

RESEARCH ARTICLE

Sensory Processing

Differential motor system entrainment to auditory and visual rhythms

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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 the entrainment of both auditory and visual rhythms from the motor cortex while subjects either tapped in synchrony with or passively attended to the presented rhythms. To isolate activity from motor cortex, we used independent component 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, which helped select motor components. Our findings suggest neural entrainment in motor components was stronger for visual rhythms than 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 use the timing information made available to it.

NEW & 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 than for auditory rhythms. Motor system activity was isolated with a novel procedure using independent component analysis as a means of blind source separation, along with known markers of mu activity from the motor system to identify motor components.

EEG; entrainment; motor system; mu rhythms; rhythm cognition

INTRODUCTION

Human capability for sensorimotor synchronization (SMS) to auditory rhythms has been shown to be more precise than SMS to visual rhythms (1), but the exact reasons why are yet to be uncovered. It has been shown through fMRI work that activation of motor structures is more pronounced for auditory rhythms than for visual rhythms during SMS tasks (2). 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 that 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

(3–5). 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 of 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 premotor cortices (6). Other works have highlighted the importance of the supplementary motor area (SMA) and basal ganglia in rhythm perception (7–10). These structures are believed to work in concert with the auditory system to drive the precise timing required in rhythm perception. In their action

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simulation for auditory prediction (ASAP) hypothesis, Patel and Iverson (11) propose that this audiomotor facilitation is achieved through the dorsal auditory stream. Likewise, Merchant and Honing (12) 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 (13–15), and this signal is increased during an SMS task (16). 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 Ref. 17). It is unclear to what extent activity at f0 induced from 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 (18–20). 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 (21). One method used to solve this issue is to use independent component analysis (ICA), which has been shown to be an effective method of separating out sources of neural activity in the brain (22). Although the blind source separation of ICA allows for separating sources, a method of selecting appropriate sources for each study is required. As 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 (23). 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 (18-20) as well as during movement imagery (18, 24). Isolating mu activity using ICA based on component location and characteristics has been previously done in research into the mirror neuron system (25-27) and more recently to understand the role of mu in music perception (28). Mu components could be made further identifiable by using a study design with both a sufficient motor task and a nonmotor task that could be expected to induce modulation of mu rhythms.

Although 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. (28) showed that listening to music while remaining still results in mu ERS relative to silence. That study was motivated by the premise of the ASAP hypothesis that the motor system is simulating the beat in music (11). Although 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 (5, 29, 30). The findings in the study by Ross et al. (28) 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 (19, 20). 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 nontapping conditions. In addition, 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

Twenty-one subjects participated in the experiment (11 females, M = 21.62 yr, SD = 3.58). Data from three subjects were not used, two for computer error and one due to poor signal-to-noise ratio leaving in no discernible motor components, resulting in an n of 18 subjects. Ten subjects reported having some musical training (M = 6.6 yr 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 before 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. Eight of the trains were of auditory tones (1,000 Hz sine wave, 50 ms duration with 10 ms rise and 30 ms fall), and the other eight were visual flashes

(light gray flash with 50 ms duration). For both tones and flashes, the subjects faced a black computer screen with a gray fixation cross at the center that remained visible during both flashes and tones. All stimuli were presented with an interonset 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 recording, 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 nontapping, visual tapping, and visual nontapping) 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 two groups from each modality were always presented one after the other, and the tapping order was preserved across modalities, e.g., visual nontapping, visual tapping, auditory nontapping, and auditory tapping. To ensure subjects were actively attending to 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 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 6 s.

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 (31) and Matlab 2020b (32). Data were first downsampled from 1,024 to 256 Hz, then high pass-filtered with passband edge at 1 Hz and -6 dB cutoff at 0.5 Hz. Data were then pruned so only the stimulus trains and 5 s before 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 Artifact Subspace Reconstruction (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 (33). 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 (34) 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, and mu modulation based on condition (mu ERD during tapping



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 nontapping conditions (*B*). The topography of the component suggests its source is from the left motor cortex (*C*), whereas 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*). ERP, event-related potential.

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 Fig. 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 (23). In this experiment, movement onset is expected to occur just before stimulus onset as participants move to tap in synchrony with the stimulus. All selected motor components followed the expected pattern of beta modulation: clear beta power attenuation before stimulus onset followed by increased beta power after stimulus onset during tapping conditions, but not for the nontapping conditions.

Three separate time-frequency calculations were performed on the processed component data: an analysis to inspect beta power modulation, an analysis to calculate phase coherence, and an analysis to calculate mu power. To calculate beta power modulation, the data were epoched into 3-s 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 the 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 unepoched trials using Morlet wavelets between 1.066 and 14.066 Hz with a constant wavelet length of 6,563 ms 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 four conditions. Using the unepoched 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 0.3 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 and Poeppel (35), 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 unepoched trials using a fast Fourier transform between 7 and 30 Hz with a window length of 2 s. A divisive baseline specific to each condition was used with the period defined as the 5 s before 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 unepoched 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 was 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. (13).

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., Nozaradan et al. (13, 16) and Doelling and Poeppel (35). 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 with 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

Left Motor Component ERSP



Figure 2. Average event-related spectral perturbation (ERSP) plots from motor components for each condition showing time-frequency power response compared with 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 plots depicting the distribution of power in the mu range (8– 13 Hz) compared with baseline across conditions for left motor component activity. The center line of each box depicts the median and 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.

motor component data to test if the noise-corrected amplitude at f0 was greater than zero. As ITC activity is effectively always greater than zero, paired-sample *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, false discovery rate was used on all test results (36).

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 withinsubject factors being modality (audition and vision) and tap condition (no tapping and tapping). All statistical

Left Motor f0 Amplitude

SD

0.122

0.177

0 164

t df

1.37

4.37 17

172

17

17

n

18

18

18

Mean

0.040

0.182

0.066

Condition

L. Motor Aud No Tap

Motor Vis No Ta

L. Motor Aud Tap

analyses were performed using Jamovi (v. 2.2; 37) statistical software.

RESULTS

Mu Power

One-sample *t* tests of mu activation in response to stimuli revealed increased mu activity compared with baseline for the visual nontapping conditions [M = 2.316, SD = 3.08, t(17) = 3.192, P = 0.021] and for the auditory nontapping conditions [M = 2.208, SD = 3.34, t(17) = 2.801, P = 0.025], but not for either tapping condition (Figs. 2 and 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 nontapping conditions (M = 2.262, SE = 0.713) than during tapping conditions (M = -0.248, SE = 0.293).

Beat Induction at fO

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 1, Fig. 4). Amplitude at f0 for the visual non-tapping motor components neared significance at P = 0.059 (Table 1). 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 1, Fig. 6).

Amplitude at f0

Condition

Avg. Aud No Tap

Avg. Aud Tap

Ava Vis No Tan

n

18

18

18

Mean

0 5 9 3

0.708

0 984

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) (Fig. 4D). We report no interaction effects, and therefore no post hoc tests. The

Grand Average f0 Amplitude

SD

0.364

0.581

0 606

t

6.92

5.17 17

6 89 17

df

17

One-sample t test

P

< 0.001

< 0.001

< 0.001

Effect Size

1.63

1.219

1624

L. Motor Vis Tap	18	0.25	0 0.19	8 5.37	17	<0.0	001 1	1.267	Avg. Vis Tap 18	8 1	1.204	0.49	2 10.3	9 17	<0	.001 2	2.45
Left Motor f0 ITC									Grand Average f0 ITC								
				Paired-samples t test									Paired-samples t test				
								Effect									Effect
Condition		n	Mean	SD	t	df	Р	Size	Condition		n	Mean	SD	t	df	Р	Size
L. Motor Aud No Tap		18	0.244	0.121	7.44	17	< 0.001	1.750	Avg. Aud No Tap		18	0.286	0.031	34.15	17	< 0.001	8.050
L. Motor Aud No Tap r	Sam	p 18	0.031	0.003					Avg. Aud No Tap rSa	amp	18	0.031	0.002				
L. Motor Aud Tap		18	0.473	0.256	7.32	17	< 0.001	1.720	Avg. Aud Tap		18	0.335	0.058	22.16	17	< 0.001	5.220
L. Motor Aud Tap rSan	np	18	0.031	0.003					Avg. Aud Tap rSamp)	18	0.031	0.002				
L. Motor Vis No Tap		18	0.384	0.158	9.42	17	< 0.001	2.220	Avg. Vis No Tap		18	0.334	0.048	27.08	17	< 0.001	6.380
L. Motor Vis No Tap rS	Samp	18	0.030	0.004					Avg. Vis No Tap rSar	пp	18	0.031	0.002				
L. Motor Vis Tap		18	0.577	0.172	13.35	17	< 0.001	3.150	Avg. Vis Tap		18	0.394	0.080	19.30	17	< 0.001	4.550
L. Motor Vis Tap rSam	р	18	0.031	0.004					Avg. Vis Tap rSamp		18	0.031	0.002				

Effect Size

0.323

1.03

0 4 0 5

One-sample t test

0.094

0.059

< 0.001

P

One-sample *t* test results comparing amplitude at f0 to zero for both motor components and grand average. Paired-sample *t* tests to assess if f0 ITC is significantly different from randomly selected ITC values for both motor components and grand average. Randomly sampled ITC values are denoted as rSamp. All *P* values are corrected for multiple comparisons using false discovery rate correction. Aud, auditory; ITC, intertrial phase coherence; Vis, visual. Tap and No Tap refer to tapping in synchrony with the stimulus rhythm or remaining still while attending the stimulus rhythm, respectively.

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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 and 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 nontapping conditions in the left motor components (*B*).

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 nontapping conditions (*M* = 0.053, SE = 0.03) (Fig. 4*B*).

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 nottapping 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. (Fig. 5).

ITC at f0

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 nontapping conditions (M = 0.31, SE = 0.007) (Fig. 6D). 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 the auditory conditions (M = 0.359, SE = 0.031), and that left motor f0 ITC was greater in tapping conditions (M = 0.314, SE = 0.027) (Fig. 6B).

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



f0 Spectral Topography

Figure 5. Scalp topography of f0 amplitude from grand-average data. Aud, auditory; Vis, visual. Tap and No Tap refer to tapping in synchrony with the stimulus rhythm or remaining still while attending the stimulus rhythm, respectively.

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 (Figs. 4 and 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 with passively attending the rhythms, where tapping in synchrony increases both power (Fig. 4) and phase-coherence (Fig. 6) at the beat frequency while decreasing mu power (Figs. 2 and 3). Surprisingly, we find evidence of stronger induced activation at the beat frequency from visual rhythms over auditory rhythms in ITC measures (Fig. 6), yet see no evidence of differential activation of mu rhythms nor of noise-corrected amplitude across modalities (Figs. 2, 3, and 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 fo power posteriorly (Fig. 5). Although 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 (Fig. 4). Yet when looking at ITC at f0, there appears to be stronger activation for all conditions in the motor components compared with the grand-averaged data (Fig. 6), indicating stronger phase locking to the rhythms.

Mu Power

Mu rhythm activity is thought to increase during movement suppression (19, 20), and has been shown that it can serve as a marker for rhythmic timing processing (28), based on the idea that the motor system is simulating the beat (11, 38), 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. (39) reported mu ERD while listening to music, whereas Ross et al. (28) reported mu ERS. Our results are in line with those reported by Ross et al. (28) where they showed mu ERS during music listening compared with 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. (39) 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 nonmusicians, or 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 Ref. 40 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 (11, 38), whereas more recent work has suggested that the visual system is able to do some rhythmic timing in-house (3, 5). Under those conditions, and given the assumptions that mu ERD is seen during motor imagery, it could be expected that auditory rhythms would elicit greater mu ERD compared with 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. (28) 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 nontapping 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 (19, 20). 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 of the mu results is that mu activity arising from the primary motor cortex is known to be modulated by the premotor areas including SMA (41). Given that the SMA has been implicated in rhythm processing (11, 12, 40), and as this study did not isolate premotor or SMA activity, it may be premotor activity that would show the differentiation we hypothesized between modalities.



Figure 6. Frequency domain representation of intertrial phase coherence (ITC) left motor components (*A*) and grand average (*C*). Subject average ITC is represented with the thick 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 and 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 nontapping conditions.

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 (13-16, 35). Likewise, visual rhythms have been long known to entrain to flashing rhythms (17), although visual rhythm studies usually look at activity at higher frequency ranges, e.g., 10-12 Hz, rather than at the lower frequencies used for SMS or auditory rhythm perception tasks. A recent study (42) has shown that audio-visual rhythms can elicit beta-coherence between EMG activity from a subject's nonmoving finger and EEG activity over the cortical motor region that was stronger than elicited by audio rhythms alone, suggesting that information on 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 for 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 the greater entrainment ability of one modality over the other, but rather in how that entrained activity is used.

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 with the synchronizing movement (43, 44). Further improvements have been seen when the moving visual rhythm follows an ecologically valid movement pattern, such as with a bouncing ball (45–47). Yet, the benefit of using moving visual rhythms does not appear to apply when there is no explicit motor task (48, 49). 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 visuomotor 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 of applying a Fourier transform to rhythmic stimulus to evoked potentials (50-52). 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 (53, 54). 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 than in 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.

In addition, we cannot entirely rule out effects of possible attentional differences between stimuli conditions. If the visual rhythms resulted in increased attentional focus compared with 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 the 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. Furthermore, 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 used 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.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

D.C.C. and R.B. conceived and designed research; D.C.C. performed experiments; D.C.C. analyzed data; D.C.C. and R.B. interpreted results of experiments; D.C.C. prepared figures; D.C.C. drafted manuscript; D.C.C. and R.B. edited and revised manuscript; D.C.C. and R.B. approved final version of manuscript.

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