

RESEARCH ARTICLE

Sensory Processing

Cortical mu rhythms during action and passive music listening

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Abstract

Brain systems supporting body movement are active during music listening in the absence of overt movement. This covert motor activity is not well understood, but some theories propose a role in auditory timing prediction facilitated by motor simulation. One question is how music-related covert motor activity relates to motor activity during overt movement. We address this question using scalp electroencephalogram by measuring mu rhythms—cortical field phenomena associated with the somatomotor system that appear over sensorimotor cortex. Lateralized mu enhancement over hand sensorimotor cortex during/just before foot movement in foot versus hand movement paradigms is thought to reflect hand movement inhibition during current/prospective movement of another effector. Behavior of mu during music listening with movement suppressed has yet to be determined. We recorded 32-channel EEG ($n = 17$) during silence without movement, overt movement (foot/hand), and music listening without movement. Using an independent component analysis-based source equivalent dipole clustering technique, we identified three mu-related clusters, localized to left primary motor and right and midline premotor cortices. Right foot tapping was accompanied by mu enhancement in the left lateral source cluster, replicating previous work. Music listening was accompanied by similar mu enhancement in the left, as well as midline, clusters. We are the first, to our knowledge, to report, and also to source-resolve, music-related mu modulation in the absence of overt movements. Covert music-related motor activity has been shown to play a role in beat perception (Ross JM, Iversen JR, Balasubramaniam R. *Neurocase* 22: 558–565, 2016). Our current results show enhancement in somatotopically organized mu, supporting overt motor inhibition during beat perception.

NEW & NOTEWORTHY We are the first to report music-related mu enhancement in the absence of overt movements and the first to source-resolve mu activity during music listening. We suggest that music-related mu modulation reflects overt motor inhibition during passive music listening. This work is relevant for the development of theories relating to the involvement of covert motor system activity for predictive beat perception.

electroencephalography; independent component analysis; neural oscillation; premotor; sensorimotor

INTRODUCTION

Mu-rhythm activity in the scalp electroencephalogram (EEG) has long been associated with action and is consistently reduced in mean power during and in preparation for body movements, as most commonly observed in paradigms using hand movements. Mu power reduction with movement, known as mu event-related desynchronization (ERD),

mu suppression, or mu blocking, may arise from a decrease in synchrony of local field potential (LFP) activity in one or more areas of cortex related to cortical action processing (1). The EEG mu rhythm is most dominant in the same 8–12 Hz frequency band as posterior alpha rhythms, but unlike posterior alpha recorded over occipital cortex, mu activity is recorded from scalp electrode sites near sensorimotor areas. Both posterior alpha and sensorimotor mu rhythms have

been associated with cortical inhibition, but of different processes (2); posterior alpha activity in visual cortex is suppressed during covert visual attention (3, 4) and visual working memory maintenance (5), whereas sensorimotor mu activity is associated with active inhibition of body movements (2). Mu oscillations, unlike alpha, appear as sharp convex arc-shaped (i.e., suggestively “ $\mu\mu\mu$ ”-shaped) periodic waveforms that, when converted to the frequency domain, exhibit a strong fundamental in the alpha range and smaller harmonics in the beta and high-beta range. The alpha-range and first harmonic peaks are modulated in parallel during ERD and during ERS (event-related desynchronization/synchronization) or in a state-related mu power decrease or increase, so a decrease or increase in one band typically also occurs in the other (1).

There is some evidence that mu activity is sensitive to motor system activity not tied to overt movements, best demonstrated by modulation during imagined movements (6). Pfurtscheller and Neuper (7) provided evidence for mu sensitivity to motor cortical inhibition. They found that dorsal flexion of the right foot resulted in a transient mu power increase in both left and right hemispheres, over what appeared to be sensorimotor hand areas, suggesting that excitation of the foot sensorimotor areas may have been accompanied by inhibition of other sensorimotor areas (e.g., the hands in their hand-vs.-foot movement paradigm). Importantly, this study shows that rather than simply representing an “idling” (passive resting) state or instructed abeyance of action in general, willful movement inhibition of a specific effector may produce enhanced mu rhythms, for example, in response to or in preparation for instructed movements of other effectors.

The brain-computer interface literature on nonmuscle-mediated communication supports that mu activity is present in the idle awake state and during instructed abeyance of action and is suppressed during movements, action imagination, and action observation (for a review, see Ref. 8). This brain-computer interface (BCI) literature provides the most consistent demonstration of mu modulation with imagined movement. Pfurtscheller et al. (9) were able to discriminate between EEG mu power in imagined movement of the left and right hands in three subjects, suggesting sensitivity of mu power to unilateral imagined movement (also reviewed in Ref. 10). Shortly following, mu ERD with imagined movement was shown in more detail using voltage and spectral changes across the scalp with a larger sample of adults by McFarland et al. (11). Mu ERD with unilateral hand movement designs appears to be replicable (12, 13) and have high classification accuracy at the individual subject level (12). When compared with actual movement, imagined movement can induce from 25% of the ERD to more than 100% with biofeedback-based training (13), as shown in this study using ECoG. Miller et al. (13) highlighted the importance of primary motor cortex for the mu ERD response and its relevance for user-controlled BCI systems.

An open question is whether mu activity is also sensitive to brain motor system activations that are known to occur during perception of musical rhythm. Music listening appears to be tightly bound to the motor system. To move to music is so compelling that it often occurs without intention and appears to reinforce positive affect during music

listening (14). This music-movement relationship is strong enough to be used for optimizing body movement, as in the case of atypical gait (15, 16). Music has measurable impacts on distributed muscle activity, including those used for postural control (17). The connection is strong enough that even when we are not overtly moving, motor structures in the brain and corticospinal pathways are active when we listen to rhythmically patterned sounds including music, as shown with functional brain imaging (18–21), magnetoencephalography (MEG) (22, 23), transcranial magnetic stimulation (TMS), and electromyography (EMG) (24, 25).

Although an intimate music-movement relationship is apparent, it is not known what role this so easily recruited motor activity has in rhythm perception per se. It has been suggested for some time that covert motor activity may serve to perceptually scaffold the beat (22, 26) or guide temporal expectations (22, 27, 28). In one synthesis of this work, Patel and Iversen, in their action simulation for auditory prediction (ASAP) hypothesis, propose that internal motor planning activity has a necessary role in the predictive aspect of beat-based auditory rhythm perception (29; see Ref. 30 for a review on this topic). However, this debate is missing some foundational knowledge about how covert motor activity during music listening relates to motor activity during overt movement. Understanding the relationship between covert music-induced motor system activity and motor system activity tied to overt movement is needed to better define internal motor simulation in this context. Because mu rhythms can be used to address questions of motor activity and inhibition without overt movement, they can be used to examine covert motor processes including those that occur during music listening. Furthermore, prior studies have typically focused on event-related potential (ERP) and beta-band modulations with beat perception, whereas mu has been largely unexamined. It is unknown whether the beta desynchronization studied previously (22, 23) was the first harmonic of mu or a separate phenomenon, although scalp topography, relationship to movement, and independent component analysis (ICA)- (31, 32) and principal component analysis (PCA)-based methods (11), as well as simultaneous EEG with functional magnetic resonance imaging (fMRI) (33), all support there is somatomotor cortical beta-band activity distinct from mu harmonic. Isolating mu harmonic from other beta sources is needed to fully understand the relationship between movement, beat perception and prediction, and underlying motor processes.

The relevance of mu activity to action and action planning is backed by an extensive literature, but previous examinations of mu activity during music listening are scarce. Li et al. (34) reported mu suppression during music listening, but the sound stimuli they used were produced by people playing a game that made noise when the player performed certain key presses. Although these stimuli might have sounded musical to some extent, they were not musical compositions with predictable rhythms and beat structure and were in any case confounded by motor actions. The stimuli were presented to subjects who had played the game previously and, therefore, had associations between the sounds and the movements that would have produced the sounds. Although Li et al.’s results cannot be extended to understanding of

changes in mu activity during musical rhythm perception, their study shows that motor imagery induced by sounds can be associated with changes in mu power (34).

Mercadié et al. (35) asked whether there are interactions between mu ERD during music listening and osteopathic treatments involving two people listening to music that is synchronized or desynchronized across the dyad. Although their results suggest there could be mu ERD with music listening, their results in fact show no significant main effects. Regardless, whether or not the subjects were asked to sit still while listening was not stated.

Recent work from Wu et al. (36), and later Wu et al. (37), demonstrated that mu modulations may occur with specificity related to training—in subjects with piano training who listen to piano tones. The authors concluded that the effect is specific to trained sound-action mappings.

Much of the work on mu during movement has used a hand or finger as the movement effector. It is not yet agreed whether mu activity in these experiments originates specifically in hand sensorimotor areas, or if the cortical mu source area is less focal (38). Although the results described in Pfurtscheller and Neuper (7) may be interpreted to imply that the sources of mu activity have a topographical organization in accord with the well-known somatomotor homunculus, this topographical organization of mu source activity has often been implicitly assumed because sensorimotor cortical activity is generally topographically organized in both primary motor and facing somatosensory cortices. Some more recent EEG-fMRI evidence, however, does support this topographical organization of mu source activity (39).

Here, we source-resolved mu during music listening, and use mean mu-rhythm power changes to study movement planning and simulation, both of overt movements of different effectors and during music listening without overt movements. In the experiment reported here, we observed mu activity during movement of the right hand or right foot and during sitting without movement in silence and during music listening. We hypothesized that mu activity would be relatively strong during quiet sitting and weakest during hand movements. We expected to replicate the findings of Pfurtscheller and Neuper (7) of mu power increase during foot movements. We also expected to observe modulation of mu activity during music listening because of its concomitant motor system activation. Based on the limited existing reports on mu rhythms during music listening, we were unsure whether to expect an increase or decrease in mu power. However, our predictions were that if mu is related to action inhibition, then we expected an increase in mu while listening to music, but if mu is related to motor imagery, then we expected a decrease in mu while listening to music.

Based on existing evidence (7, 8), we expected that mu power modulations would be unilateral. Specifically, left hemisphere mu activity contralateral to the right hand and foot movements would be expected to decrease in power in left somatomotor cortex controlling right hand/foot movements, but not in the hemisphere ipsilateral to movement.

To our knowledge, this is the first study to examine mu activity systematically during musical listening, as well as during motor action and silent inaction.

MATERIALS AND METHODS

Participants

Seventeen healthy adults (15 females, 2 males) between the ages of 18 and 26 (mean age = 21.765 ± 2.73 yr) were recruited from the University of California, Merced student population. All subjects were right-hand dominant. There was a range in the number of years of musical training and/or experience; 5 subjects reported 3 or more years, 1 subject 2 yr, 1 subject 1 yr, and 10 subjects reported none. All subjects were screened for hearing impairment, amusia, neurological or movement conditions, and recent injury to arms or legs. The experimental protocol was carried out in accordance with the Declaration of Helsinki, and all participants gave written informed consent before testing.

Experimental Protocol

Participants were asked to remain seated without moving while maintaining eyes-open fixation on a cross in front of them during the experimental trials. The experiment was controlled using Paradigm software (version 2.5.0.68). There were four conditions, presented in a randomized order, each comprised of 36 10-s-long trials. In the silent condition, subjects were instructed to sit motionless in silence. In the finger-tapping condition, subjects were instructed to tap freely at an approximate rate of two taps per second with the index finger of their right hand. In the foot-tapping condition, subjects were instructed to tap freely, also at an approximate rate of two taps per second, with their right foot. In the music listening condition, subjects were instructed to listen to clips of music while sitting motionless. Although all subjects were instructed not to move in the silent and music conditions, and were monitored visually by experimenters, it is impossible to quantify how much subjects in fact moved during those trials without kinematic recordings. However, instructions to sit motionless were clearly presented to subjects, and subjects were observed to be compliant in all conditions (as in they did not make any noticeable voluntary or involuntary movements).

Musical stimuli were created from the 12 instrumental musical excerpts used in the Beat Alignment Test (BAT), Version 2 (40). Musical excerpts were presented without an overlying metronome beep (in contrast to their use in the BAT). These excerpts were taken from several genres (jazz, rock, orchestral), were each 11 s in length with an amplitude ramp up at the beginning of the stimulus and an amplitude ramp down at the end of the stimulus (up and down ramps were both over a 500 ms length of time), and were digitized at 44.1 kHz (mono). The musical excerpts were normalized and compressed to have equal mean, minimum, and maximum volume.

EEG was collected during all trials using an ANT Neuro Waveguard 32-channel 10-20 EEG system with sintered Ag/AgCl electrodes, an Asalab amplifier and Asalab software. The EEG cap was placed at a known location relative to fiducials (channel Cz on the midpoint of line between nasion and inion). Data were sampled at 1,024 Hz. At the beginning of each trial, an event was sent from Paradigm to Asalab to mark the start of a new trial in the EEG recording. Tap times were not recorded. Segments of EEG were extracted for each

trial, starting at the recorded trial onset and lasting 10 s. This protocol was reviewed and approved by the University of California Merced (UCM) Institutional Review Board.

Analyses

All EEG preprocessing and analyses were performed in MATLAB R2019a (MathWorks, Natick, MA) using the EEGLAB v2019.0 toolbox (41), following “Makoto’s Preprocessing Pipeline” (https://scn.ucsd.edu/wiki/Makoto's_preprocessing_pipeline). EEG data were down sampled to 256 Hz, then 1-Hz high-pass and 50-Hz low-pass filters were applied (basic FIR; Ref. 42). Line noise was removed using the *pop_cleanline* plugin (60 and 120 Hz), and channel rejection and noise removal was applied using the *clean_rawdata* plug-in (5 s flatline criteria, [1 2] Hz transition band, minimum channel correlation criteria 0.80, line noise criteria 5 standard deviations, 5 standard deviation cutoff for automated subspace removal (ASR) of bursts, and maximum fraction of contaminated channels tolerated in each window 0.5). Data were re-referenced to the sample-by-sample all-channels average. Data were epoched (from trial onset to 10 s) and aberrant epochs were rejected based on conservative criteria (43), by applying an amplitude threshold of ± 500 μ V. In addition, we applied a data improbability test. This method of excluding artifacts computes the statistical probability of observing a value in the observed distribution, and we used a 6 standard-deviation threshold for single-channel and a 2 standard-deviation data rejection threshold for all-channels activity level, as recommended by Delorme et al. (43).

Extended infomax independent component analysis (ICA) decomposition was performed separately on each subject’s preprocessed data (converted to average reference) after applying principal component analysis (PCA) to reduce the data dimension by 1 before ICA decomposition. Single (or rarely, dual-symmetric) equivalent dipole model fitting (using *dipfit3.3*) was performed for brain-based independent component (IC) processes (defined as ICs having a brain-centered equivalent dipole model with scalp map residual variance, after subtracting the equivalent dipole model scalp projection, below 15%). Equivalent dipole fitting used a head model based on a standard Montreal Neurological Institute (MNI) magnetic resonance (MR) head image. Thereafter, across-subjects IC cluster analysis was performed (as described in *Analyses*, paragraph 5) based on similarities in component equivalent dipole locations.

ICA decomposition is a data-driven signal analysis technique for blind source separation (44). ICA separates a signal into maximally temporally independent components (ICs) and can be used to interpret scalp EEG recorded during experimental tasks as the sum of localizable brain processes plus nonbrain (“artifact”) and small noise-like processes (21, 45–47). Scalp data accounted for by any IC can be backprojected into the electrode montage by multiplying the IC activation time course by the IC scalp map representing the topographic distribution of its projection to the scalp channels (48, 49). In the current study, the locations of the equivalent dipole models for the brain-based ICs, as well as their spectra and other signal properties, were used to determine which ICs were mu-related (50). This allowed analysis of mu-related maximally independent EEG signal source processes in individual subjects for the four conditions.

Visual inspection of the raw time series data revealed the presence of sharp convex arc-shaped periodic waveforms with alpha-band frequencies of oscillation in every subject. We studied the IC topographic (scalp) maps and frequency profiles to determine the presence of components that were mu-related, using criteria set out in Pfurtscheller and McFarland (50). We looked for sources projecting to both scalp hemispheres, typically with opposing signs dominating, that project more strongly to central than to occipital scalp. Furthermore, mu IC source activity spectra should have near-harmonically related peaks in the alpha and beta bands, due to converting the mu waveform shape to the frequency domain, although beta-band activity can have mixed sources resulting in flattened or unclear harmonics in some subjects. However, all the ICs that met these criteria (alpha and beta peaks, with project more strongly to central than occipital) had equivalent dipoles that were compatible with the source being generated in or near primary somatomotor or premotor areas.

To compare spectral power across conditions and subjects in mu clusters, a *k*-means IC clustering method was used on all brain components (51) before identifying mu-related clusters. IC clustering is used to group ICs from different data sets that are most likely generated in the same cortical area. The *k*-means clustering of ICs is based on an IC distance measure composed from selected spatial and/or activity measures; here, we used dipole location only. To determine the appropriate number of clusters, we applied three measures for cluster number optimization (Calinski-Harabasz, Silhouette, and Davies-Bouldin) for between 10 and 30 clusters. The optimal number of clusters was determined to be 21 using the Calinski-Harabasz method, 30 using the Silhouette method, and 18 using the Davies-Bouldin method. We used 18 clusters to maximize the number of unique subjects per cluster, plus 1 outlier cluster for components with dipole positions 3 or more standard deviations from any of the cluster centers. We then calculated cluster centroids, defined as the points in the template head model that minimized the total root mean square distance from all of the cluster ICs (51). Cluster-mean scalp maps and activity spectra were used to define which clusters were mu-related. Mu clusters were determined based on sources projecting to both hemispheres with opposite signs dominating, more central than occipital, with near-harmonically related peaks in the alpha and beta bands. Visual inspection confirmed that all the individual ICs in each mu-related cluster had consistent scalp map appearance. It should be noted that although the number of clusters used for this technique is predefined, the experimenter is agnostic to the number of ICs that cluster together, or number of ICs per subject that get assigned to the same cluster. For these reasons, it is important to report these details.

A one-way repeated-measures ANOVA was used to compare mean power in the (8–12 Hz) alpha range between the four conditions in each identified mu-related cluster (7, 50). Another one-way repeated-measures ANOVA was used to compare mean power in the (16–24 Hz) beta-band range including the first mu harmonic across the four conditions for each mu-related cluster (7, 50). These ANOVAs were followed by pairwise comparisons to assess how source-resolved mu activity differed between the four conditions.

To interpret the localization results, when we describe IC source activity “corresponding to cortical region xxx,” we mean a centroid that when projected radially toward the scalp surface “is IN cortical region xxx,” as due to the inaccuracies of using a template head model for dipole localization some dipoles may be displaced more deeply into the brain for some participants than for others (52).

Accessibility

The EEGLAB (v2019.0) tools that were used to analyze all the data can be downloaded from the Swartz Center for Computational Neuroscience website: <https://sccn.ucsd.edu/eeGLAB/download.php>. Paradigm software (version 2.5.0.68) was used to present the instructions and to sync the start of each trial with the EEG data. EEG data were collected using a

32-channel ANT Neuro Waveguard 10-20 system with sintered Ag/AgCl electrodes, an Asalab amplifier and Asalab software.

RESULTS

Three clusters met the topographic and spectral criteria and were thereby determined to account for mu-related brain activity. One cluster centroid was localized by equivalent dipole analysis to the left hemisphere (Fig. 1), one to the right hemisphere (Fig. 2), and one to the central sulcus but including component scalp maps that suggest bilateral source contributions (Fig. 3).

Left Hemisphere Mu Cluster

The left hemisphere IC cluster was a group of 19 ICs that included 1–3 ICs per subject (mean = 1.58, SD = 0.7) from 12 subjects. The centroid was at Talairach coordinates (−39,

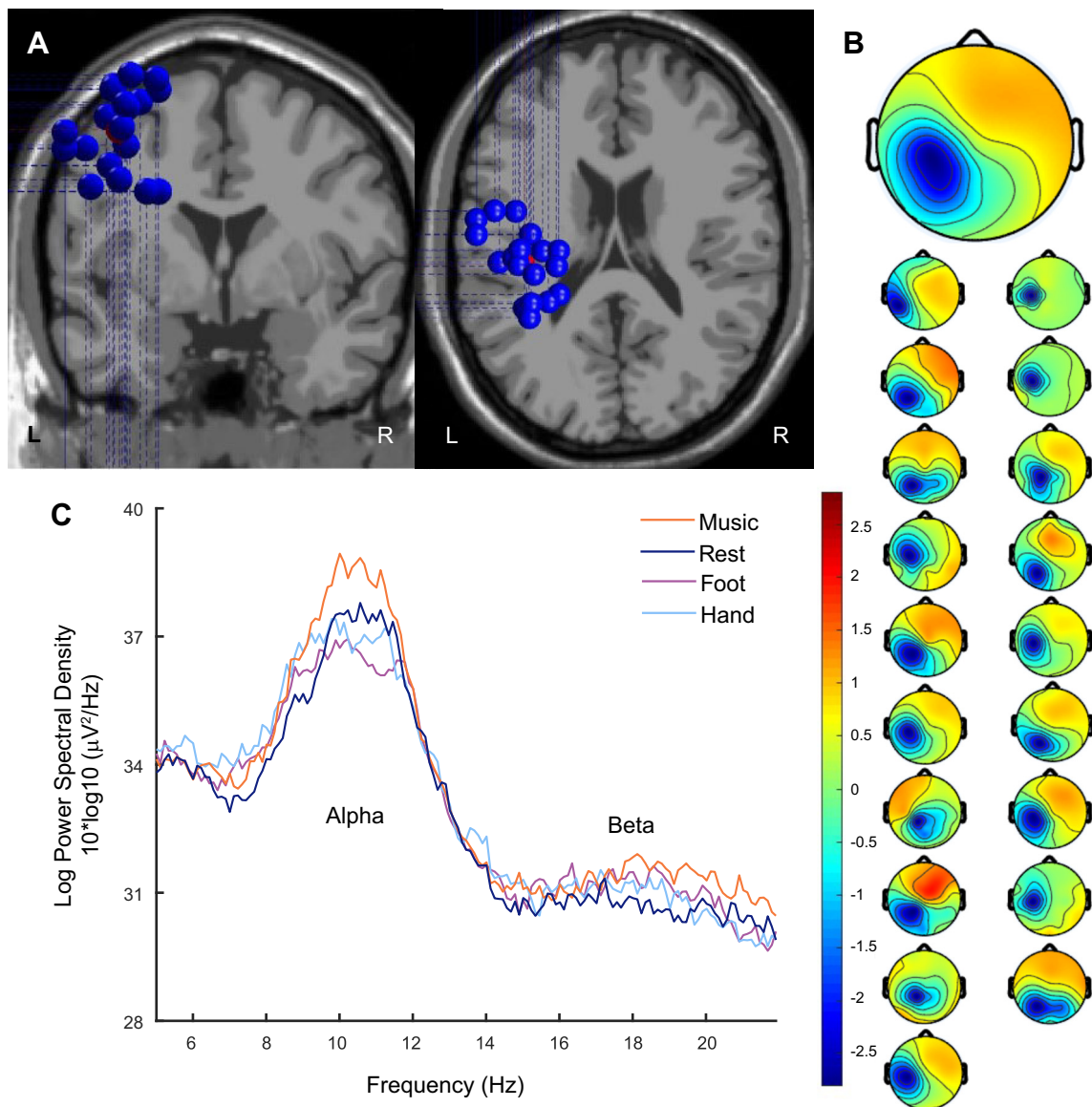


Figure 1. Left hemisphere mu-rhythm cluster (19 independent components from 12 participants). *A*: cluster component equivalent dipoles in blue and dipole centroid in red. Centroid localized to Talairach (−39, −22, 51), left BA4 in or near right hand somatomotor cortex. *B*: cluster mean (top) and individual independent component (IC) scalp maps (bottom). + [red]; 0 [green]; − [blue]. *C*: cluster mean log power spectra in the 4 experimental conditions. The broad 16–24 Hz beta-band peak comprises mu harmonic and other beta-band activity.

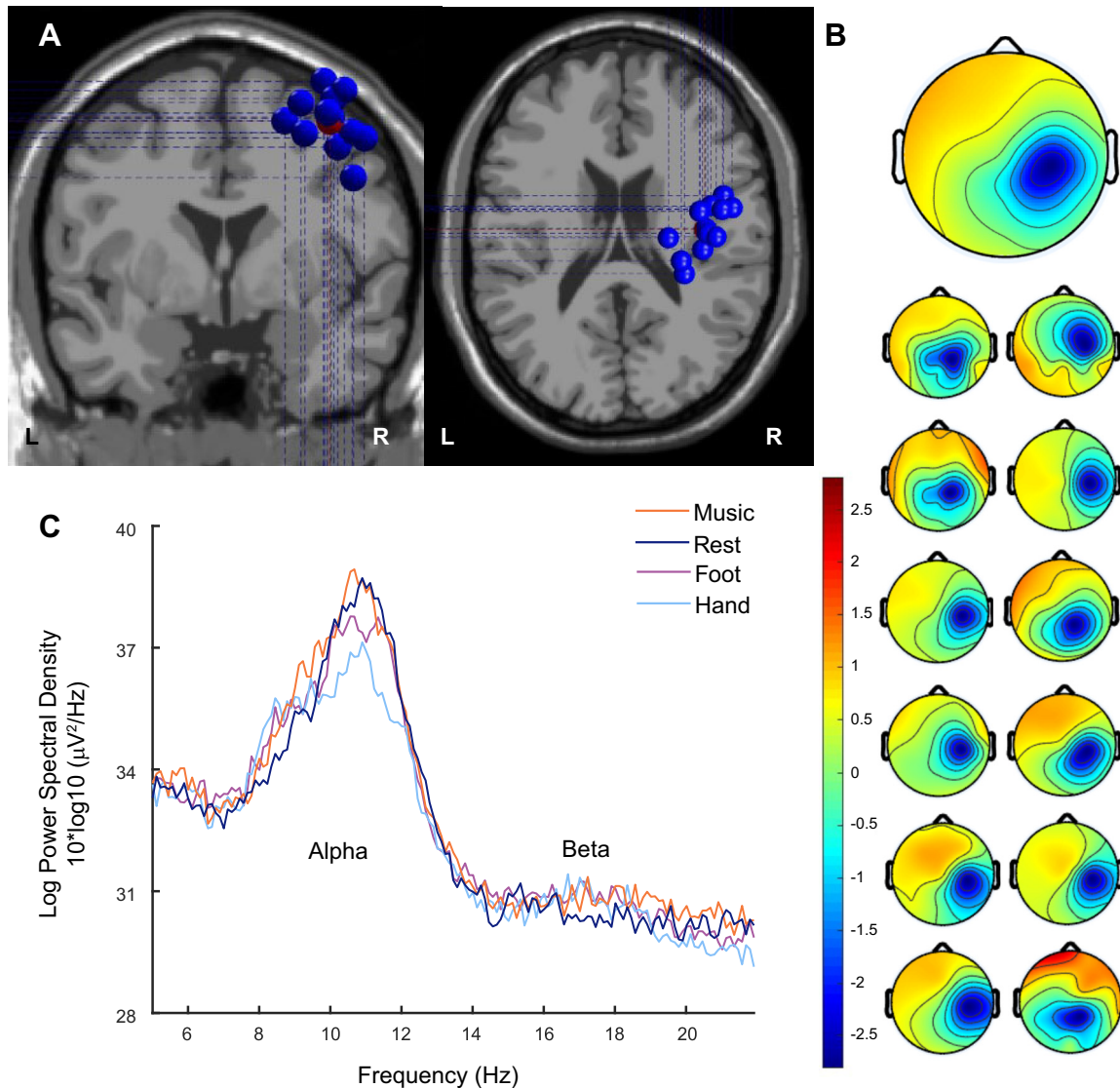


Figure 2. Right hemisphere mu-rhythm cluster (12 independent components from 10 participants). **A:** cluster component equivalent dipoles in blue and dipole centroid in red. Centroid localized to Talairach (38, −9, 52), right BA6 near left hand somatomotor cortex. **B:** cluster mean (top) and individual independent component (IC) scalp maps (bottom). + [red]; 0 [green]; − [blue]. **C:** mean log power spectra in the 4 experimental conditions. Note evidence for 2 mu peaks in each condition (near 9 and 11 Hz) and the broad, shallow beta-band peak with some suggestion of inflection points near mu first harmonics (18 and 22 Hz).

−22, 51), corresponding to left primary motor cortex in Brodmann area 4 (MRIcon, v1.0.20190902). See Fig. 1 for the cluster component and mean equivalent dipoles, mean and individual IC scalp maps, and cluster mean spectra in the four conditions. In each condition, the cluster activity spectrum exhibited both sharper alpha and broader beta that peaked at the first harmonic of the alpha power maximum.

The left mu cluster exhibited 8–12 Hz alpha-band spectral power differences between conditions [$F(3,140) = 8.63$, $P < 0.00003$; Figs. 1C and 4A]. There were also differences in 16–24 Hz beta-band spectral power between conditions [$F(3,212) = 23.22$, $P < 4.9 \times 10^{-13}$; Figs. 1C and 4B].

Pairwise comparisons revealed the following: that mu power was higher during music listening than rest, hand or foot movement. During right foot tapping, mean peak power was larger than in the resting condition in the beta range ($P = 0.006$),

consistent with the ERS during foot tapping and topographical organization of mu sources in cortex found by Pfurtscheller and Neuper (7). Music listening while sitting motionless produced mu-source spectra with a power increase (ERS) compared with rest in both the alpha ($P = 0.0007$) and beta ($P < 0.0001$) ranges. Mu power during music listening was also higher than during right hand movement in both the alpha ($P = 0.01$) and the beta ($P = 0.0001$) ranges and higher than during right foot movement in both the alpha ($P < 0.0001$) and the beta ($P = 0.0001$) ranges. All statistical analyses were run on mean power (Fig. 1C), but we also show ratios of hand, foot, or music conditions over silent rest in Fig. 4, A and B.

Right Hemisphere Mu Cluster

The right hemisphere mu cluster was a group of 12 ICs that included 1–2 ICs per subject (mean = 1.20, SD = 0.4) from

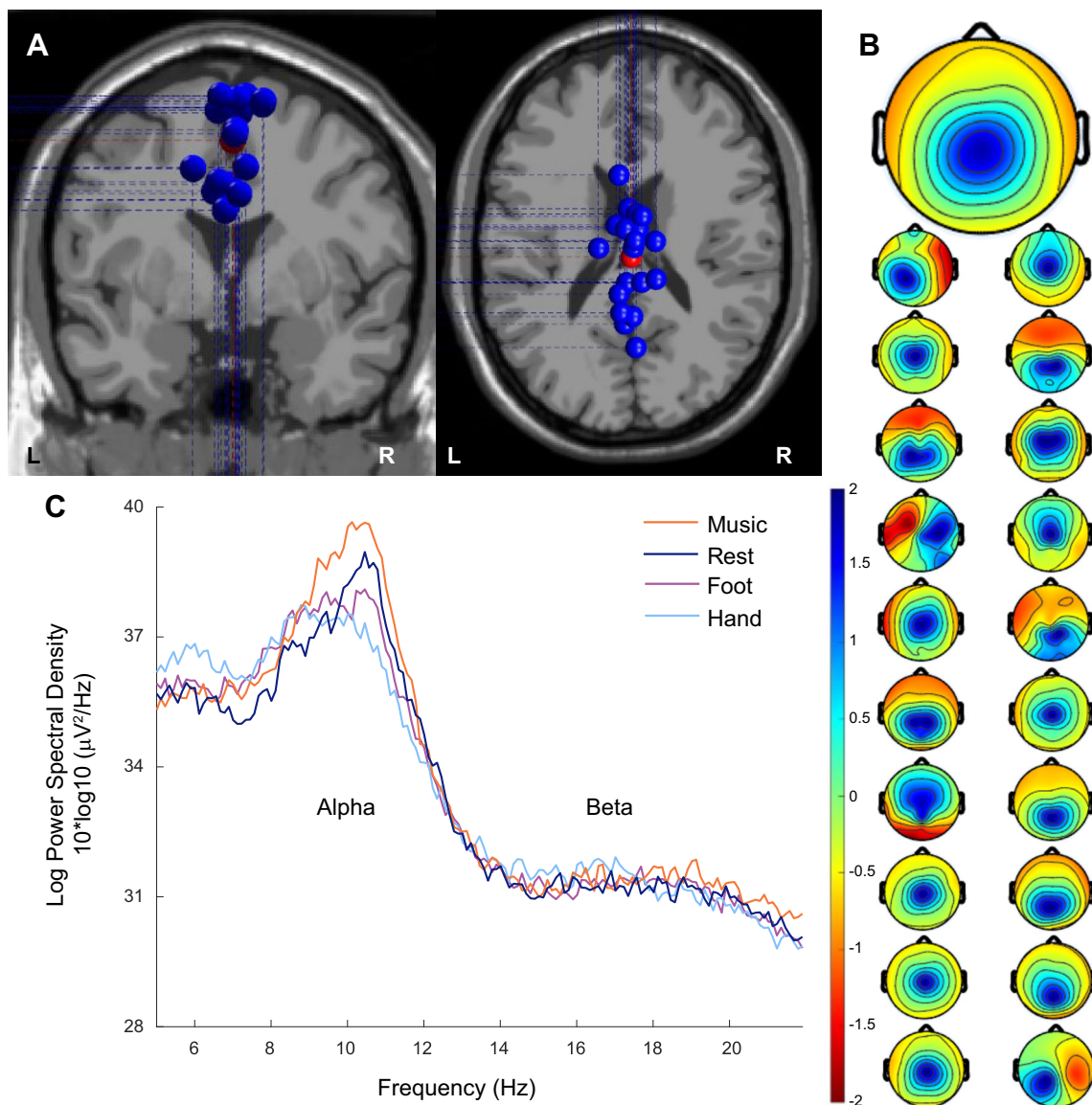


Figure 3. Midline mu-rhythm cluster (20 independent components from 12 of the participants). **A:** cluster component equivalent dipoles in blue and dipole centroid in red. Centroid localized to Talairach (1, −19, 49), BA6 possibly near foot sensorimotor cortex. **B:** cluster mean (top) and individual independent component (IC) scalp maps (bottom). + [blue]; 0 [green]; − [red]. **C:** mean log power spectra in the four experimental conditions.

10 subjects. The cluster centroid was at (Talairach: 38, −9, 52), corresponding to right premotor cortex, in Brodmann area 6 (MRIcon, v1.0.20190902). See Fig. 2 for the cluster component and centroid equivalent dipole positions, mean and individual IC scalp maps, and cluster centroid mean spectra in the four conditions. Each condition again exhibited alpha and beta range peaks. In each condition, the mean spectra gave evidence for two alpha peaks at ~9 Hz and 11 Hz.

There were differences between conditions only in mean 8–12 Hz alpha-band spectral power [$F(3,140) = 8.01$, $P < 0.00006$; Figs. 2C and 4C]. The pattern of relative alpha-band power was very different from the left mu cluster. Only the right hand finger tapping condition differed from rest, showing a significant decrease in alpha power ($P = 0.03$). Right hand finger tapping was also significantly less than during right foot tapping ($P = 0.03$)

and during music listening ($P < 0.0001$). Figure 4, C and D, depicts condition ratios of hand, foot, and music to the rest condition.

Midline Mu Cluster

The midline mu cluster was a group of 21 ICs that included 1–3 ICs per subject (mean = 1.62, SD = 0.8) from 13 of the subjects. The cluster centroid was at (Talairach: 1, −19, 49), corresponding to premotor cortex, Brodmann area 6 (MRIcon, v1.0.20190902). See Fig. 3 for the component and cluster centroid equivalent dipole positions, mean and individual IC scalp maps, and the cluster centroid mean spectra in the four conditions. Each condition exhibited an alpha range peak and possible increased power in a broad beta range.

There were significant differences between conditions only in mean 8–12 Hz alpha-band spectral power [$F(3,140) =$

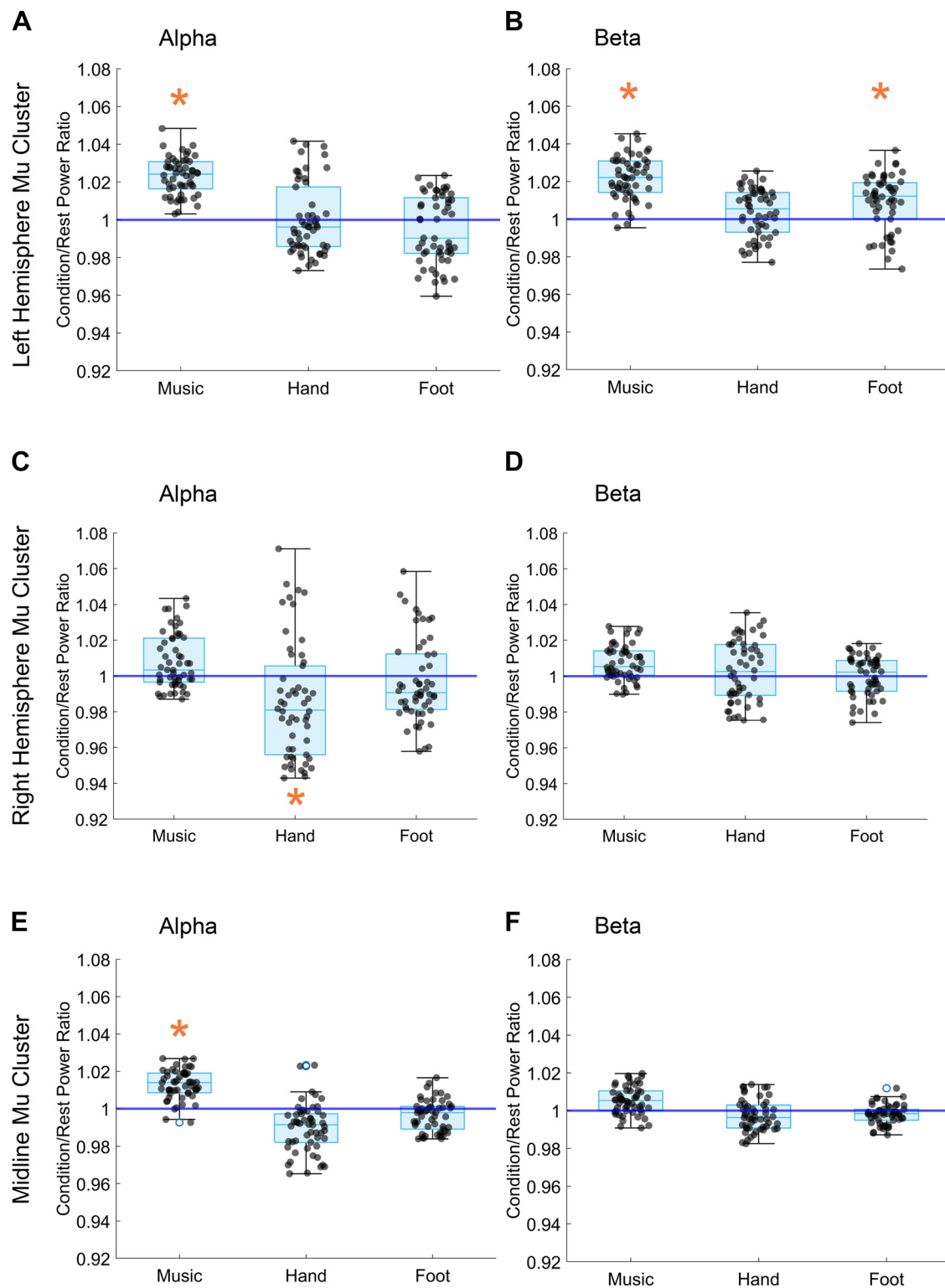


Figure 4. Ratios of mean power during music listening, hand movement, and foot movement conditions to mean power in the rest condition (ERD, this ratio < 1; ERS, this ratio > 1). Asterisks mark conditions significantly different from the rest condition. Left hemisphere mu-rhythm cluster spectral power change from rest in alpha (A) and beta (B) ranges. In addition, in the left hemisphere, music listening produced more power than right hand movement and right foot movement in both alpha and beta ranges. Alpha (C) and beta (D) right hemisphere source cluster spectral power changes compared with rest. In right hemisphere sources, right hand movement produced less power than rest, right foot movements, and during music listening. Midline mu-rhythm cluster spectral power changes from rest in alpha (E) and beta (F) ranges. Music listening produced more mean mu power than rest, right hand movement, and right foot movement. ERD, event-related desynchronization; ERS, event-related synchronization.

9.57, $P = 8.6 \times 10^{-6}$; Figs. 3C and 4E]. Pairwise comparisons revealed that music listening while sitting produced more mean alpha power than in the resting condition ($P = 0.02$), during right hand finger tapping ($P < 0.0001$), or during right foot tapping ($P = 0.002$). Figure 4, E and F, depicts condition ratios of hand, foot, and music to the rest condition.

DISCUSSION

We measured source-resolved mu activity in the 8–12 Hz alpha range, as well as in a broader beta-band peak in the 16–24 Hz range (7, 50) during four conditions: movement of the 1) right hand or 2) right foot, and during sitting still 3) without moving in silence and 4) during music listening. Our findings during hand and foot movement conditions are consistent with past reports showing suppression of mu over hand somatomotor cortex during hand movement, and increased mu over hand somatomotor cortex during foot movement, which might support active movement inhibition of the right hand during directed foot movements. Right foot movement was accompanied by a left lateralized mu modulation, as was found by Pfurtscheller and Neuper (7). Although we did not observe a corresponding modulation in the right hemisphere, in contrast to Pfurtscheller and Neuper (7), our result supports their interpretation that mu-rhythm activity is associated with movement inhibition, in this case of the hand while tapping the foot.

We expected that while sitting still while listening to music the level of mu activity might differ from its level in the “sitting still in silence” condition, related to concomitant covert music-related motor cortical activity supporting music listening, but we were unsure whether to expect a mean power increase or decrease based on the limited reports on mu rhythms during music listening. In addition, there were theoretical reasons for expecting either an increase in mu (movement suppression) or decrease (movement imagery). Here, sitting still while listening to music was, in fact, accompanied by mu power increases that correspond to left and midline somatomotor areas relative to sitting in silence. If interpreting increased mu power as due to cortical inhibition (7), our results are consistent with the occurrence of active hand (or other upper body limb) movement inhibition during music listening. Supporting this interpretation, we report a relative mu increase in the left hemisphere mu cluster during music listening without movement that was even greater than during right foot movements (without music). During still music listening, mu activity also increased in the midline cluster.

The increased mu activity during music listening may reflect active suppression of an urge to move, possibly an urge to move the hand, or more global upper limb, feet, or more global lower limb. As work on musical “groove” shows sensorimotor coupling is pleasurable and listening to music can lead to an urge to move in time to the rhythms of the music (14). Motor systems are active when we listen to rhythms (18, 19, 23) and suppression of overt body movement is natural during restful listening or as required in social settings inappropriate for music-related movement, and in experimental paradigms in which the participant is asked to sit still such as in the task reported here.

The nature of and particular role of music-listening-related motor network activity without overt movement is unknown, but there is mounting evidence that it is necessary to support auditory timing predictions (53–56). However, active suppression of overt movement may be a separate process invoked in addition to hypothesized covert motor activation supporting temporal expectations. As our task included an instruction to remain still during music listening, our EEG results may be evidence for enhanced motor inhibition during the music listening condition, but do not rule out other forms of motor planning activity, and indeed may support the involvement of motor planning during music listening (for presumably movement would only need to be suppressed if it was intended).

It is unknown which acoustic properties of the musical stimuli contributed most to mu modulation. The 12 BAT stimuli vary on a number of audio features, and features such as tempo and pulse clarity can impact the listener's urge to move in time with the music (57), and conceivably also modulation of mu. In addition, it is possible that mu modulation may have a time course related to acoustic changes over the course of a musical excerpt. Further work is needed to determine the musical contributors to mu modulation, and to examine the time course of mu modulation during music listening. For details on the BAT stimuli, see Iversen and Patel (40) and Supplemental Table S1 (all Supplemental material is available at <https://doi.org/10.6084/m9.figshare.17203955.v1>).

One limitation of many imaging techniques is that it can be difficult to distinguish between excitatory and inhibitory processes. Our focus on mu during movement and during music reveals possible motor suppression during music listening. Further investigations are needed with designs that can distinguish music-listening-related motor network activity and motor inhibitory activity. One technique that is more commonly used to contrast excitatory and inhibitory processes is to measure motor-evoked potentials (MEPs) following single- or paired-pulse transcranial magnetic stimulation (TMS). Stupacher et al. (24) used single-pulse TMS in this way and showed that high-groove music reduced MEP amplitude when compared with low-groove music (see Ref. 14 for more on the phenomenon of “groove”), supporting that listening to music that compels movement may be accompanied by corticospinal motor inhibition. Interestingly, the opposite effect was found for subjects with musical training. Our sample of subjects had very little musical training in the current study, but based on Stupacher et al. (24), it might be predicted that the music-mu effect may be sensitive to musical training. In fact, it has been shown that mu modulation while listening to piano tones may have specificity related to musical experience and sensitivity to trained sound-action mappings (36, 37).

One cortical region implicated in tasks of beat-based timing and synchronization is supplementary motor area (SMA) (18, 55, 58, 59), often discussed in the context of internally generated periodicity (60, 61). The literature on mu, as well as our results, support mu source along the somatomotor areas. However, a direct link between music-related motor inhibition reflected in mu signal and internally generated

beat tracking in the SMA and striato-thalamo-cortical network is open territory for future research.

Some evidence suggests that auditory stimulation that is nonmusical can modulate motor system activity. Novembre et al. (62) compared vertex EEG response to auditory tones with pinch grip variations on a force transducer. These data suggest tight auditory-motor coupling as early as 100 ms after tone onset. One limitation in our design is that we do not have an auditory control condition, so it is possible that mu modulation with the musical sounds may not be specific to musical rhythms, but a result of auditory stimulation. Future work on music and mu should use an auditory control condition that is not rhythmically predictable.

Several forms of beta activity are known to exist, including frontal beta, rolandic beta, and high beta (63). This diversity strongly suggests that beta-band activity may encompass several different phenomena, as reported by Onton and Makeig (31), including mu-harmonic-related activity (63). Our analysis was designed to focus on mu-related signal, but because the beta range is a highly mixed region of the spectrum, we analyzed mu activity in alpha and beta bands separately to clearly show that the EEG effective source activities we isolated using ICA decomposition exhibited known mu activity characteristics. Evidence in support of activity in the two reported mu-activity source clusters being typical mu activity includes its stereotypical scalp distribution, frequency peak in the 8–12 Hz range, a beta-band activity peak including twice the frequency of the first peak, and stronger suppression during hand movement (50). Furthermore, condition differences in beta-band power in the mu-related clusters generally followed the mu-band power differences. Beta-band activity in nonmotor regions has been suggested to be involved in timing and anticipation, most likely independent of mu (22, 64), although how mu-harmonic activity is related to other beta activity that has been reported during music listening or other motor tasks is not yet known. Our beta-band activity was identified with the intention of focusing on mu-related signal and is, therefore, not necessarily relevant to the literature on nonmotor beta and musical beat perception. Development of the independent modulator analysis (IMA) plug-in for EEGLAB shows promise for future efforts to separate mu-rhythm first harmonic from other beta-band fluctuations (<https://github.com/scn/imat>; Refs. 31, 32).

The mu activity sources localized in our data to left and right motor or premotor cortex exhibited spectral power differences between hand and foot movement conditions, supporting previous proposals concerning topographical organization of mu source activity in primary somatomotor cortex.

Here, the left hemisphere source corresponded to primary motor cortex, and both right hemisphere and midline sources corresponded to premotor cortex, just anterior to primary motor. Although rostral divisions of premotor cortex do not project directly to primary motor, there is some evidence of somatotopy in caudal premotor areas just anterior to primary motor (65) from research using microstimulation (66, 67) and histological tracers (68) in nonhuman primates and single-pulse transcranial magnetic stimulation (TMS) in humans (69). At present, however, we cannot make strong anatomical claims about these localizations to specific effectors given the limitations of our data, for example, our lack of

individual electrode position measurements and our use of template rather than individual head models using standard rather than individualized estimates of skull conductance (70). Magnetoencephalographic (MEG) studies using precisely measured sensor positions, and less sensitive to head-model inaccuracies than for EEG, have localized hand-movement-related mu activity to small areas in primary somatomotor cortex in or close to the hand projection area (71, 72).

This work, to our knowledge, is the first to study music-listening-related mu modulation in the absence of overt movement and is also the first to source-resolve mu during music listening, reinforcing confidence that mu source activity is topographically organized in somatomotor cortex, something previously assumed from scalp projection patterns but not clearly demonstrated at the effective source level.

It is not yet clear how these findings and findings suggesting an active role for the motor system in precise temporal prediction relate. There is mounting evidence in fMRI blood oxygenation level-dependent (BOLD) studies for an active role of the motor system for auditory predictive timing and in brain stimulation studies for a necessary role. It is unknown what the correspondence is between fMRI BOLD activity, brain stimulation responses, and EEG mu, but the findings here suggest that inhibitory mechanisms in motor networks may accompany auditory-motor predictive processes.

SUPPLEMENTAL DATA

Supplemental Table S1: <https://doi.org/10.6084/m9.figshare.17203955.v1>.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

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

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