
	Transposed	.018	.005	.007	.029
Fz	Scrambled	.011	.004	.003	.020
	Learned	.010	.003	.003	.016
	Transposed	.017	.005	.006	.028
F4	Scrambled	.012	.004	.003	.020
	Learned	.011	.004	.004	.019
	Transposed	.017	.005	.007	.028
C3	Scrambled	.009	.006	-.004	.022
	Learned	.014	.004	.005	.022
	Transposed	.020	.005	.009	.031
Cz	Scrambled	.006	.005	-.005	.017
	Learned	.008	.004	.000	.016
	Transposed	.017	.006	.005	.029
C4	Scrambled	.013	.005	.001	.024
	Learned	.011	.004	.003	.019
	Transposed	.017	.005	.007	.027
P3	Scrambled	.007	.006	-.006	.020
	Learned	.007	.006	-.005	.019
	Transposed	.016	.005	.004	.028
Pz	Scrambled	.005	.006	-.008	.017
	Learned	.005	.005	-.006	.016
	Transposed	.014	.006	.001	.026
P4	Scrambled	.012	.006	-.001	.025
	Learned	.007	.005	-.003	.017
	Transposed	.013	.004	.004	.021
T5	Scrambled	.009	.006	-.003	.021
	Learned	.007	.005	-.004	.019
	Transposed	.016	.005	.006	.026
T6	Scrambled	.011	.005	.000	.023
	Learned	.008	.005	-.003	.018
	Transposed	.012	.004	.004	.020
O1	Scrambled	.003	.004	-.006	.012
	Learned	.005	.004	-.004	.013
	Transposed	.010	.005	.000	.021
O2	Scrambled	.002	.004	-.006	.010
	Learned	.006	.004	-.002	.013
	Transposed	.012	.004	.003	.021
T3	Scrambled	.007	.006	-.005	.018
	Learned	.010	.005	.001	.020
	Transposed	.013	.005	.002	.024
T4	Scrambled	.013	.006	.000	.026
	Learned	.009	.005	-.002	.020
	Transposed	.013	.005	.002	.025
FP1	Scrambled	.012	.004	.004	.019
	Learned	.010	.003	.002	.017
	Transposed	.018	.006	.006	.030
FP2	Scrambled	.012	.003	.005	.019
	Learned	.011	.004	.004	.019
	Transposed	.020	.005	.009	.031

Table 6.5: Examining the effect of Electrode by Condition in the Theta frequency band

electrode	condition	Mean	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
F7	Scrambled	.764	.006	.751	.777
	Learned	.766	.006	.753	.779
	Transposed	.777	.009	.758	.797
F8	Scrambled	.760	.007	.745	.775
	Learned	.764	.006	.751	.776
	Transposed	.771	.010	.751	.791
F3	Scrambled	.759	.007	.743	.774
	Learned	.753	.006	.740	.766
	Transposed	.767	.009	.748	.785
Fz	Scrambled	.754	.007	.740	.768
	Learned	.753	.007	.739	.767
	Transposed	.756	.007	.742	.771
F4	Scrambled	.763	.007	.747	.779
	Learned	.766	.007	.750	.781
	Transposed	.767	.007	.752	.783
C3	Scrambled	.764	.008	.747	.781
	Learned	.758	.008	.741	.775
	Transposed	.768	.010	.747	.789
Cz	Scrambled	.755	.009	.736	.774
	Learned	.749	.009	.731	.768
	Transposed	.752	.009	.733	.772
C4	Scrambled	.765	.008	.748	.782
	Learned	.762	.008	.745	.780
	Transposed	.772	.008	.754	.790
P3	Scrambled	.762	.009	.743	.781
	Learned	.755	.010	.734	.775
	Transposed	.762	.009	.742	.781
Pz	Scrambled	.751	.009	.732	.770
	Learned	.743	.010	.723	.763
	Transposed	.749	.009	.730	.768
P4	Scrambled	.760	.008	.742	.778
	Learned	.757	.009	.738	.775
	Transposed	.763	.008	.746	.780
T5	Scrambled	.774	.009	.755	.794
	Learned	.770	.009	.750	.789
	Transposed	.782	.011	.758	.806
T6	Scrambled	.769	.007	.754	.783
	Learned	.764	.007	.750	.779
	Transposed	.777	.008	.760	.794
O1	Scrambled	.777	.011	.754	.800
	Learned	.777	.011	.754	.799
	Transposed	.779	.011	.755	.802
O2	Scrambled	.776	.009	.757	.795
	Learned	.777	.009	.759	.795
	Transposed	.779	.009	.761	.798
T3	Scrambled	.780	.009	.761	.800
	Learned	.776	.009	.757	.795
	Transposed	.791	.009	.771	.811
T4	Scrambled	.772	.009	.753	.791
	Learned	.769	.009	.748	.789
	Transposed	.783	.010	.763	.803
FP1	Scrambled	.758	.006	.746	.770
	Learned	.762	.006	.749	.774
	Transposed	.764	.007	.748	.779
FP2	Scrambled	.757	.007	.742	.772
	Learned	.760	.006	.746	.773
	Transposed	.764	.008	.748	.780

Chapter 7

Apendix B - Synchronizing Moving and Listening via Tapping

Supplementary Tables

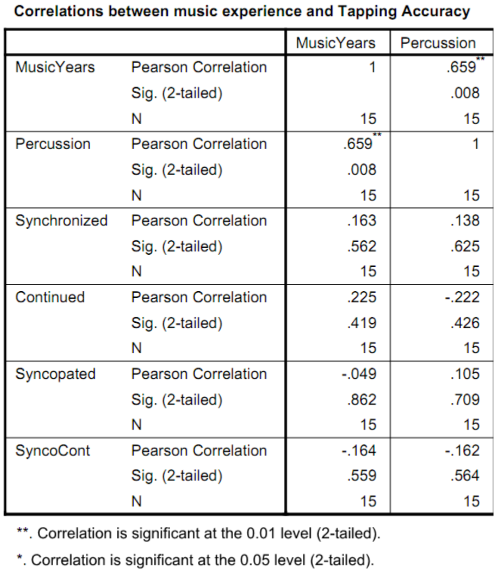
Supplementary Figures

Channel Space Results

Event Related Potential validation

Event related potentials were used to validate the use of this task with the Biosemi EEG recordings. During the listen-only condition, the average waveform time locked to onset of tone presentation showed an ERP consistent with auditory effects reported in literature. Two negative deflections were seen post stimulus presentation: the first at approximately 25-50 ms, and the second about 100 ms later (see Fig. 7.3a). The early response could indicate a middle latency auditory response, whereas the later response falls in the time window expected of a cortical

Table 7.1: Correlations between music experience and tapping accuracy.



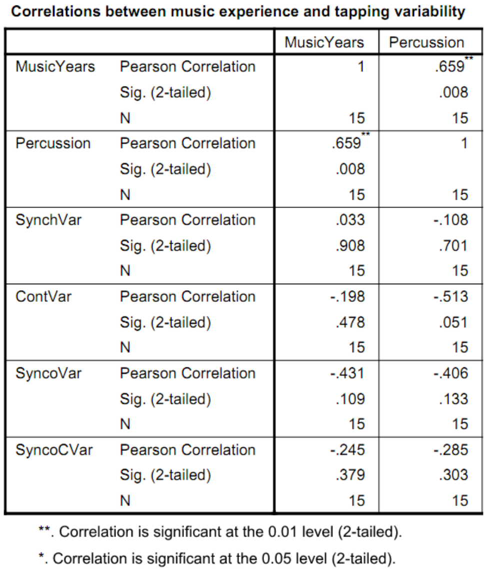
Correlations between music experience and Tapping Accuracy

		MusicYears	Percussion
MusicYears	Pearson Correlation	1	.659**
	Sig. (2-tailed)		.008
	N	15	15
Percussion	Pearson Correlation	.659**	1
	Sig. (2-tailed)	.008	
	N	15	15
Synchronized	Pearson Correlation	.163	.138
	Sig. (2-tailed)	.562	.625
	N	15	15
Continued	Pearson Correlation	.225	-.222
	Sig. (2-tailed)	.419	.426
	N	15	15
Syncopated	Pearson Correlation	-.049	.105
	Sig. (2-tailed)	.862	.709
	N	15	15
SyncoCont	Pearson Correlation	-.164	-.162
	Sig. (2-tailed)	.559	.564
	N	15	15

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

Table 7.2: Correlations between music experience and tapping variability.



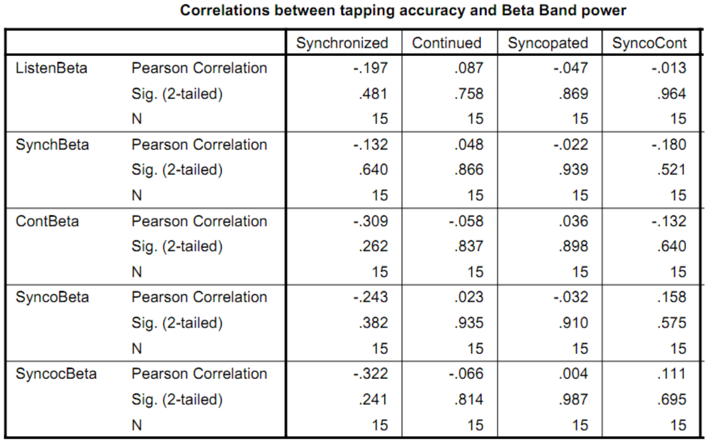
Correlations between music experience and tapping variability

		MusicYears	Percussion
MusicYears	Pearson Correlation	1	.659**
	Sig. (2-tailed)		.008
	N	15	15
Percussion	Pearson Correlation	.659**	1
	Sig. (2-tailed)	.008	
	N	15	15
SynchVar	Pearson Correlation	.033	-.108
	Sig. (2-tailed)	.908	.701
	N	15	15
ContVar	Pearson Correlation	-.198	-.513
	Sig. (2-tailed)	.478	.051
	N	15	15
SyncoVar	Pearson Correlation	-.431	-.406
	Sig. (2-tailed)	.109	.133
	N	15	15
SyncoCVar	Pearson Correlation	-.245	-.285
	Sig. (2-tailed)	.379	.303
	N	15	15

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

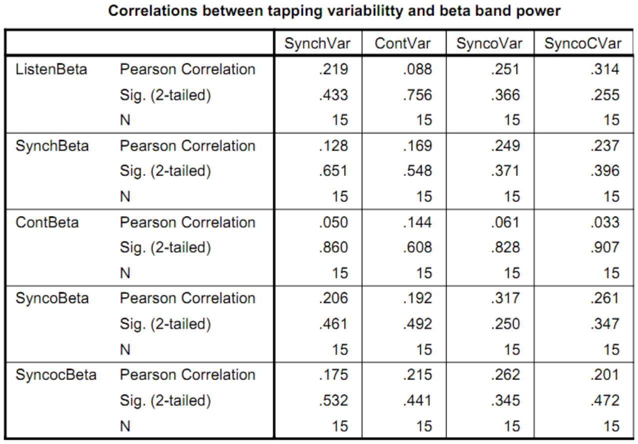
Table 7.3: Correlations between tapping accuracy and beta band measures over sensorimotor cortex.



Correlations between tapping accuracy and Beta Band power

		Synchronized	Continued	Syncopated	SyncoCont
ListenBeta	Pearson Correlation	-.197	.087	-.047	-.013
	Sig. (2-tailed)	.481	.758	.869	.964
	N	15	15	15	15
SynchBeta	Pearson Correlation	-.132	.048	-.022	-.180
	Sig. (2-tailed)	.640	.866	.939	.521
	N	15	15	15	15
ContBeta	Pearson Correlation	-.309	-.058	.036	-.132
	Sig. (2-tailed)	.262	.837	.898	.640
	N	15	15	15	15
SyncoBeta	Pearson Correlation	-.243	.023	-.032	.158
	Sig. (2-tailed)	.382	.935	.910	.575
	N	15	15	15	15
SyncocBeta	Pearson Correlation	-.322	-.066	.004	.111
	Sig. (2-tailed)	.241	.814	.987	.695
	N	15	15	15	15

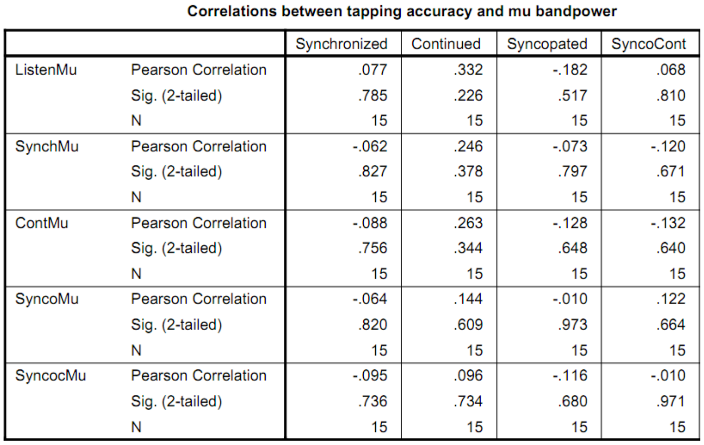
Table 7.4: Correlations between tapping variability and beta band measures over sensorimotor cortex.



Correlations between tapping variabilitty and beta band power

		SynchVar	ContVar	SyncoVar	SyncoCVar
ListenBeta	Pearson Correlation	.219	.088	.251	.314
	Sig. (2-tailed)	.433	.756	.366	.255
	N	15	15	15	15
SynchBeta	Pearson Correlation	.128	.169	.249	.237
	Sig. (2-tailed)	.651	.548	.371	.396
	N	15	15	15	15
ContBeta	Pearson Correlation	.050	.144	.061	.033
	Sig. (2-tailed)	.860	.608	.828	.907
	N	15	15	15	15
SyncoBeta	Pearson Correlation	.206	.192	.317	.261
	Sig. (2-tailed)	.461	.492	.250	.347
	N	15	15	15	15
SyncocBeta	Pearson Correlation	.175	.215	.262	.201
	Sig. (2-tailed)	.532	.441	.345	.472
	N	15	15	15	15

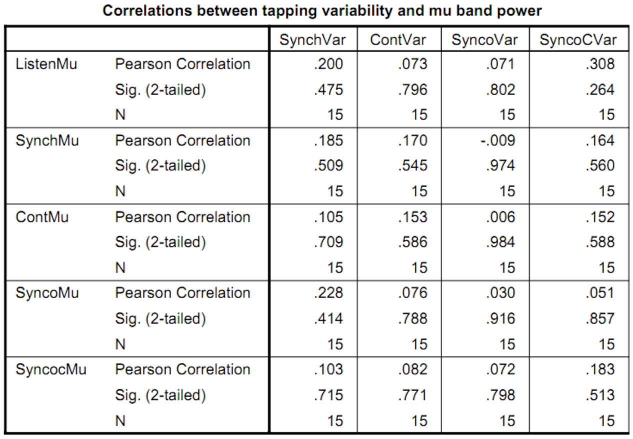
Table 7.5: Correlations between tapping accuracy and mu band measures over sensorimotor cortex.



Correlations between tapping accuracy and mu bandpower

		Synchronized	Continued	Syncopated	SyncoCont
ListenMu	Pearson Correlation	.077	.332	-.182	.068
	Sig. (2-tailed)	.785	.226	.517	.810
	N	15	15	15	15
SynchMu	Pearson Correlation	-.062	.246	-.073	-.120
	Sig. (2-tailed)	.827	.378	.797	.671
	N	15	15	15	15
ContMu	Pearson Correlation	-.088	.263	-.128	-.132
	Sig. (2-tailed)	.756	.344	.648	.640
	N	15	15	15	15
SyncoMu	Pearson Correlation	-.064	.144	-.010	.122
	Sig. (2-tailed)	.820	.609	.973	.664
	N	15	15	15	15
SyncocMu	Pearson Correlation	-.095	.096	-.116	-.010
	Sig. (2-tailed)	.736	.734	.680	.971
	N	15	15	15	15

Table 7.6: Correlations between tapping variability and mu band measures over sensorimotor cortex.



Correlations between tapping variability and mu band power

		SynchVar	ContVar	SyncoVar	SyncoCVar
ListenMu	Pearson Correlation	.200	.073	.071	.308
	Sig. (2-tailed)	.475	.796	.802	.264
	N	15	15	15	15
SynchMu	Pearson Correlation	.185	.170	-.009	.164
	Sig. (2-tailed)	.509	.545	.974	.560
	N	15	15	15	15
ContMu	Pearson Correlation	.105	.153	.006	.152
	Sig. (2-tailed)	.709	.586	.984	.588
	N	15	15	15	15
SyncoMu	Pearson Correlation	.228	.076	.030	.051
	Sig. (2-tailed)	.414	.788	.916	.857
	N	15	15	15	15
SyncocMu	Pearson Correlation	.103	.082	.072	.183
	Sig. (2-tailed)	.715	.771	.798	.513
	N	15	15	15	15

Table 7.7: Correlations between tapping accuracy and variability with mu and beta suppression over sensorimotor cortex.

Correlations between tapping measures and motor rhythm suppression

		MuSuppress	BetaSuppress
Synchronized	Pearson Correlation	-.341	.102
	Sig. (2-tailed)	.214	.718
	N	15	15
Continued	Pearson Correlation	-.267	-.088
	Sig. (2-tailed)	.336	.756
	N	15	15
Syncopated	Pearson Correlation	.311	.043
	Sig. (2-tailed)	.259	.878
	N	15	15
SyncoCont	Pearson Correlation	-.451	-.437
	Sig. (2-tailed)	.091	.103
	N	15	15
SynchVar	Pearson Correlation	-.042	-.198
	Sig. (2-tailed)	.883	.480
	N	15	15
ContVar	Pearson Correlation	.233	.251
	Sig. (2-tailed)	.402	.366
	N	15	15
SyncoVar	Pearson Correlation	-.188	.058
	Sig. (2-tailed)	.503	.837
	N	15	15
SyncoCVar	Pearson Correlation	-.378	-.107
	Sig. (2-tailed)	.165	.704
	N	15	15

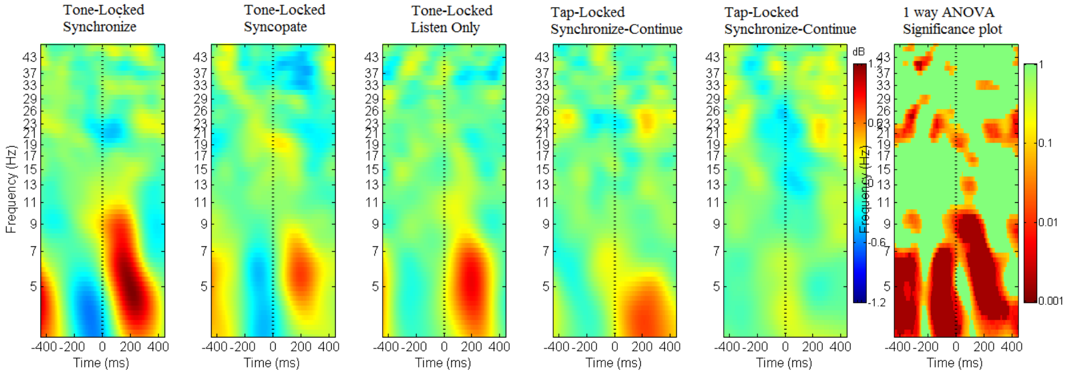


Figure 7.1: Event related spectral perturbations for brain data across conditions at electrode C4. A significance plot showing FDR corrected probabilities for significant differences across conditions is featured on the right.)

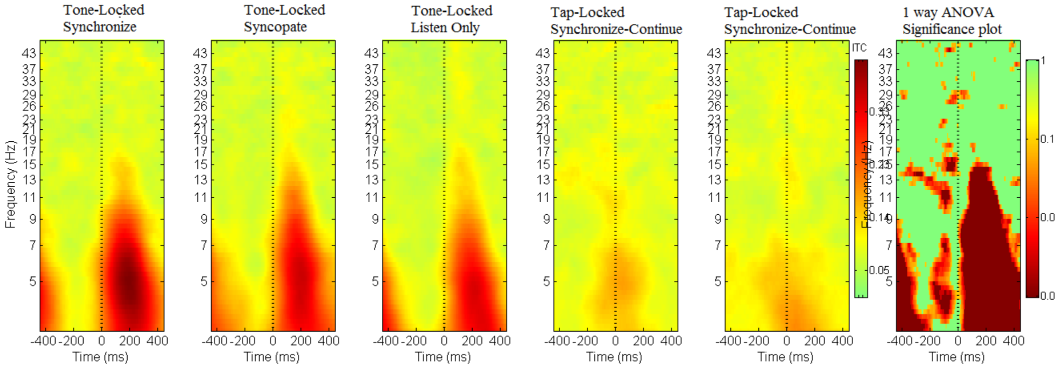


Figure 7.2: Inter-trial coherence measures for brain data across conditions at electrode C4. A significance plot showing FDR corrected probabilities for significant differences across conditions is featured on the right.)

auditory N100 potential (Hillyard et al., 1973). The continue tapping portion of the synchronized (not syncopated) trial with averaged waveform time locked to the execution of tap revealed a negative deflection starting at about 400 ms prior to tap detection. The negative potential changed polarity at about 225 ms prior to tap. This corresponds to a pre-motion positivity (Deecke et al., 1969), as the EMG sensor showed muscle activity starts around 175 ms prior to tap (see Fig. 7.3b).

Time-Frequency Results

Theta Band Visual inspection of the time frequency plots revealed a theta band oscillation (Fig. 7.4) for the listen-only condition that showed a slow positive perturbation time locked to the tone onset. The time locking nature of the oscillation is further corroborated by the same response in terms of latency and power in both the synchronized tapping (correlation coefficient r=0.98, p<0.0001) and syncopated tapping conditions (r=0.91, p<0.0001). In the synchronized tapping condition the oscillation time locked to tap onset followed the same positive deflection initiated just prior to tap onset as the sound-locked, listen-only curve (r=0.8,

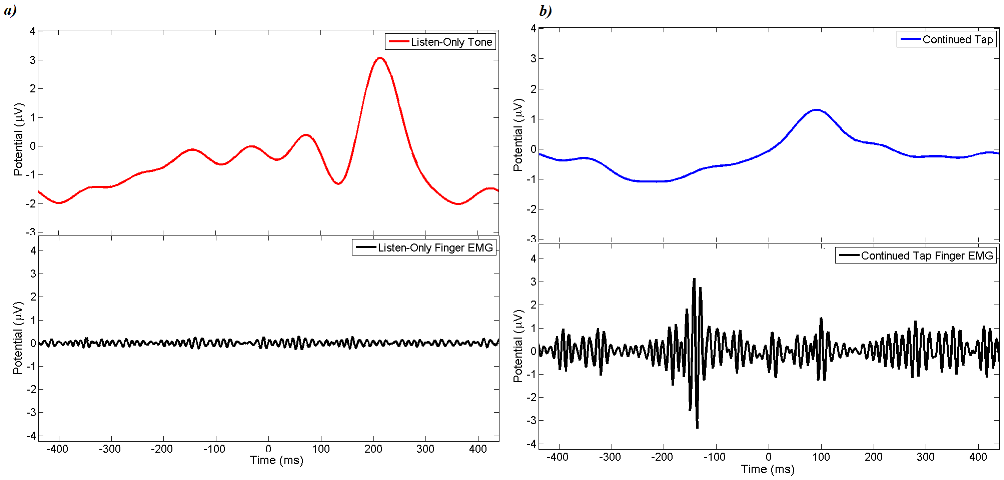


Figure 7.3: Event related brain and finger muscle potentials for a) listen-only condition and b) continued-tap.

p<0.0001). These two graphs represent the same data, just time-locked to different events. The slightly lower peak amplitude in the synchronized tap-locked curve can be explained by the increased variance in human tapping response as well as the latency lining up approximately 50 ms behind the sound locked curve. The continued tap-locked curve showed very little change in power over the whole window. The continued-tap condition did not contain any auditory information so a noticeable decrease in theta oscillations supports an interpretation that the theta band is carrying primarily auditory information. Comparing the syncopated condition sound locked and tap locked curves further supports this interpretation as the sound and tap were 180 degrees out of phase with each other and the curves were shifted out of phase with each other as well. The tap locked curve showed its positive peak approximately 375 ms prior to the sound locked curve. Note the continued tap-locked curve, like its counterpart from the synchronized trial, did not show any fluctuations on the order of the same power as the sound + movement, or sound only conditions.

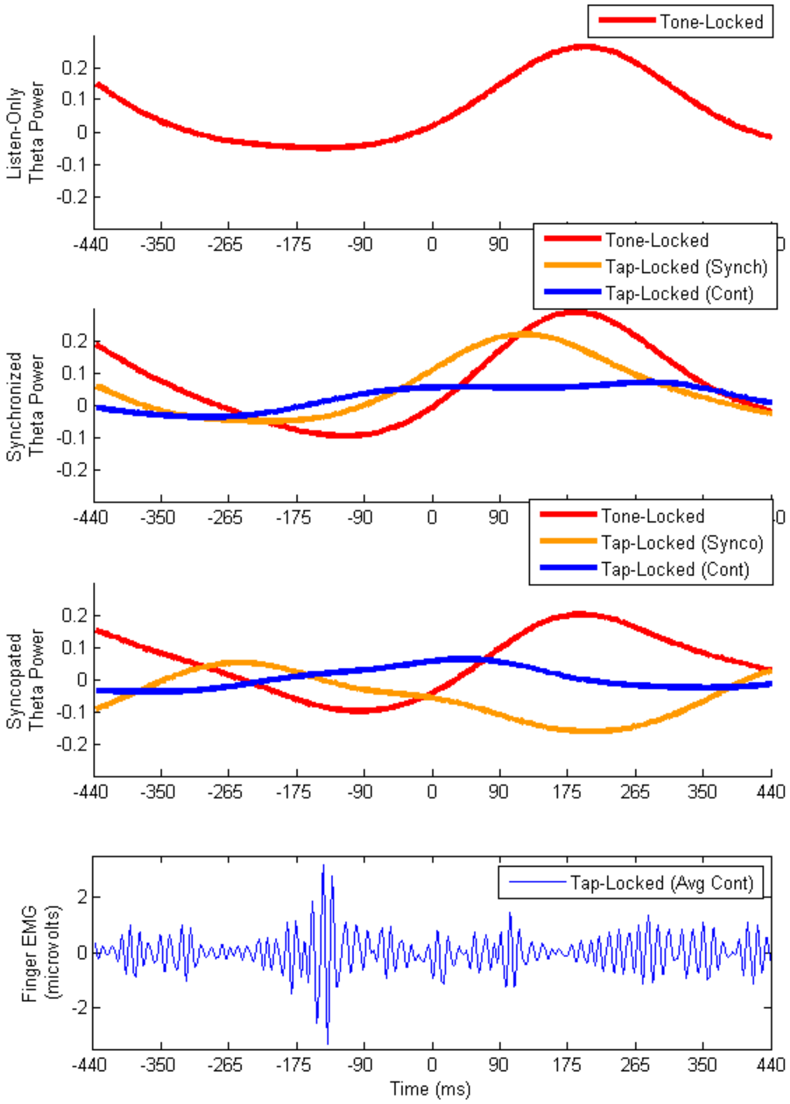


Figure 7.4: Theta bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

Gamma Band Tone locked gamma band responses from the listen only condition showed a characteristic increase in power, peaking quickly (90 ms) post tone onset (Fig. 7.5). During conditions when taps also occur, this response was attenuated in the tone locked oscillations. In both the synchronized and syncopated conditions the tap locked conditions showed a similar suppression that reached its peak just prior to finger movement. This could be indicative of a motor planning response. That the tone locked and tap-locked oscillations for the syncopated condition appeared synchronized in the -350 to -175 ms time window is likely coincidence as there was not a similar negative deflection in either of the other tone locked conditions. It would appear this frequency band contains information time-locked to both listen and moving, however it is difficult to see both at the same time, such as the influence of simultaneous movement in the mu band. It is possible the motor activity perturbed the auditory response when both types of information co-occur in the same trial. Indeed during the syncopated condition, the waveforms locked to tapping between sounds, and continued after sounds were highly correlated over the whole window ($r= 0.88$, $p<0.0001$), and particularly during the motor preparation from -440 to -90 seconds ($r=0.96$, $p<0.0001$). During the synchronized condition they were less correlated ($r=0.47$, $p<0.0001$). As the two tap locked waveforms continued to diverge across the rest of the window for the synchronized condition, this implies the motor response is perturbed by presence of auditory information.

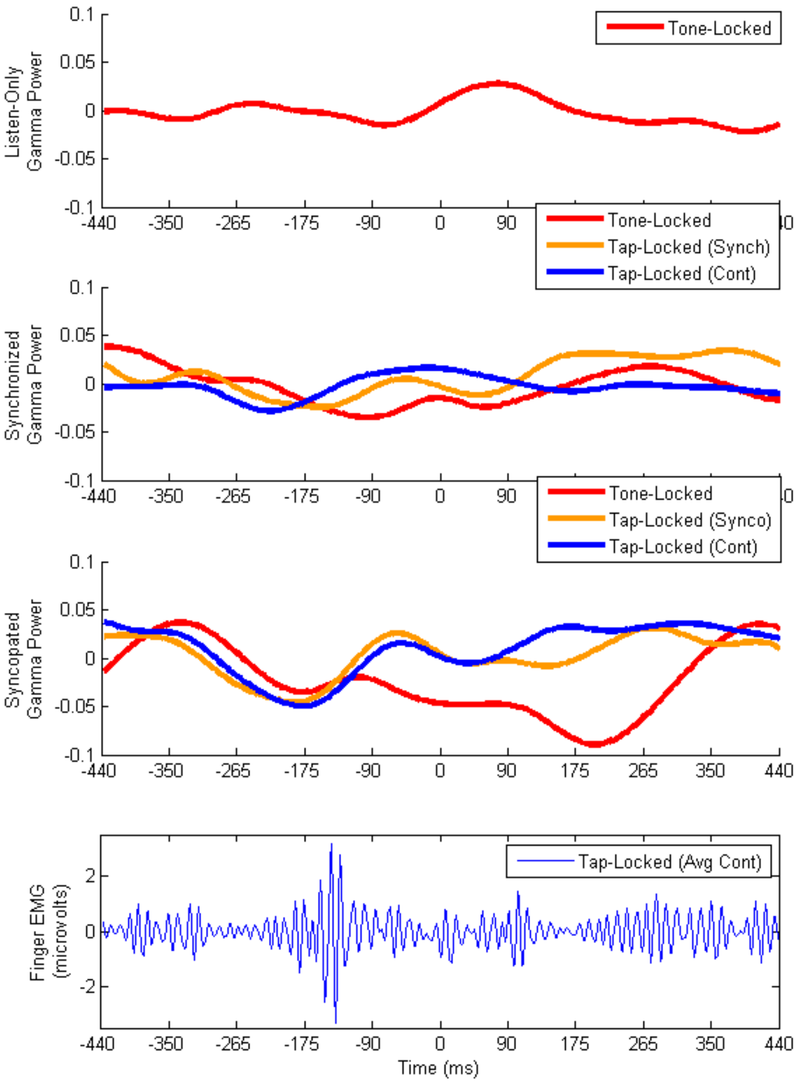


Figure 7.5: Gamma bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

Source Space Results

Time-Frequency Analysis

Cluster 11 - right Medial Temporal Gyrus Unlike the theta band power recorded over left sensorimotor cortex, there was not a clear increase in theta power post tone onset in the rMTG estimated cluster during the listen only condition. I did see a return of the oscillation during the synchronized tapping, with similar oscillatory activity across the different event-locked curves with strong correlations between the two tap locked curves ($r=0.74$, $p<0.0001$). In the syncopated tapping there was an increase in theta power associated with the tap-locked curves, and also seen as a phase shifted response in the tone-locked curve that corresponds to the movement, as evidenced by negative correlation ($r=-0.68$, $p<0.0001$).

In gamma band power there was a lack of similarity across the three tone-locked conditions, however this was not a significant difference ($F(2,45)=1.68$, $p=0.2$). The tap-locked oscillations showed differences between synchronized and syncopated conditions, mostly in the form of shifted latency of peaks.

Cluster 13 - left Medial Temporal Gyrus Theta oscillations in the dipole cluster localized to the lMTG showed more consistency with the channel space reports of theta activity than the right hemisphere localized MTG cluster. Across the three listen conditions there was an increase in theta that started around or prior to tone onset and continued until it peaked around 200 ms post stimulus in the listen-only and synchronized trials. The listen-only and synchronized trials showed a higher correlation ($r=0.79$, $p<0.0001$) than the listen-only and syncopated trials ($r=0.4$, $p<00.1$) which suggests contamination from movement information such that the tone-locked oscillation is perturbed from normal functioning when a movement occurs in the rebound window, since motor preparation should

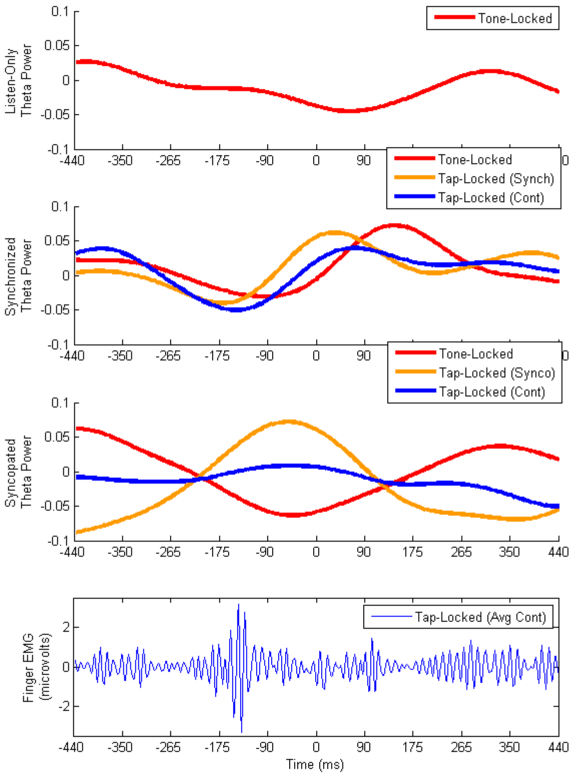


Figure 7.6: Theta bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

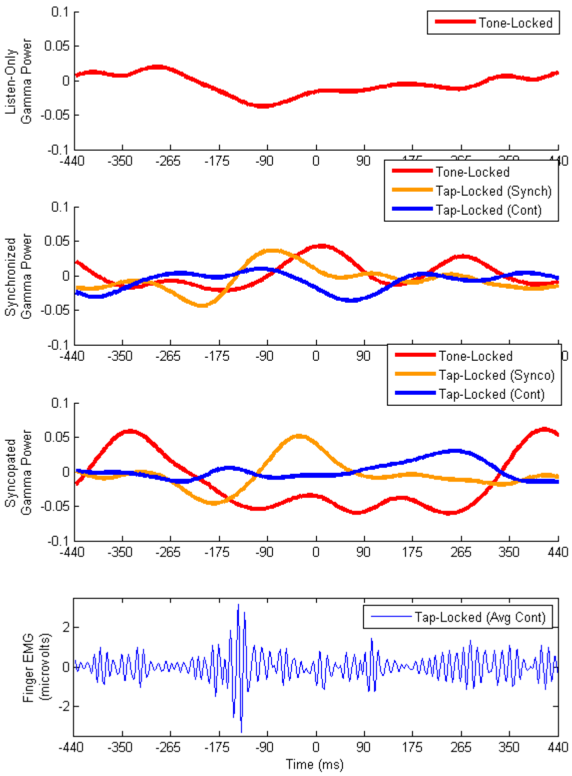


Figure 7.7: Gamma bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

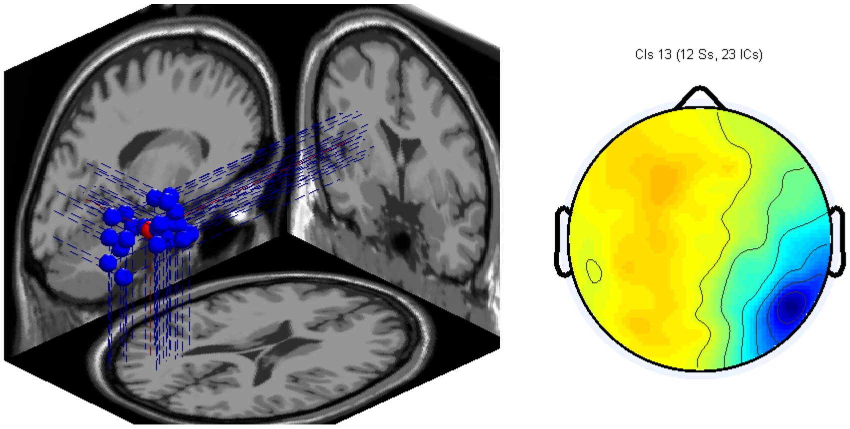


Figure 7.8: Dipole source estimate (L) and scalp projection (R) for left medial temporal gyrus cluster.)

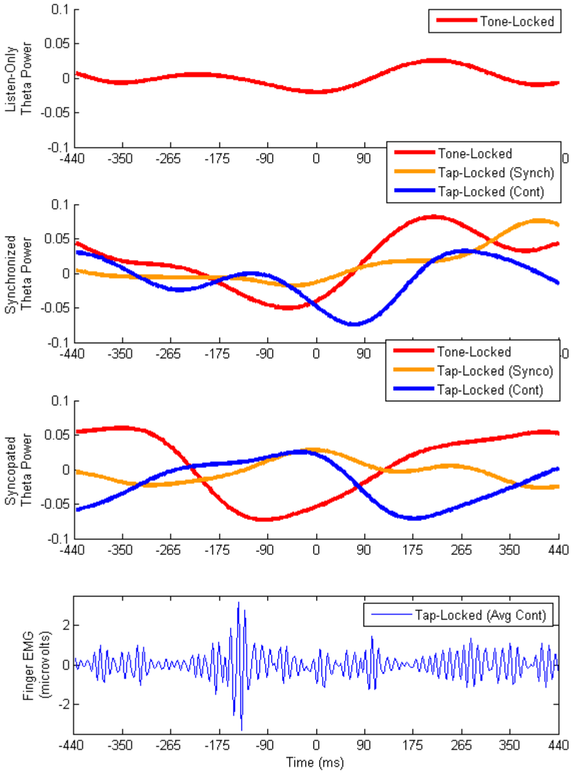


Figure 7.9: Theta bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

initiate around 200 ms post tone.

The mu band did not exhibit the same tone-locked suppression indicated in the rMTG cluster. During the syncopated tapping, tone-locked mu showed enhancement, though this is not significantly different than the other conditions at this time point (F(2,66)=0.91, p=41). The tap-locked oscillations show slight suppression prior to tap registration, however the lack of strong suppression, as seen over sensorimotor cortex, indicates this cluster is not representing much motor information, and only minimal auditory processing.

The beta band did not show any significant similarities or differences across

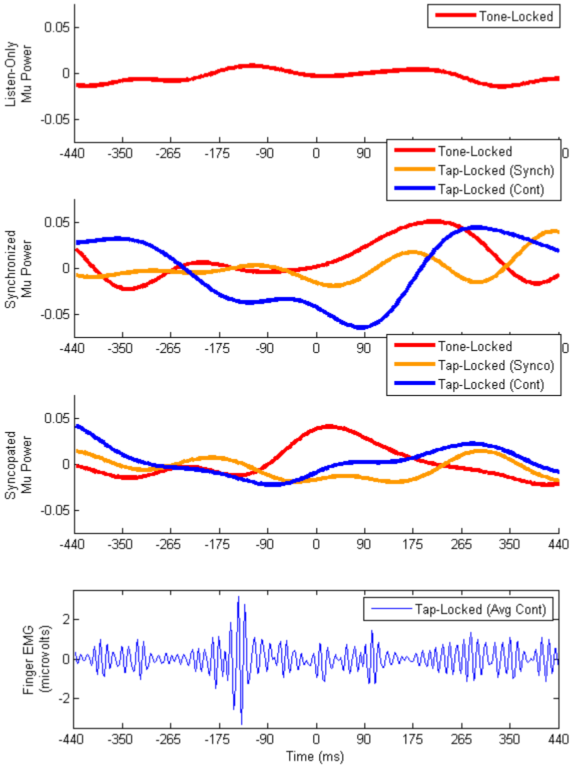


Figure 7.10: Mu bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

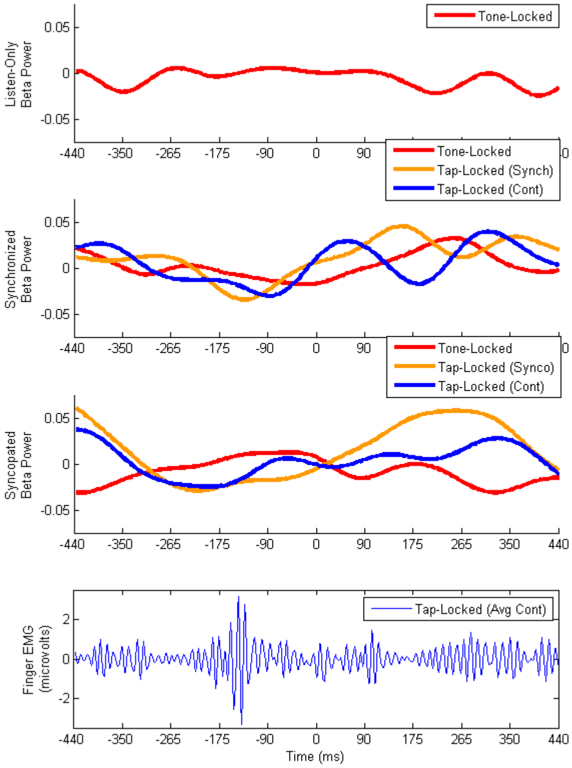


Figure 7.11: Beta bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

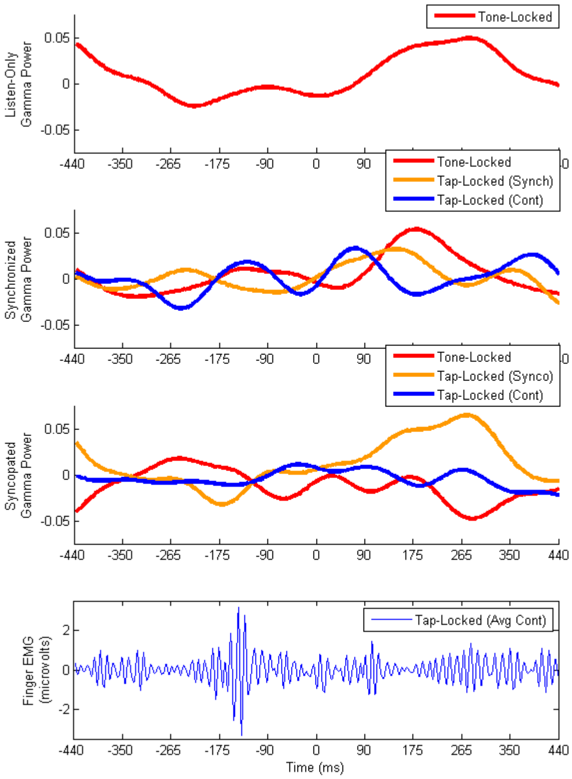


Figure 7.12: Gamma bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

conditions in this cluster, nor did the gamma band.

Cluster 16 - Precentral Gyrus Tone-locked theta oscillations in the PCG corresponded to those observed in channel space that were associated with listen effects, for the listen-only condition. The tap-locked and tone-locked oscillations from the synchronzied condition also showed a slow increase in power starting prior to tone onset, but seemed to have a shorter peak and fall in power more quickly. The correlation between listen-only and synchronized tone-locked waves was small indeed (r=0.11, p=0.12). In this cluster there was more likely an in-

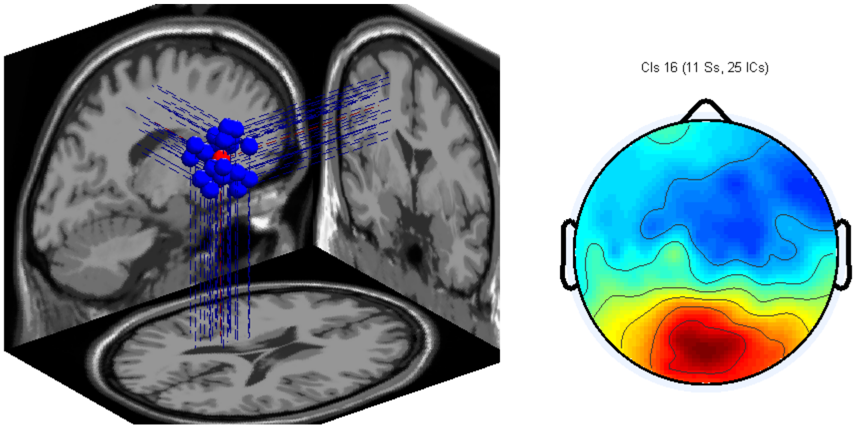


Figure 7.13: Dipole source estimate (L) and scalp projection (R) for precentral gyrus cluster.)

teraction between auditory and motor information such that the listen response seen in other sources/recording sites is contaminated. However whether the actual contamination is motor based is unclear based on these findings. If there was a theta motor effect, then one would expect the tap-locked activity to be similar between synchronized and syncopated conditions, particularly for the continued phase of tapping. This was not the case, as at the registration of tap, the syncopated continue is significantly enhanced relative to the synchronized-continue tap (t(24)=3.21, p=0.003).

Mu rhythm suppression was observed for synchronized tap-locked waves. Suppression was greater for continued taps than synchronized taps, but the same pattern was not present for the syncopated taps. The continued taps showed a significant correlation between syncopated and synchronized conditions (r=0.81, p<0.0001). The correlation between syncopated and synchronized taps is negative (r=-0.62, p<0.0001) and did not reveal expected mu suppression. Consistently across conditions, the tone-locked response showed a decrease in power from approximately 90 ms prior to tone onset, indicating a potential auditory expectation response, however the responses diverged in the rebound phase.

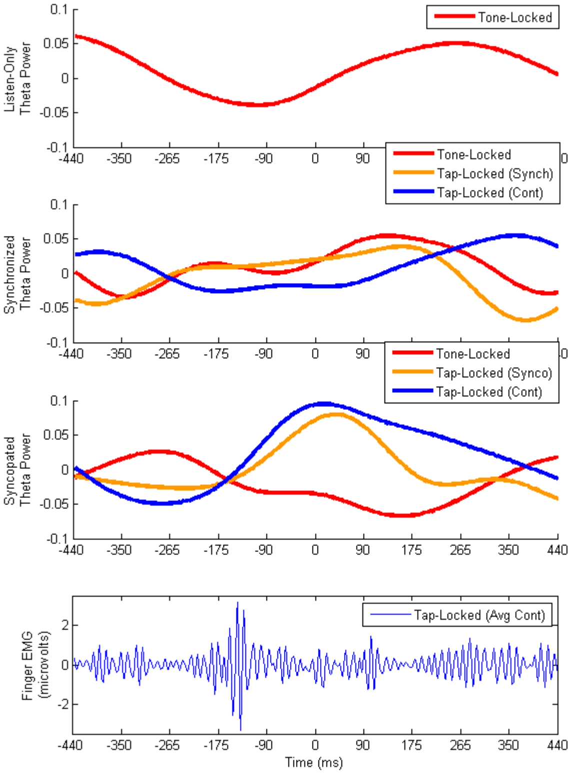


Figure 7.14: Theta bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

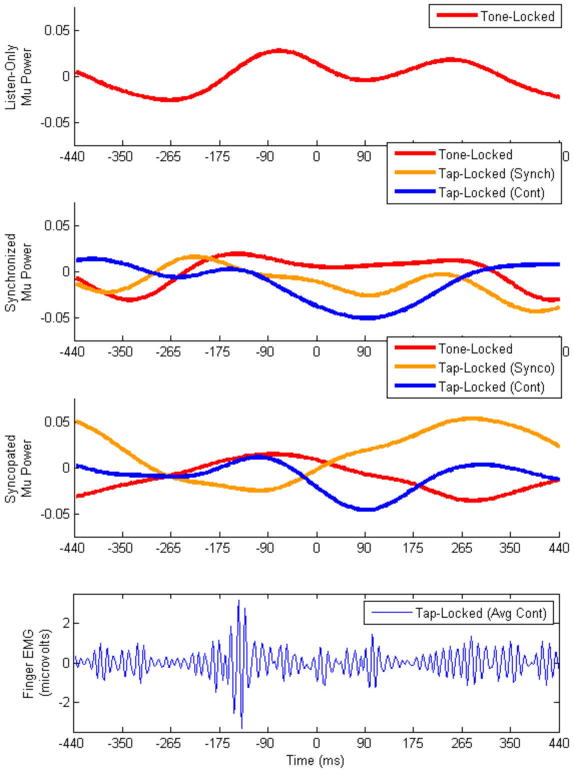


Figure 7.15: Mu bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

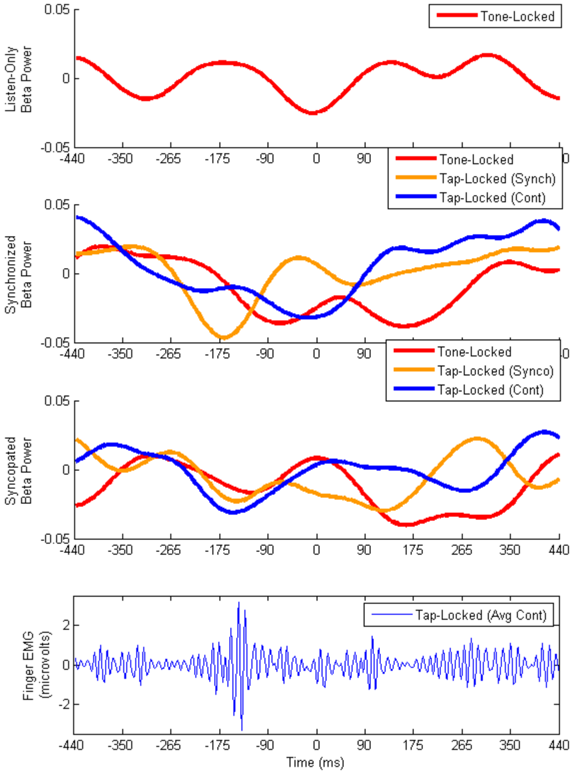


Figure 7.16: Beta bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

Across conditions, the tone-locked beta oscillation showed a decrease in power prior to tone onset, however, the ensuing positive rebound was different in latency for all three conditions. Tap-locked responses showed a suppression prior to movement onset that was most synchronized between different conditions during syncopated tapping. The pre-movement suppression across conditions was consistent with latency observed over sensorimotor cortex (-265 ms), and preceded the onset of finger activity (-150 ms). This likely represents motor planning. The negative deflection in listen-only condition may reflect an anticipatory response, but without concurrent motor planning demands, is shifted later in latency.

Gamma band responses are difficult to interpret for the tone-locked oscillations. They all collapse close to 0 power relative to baseline at the onset, but what they did before and after is divergent. This likely corroborates channel space interpretations that gamma band encodes both auditory and motor information. This interpretation is further supported by the observation that the continued tap showed similar activity in both syncopated and synchronized conditions ($r=0.57$, $p<0.0001$), particularly during tap preparatory phases ($r=0.82$, $p<0.0001$). If this band is carrying auditory information, it is not likely carrying auditory imagery during the syncopated condition. If it was, the syncopated continued tap would presumably have looked different than the synchronized continued tap.

Cluster 22 - Medial Frontal Gyrus The medial frontal cluster showed an attenuated theta band response to the listen-only tone-locked condition. Across tone-locked oscillations, the band still had a positive deflection post tone onset, but of varying latencies, with the listen-only theta enhancement starting just prior to tone onset, synchronized tone following after, and syncopated tone-locked positive response more synchronized with the occurrence of a tap than tone. The continued tap showed a similar profile of increase in power starting prior to muscle movement in both syncopated and synchronized conditions ($r=0.65$, $p<0.0001$), however a shortened period of enhancement in the syncopated condition. The synchronized and syncopated tap-locked responses showed an even stronger correlation ($r=0.86$, $p<0.0001$).

Gamma band activity showed a relatively flat response across event-locking oscillations for the synchronized condition. The listen-only condition showed the similar post tone increase in power that starts before the tone onset with varying latencies between different clusters. This was present in the syncopated tapping

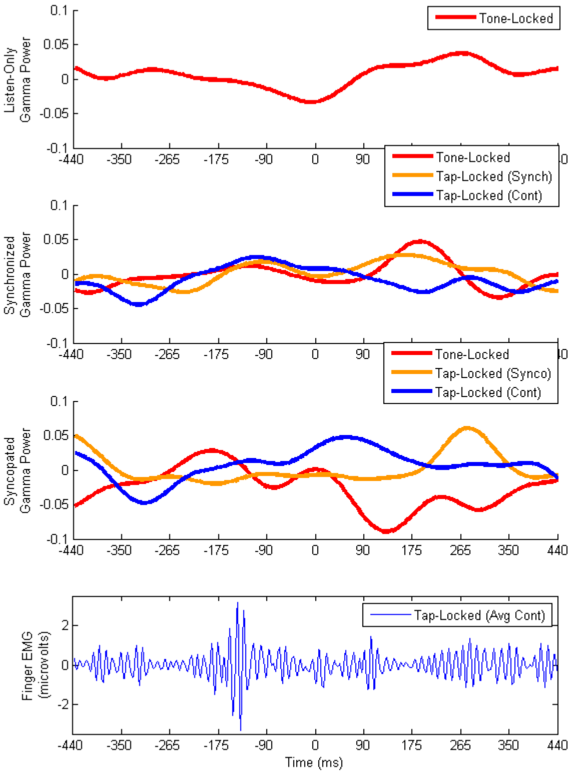


Figure 7.17: Gamma bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

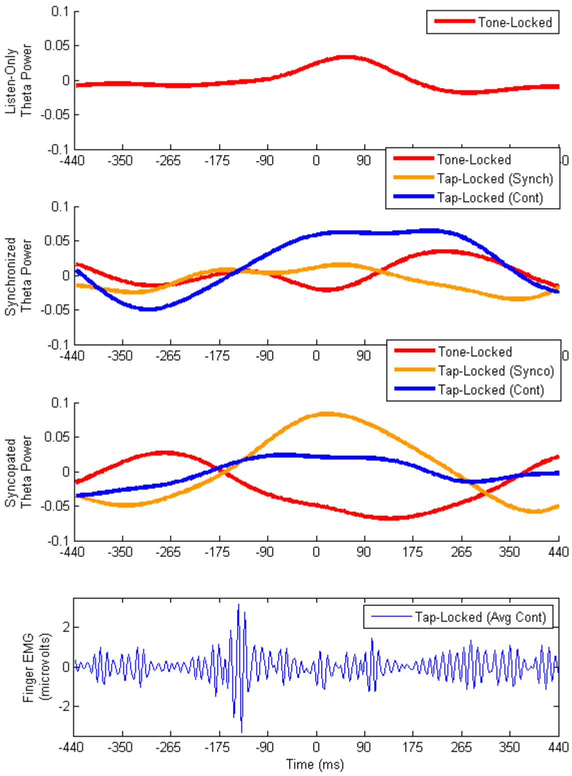


Figure 7.18: Theta bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

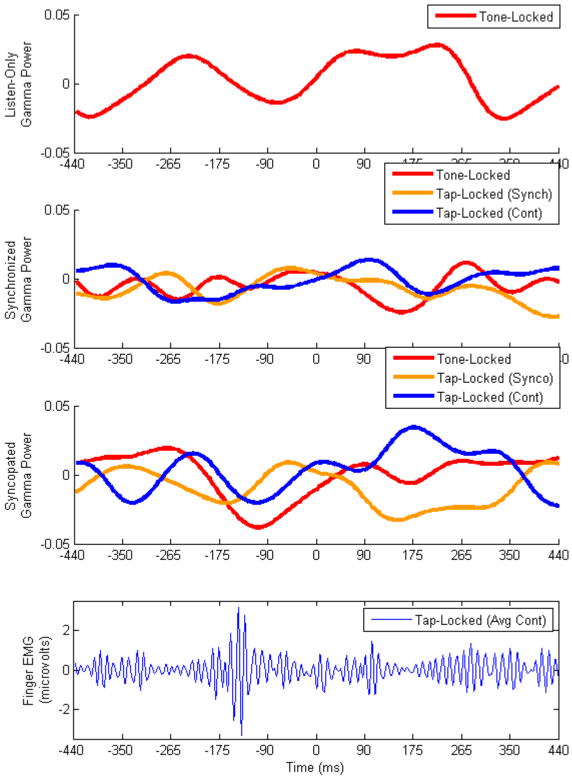


Figure 7.19: Gamma bandpower plots comparing 1. listen-only condition, 2. synchronized tapping, 3. syncopated tapping, and 4. finger muscle response from motor-only condition.

tone-locked oscillation as well, but was not present in the synchronized tapping.

Chapter 8

Appendix C - Synchronizing Moving and Listening via Hand Drumming

8.1 Methodological Considerations

Latency Since this was a prototype EEG system, and used in conjunction with a novel task, it was necessary to perform latency calibration measures. As the listen and play conditions were epoched according to a time stamp based on iterations of the drum sample, it was necessary to estimate the length of time that would occur between the production of sound in speakers and the appearance of the time stamp in the EEG stream. QUASAR's prototype headset had an analog voltage trigger that acted as a binary switch. If voltage detected above threshold, then time stamp the EEG stream. The stimulus machine playing the sounds and recording drum hits was an older pentium 3 era desktop computer with dedicated soundcard. The EEG trigger was sent from the 9 pin COM port, which is a digital signal, that is

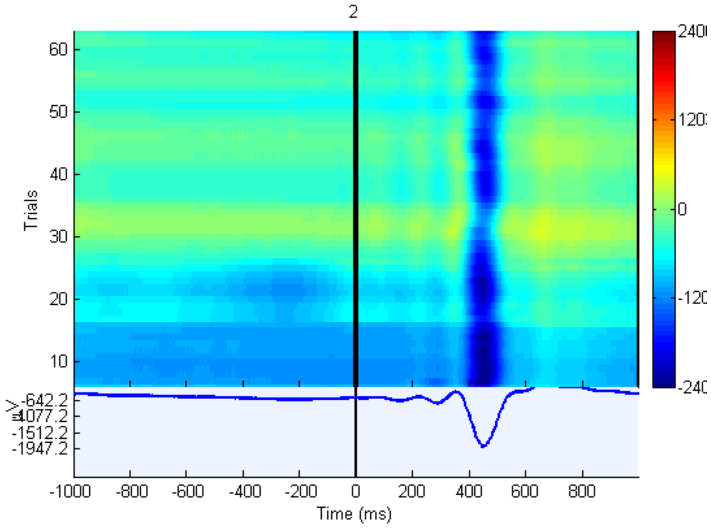


Figure 8.1: Event related potential from speaker electrical field time locked to the trigger event code.

detected as an analog signal, and converted back to digital. To estimate the time between a sound and a serial port trigger, a computer speaker was placed inside the headset. The assumption was that the electrical signal terminating at the speaker would create an electrical field detectable by the headset sensors. Figure 8.1 shows that the speaker field starts approximately 180 ms post trigger, reaching maximum field distortion by about 425 ms. The stacked trials in the histogram reveal the relative stability of the latency over time. Using the time course of well validated auditory and motor event related potentials we were able to calibrate the system to within a reasonable tolerance.

The solo condition was time stamped initially based on drum head triggers. A piezo element mounted on the drum head recorded surface vibrations for the duration of the experiment, but as the QUASAR prototype trigger system was just an analog input treated as a binary switch, there was only one event code available, so the drum sensor was only used as an EEG trigger during the solo condition when there was no auditory clip to use for epoching. This required a second round of latency tests. The piezo trigger fed an analog signal into the microphone input on the soundcard where it was converted to a digital signal. The stimulus and recording software I wrote in MAXmsp filtered the signal to prevent small vibrations that were clearly not drum hits from becoming EEG triggers. It also applied a 100 ms refractory window in which after an initial drum hit, the time code could not be sent for at least 100 ms which prevented double triggers from particularly heavy handed drum hits, or a rebound effect from a hand resting on the drum membrane from suddenly being pulled off. This digital signal then followed the same path as the auditory trigger previously described. To test the calibration, the time stamp is based on an input trigger from the drum, and simultaneously routed through the computer speaker still placed in the headset which replicated the noise of the drum head. Note that the drum sensor was directly routed to the speaker free of the digital filters such that its initially perceived latency was shorter than the auditory trigger. This indicates that even with the digital filter and additional analog to digital conversion, it still was reduced to the same bottleneck in terms of registering in the speaker in the cap for similar latency.

Segmenting solo condition Making direct comparisons in the time domain between the listening and play conditions, which were tightly time locked to the drum sample, and the self paced solo condition was difficult. There was a precise length of time window afforded the first two conditions, and given tempo drift during free drumming, the length of a drum pattern window was subject to change over time. The way I dealt with this was to write an algorithm that searched for features from the drum loop in the drum triggers in the EEG event log. Note the longest interval between drum hits is between the first and the second, which comes

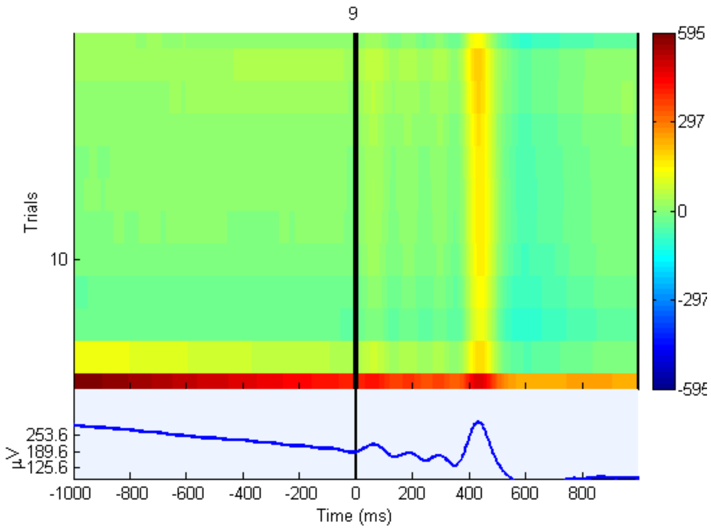


Figure 8.2: Event related potential from drum sensor to speaker electrical field time locked to the trigger event code.

out to about 600 ms. My script searched for this 600 ms gap. It then counted to see if it was followed by a 200 ms rest, and then two 400 ms rests. As even the best musicians have up to 10s of ms variability in tempo matching, I factored in a tolerance based on 1 standard deviation from the mean value of the past four drum loops. The first four drum loops were compared to the expected values +/- 75 ms, and then the subsequent iterations were compared to these first four. If there were not 4 drum hits in a row conforming to this pattern, the trial was dropped and the algorithm went on to find the next 600 +/- 1 std ms rest. When a correct window was identified, one event marker was placed at the start of the drum loop (accounting for latency described above) such that it should match up with the onset of the drum windows in the recorded drum loop used for epoching the other conditions. This algorithm had an added benefit of automatically rejecting bad epochs where subjects lost the drum beat, as they would not have the requisite number of drum hits following a long break prior to the next long break.

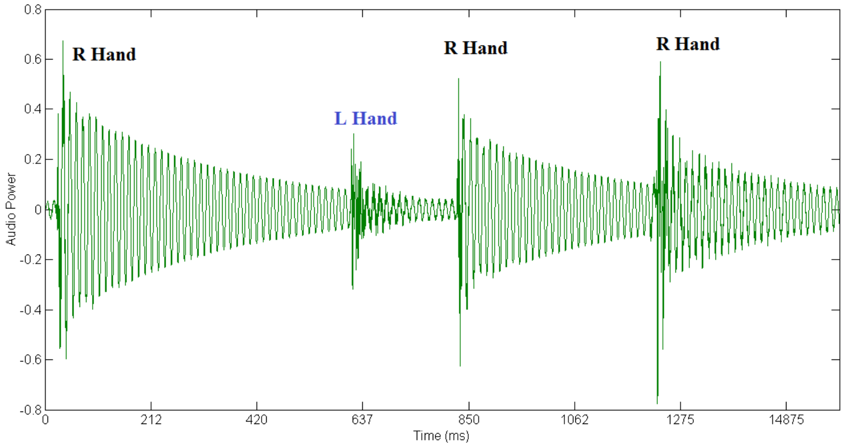
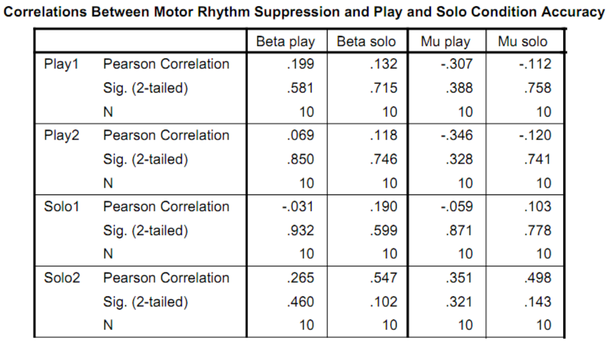


Figure 8.3: Raw waveform of sampled drum pattern for one measure/iteration.

Table 8.1: Correlation of behavioral drumming data with mu and beta suppression measures.



Correlations Between Motor Rhythm Suppression and Play and Solo Condition Accuracy

		Beta play	Beta solo	Mu play	Mu solo
Play1	Pearson Correlation	.199	.132	-.307	-.112
	Sig. (2-tailed)	.581	.715	.388	.758
	N	10	10	10	10
Play2	Pearson Correlation	.069	.118	-.346	-.120
	Sig. (2-tailed)	.850	.746	.328	.741
	N	10	10	10	10
Solo1	Pearson Correlation	-.031	.190	-.059	.103
	Sig. (2-tailed)	.932	.599	.871	.778
	N	10	10	10	10
Solo2	Pearson Correlation	.265	.547	.351	.498
	Sig. (2-tailed)	.460	.102	.321	.143
	N	10	10	10	10

8.2 Supplementary Results

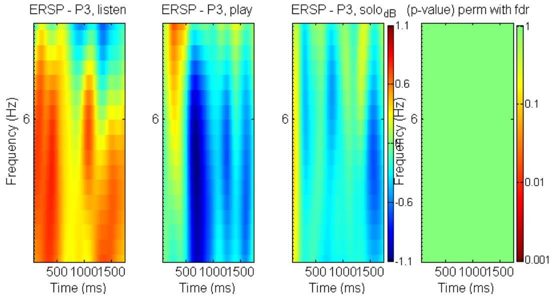


Figure 8.4: Event Related Spectral Perturbations for theta band (4-8 Hz)at electrode P3. Significance plot on the right shows results from 1 way ANOVA at each frequency and each time point, corrected by FDR.

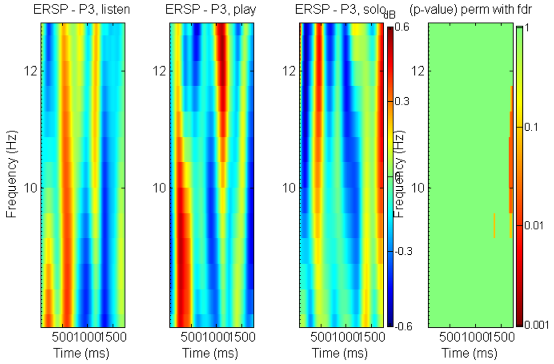


Figure 8.5: Event Related Spectral Perturbations for mu band (8-13 Hz)at electrode P3. Significance plot on the right shows results from 1 way ANOVA at each frequency and each time point, corrected by FDR.

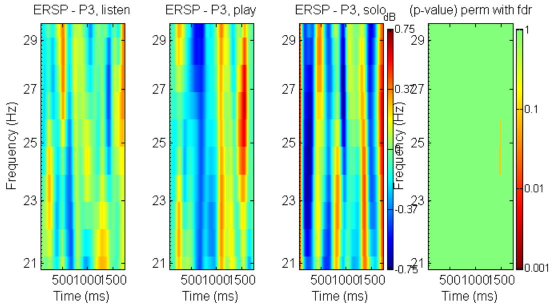


Figure 8.6: Event Related Spectral Perturbations for beta band (20-30 Hz)at electrode P3. Significance plot on the right shows results from 1 way ANOVA at each frequency and each time point, corrected by FDR.

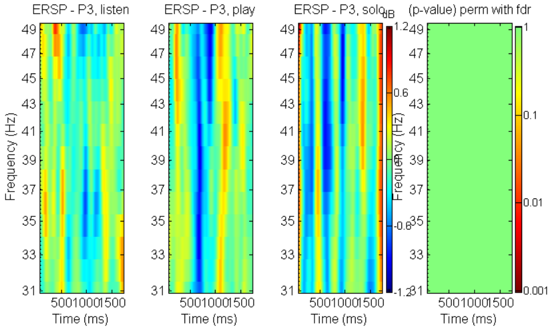


Figure 8.7: Event Related Spectral Perturbations for gamma band (30-50 Hz)at electrode P3. Significance plot on the right shows results from 1 way ANOVA at each frequency and each time point, corrected by FDR.

Table 8.2: Mean Correlation per frequency band for Listen-Play.

	Theta	Mu	Beta	Gamma
P3	0.87	0.71	0.79	0.90
C3	0.85	0.66	0.81	0.91
F3	0.64	0.72	0.60	0.73
FZ	0.91	0.76	0.90	0.94
F4	0.84	0.70	0.92	0.94
C4	0.87	0.52	0.74	0.89
P4	0.89	0.73	0.81	0.89
CZ	0.82	0.64	0.80	0.91
FP1	0.91	0.85	0.92	0.95
F7	0.81	0.63	0.70	0.84
O1	0.94	0.88	0.90	0.94
T5	0.84	0.84	0.87	0.88
T6	0.90	0.85	0.90	0.92
O2	0.90	0.85	0.91	0.90
T3	0.88	0.80	0.72	0.85
T4	0.91	0.72	0.60	0.69
FP2	0.94	0.85	0.94	0.96

Table 8.3: Mean Correlation per frequency band for Listen-Solo.

	Theta	Mu	Beta	Gamma
P3	0.72	0.59	0.70	0.87
C3	0.82	0.60	0.74	0.88
F3	0.42	0.58	0.58	0.74
FZ	0.88	0.67	0.86	0.92
F4	0.85	0.62	0.87	0.93
C4	0.71	0.29	0.61	0.85
P4	0.82	0.60	0.74	0.87
CZ	0.80	0.53	0.71	0.88
FP1	0.88	0.83	0.92	0.96
F7	0.59	0.50	0.74	0.84
O1	0.90	0.82	0.86	0.91
T5	0.73	0.70	0.80	0.80
T6	0.80	0.75	0.84	0.88
O2	0.83	0.72	0.85	0.84
T3	0.89	0.76	0.73	0.87
T4	0.87	0.51	0.48	0.60
FP2	0.90	0.83	0.93	0.96

Table 8.4: Mean Correlation per frequency band for Play-Solo.

	Theta	Mu	Beta	Gamma
P3	0.88	0.93	0.93	0.96
C3	0.97	0.94	0.92	0.95
F3	0.77	0.91	0.91	0.94
FZ	0.95	0.92	0.95	0.96
F4	0.87	0.91	0.87	0.92
C4	0.85	0.89	0.92	0.95
P4	0.92	0.93	0.95	0.96
CZ	0.90	0.90	0.92	0.96
FP1	0.94	0.96	0.96	0.97
F7	0.73	0.85	0.81	0.91
O1	0.95	0.96	0.96	0.96
T5	0.92	0.93	0.93	0.92
T6	0.91	0.92	0.96	0.97
O2	0.94	0.92	0.94	0.94
T3	0.93	0.93	0.94	0.96
T4	0.92	0.87	0.92	0.96
FP2	0.94	0.96	0.96	0.97

Table 8.5: Correlations between theta band and drum sample.

	Listen	Play	Solo
P3	0.52	0.64	0.48
C3	0.07	0.50	0.01
F3	0.35	0.20	-0.02
FZ	0.58	0.31	0.13
F4	0.22	0.25	0.28
C4	0.41	0.44	0.08
P4	0.45	0.38	-0.02
CZ	0.72	0.58	0.19
FP1	0.69	0.37	0.20
F7	0.55	0.08	-0.06
O1	0.65	0.29	0.18
T5	0.36	0.37	0.18
T6	0.27	0.40	0.16
O2	0.25	0.29	0.14
T3	0.61	0.30	0.08
T4	0.23	0.16	0.12
FP2	0.55	0.16	0.31

Table 8.6: Correlations between mu band and drum sample.

	Listen	Play	Solo
P3	-0.31	0.48	-0.43
C3	-0.36	0.24	-0.06
F3	-0.05	0.32	0.01
FZ	-0.19	-0.06	0.08
F4	-0.37	-0.15	0.07
C4	0.05	0.07	0.03
P4	-0.15	0.25	-0.05
CZ	-0.35	0.11	0.03
FP1	-0.26	-0.08	0.07
F7	-0.08	-0.09	0.02
O1	-0.26	0.15	-0.15
T5	-0.51	0.18	-0.09
T6	-0.32	0.41	0.06
O2	-0.46	0.20	0.05
T3	0.11	0.36	-0.16
T4	0.35	-0.01	-0.06
FP2	-0.13	-0.04	0.22

Table 8.7: Correlations between beta band and drum sample.

	Listen	Play	Solo
P3	-0.20	0.23	-0.40
C3	0.03	-0.27	-0.39
F3	-0.16	-0.07	-0.40
FZ	-0.08	0.12	-0.30
F4	0.02	0.20	-0.34
C4	0.05	0.23	-0.28
P4	0.14	0.31	-0.30
CZ	-0.11	0.29	-0.32
FP1	-0.26	0.03	-0.33
F7	-0.34	-0.01	-0.30
O1	-0.04	0.24	-0.27
T5	-0.06	0.13	-0.26
T6	0.08	0.25	-0.24
O2	0.06	0.22	-0.18
T3	-0.29	0.03	-0.29
T4	-0.07	0.26	-0.40
FP2	-0.51	0.03	-0.36

Table 8.8: Correlations between gamma band and drum sample.

	Listen	Play	Solo
P3	-0.20	0.38	-0.23
C3	0.03	0.36	-0.19
F3	-0.16	0.36	-0.12
FZ	-0.08	0.50	-0.10
F4	0.02	0.45	-0.13
C4	0.05	0.46	-0.13
P4	0.14	0.43	-0.07
CZ	-0.11	0.47	-0.12
FP1	-0.26	0.39	-0.14
F7	-0.34	0.20	-0.14
O1	-0.04	0.34	-0.18
T5	-0.06	0.26	-0.21
T6	0.08	0.21	-0.06
O2	0.06	0.30	0.01
T3	-0.29	0.33	-0.15
T4	-0.07	0.21	-0.16
FP2	-0.51	0.43	-0.09

Table 8.9: Correlations between theta band and drum sample for drummers.

	Listen	Play	Solo
P3	0.12	0.59	0.36
C3	0.26	0.49	0.23
F3	0.13	0.10	0.03
FZ	0.31	0.24	0.17
F4	0.20	0.36	0.25
C4	0.28	0.50	0.27
P4	0.18	0.34	0.14
CZ	0.35	0.52	0.25
FP1	0.53	0.42	0.16
F7	0.52	0.26	-0.08
O1	0.37	0.08	0.17
T5	0.48	0.19	0.25
T6	-0.20	0.47	0.14
O2	0.05	0.25	0.20
T3	0.48	0.30	0.18
T4	0.59	0.22	-0.11
FP2	0.48	0.22	0.35

Table 8.10: Correlations between theta band and drum sample for novices.

	Listen	Play	Solo
P3	0.54	0.51	0.43
C3	-0.08	0.40	-0.30
F3	0.33	0.35	-0.04
FZ	0.46	0.39	0.06
F4	0.13	0.12	0.23
C4	0.17	0.24	-0.03
P4	0.39	0.24	-0.11
CZ	0.38	0.58	0.11
FP1	0.51	0.26	0.14
F7	0.44	-0.06	-0.03
O1	0.45	0.40	0.16
T5	0.14	0.41	0.12
T6	0.30	0.31	0.15
O2	0.21	0.22	0.08
T3	0.54	0.21	-0.06
T4	-0.02	0.11	0.29
FP2	0.42	0.07	0.21

Table 8.11: Correlations between mu band and drum sample for drummers.

	Listen	Play	Solo
P3	-0.33	0.24	-0.01
C3	-0.43	-0.09	-0.07
F3	-0.16	0.15	0.10
FZ	-0.26	0.05	0.13
F4	-0.25	-0.13	0.29
C4	0.20	0.01	-0.09
P4	0.18	0.18	-0.05
CZ	-0.28	0.07	0.03
FP1	-0.14	0.13	0.11
F7	-0.38	0.34	0.10
O1	-0.15	-0.02	0.13
T5	-0.25	0.15	0.14
T6	-0.42	0.37	0.02
O2	-0.24	0.13	0.10
T3	-0.09	0.14	-0.01
T4	0.27	0.15	-0.24
FP2	-0.15	0.05	0.29

Table 8.12: Correlations between mu band and drum sample for novices.

	Listen	Play	Solo
P3	-0.20	0.47	-0.57
C3	-0.04	0.37	-0.05
F3	0.09	0.38	-0.06
FZ	0.01	-0.21	0.01
F4	-0.23	-0.12	-0.09
C4	-0.08	0.07	0.07
P4	-0.43	0.22	-0.04
CZ	-0.32	0.11	0.03
FP1	-0.38	-0.27	0.01
F7	0.21	-0.41	-0.06
O1	-0.15	0.23	-0.43
T5	-0.28	0.16	-0.35
T6	0.13	0.35	0.07
O2	-0.39	0.20	-0.02
T3	0.29	0.40	-0.28
T4	0.11	-0.16	0.09
FP2	-0.03	-0.14	0.13

Table 8.13: Correlations between beta band and drum sample for drummers.

	Listen	Play	Solo
P3	-0.13	0.15	-0.19
C3	-0.13	-0.22	-0.13
F3	0.04	-0.17	-0.32
FZ	0.15	0.13	-0.17
F4	0.07	0.08	-0.23
C4	0.17	0.16	-0.20
P4	0.15	0.28	-0.22
CZ	0.01	0.18	-0.07
FP1	-0.03	-0.12	-0.26
F7	-0.46	-0.22	-0.29
O1	0.13	0.16	-0.14
T5	0.09	0.10	-0.05
T6	0.06	0.10	-0.28
O2	0.13	0.12	-0.11
T3	-0.33	-0.13	-0.28
T4	0.27	0.13	-0.27
FP2	-0.18	-0.06	-0.24

Table 8.14: Correlations between beta band and drum sample for novices.

	Listen	Play	Solo
P3	-0.11	0.24	-0.41
C3	0.16	-0.08	-0.46
F3	-0.20	0.06	-0.38
FZ	-0.25	0.07	-0.34
F4	-0.02	0.19	-0.36
C4	-0.12	0.25	-0.28
P4	0.07	0.27	-0.26
CZ	-0.12	0.21	-0.39
FP1	-0.28	0.17	-0.34
F7	0.08	0.21	-0.27
O1	-0.18	0.28	-0.28
T5	-0.16	0.13	-0.38
T6	0.05	0.24	-0.14
O2	-0.04	0.23	-0.17
T3	-0.17	0.15	-0.24
T4	-0.25	0.28	-0.42
FP2	-0.42	0.10	-0.36

Table 8.15: Correlations between gamma band and drum sample for drummers.

	Listen	Play	Solo
P3	-0.13	0.22	-0.31
C3	-0.13	0.14	-0.33
F3	0.04	0.08	-0.21
FZ	0.15	0.26	-0.04
F4	0.07	0.13	-0.09
C4	0.17	0.21	-0.27
P4	0.15	0.23	-0.20
CZ	0.01	0.26	-0.21
FP1	-0.03	0.15	-0.14
F7	-0.46	-0.04	-0.27
O1	0.13	0.19	-0.16
T5	0.09	0.20	-0.22
T6	0.06	-0.06	-0.31
O2	0.13	0.11	-0.13
T3	-0.33	0.04	-0.39
T4	0.27	-0.12	-0.15
FP2	-0.18	0.18	-0.05

Table 8.16: Correlations between gamma band and drum sample for novices.

	Listen	Play	Solo
P3	-0.11	0.41	-0.15
C3	0.16	0.44	-0.09
F3	-0.20	0.46	-0.06
FZ	-0.25	0.60	-0.12
F4	-0.02	0.52	-0.13
C4	-0.12	0.52	-0.05
P4	0.07	0.47	0.01
CZ	-0.12	0.50	-0.06
FP1	-0.28	0.49	-0.12
F7	0.08	0.38	-0.06
O1	-0.18	0.41	-0.14
T5	-0.16	0.26	-0.16
T6	0.05	0.38	0.11
O2	-0.04	0.39	0.09
T3	-0.17	0.39	-0.04
T4	-0.25	0.36	-0.16
FP2	-0.42	0.46	-0.10

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