Differential Motor System Entrainment to Auditory and Visual Rhythms

Daniel C. Comstock[1,2], Ramesh Balasubramaniam[2]

[1]Center for Mind and Brain, University of California, Davis, CA, 95618, USA
[2]Cognitive and Information Sciences, University of California, Merced, CA, 95343, USA

Running Title: Motor System Entrainment to Auditory and Visual Rhythms

Keywords: EEG, Entrainment, Rhythm Cognition, Mu Rhythms, Motor System

Address for Correspondence:

Daniel C. Comstock
Center for Mind and Brain
University of California, Davis
267 Cousteau Pl, Davis, CA 95618
Ph: 530.754.4526
dccomstock@ucdavis.edu

Abstract

Perception of, and synchronization to, auditory rhythms is known to be more accurate than with flashing visual rhythms. The motor system is known to play a role in the processing of timing information for auditory rhythm perception, but it is unclear if the motor system plays the same role for visual rhythm perception. One demonstrated component of auditory rhythm perception is neural entrainment at the frequency of the auditory rhythm. In this study we use EEG to measure entrainment of both auditory and visual rhythms from the motor cortex while subjects either tapped in synchrony with, or passively attended the presented rhythms. In order to isolate activity from motor cortex, we used independent components analysis to first separate out neural sources, then selected components using a combination of component topography, dipole location, mu activation, and beta modulation. This process took advantage of the fact that tapping activity results in reduced mu power, and characteristic beta modulation, that helped select motor components. Our findings suggest neural entrainment in motor components was stronger for visual rhythms than auditory rhythms, and strongest during the tapping conditions for both modalities. We also find mu power increased in response to both auditory and visual rhythms. These findings indicate that the generally greater rhythm perception capabilities of the auditory system over the visual system may not depend entirely on neural entrainment in the motor system, but rather how the motor system is able to utilize the timing information made available to it.

New and Noteworthy

We investigated neural entrainment in the motor system for both auditory and visual isochronous rhythms using electroencephalogram. Counter to expectations, our findings suggest stronger entrainment for visual rhythms compared to auditory rhythms. Motor system activity was isolated with a novel procedure using independent components analysis as a means of blind source separation, along with known markers of mu activity from the motor system to identify motor components.

Introduction

Human capability for sensorimotor synchronization (SMS) to auditory rhythms has been shown to be more precise than SMS to visual rhythms (Repp, 2003), but the exact reasons why are yet to be uncovered. It has been shown through fMRI work that activation of motor structures are more pronounced for auditory rhythms than for visual rhythms during SMS tasks as (Hove et al., 2013). This has led us to the suggestion that the auditory system is more tightly tied to the motor system for temporal processing, such as needed for rhythm perception, than the visual system which specializes in spatial processing. In previous works, we have suggested that a corollary to this is that the visual system performs some rhythm processing in house (Comstock & Balasubramaniam, 2018; Comstock et al; 2018; Comstock et al 2021). Based on that suggestion, we would expect to see differences in electrophysiological measures of rhythm processing in the motor system between auditory and visual rhythms that match those seen in fMRI data.

The motor system plays a crucial role in the processing of music and auditory rhythms. A meta-analysis on fMRI studies indicated activation of multiple regions of the motor system during passive listening including right cerebellum, right primary motor cortex, and left and right pre-motor cortices (Gordon et al., 2018). Other works have highlighted the importance of the supplementary motor area (SMA) and basal ganglia in rhythm perception (Grahn & Brett, 2007; Chen et al., 2008; Grahn & Rowe, 2009; Merchant et al., 2015). These structures are believed to work in concert with the auditory system in order to drive the precise timing required in rhythm perception. In their Action Simulation for Auditory Prediction (ASAP) hypothesis, Patel and Iversen (2014) propose that this audio-motor facilitation is achieved through the dorsal auditory stream. Likewise, Merchant and Honing (2014) also suggest a key role for the dorsal auditory stream in rhythm processing in their Gradual Audiomotor Evolution (GAE) hypothesis, and also highlight a central role for the motor cortico-basal ganglia thalamo-cortical circuit as a key player in general timing processing. It is, however, not clear if there is a visuomotor equivalent to the audiomotor coupling for the processing of auditory rhythms, or to what extent visual rhythm timing is performed in the absence of motor system involvement. Further investigations are needed to determine what role, if any, the motor system may play in visual rhythm processing.

It has been demonstrated using EEG that listening to auditory rhythms elicits an increase in power and phase coherence at the frequency of the beat of the rhythm (f0), that is measured most strongly over frontal-central regions (Nozaradan et al., 2011, 2012a, 2012b), and this signal is increased during an SMS task (Nozaradan et al., 2015). Likewise, it has long been known that the visual system can elicit power at the rhythm of visual flashes in what are dubbed steady-state visually evoked potentials (SSVEPs) (for review see Vialatte et al., 2010). It is unclear to what extent activity at f0 induced for auditory rhythms and visual rhythms would both be present in the motor system. If the auditory system is more tightly tied to the motor system than the visual system however, we would expect measures of power and phase coherence in the motor system to be stronger for auditory rhythms than visual rhythms.

Many previous EEG studies investigating activity from the motor system have attempted to isolate motor system activity by selectively measuring activity from channels that lie over motor regions (Pfurtscheller & Neuper, 1994; Pfurtscheller et al., 1997; McFarland et al., 2000). One downside of this approach is that EEG activity arriving at the scalp level is a mix of all sources of activity in the brain (Makeig et al., 2004). One method used to solve this issue is to use independent components analysis (ICA), which has been shown to be an effective method of

separating out sources of neural activity in the brain (Delorme et al., 2012). While the blind source separation of ICA allows for separating out sources, a method of selecting appropriate sources for each study is required. Since this study aims to determine the role of the motor cortex in rhythm processing, a clear marker of motor system activity will be needed.

One such marker can be found in Mu rhythms, which are a well-known marker of motor system activity, and originate from the primary motor cortex in the range 8-13 Hz (Pfurtscheller & Lopes da Silva 1999). Mu rhythms are known to reflect cortical idling and have been shown to increase in power, or what is termed event-related synchronization (ERS), during movement suppression, and decreased power or event-related desynchronization (ERD), during active movements (Pfurtscheller & Neuper, 1994; Pfurtscheller et al., 1997; McFarland et al., 2000) as well as during movement imagery (McFarland et al., 2000; Solomon et al., 2019). Isolating mu activity using ICA based on component location and characteristics has been previously done in research into the mirror neuron system (Nyström et al., 2011; McGarry et al., 2012; Behmer & Fournier, 2016), and more recently to understand the role of mu in music perception (Ross et al., 2022). Using a study design with a sufficient motor task, and a non-motor task could be expected to induce modulation of mu rhythms that would make mu components further identifiable.

While previous work has primarily identified premotor and subcortical regions for measuring rhythm processing, measuring activity generated from the primary motor cortex through mu rhythm identified components is important as it is speculated that mu rhythms may additionally serve as markers of rhythm perception, suggesting the primary motor cortex is playing an additional role in processing rhythms. In previous work Ross et al., (2022) showed that listening to music while remaining still results in mu ERS relative to silence. That study was motivated by the premise in the ASAP hypothesis that the motor system is simulating the beat in music (Patel & Iversen, 2014). While it remains unclear if beat simulation reflects covert motor imagery of movement plans to a beat, or of a more abstract simulation of the beat in time, the result is the motor system is able to send temporal predictions to the auditory system, as has been measured through modulation of beta power (Fujioka et al., 2012, 2015, Comstock et al., 2021). The findings in Ross et al., (2022) are then somewhat surprising given the previously stated findings that mu activity reflects cortical idling as opposed to inhibition. A possible explanation follows from reports that hand-area mu ERS has also been reported during foot movements (Pfurtscheller & Neuper, 1994; Pfurtscheller et al., 1997). It may be that mu ERS during music listening reflects an interaction between holding the hand still, and cortical processing for movement or movement imagery elsewhere in the motor system, such as beat simulation.

In this study we used EEG to measure changes in mu rhythms and activity at the beat frequency (f0) induced by attending to isochronous auditory or visual rhythms. Based on the idea that the auditory system is more tightly connected to the motor system than the visual system for temporal processing, and that listening to music induces mu ERS as a result of motor system beat simulation, we hypothesized that mu ERS would be greater for auditory rhythms than visual rhythms during non-tapping conditions. Additionally, we hypothesized that activity at f0, as measured by power and phase coherence, would reflect auditory rhythms more strongly than visual rhythms in the motor cortex.

Materials and Methods

Participants

21 subjects participated in the experiment (11 female, $M = 21.62$ years, $SD = 3.58$). Data from 3 subjects were not used, 2 for computer error and 1 due to poor signal to noise ratio resulting in no discernable motor components. 10 subjects reported have some musical training ($M = 6.6$ years training, $SD = 3.21$). All subjects had typical hearing and typical or corrected vision, and reported being right handed. This study was approved by the UC Merced Institutional Review Board for Research Ethics and Human subjects, and was carried out in accordance with the Declaration of Helsinki. All participants gave written informed consent prior to testing.

Task

Subjects were seated and fitted with a 32 electrode EEG cap, and were presented with 16 stimulus trains with each train consisting of 40 events. 8 of the trains were of auditory tones (1000 Hz sine wave, 50 ms duration with 10 ms rise and 30 ms fall), and the other 8 being visual flashes (light grey flash with 50 ms duration). For both tones and flashes the subjects faced a black computer screen with a grey fixation cross at the center that remained visible during both flashes and tones. All stimuli were presented with an inter-onset interval of 600 ms, resulting in beat frequency (f0) of 1.667 Hz. Subjects were either instructed to tap in synchrony to the tones or flashes using their right index finger, or to attend to the stimuli while remaining motionless. During recorded subjects were observed to ensure they remained motionless except for tapping in the appropriate conditions. Tap times were not recorded. The resulting four groups of stimulus trains (auditory tapping, auditory non-tapping, visual tapping, visual non-tapping) were presented as separate blocks, with each block having stimuli from only one condition. The order of the groups was randomized with the exception that the 2 groups from each modality were always presented one after the other, and the tapping order was preserved across modalities, e.g., visual non-tapping, visual tapping, auditory non-tapping, auditory tapping. In order to ensure subjects were actively attending the stimuli, subjects were presented with an additional short test-stimulus train immediately following each stimulus train, and were asked to compare the tempos of the stimulus train with the short test stimulus train. The test-stimulus train was always of the same modality as the stimulus train it followed, with tempo that was either slightly slower or faster than the preceding train was presented. After the test-stimulus train was presented, subjects were tasked with reporting if the later train was faster or slower than the previous train. Following the end of each test-stimulus train and the start of each new stimulus train, participants had a short break of a minimum of a 6 seconds.

EEG Processing

EEG data were recorded using an ANT-Neuro 32 channel amplifier using an ANT-Neuro 32 electrode Waveguard with electrode locations following the 10-20 International system. EEG data were processed using EEGLAB 2021 (Delorme & Makeig, 2004) and Matlab 2020b. Data were first downsampled from 1024 to 256 Hz, then high pass filtered with passband edge at 1 Hz and -6 dB cutoff at .5 Hz. Data were then pruned so only the stimulus trains and 5 seconds prior to each stimulus train remained, after which the data were inspected and bad channels were removed. Spherical interpolation was used to fill the removed channels, after which ASR correction was used to fix noisy bursts in single channels. Data were then referenced to average and ICA was applied using the AMICA algorithm (Palmer et al., 2012). After ICA Dipoles were

fitted to the resulting components. Eye blink, eye movement, and heart artifact components were selected by hand for each subject and removed from the data.

The independent components were then inspected using the IC Label toolbox (Pion-Tonachini et al., 2019) to visualize and help determine which component corresponded to the left hemisphere primary motor cortex for each subject based on the following criteria: Scalp topography and dipole location indication that the component source was in the left motor cortex, evidence of mu ERS in the spectral power, evidence of mu ERS in the time series based on the distinctive mu wave shape, mu modulation based on condition (mu ERD during tapping conditions). Left primary motor cortex components were found for all but 1 subject, resulting in 18 subjects. An example of a motor component can be seen in figure 1, along with the scalp topography of all selected motor components. Further confirmation of the veracity of the motor components was made following the time-frequency calculations by inspecting and comparing beta power modulation between the tapping and no tapping conditions, as beta band power attenuation from the motor cortex is known to occur during movement onset (Pfurtscheller & Lopes da Silva, 1999). In this experiment, movement onset is expected to occur just prior to stimulus onset as participants move to tap in synchrony with stimulus. All selected motor components followed the expected pattern of beta modulation: clear beta power attenuation prior to stimulus onset followed by increased beta power after stimulus onset during tapping conditions, but not for the non-tapping conditions.

Figure 1 about here

Three separate time-frequency calculations were performed on the processed component data: an analysis to inspect beta power modulation, and an analysis to calculate phase coherence in the lower frequencies. To calculate beta power modulation, the data were epoched into 3 second epochs centered on the stimulus onset. Single-trial time-frequency analysis was performed on the resulting epochs using Morlet wavelets between 8 and 35 Hz with a constant wavelet length of 500 ms achieved using 4 cycles at 8 Hz and scaling up to 17.5 cycles at 35 Hz. A divisive baseline consisting of the entire epoch length for each condition was used to highlight power modulation of each frequency. The resulting time-frequency activity was used solely to confirm that the selected motor components did indeed correspond to motor activity.

A second time-frequency calculation was performed on the un-epoched trials using Morlet wavelets between 1.066 and 14.066 Hz with a constant wavelet length of 6563 ms seconds achieved using 7 cycles at 1.066 Hz and 92.31 cycles at 14.066 Hz. The frequencies used were linearly spaced at 0.1 Hz intervals so that the beat frequency of 1.666 Hz could be captured. No baseline was used so that power could be compared across all 4 conditions. Using the un-epoched data allowed for a wider window, removing potential edge artifacts that can arise from using a narrow window, and additionally allowed for better bandwidth resolution with a resulting constant bandwidth for each frequency of .3 Hz. Intertrial Phase Coherence (ITC) was calculated by extracting the phase angles from the time-frequency calculations and epoching them centered on each stimulus (+/- 300 ms), in a similar manner as implemented by Doelling & Poeppel (2015). ITC was then calculated as phase coherence across epochs for each condition at each time-frequency point for each component. Average ITC at each frequency was then calculated by averaging across time.

A third time-frequency calculation was performed to extract mu activity from the selected components on the un-epoched trials using a fast Fourier transform between 7 and 30 Hz with a

window length of 2 seconds. A divisive baseline specific to each condition was used with the period defined as the 5 seconds prior to the start of each stimulus-train. Mu activity used for analysis was the average power between 8 and 13 Hz and taken from the onset of the second stimulus in each train to the end of the stimulus train.

To extract amplitude, a discrete Fourier transform was applied to the un-epoched data from start of the second stimulus in each stimulus train, to the end of the train, using the length of the entire stimulus train as the window size resulting in a frequency resolution of 0.0439 Hz. To extract amplitude induced by the beat frequency, signal power for the individual frequencies were noise corrected by subtracting the average power of the neighboring frequencies (+ 0.088 to 0.132 Hz and – 0.088 and 0.132 Hz) in a similar fashion as used by Nozaradan et al (2011).

Statistical Analysis

Analyses were carried out on the selected motor components for mu power, f0 amplitude, and ITC. Analyses were also carried out on grand average activity for f0 amplitude and ITC to assess overall activity without location bias as a point of comparison to other existing works, e.g., Nozearadan et al (2011, 2015), Doelling & Poeppel (2015). The grand averages were calculated for each subject for each condition, and consisted of the averages of the measures of all components, which is equivalent to the grand scalp-average. One sample t-tests were used to investigate if average calculated mu activity significantly increased in response to the stimuli compared to baseline for each condition. To test if the rhythms induced a significant neural response at f0, one sample-tests were used for each condition on the grand averaged data and motor component data to test if the noise-corrected amplitude at f0 was greater than zero. Since ITC activity is effectively always greater than zero, paired-sampled t-tests were used to investigate if the rhythms induced significant phase coherence. ITC for both selected motor components and for the grand averaged data was tested against randomly sampled ITC activity at frequencies not likely to contain f0 activity or from any of the harmonics. To correct for multiple comparisons, FDR was used on all test results (Benjamini & Hochberg, 1995).

To compare changes in mu power, noise corrected f0 power and f0 ITC across the four conditions, separate 2 by 2 repeated measures ANOVAs were used with within-subject factors being modality (audition and vision), and tap condition (no tapping and tapping). All statistical analyses were performed using Jamovi (Version 2.2; The jamovi project 2021) statistical software.

Results

Mu Power

one sample t-tests of mu activation in response to stimuli revealed increased mu activity compared to baseline for the visual non-tapping conditions ($M = 2.316$, $SD = 3.08$) $t(17) = 3.192$, $p = 0.021$ and for the auditory no-tapping conditions ($M = 2.208$, $SD = 3.34$) $t(17) = 2.801$, $p = 0.025$, but not for either tapping condition (figures 2 & 3)

Analysis of power for mu activity from left motor component data showed a main effect only for tapping $F(1,17) = 13.072$, $p = 0.002$, $n_p^2 = 0.445$, indicating mu activity was greater during non-tapping conditions ($M = 2.262$, $SE = 0.713$) than during tapping conditions ($M = -0.248$, $SE = 0.2.93$).

Figure 2 about here

Figure 3 about here

Beat induction at f0

Single-sample t-tests of amplitude at f0 indicated all conditions induced significant amplitude in the grand average conditions, and for both tapping conditions in the motor components (table 1a, 1b, figure 4). Amplitude in f0 for the visual non-tapping conditions near significant at $p = 0.059$ (table 1a). Paired-sample t-tests of ITC at f0 indicated all conditions induced significant phase-coherence for both grand averaged and left motor component data (table 1c, 1d, figure 5).

Table 1 about here

Amplitude at f0

The repeated measures ANOVA of amplitude at f0 for the grand averaged data show only a main effect for modality $F(1,17) = 8.439$, $p = 0.010$, $n_p^2 = 0.332$, indicating greater f0 amplitude for the visual modality ($M = 1.094$, $SE = 0.111$) than the auditory modality ($M = 0.65$, $SE = 0.091$) (figure 4 d). We report no interaction effects, and therefore no post-hoc tests. The repeated measures ANOVA of amplitude at f0 for the left motor component data shows only a main effect for tapping $F(1,17) = 17.346$, $p < 0.001$, $n_p^2 = 0.509$, indicating greater f0 amplitude in the tapping conditions ($M = 0.216$, $SE = 0.032$) than in the non-tapping conditions ($M = 0.053$, $SE = 0.03$) (figure 4b).

Figure 4 about here

Examination of the scalp topography of f0 power indicates power peaking in the frontal-central region for auditory conditions, with stronger activity for the auditory tapping condition than the auditory not-tapping condition. Similar activity in the topography is seen in the visual conditions except there is additional stronger activity peaking over the posterior regions that does not appear to change between tapping conditions. (figure 5)

Figure 5 about here

ITC

The repeated measures ANOVA of ITC on grand averaged data revealed main effects for modality $F(1,17) = 17.653$ $p < 0.001$, $n_p^2 = 0.509$, indicating visual ITC at f0 ($M = 0.364$, $SE = 0.014$) was greater than auditory ITC at f0 ($M = 0.311$, $SE = 0.009$). We additionally find a main effect for tapping $F(1,17) = 26.283$, $p < 0.001$, $n_p^2 = 0.607$, showing the tapping conditions ($M = 3.65$, $SE = 0.014$) had greater f0 ITC than the non-tapping conditions ($M = 0.31$, $SE = 0.007$) (figure 6 d). There were no interaction effects seen in the grand averaged f0 ITC. The repeated measures ANOVA of ITC on left motor components data revealed main effects for modality $F(1,17) = 11$, $p = 0.004$, $n_p^2 = 0.394$, and for tapping $F(1,17) = 19.961$, $p < 0.001$, $n_p^2 = 0.54$, with no interaction effects. The main effects result indicate left motor f0 ITC was greater in the visual conditions ($M = 0.481$, $SE = 0.032$) than in auditory conditions ($M = 0.359$, $SE = 0.031$),

and that left motor f0 ITC was greater in tapping conditions (M = 0.525, SE = 0.041) than in non-tapping conditions (M = 0.314, SE = 0.027) (figure 6b).

Figure 6 about here

Discussion

Summary of Results

In this experiment, we compared the effects of synchronizing to, or passively attending, auditory and visual rhythms on neural activations at the beat frequency and on mu rhythms. Our results show clear activation of the beat frequency for both auditory and visual rhythms in the motor system in ITC and in both ITC and noise-corrected power in grand averaged data, suggesting both modalities can entrain rhythms at the beat frequency in neural populations (figures 4 & 6). We additionally show strong differential activation at the beat frequency and in mu power between tapping in synchrony to auditory and visual rhythms compared to passively attending the rhythms, where tapping in synchrony increases both power (figure 4) and phase-coherence (figure 6) at the beat frequency, while decreasing mu power (figures 2 & 3). Surprisingly, we find evidence of stronger induced activation at the beat frequency from visual rhythms over auditory rhythms in ITC measures (figure 6), yet see no evidence of differential activation of mu rhythms nor of noise-corrected amplitude across modalities (figures 2, 3, & 4). Inspections of the spectral topography plots of noise corrected amplitude for all components at f0 indicate that f0 amplitude is most modulated by tapping in the frontal-central regions for both modalities, while both visual conditions show relatively high f0 power posteriorly (figure 5). While we make no direct statistical comparisons between the activity from the left-motor components and grand-averaged data, it does appear that amplitude at the beat frequency is seen in the motor components clearly only when tapping, as opposed to in all cases in the grand averaged data (figure 4). Yet when looking at ITC at f0, there appears to be stronger activation for all conditions in the motor components compared to the grand averaged data (figure 6) indicating stronger phase locking to the rhythms.

Mu Power

Mu rhythm activity is thought to increase during movement suppression (Pfurtscheller & Neuper, 1994; Pfurtscheller et al., 1997), and has been shown that it can serve as a marker for rhythmic timing processing (Ross et al., 2022), based on the idea that the motor system is simulating the beat (Iversen & Patel, 2014; Ross et al., 2016), and that the work of beat simulation may result in mu ERS. Existing work made it unclear if attending rhythms would result in mu ERS or ERD as Wu et al., (2016) reported mu ERD while listening to music while Ross et al., (2022) reported mu ERS. Our results are in line with those reported by Ross et al (2022) where they showed mu ERS during music listening compared to baseline. We show mu ERS in response to both auditory and visual rhythms, suggesting a modality general response to rhythms at the level of the motor cortex. The effect found by Wu et al., (2016) may be due to motor imagery, as the ERD was seen in trained pianists while they listened to piano pieces they were familiar with, and therefore may have been imagining the movements required to play the pieces. As the study did not test non-musicians, nor musicians with music they were not familiar

with, it cannot be confirmed that the mu ERD was a result of simply attending or processing of music

It is well known that humans synchronize with greater precision and across a greater range of tempi to auditory rhythms than to visual rhythms (see Repp & Su, 2013 for review). One prominent explanation is that the auditory system is tightly tied into the motor system to use the motor system for auditory rhythmic timing processing (Iversen & Patel, 2014; Ross et al., 2016), while more recent work has suggested that the visual system is able to do some rhythmic timing in house (Comstock & Balasubramaniam, 2018; Comstock et al., 2021). Under those conditions, and given the assumptions that mu ERD is seen during motor imagery, it could be expected that auditory rhythms would elicit mu greater ERD compared to visual rhythms if the motor system is involved in beat simulation as stated in the ASAP hypothesis. Yet our results are in line with Ross et al., (2022) showing mu ERS during the auditory rhythms, and we surprisingly also show mu ERS during visual rhythms, with no significant differences between the two.

These results can be interpreted in several ways. The simplest interpretation is as evidence that the motor cortex is not simulating the beat for either auditory or visual rhythms. However, we urge caution in interpreting the results in this way as mu ERS during the non-tapping tasks may reflect an interaction between holding the hand still, and cortical processing for movement or movement imagery elsewhere in the motor system, such as reported in the interactions between hand-area mu during foot movements (Pfurtscheller & Neuper, 1994; Pfurtscheller et al., 1997). This would suggest an unexpected result: the motor system is engaging in rhythm processing equally for both auditory and visual rhythms. A further explanation may be that the isochronous rhythms used in this study did not modulate mu activity in the same way music would. This could be due to the isochronous rhythms simply not driving motor beat simulation in a way that would differentiate between auditory and visual rhythms. A final consideration on the mu results is that mu activity arising from the primary motor cortex is known to be modulated by the premotor areas including SMA (Ulloa & Pineda, 2007). Given that the SMA has been implicated in rhythm processing (Iversen & Patel, 2014; Merchant & Honing, 2014; Ross et al., 2016), and since this study did not isolate pre-motor or SMA activity, it may be pre-motor activity would show the differentiation we hypothesized between modalities.

Activity at f0

Numerous studies have shown neural activation at the beat frequency of a rhythm in power and phase coherence measures using a frequency tagging approach (Nozaradan et al., 2011, 2012a, 2012b, 2015; Doelling & Poeppel, 2015). Likewise, visual rhythms have been long known to entrain to flashing rhythms (Vialatte et al., 2010), although visual rhythms studies usually look at activity at higher frequency ranges, e.g. 10 to 12 Hz, rather than at the lower frequencies used for SMS or auditory rhythm perception tasks. A recent study (Varlet et al 2020) has shown that audio-visual rhythms can elicit beta-coherence between EMG activity from a subject's non-moving finger and EEG activity over the cortical motor region that was stronger than elicited by audio rhythms alone, suggesting that information of the timing of the visual rhythms is present in the motor system, even when the subject is instructed to remain motionless. Counter to our hypothesis, the f0 activity localized to the left motor cortex in the current study revealed greater ITC for visual rhythms than auditory rhythms, although we find no modality differences in the motor component data in mu activation or in noise-corrected f0 amplitude. This finding suggests that differences in SMS and rhythm perception capabilities between

auditory and visual rhythms may not be due to greater entrainment ability of one modality over the other, but rather in how that entrained activity is utilized.

Recent findings have shown that synchronization to visual rhythms can be achieved with similar levels of accuracy found in synchronization to auditory rhythms when those rhythms are moving. Importantly, the rhythm must move in a compatible way to the synchroning movement (Hove et al., 2010; Varlet et al., 2014). Further improvements have been seen when the moving visual rhythm follows an ecologically valid movement pattern, such as with a bouncing ball (Gan et al., 2015; Iversen et al., 2015; Huang et al., 2018). Yet, the benefit of using moving visual rhythms does not appear to apply when there is no explicit motor task (Silva & Castro, 2016; Gu et al., 2020). When these findings are taken into consideration with the motor cortex f0 ITC activity we report in response to visual rhythms, it suggests the visual system is tightly connected to the motor system in a way that allows for precise timing in response to visual stimuli in the same way the motor system can with auditory stimuli. However, that tight visuo-motor timing is only facilitated when visual stimuli are action compatible. When the stimuli are not action compatible, such as a flashing rhythm, or when there is no action intention, the motor system is not able to facilitate the same level of timing precision as is seen in synchronizing to a bouncing ball.

Limitations and Future Directions

One major limitation of this study is in its use of isochronous rhythms, and interpreting the resultant frequency domain activity. There has been controversy over whether or not activity at the beat frequency of a rhythm represents neural entrainment to a rhythm, or if the activity at the beat frequency is essentially an artifact from applying an FFT to rhythmic stimulus to evoked potentials (Capilla et al., 2011; Novembre & Iannetti, 2018; Rajendran & Schnupp, 2019). One way around the issues is to use syncopated or metered stimuli that would produce little or no increase in frequency power at the frequency of interest (Lenc et al., 2019, Nozaradan et al., 2018). As this study was designed to use as simple stimuli as possible, one needs to take care to not over interpret the results. Indeed, it is possible that greater f0 activity seen in visual rhythms compared to auditory rhythms is simply due to the evoked potentials to visual stimuli being generally more pronounced than those evoked from similar auditory stimuli. However, this concern applies primarily only to the grand-averaged f0 ITC and noise-corrected power, as we see it as unlikely that the activity measured from the components isolated in the left motor cortex would contain large sensory evoked potentials, as those components are not sourced in either auditory or visual regions.

Additionally, we cannot entirely rule out effects of possible attentional differences between stimuli conditions. If the visual rhythms resulted in increased attentional focus compared to the auditory rhythms, we may expect to see greater entrainment for visual conditions. As we did not have a direct measure of attentional effort, nor did we inquire about the participants level of effort, it is unclear if there were attentional differences between our conditions.

A further limitation is taps were not recorded. Future studies of a similar design would be able to directly connect SMS performance metrics with the neural data. This may be particularly useful in understanding how musical expertise affects neural processing of rhythms. Further explanations such as a role for error correction in driving auditory and visual rhythm processing differences should be tested in future studies.

Conclusions

We showed that mu rhythm activity in response to passively attending and synchronizing to simple isochronous rhythms is not modulated by the modality of that rhythm. Further we find evidence that entrainment to visual rhythms may be stronger than auditory rhythms, even though humans are generally able to perceive and synchronize to auditory rhythms more precisely than to visual rhythms. This indicates that how the entrainment activity is utilized by the motor system is just as important as the entrainment activity itself. We suggest that how, and to what extent, the motor system is able to couple with the visual system for rhythm processing is dependent on the stimulus appropriateness and the action intention regarding that stimulus.

Acknowledgement

The work was supported by NSF grant BCS 1626505. A portion of this work was submitted in partial fulfillment of the dissertation of Daniel C Comstock.

Conflict of Interest

The authors do not have any conflicts of interest to declare.

Author Contributions

DCC and RB conceived and designed this study together. DCC ran all participants and conducted analyses. DCC and RB co-wrote the paper.

References

Bangert, M., & Altenmüller, E. O. (2003). Mapping perception to action in piano practice: a longitudinal DC-EEG study. *BMC neuroscience*, *4*(1), 1-14.

Behmer Jr, L. P., & Fournier, L. R. (2016). Mirror neuron activation as a function of explicit learning: changes in mu-event-related power after learning novel responses to ideomotor compatible, partially compatible, and non-compatible stimuli. *European Journal of Neuroscience, 44*(10), 2774-2785.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal statistical society: series B (Methodological), 57*(1), 289-300.

Capilla, A., Pazo-Alvarez, P., Darriba, A., Campo, P., & Gross, J. (2011). Steady-state visual evoked potentials can be explained by temporal superposition of transient event-related responses. *PloS one*, *6*(1), e14543.

Chen, J. L., Penhune, V. B., & Zatorre, R. J. (2008). Listening to musical rhythms recruits motor regions of the brain. *Cerebral cortex, 18*(12), 2844-2854.

Comstock, D.C. & Balasubramaniam, R. (2018). Neural responses to perturbations in visual and auditory metronomes during sensorimotor synchronization. *Neuropsychologia* http://doi.org/10.1016/j.neuropsychologia.2018.05.013.

Comstock, D. C., Hove, M. J., & Balasubramaniam, R. (2018). Sensorimotor synchronization with auditory and visual modalities: behavioral and neural differences. *Frontiers in computational neuroscience*, *12*, 53.

Comstock, D. C., Ross, J. M., & Balasubramaniam, R. (2021). Modality-specific frequency band activity during neural entrainment to auditory and visual rhythms. *European Journal of Neuroscience, (in press)*

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of neuroscience methods*, *134*(1), 9-21.

Delorme, A., Palmer, J., Onton, J., Oostenveld, R., & Makeig, S. (2012). Independent EEG sources are dipolar. *PloS one*, *7*(2), e30135.

Doelling, K. B., & Poeppel, D. (2015). Cortical entrainment to music and its modulation by expertise. *Proceedings of the National Academy of Sciences*, *112*(45), E6233-E6242.

Foxe, J. J., & Snyder, A. C. (2011). The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Frontiers in psychology*, *2*, 154.

Fujioka, T., Trainor, L. J., Large, E. W., & Ross, B. (2012). Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations. *Journal of Neuroscience, 32*(5), 1791-1802.

Fujioka, T., Ross, B., & Trainor, L. J. (2015). Beta-band oscillations represent auditory beat and its metrical hierarchy in perception and imagery. *Journal of Neuroscience, 35*(45), 15187-15198.

Gan, L., Huang, Y., Zhou, L., Qian, C., & Wu, X. (2015). Synchronization to a bouncing ball with a realistic motion trajectory. *Scientific reports, 5*(1), 1-9.

Gordon, C. L., Cobb, P. R., & Balasubramaniam, R. (2018). Recruitment of the motor system during music listening: An ALE meta-analysis of fMRI data. *PloS one, 13*(11), e0207213.

Grahn, J. A., & Brett, M. (2007). Rhythm and beat perception in motor areas of the brain. *Journal of cognitive neuroscience, 19*(5), 893-906.
Grahn, J. A., & Rowe, J. B. (2009). Feeling the beat: premotor and striatal interactions in musicians and nonmusicians during beat perception. *Journal of Neuroscience, 29*(23), 7540-7548.
Gu, L., Huang, Y., & Wu, X. (2020). Advantage of audition over vision in a perceptual timing task but not in a sensorimotor timing task. *Psychological Research, 84*(7), 2046-2056.
Hove, M. J., Fairhurst, M. T., Kotz, S. A., & Keller, P. E. (2013). Synchronizing with auditory and visual rhythms: an fMRI assessment of modality differences and modality appropriateness. *Neuroimage*, *67*, 313-321.
Hove, M. J., Spivey, M. J., & Krumhansl, C. L. (2010). Compatibility of motion facilitates visuomotor synchronization. J*ournal of Experimental Psychology: Human Perception and Performance, 36*(6), 1525.
Huang, Y., Gu, L., Yang, J., Zhong, S., & Wu, X. (2018). Relative contributions of the speed characteristic and other possible ecological factors in synchronization to a visual beat consisting of periodically moving stimuli. *Frontiers in Psychology, 9*, 1226.
Iversen, J. R., Patel, A. D., Nicodemus, B., & Emmorey, K. (2015). Synchronization to auditory and visual rhythms in hearing and deaf individuals. *Cognition, 134*, 232-244.
Lenc, T., Keller, P. E., Varlet, M., & Nozaradan, S. (2019). Reply to Rajendran and Schnupp: Frequency tagging is sensitive to the temporal structure of signals. *Proceedings of the National Academy of Sciences*, *116*(8), 2781-2782.
Makeig, S., Debener, S., Onton, J., & Delorme, A. (2004). Mining event-related brain dynamics. *Trends in cognitive sciences*, *8*(5), 204-210.
Merchant, H., Grahn, J., Trainor, L., Rohrmeier, M., & Fitch, W. T. (2015). Finding the beat: a neural perspective across humans and non-human primates. *Philosophical Transactions of the Royal Society B: Biological Sciences, 370*(1664), 20140093.
Merchant, H., & Honing, H. (2014). Are non-human primates capable of rhythmic entrainment? Evidence for the gradual audiomotor evolution hypothesis. *Frontiers in neuroscience*, *7*, 274.
McFarland, D. J., Miner, L. A., Vaughan, T. M., & Wolpaw, J. R. (2000). Mu and beta rhythm topographies during motor imagery and actual movements. *Brain topography*, *12*(3), 177-186.
McGarry, L. M., Russo, F. A., Schalles, M. D., & Pineda, J. A. (2012). Audio-visual facilitation of the mu rhythm. *Experimental brain research, 218*(4), 527-538.
Niedermeyer, E. (1997). Alpha rhythms as physiological and abnormal phenomena. *International Journal of Psychophysiology*, *26*(1-3), 31-49.
Novembre, G., & Iannetti, G. D. (2018). Tagging the musical beat: Neural entrainment or event-related potentials?. *Proceedings of the National Academy of Sciences*, *115*(47), E11002-E11003.
Nozaradan, S., Peretz, I., Missal, M., & Mouraux, A. (2011). Tagging the neuronal entrainment to beat and meter. *Journal of Neuroscience*, *31*(28), 10234-10240.
Nozaradan, S., Peretz, I., & Mouraux, A. (2012a). Selective neuronal entrainment to the beat and meter embedded in a musical rhythm. *Journal of Neuroscience*, *32*(49), 17572-17581.
Nozaradan, S., Peretz, I., & Mouraux, A. (2012b). Steady-state evoked potentials as an index of multisensory temporal binding. *Neuroimage*, *60*(1), 21-28.

Nozaradan, S., Zerouali, Y., Peretz, I., & Mouraux, A. (2015). Capturing with EEG the neural entrainment and coupling underlying sensorimotor synchronization to the beat. *Cerebral Cortex*, *25*(3), 736-747.

Nozaradan, S., Keller, P. E., Rossion, B., & Mouraux, A. (2018). EEG frequency-tagging and input–output comparison in rhythm perception. *Brain topography*, *31*(2), 153-160.

Nyström, P., Ljunghammar, T., Rosander, K., & von Hofsten, C. (2011). Using mu rhythm desynchronization to measure mirror neuron activity in infants. *Developmental science, 14*(2), 327-335.

Palmer, J. A., Kreutz-Delgado, K., & Makeig, S. (2012). AMICA: An adaptive mixture of independent component analyzers with shared components. *Swartz Center for Computatonal Neursoscience, University of California San Diego, Tech. Rep*.

Patel, A. D., & Iversen, J. R. (2014). The evolutionary neuroscience of musical beat perception: the Action Simulation for Auditory Prediction (ASAP) hypothesis. *Frontiers in systems neuroscience*, *8*, 57.

Pion-Tonachini, L., Kreutz-Delgado, K., & Makeig, S. (2019). The ICLabel dataset of electroencephalographic (EEG) independent component (IC) features. *Data in brief*, *25*, 104101.

Pfurtscheller, G., & Da Silva, F. L. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clinical neurophysiology*, *110*(11), 1842-1857.

Pfurtscheller, G., & Neuper, C. (1994). Event-related synchronization of mu rhythm in the EEG over the cortical hand area in man. *Neuroscience letters*, *174*(1), 93-96.

Pfurtscheller, G., Neuper, C., Andrew, C., & Edlinger, G. (1997). Foot and hand area mu rhythms. *International Journal of Psychophysiology*, *26*(1-3), 121-135.

Rajendran, V. G., & Schnupp, J. W. (2019). Frequency tagging cannot measure neural tracking of beat or meter. *Proceedings of the National Academy of Sciences*, *116*(8), 2779-2780.

Repp, B. H. (2003). Rate limits in sensorimotor synchronization with auditory and visual sequences: The synchronization threshold and the benefits and costs of interval subdivision. *Journal of motor behavior*, *35*(4), 355-370.

Repp, B. H., & Su, Y. H. (2013). Sensorimotor synchronization: a review of recent research (2006–2012). *Psychonomic bulletin & review*, *20*(3), 403-452.

Ross, J. M., Comstock, D. C., Iversen, J. R., Makeig, S., & Balasubramaniam, R. (2022). Cortical mu rhythms during action and passive music listening. *Journal of neurophysiology*, *127*(1), 213-224.

Ross, J. M., Iversen, J. R., & Balasubramaniam, R. (2016b). Motor simulation theories of musical beat perception. *Neurocase*, *22*(6), 558-565.

Silva, S., & Castro, S. L. (2016). Moving stimuli facilitate synchronization but not temporal perception. *Frontiers in Psychology, 7*, 1798.

Solomon, J. P., Kraeutner, S. N., Bardouille, T., & Boe, S. G. (2019). Probing the temporal dynamics of movement inhibition in motor imagery. *Brain research, 1720*, 146310.

The jamovi project (2021). jamovi (Version 2.2) [Computer Software]. Retrieved from https://www.jamovi.org

Ulloa, E. R., & Pineda, J. A. (2007). Recognition of point-light biological motion: mu rhythms and mirror neuron activity. *Behavioural brain research*, *183*(2), 188-194.

Varlet, M., Coey, C. A., Schmidt, R. C., Marin, L., Bardy, B. G., & Richardson, M. J. (2014). Influence of stimulus velocity profile on rhythmic visuomotor coordination. *Journal of Experimental Psychology: Human Perception and Performance, 40*(5), 1849.

Varlet, M., Nozaradan, S., Trainor, L., & Keller, P. E. (2020). Dynamic Modulation of Beta Band Cortico-Muscular Coupling Induced by Audio–Visual Rhythms. *Cerebral Cortex Communications, 1*(1), tgaa043.

Vialatte, F. B., Maurice, M., Dauwels, J., & Cichocki, A. (2010). Steady-state visually evoked potentials: focus on essential paradigms and future perspectives. *Progress in neurobiology*, *90*(4), 418-438.

Wu, C. C., Hamm, J. P., Lim, V. K., & Kirk, I. J. (2016). Mu rhythm suppression demonstrates action representation in pianists during passive listening of piano melodies. *Experimental brain research*, *234*(8), 2133-2139.

Figure Legend

Figure 1
Example of left motor component from a single subject. Characteristic mu wave shape can be seen in the time-series data (a), which is present only during the non-tapping conditions (b). The topography of the component suggests its source is from the left-motor cortex (c), while the spectral power shows the characteristic 10 Hz power with a beta harmonic resultant from mu activity (d). Topographic plots of activity from the selected left motor components with activity of all components averaged together can be seen in the top topographic plot (e). All individual left-motor component plots from selected mu components are shown (f).

Figure 2
Average Event Related Spectral Perturbation (ERSP) plots from motor components for each condition showing time frequency power response compared to rest (baseline period).. The dashed line at zero indicates stimulus train onset. The area inside the dotted lines is the region of interest for mu activity.

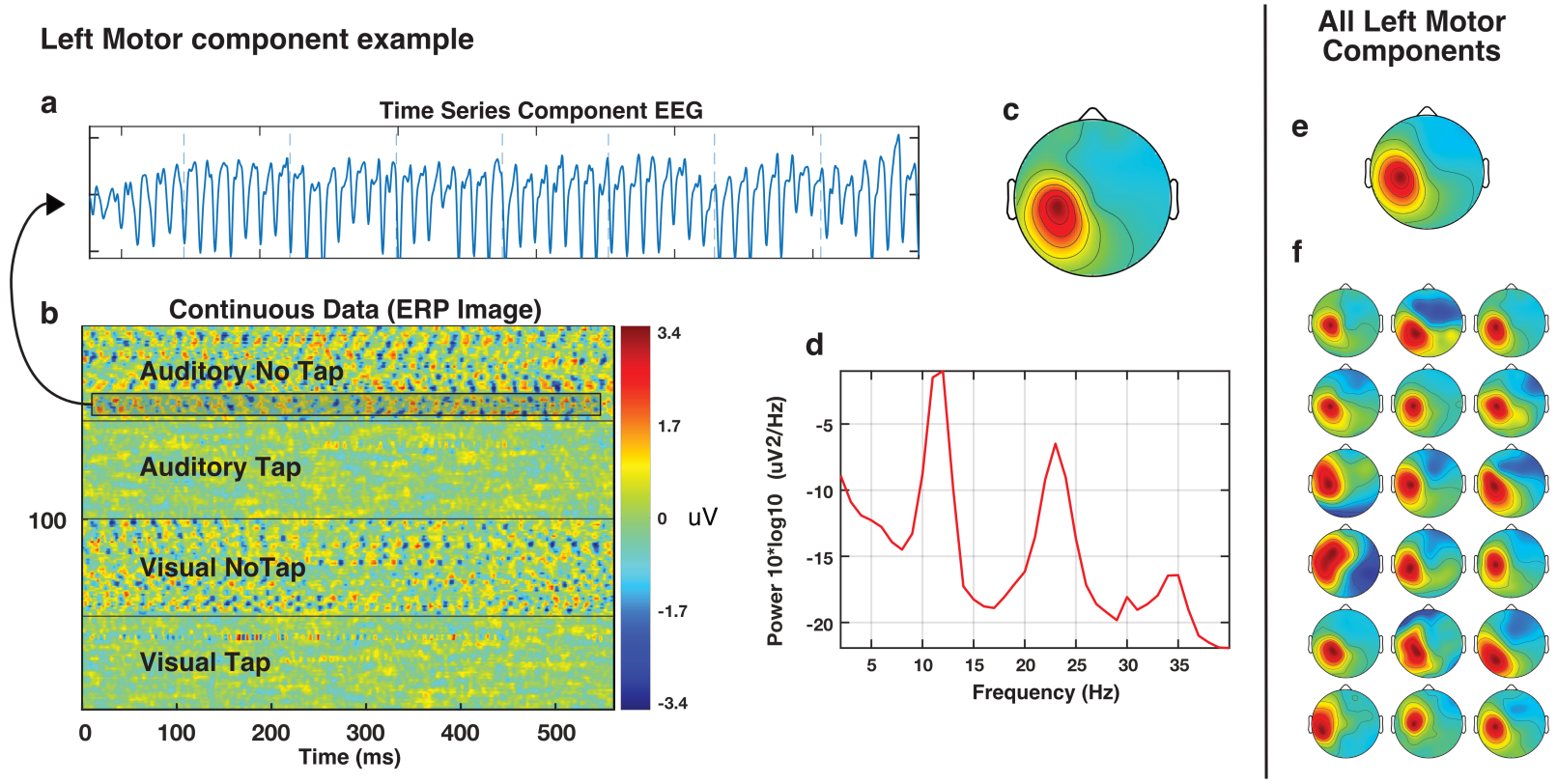
Figure 3
Box pots depicting the distribution of power in the mu range (8 - 13 Hz) compared to baseline across conditions for left-motor component activity. The center line of each box depicts the median the red circle indicates the mean. ANOVA results indicate significant mu increase for both auditory and visual no tapping conditions, but no difference across modalities.

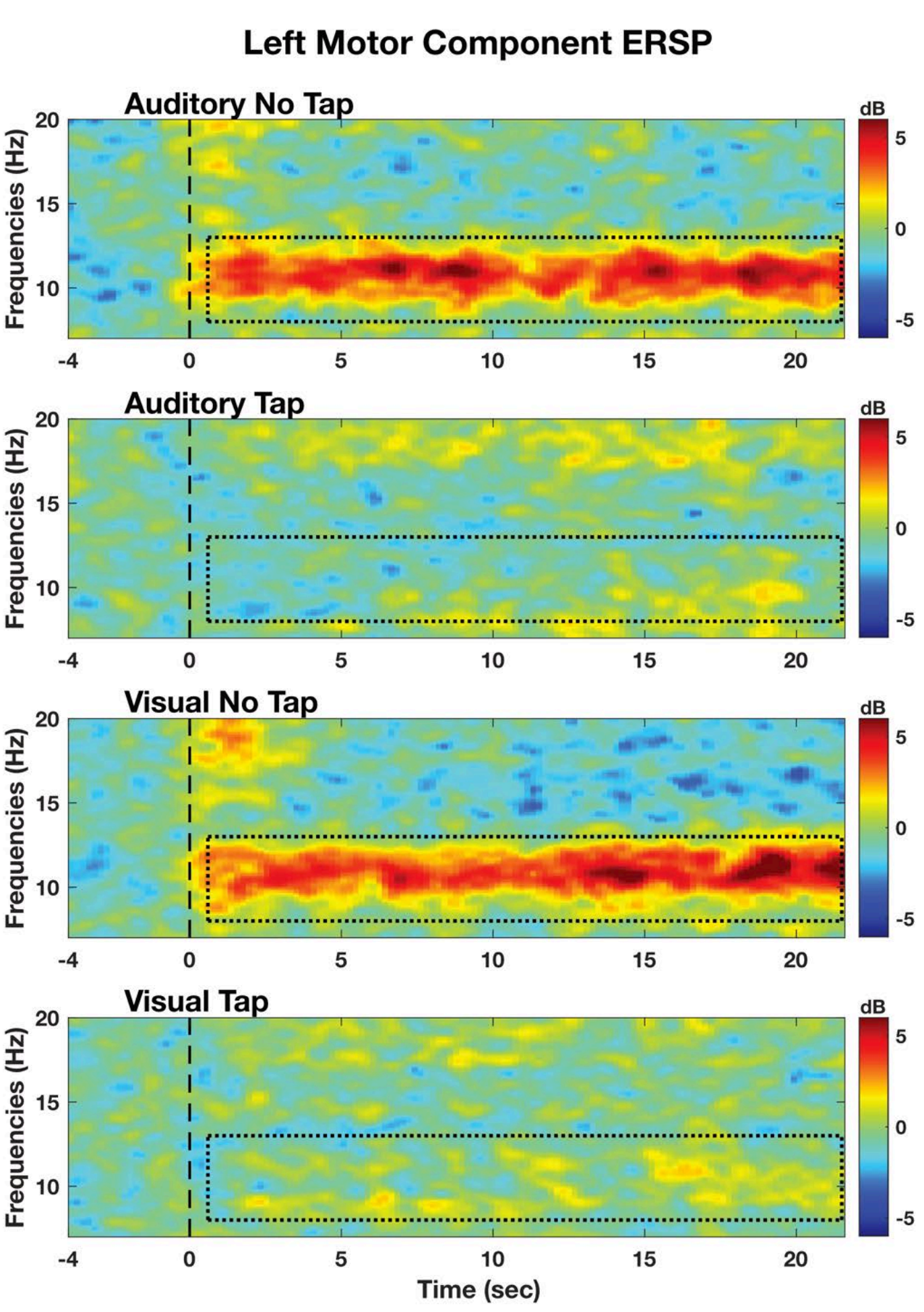
Figure 4
Frequency domain representation of noise-corrected amplitude for left motor components (a) and grand average (c). Average noise-corrected amplitude is represented with the dark blue line, and shaded areas represent 95% confidence intervals. Box plots show distribution of noise-corrected amplitude at f0 for left motor components (b) and grand average (d). The center line of each box depicts the median the red circle indicates the mean. ANOVA results indicated greater f0 amplitude in visual conditions over auditory conditions in the grand averaged data (d) and greater f0 amplitude in tapping conditions than non-tapping conditions in the left motor components (b).

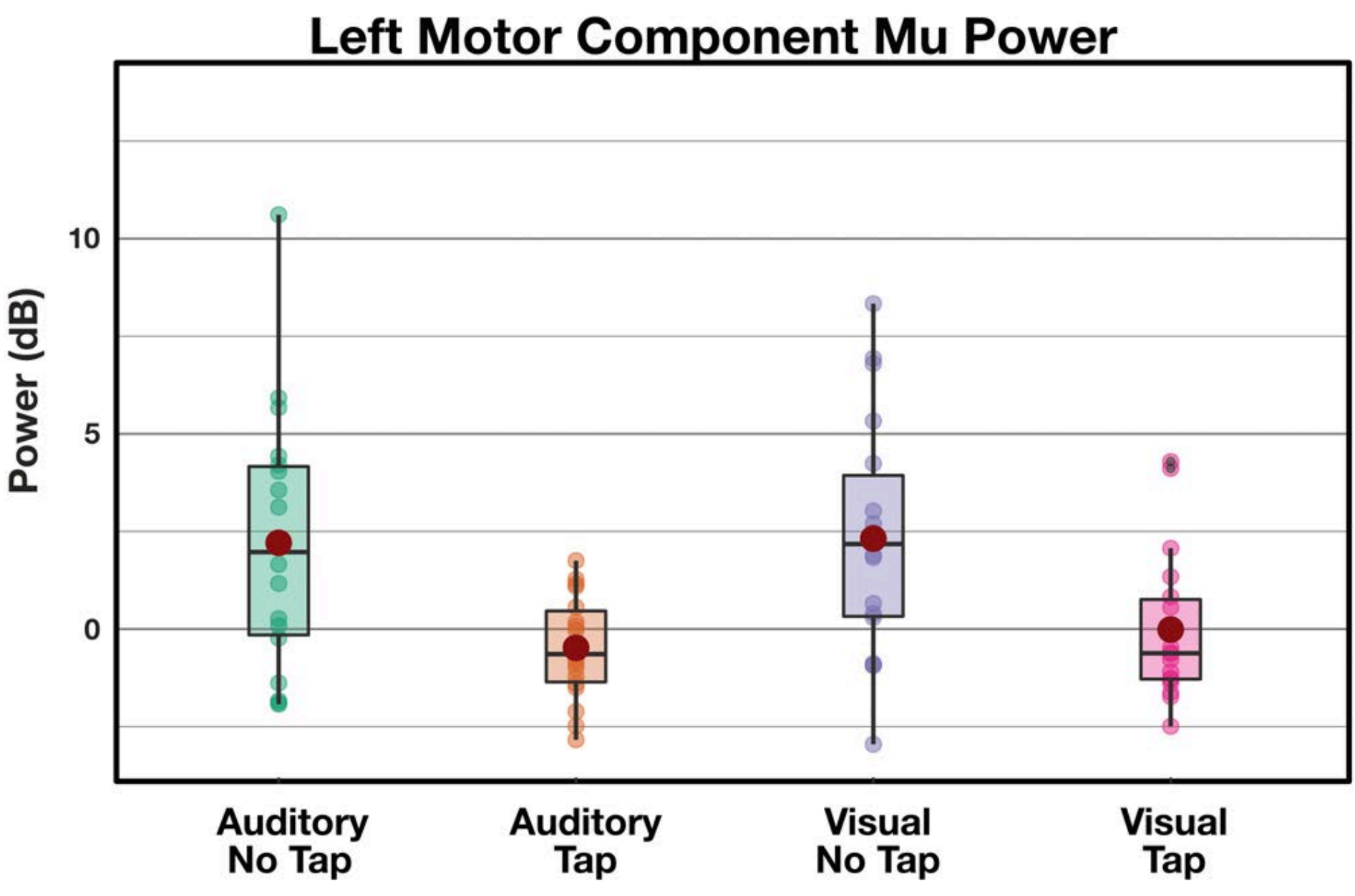
Figure 5
Scalp topography of f0 amplitude from grand average data.

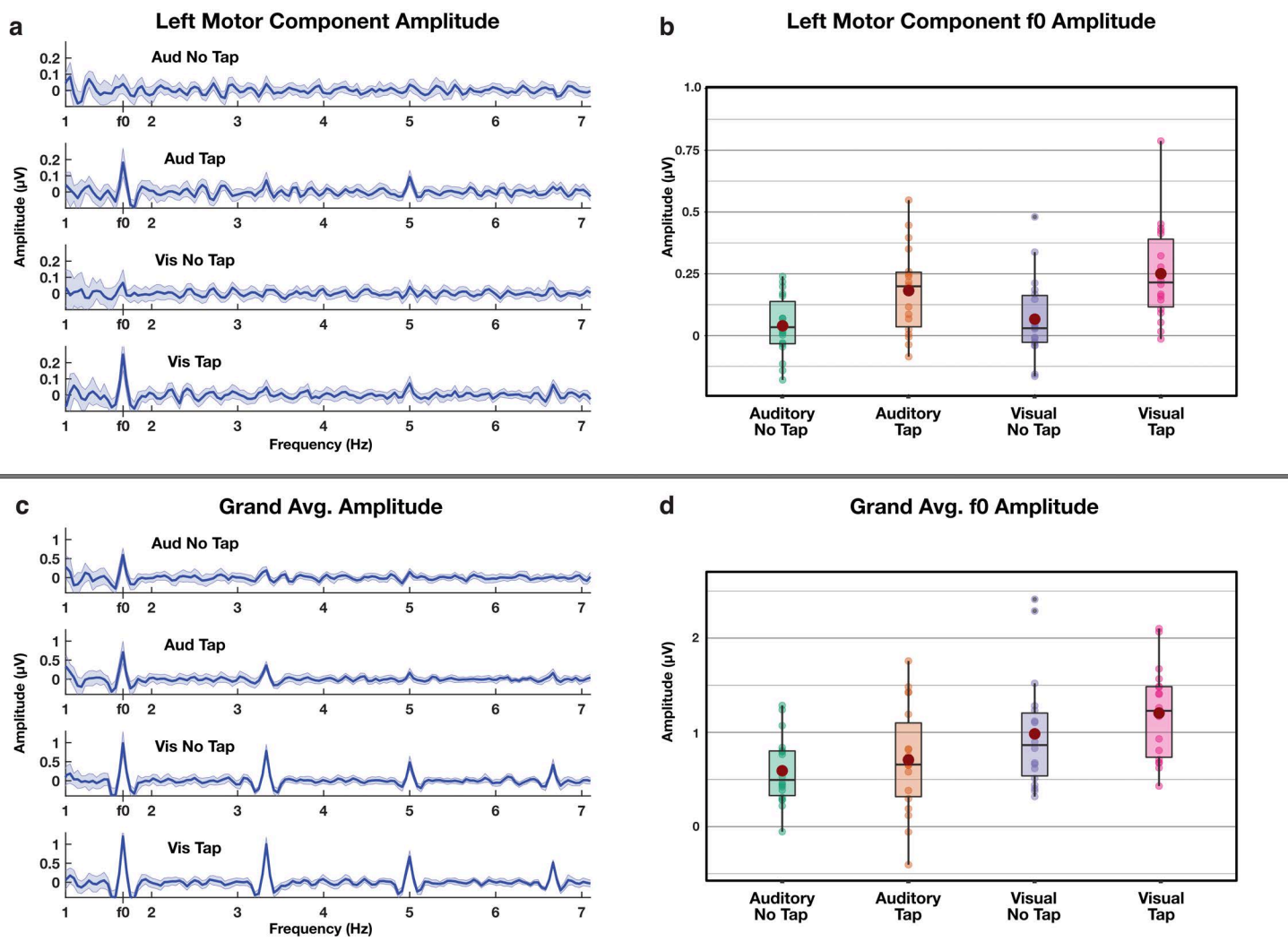
Figure 6
Frequency domain representation of ITC left motor components (a) and grand average (c). Subject average ITC is represented with the thik red line, and individual ITC are shown in thin black lines.. Box plots show distribution of ITC at f0 for left motor components (b) and grand average (d). The center line of each box depicts the median the red circle indicates the mean. ANOVA results indicated both left motor component and grand average f0 ITC was greater in visual conditions than auditory conditions and also greater in tapping conditions over non tapping conditions.

Table 1
T-test tables for f0 amplitude and ITC. One-Sample t-test results comparing amplitude at f0 to zero for both motor components (a) and grand average (b). Paired sample t-tests to assess if f0 ITC is significantly different from randomly selected ITC values for both motor components (c) and grand average (d). Randomly sampled ITC values are denoted as rSamp. All p-values are corrected for multiple comparisons using FDR correction.

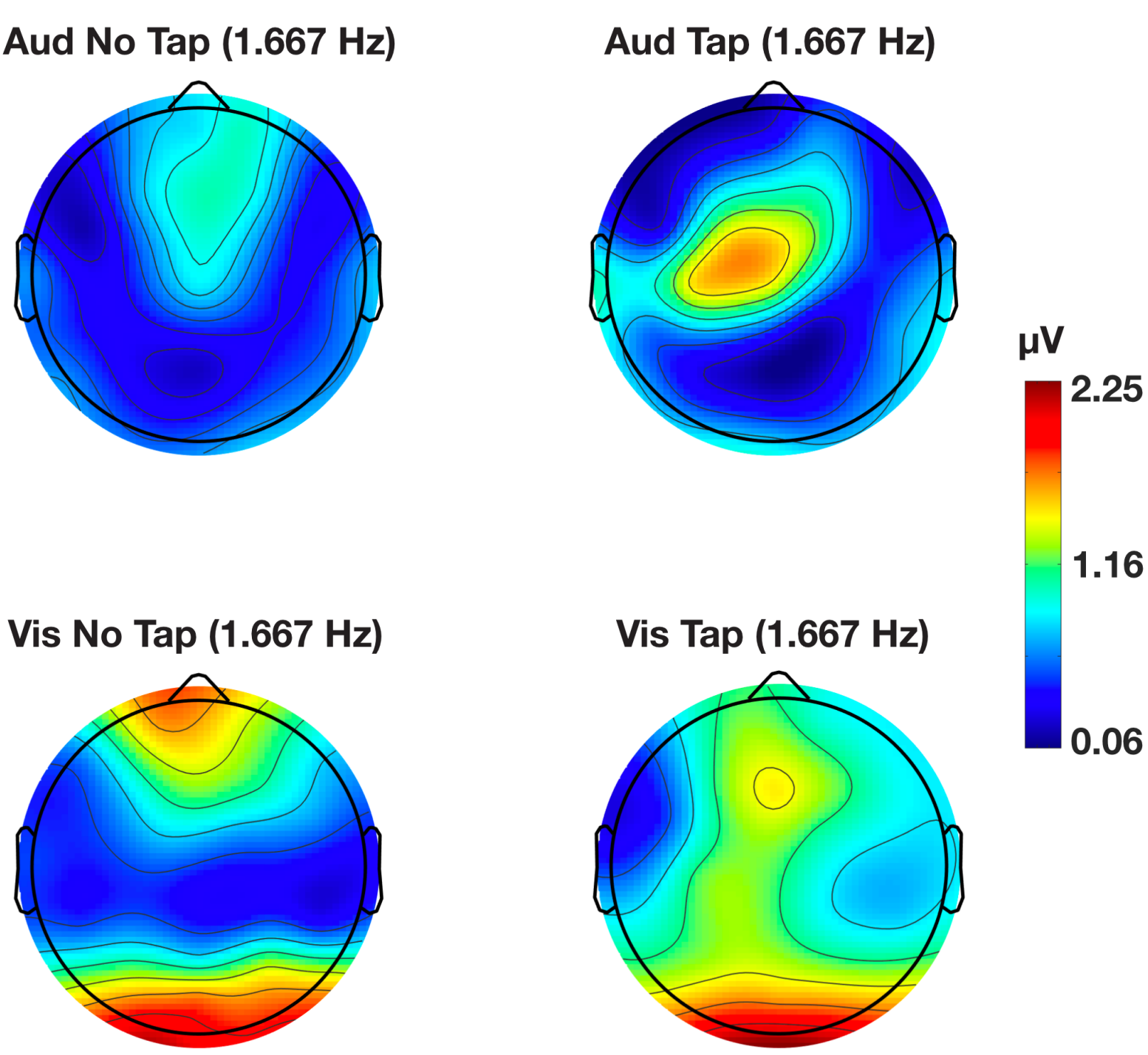

Left Motor component example
a
Time Series Component EEG
b
Continuous Data (ERP Image)
Auditory No Tap
Auditory Tap
Visual NoTap
Visual Tap
100
3.4
1.7
0
uV
-1.7
-3.4
0
100
200
300
400
500
Time (ms)
c
d
Power 10*log10 (uV2/Hz)
-5
-10
-15
-20
5
10
15
20
25
30
35
Frequency (Hz)
All Left Motor Components
e
f

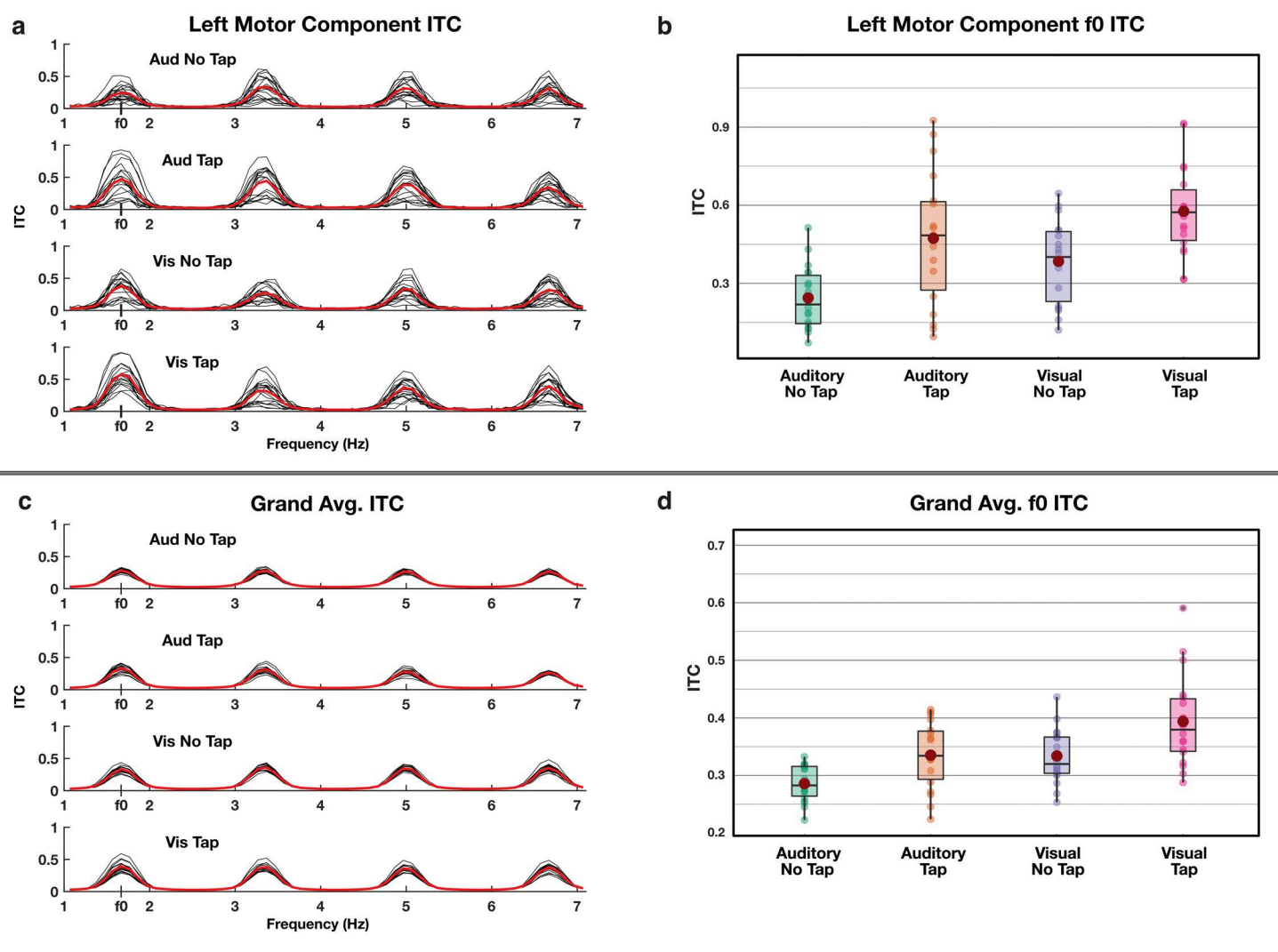

Left Motor Component ERSP
Auditory No Tap
Auditory Tap
Visual No Tap
Visual Tap
Frequencies (Hz)
20
15
10
dB
5
0
-5
-4
0
5
10
15
20
Time (sec)


Left Motor Component Mu Power
Power (dB)
10
5
0
Auditory No Tap
Auditory Tap
Visual No Tap
Visual Tap


a
Left Motor Component Amplitude
Aud No Tap
Aud Tap
Vis No Tap
Vis Tap
Amplitude (μV)
Frequency (Hz)
f0
b
Left Motor Component f0 Amplitude
Amplitude (μV)
Auditory No Tap
Auditory Tap
Visual No Tap
Visual Tap
c
Grand Avg. Amplitude
Aud No Tap
Aud Tap
Vis No Tap
Vis Tap
Amplitude (μV)
Frequency (Hz)
f0
d
Grand Avg. f0 Amplitude
Amplitude (μV)
Auditory No Tap
Auditory Tap
Visual No Tap
Visual Tap

f0 Spectral Topography




a
Left Motor Component ITC
Aud No Tap
Aud Tap
Vis No Tap
Vis Tap
ITC
f0
Frequency (Hz)
b
Left Motor Component f0 ITC
ITC
Auditory No Tap
Auditory Tap
Visual No Tap
Visual Tap
c
Grand Avg. ITC
Aud No Tap
Aud Tap
Vis No Tap
Vis Tap
ITC
f0
Frequency (Hz)
d
Grand Avg. f0 ITC
ITC
Auditory No Tap
Auditory Tap
Visual No Tap
Visual Tap

Left Motor f0 Amplitude

One Sample T-Test

Condition	N	Mean	SD	t	df	p	Effect Size
L.Motor Aud No Tap	18	0.040	0.122	1.37	17	0.094	0.323
L.Motor Aud Tap	18	0.182	0.177	4.37	17	< .001	1.03
L.Motor Vis No Tap	18	0.066	0.164	1.72	17	0.059	0.405
L.Motor Vis Tap	18	0.250	0.198	5.37	17	< .001	1.267

Grand Avg. f0 Amplitude

One Sample T-Test

Condition	N	Mean	SD	t	df	p	Effect Size
Avg. Aud No Tap	18	0.593	0.364	6.92	17	< .001	1.63
Avg. Aud Tap	18	0.708	0.581	5.17	17	< .001	1.219
Avg. Vis No Tap	18	0.984	0.606	6.89	17	< .001	1.624
Avg. Vis Tap	18	1.204	0.492	10.39	17	< .001	2.45

Left Motor f0 ITC

Paired Samples T-Test

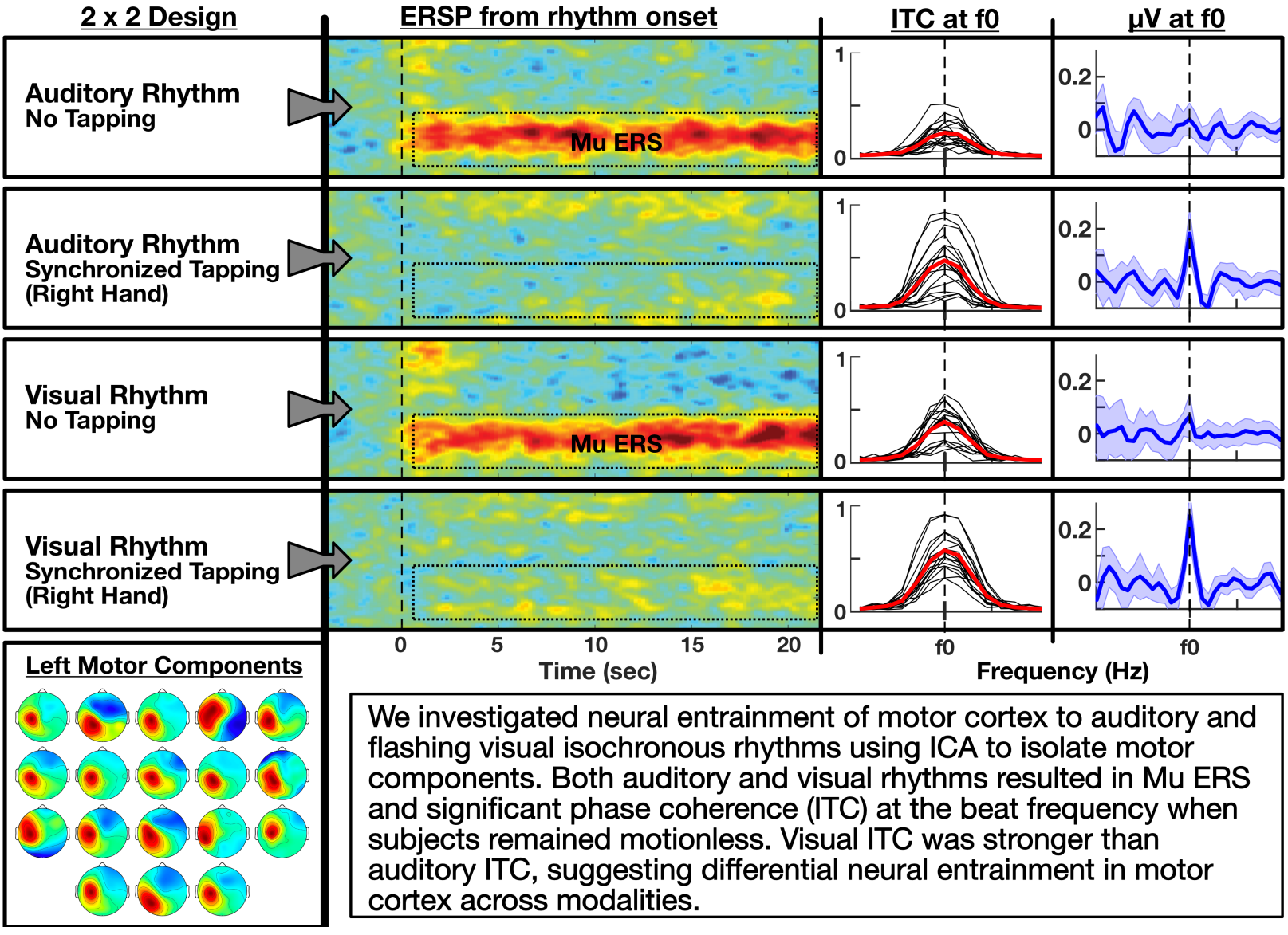
Condition	N	Mean	SD	t	df	p	Effect Size
L.Motor Aud No Tap	18	0.244	0.121	7.44	17	< .001	1.750
L.Motor Aud No Tap rSamp	18	0.031	0.003				
L.Motor Aud Tap	18	0.473	0.256	7.32	17	< .001	1.720
L.Motor Aud Tap rSamp	18	0.031	0.003				
L.Motor Vis No Tap	18	0.384	0.158	9.42	17	< .001	2.220
L.Motor Vis No Tap rSamp	18	0.030	0.004				
L.Motor Vis Tap	18	0.577	0.172	13.35	17	< .001	3.150
L.Motor Vis Tap rSamp	18	0.031	0.004				

Grand Avg. f0 ITC

Paired Samples T-Test

Condition	N	Mean	SD	t	df	p	Effect Size
Avg. Aud No Tap	18	0.286	0.031	34.15	17	< .001	8.050
Avg. Aud No Tap rSamp	18	0.031	0.002				
Avg. Aud Tap	18	0.335	0.058	22.16	17	< .001	5.220
Avg. Aud Tap rSamp	18	0.031	0.002				
Avg. Vis No Tap	18	0.334	0.048	27.08	17	< .001	6.380
Avg. Vis No Tap rSamp	18	0.031	0.002				
Avg. Vis Tap	18	0.394	0.080	19.30	17	< .001	4.550
Avg. Vis Tap rSamp	18	0.031	0.002				

Differential Motor System Entrainment to Auditory and Visual Rhythms



We investigated neural entrainment of motor cortex to auditory and flashing visual isochronous rhythms using ICA to isolate motor components. Both auditory and visual rhythms resulted in Mu ERS and significant phase coherence (ITC) at the beat frequency when subjects remained motionless. Visual ITC was stronger than auditory ITC, suggesting differential neural entrainment in motor cortex across modalities.