The Action-Perception of Musical Rhythm: A Review of EEG Findings

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Electroencephalography (EEG) research has the potential to illuminate questions of connectivity and temporal dynamics during musical rhythm perception. The phenomenon of sensorimotor synchronization observed when humans time their movements to rhythmic auditory stimuli reveals that these actions predict, rather than respond, to the beat. The phase entrainment of oscillatory activity measured by EEG and predictive modulation of beta band power offer cognitive insights to the auditory-motor relationship. Two main approaches exist to understand beat perception: motor simulation theories and dynamical systems theories. The study of mu wave suppression, considered a marker for mirror activity, has the potential to elucidate the explanatory strengths of these theories.

At its outset, this research was meant to explore the contributions of the mirror neuron system (MNS) to the perception of acoustic sounds, namely musical rhythm. The MNS is understood to activate during both the observation and execution of an action\(^1\). Mu rhythm activity is suppressed during action observation and execution and localized to motor regions where substrate for the MNS is supposed to exist in humans\(^1\). Given these temporal and spatial resemblances, mu suppression has been considered a measure of MNS activity\(^1\) and became the dependent variable of focus for this review. Mirror neurons as an associative mechanism for perception in humans has been effectively disputed on the grounds of logical and methodical shortcomings in foundational research\(^2\). Mu suppression research, however, maintains its relevancy to the perception of movement without asserting that single neurons are responsible for an imitation-based perceptual mechanism. This research arrived at an investigation of how
neurophysiological makers of motor activity inform our understanding of beat perception and how future mu suppression research can extend this knowledge.

The psychophysics of beat perception explored in this review lose relevance without first discussing the behavioral manifestation of these phenomena. Sensorimotor synchronization (SMS) describes the phase alignment of repeated sensory inputs with repeated motor output. The present review attenuates auditory stimuli and small movements such as tapping with the hand or foot. This specificity in effectors is not meant to underplay the daily significance of SMS, examples of which can be found in music performance and dance. The basic step of a social dance like west coast swing or cumbia, for example, requires that dancers alternate the distribution of weight between feet at a frequency they perceive while listening to music comprised of complex rhythms. The ubiquitous relationship between listening and coordinated movement is a bedrock from which this research springs.

The simplicity of tapping studies allows researchers to precisely relate the timing of acoustic events with movement. There is a striking observation replicated over many studies: while participants listen to a beat, on average, they tap just prior to the onset of sound when asked to synchronize with it. This beat is an isochronous sequence of clicks or volume impulses (like those of a metronome) within a perceptual range of 0.5 Hz to 4 Hz, or 30 to 240 bpm. The time interval between the beat onset and the typically preemptive tap is referred to as the negative mean asynchrony (NMA). In their review of SMS, Repp and Su suggest that this observation indicates a predictive mechanism in which movement to the beat is not responsive but predictive.
Following this research, electroencephalography (EEG) techniques have been employed to study the neural systems responsible for the predictive timing observed during SMS in certain conditions. At the level of individual neurons, post-synaptic potentials (PSPs) occurring as action potential reach axon terminals generate dipoles with a particular orientation\(^5\). The summation of dipoles with like orientation, thousands to millions of them, result in an electrical potential recordable from electrodes placed on the scalp\(^5\). It is the oscillatory activity recorded at this level considered by the present work. The high temporal resolution of this technique lends itself to the study of rhythm perception, where SMS and its neural correlates predicts stimulus onset by hundreds of milliseconds\(^5,10\).

Studies using EEG and magnetoencephalography (MEG; a similar technology achieving greater spatial resolution by measuring the magnetic fields generated by electrical current) provide evidence that large collections of neurons entrain to the beat of acoustic rhythms. Pioneering work by Nozaradan, Peretz, Missal, and Mouraux shows increased spectral power at 2.4 Hz across all electrodes while participants listened passively to a beat at 2.4 Hz\(^6\). In addition to the beat of an auditory stimulus, attentional choices can determine the enhancement of frequencies in spectral data. When asked to imagine a binary meter, where the strong beat is placed on every other note, peaks in spectral power were observed at the frequency of the acoustic beat, 2.4 Hz, and at the frequency of imagined accents, 1.2 Hz\(^6\). When participants were asked to imagine a ternary meter, where accents are placed on the first note in a group of three, spectral peaks occurred at the frequency of the acoustic beat, 2.4 Hz, and at one-third and two-thirds of that frequency, 0.8 Hz and 1.6 Hz\(^6\). In a later study, researchers observed that listening to complex rhythms can elicit spectral peaks at the frequency of the rhythm’s beat\(^7\). These observations are contiguous with the possibility that beat induction is not solely a
bottom-up process, where rhythms are detected by sensors, then processed at increasingly abstract levels to arrive at a beat percept. Instead, voluntary mental imagery acts on the auditory cortex, a “lower” sensory region, to influence electrophysiological readings that appear to impose meter on isochronous sequences and organize non-isochronous sequences around a beat.

Spectral peaks observed while participants listened to complex rhythms were less pronounced for tempi at especially fast and slow tempi⁷, reinforcing the tempo preferences noted earlier from the behavioral SMS literature. The recurrence of tempo preferences noted throughout the rhythm induction literature indicates another variety of top-down processing, where only a range of frequencies are considered danceable and register electrophysiological characteristics of musical rhythm⁷.

In an experiment where participants were presented with two streams of isochronous sequences with different frequencies, Costa-Faidella, Sussman, and Escera found spectral peaks at both frequencies in data localized to the auditory cortex⁸. In the motor cortex, however, only the task-relevant frequency exhibited an increased power and over time, the task-irrelevant frequency was suppressed in data from the auditory cortex⁸. The time course of these observations, in which attending one of two simultaneous isochronous sequence frequencies is accompanied by spectral changes in motor activity before auditory activity, support the notion that executive control over rhythm perception starts in the motor cortex.

Psychophysical correlates of motor planning and execution observed while listening to rhythms indicate that perception of these stimuli rely on both auditory and motor systems. Beta band power increases similarly during acoustic and imagined accents on an isochronous sequence⁹. In an MEG study using isochronous sequences, the same pattern of beta band power
enhancement approaching stimulus onset was observed during both imagined and perceived accents, followed by desynchronization 200 ms after onset. An earlier study by Fujioka, Trainor, Large, and Ross contextualizes this work: they observed beta amplitude modulation while listening to an isochronous sequence in the sensorimotor cortex, premotor cortex, and supplementary motor area despite the absence of movement in participants. The advantageous spatial resolution of MEG results validates EEG findings localized to the motor cortex. This data also reveals that motor system involvement is not limited to oscillations at a beat’s harmonics and subharmonics, but includes activity defined classically by the beta band.

Many theories exist to explain the phenomenon of SMS, phase entrainment, and sensory-motor coupling during rhythm perception. The Action Simulation for Auditory Prediction (ASAP) hypothesis proposed by Patel and Iversen posits that beat frequencies conveyed by musical rhythm are associated with representations of periodic movement which in turn inform the anticipation of rhythmic stimuli. Although the authors expressly distinguish between the dorsal pathway responsible for their proposed auditory-motor system and the MNS, the “action understanding” theory of mirror neurons uses associations between movement simulation and meaning in a similar way to the proposed link between movement simulation and auditory prediction. The sensory-motor theory of rhythm and beat induction developed by Todd and Lee, like the ASAP hypothesis, depends on internal representations to explain beat perception during passive listening.

Like simulation theories, approaches to understanding beat perception founded on dynamical systems theory (DST) account for a feedback loop between auditory and motor systems in the brain. This approach does not, however, rely on internal representations of movement or abstract simulations. The nonlinear oscillator models for beat perception derived
from dynamical systems theory are generalizable across physical systems and scalable within the brain. Explanations attempted by these models circumvent the mystery of simulation. Originally in opposition to the “action understanding” theory of mirror neurons, Hickok criticizes simulation as an explanation for cognitive processes because it leaves questions of how the simulation occurs unaddressed. The present work holds motor simulation theories of musical beat perception with the same skepticism. In their review of motor simulation theories, Ross, Iversen, and Balasubramaniam illuminate a gap in understanding relevant to both DST and simulation approaches, that is, whether or not the motor system activity observed while passively listening to rhythmic stimuli depicts a contribution to beat perception or an output without feedback.

Mu wave research presents an opportunity to elucidate motor responses to beat perception. In pre-print findings from Ross, Iversen, Makeig, and Balasubramaniam, mu enhancement occurred bilaterally over the hand somatomotor cortex while participants passively listened to excerpts of music. The authors attribute this finding to the inhibition of hand movement during passive listening, comparing it to the enhancement of mu over the left hand somatomotor cortex while participants tapped exclusively with their right foot. Though caution should be taken in incorporating the findings of this work given its pre-print status and small sample size of eight participants, the authors implement the best practices (aside from their number of participants) recommended by Hobson and Bishop in a comprehensive review of mu suppression literature. Especially critical is their use of a voluntary movement condition to ensure that mu suppression occurring during movement resembles that occurring while still. The relationship between these results and motor simulation theories of beat perception is unclear. Mu suppression, considered an indication of mirroring, is not present in this data during
music listening. Instead, mu enhancement occurs over the hand somatomotor region, suggesting that if action-execution is at play in the perception of naturalistic musical stimuli, it is not indicated by mu suppression.

Beat perception research has largely been concerned with delta and beta band modulation as an indicator of motor cortex participation. This review is meant to pose mu suppression studies as a compliment to the existing literature. As a correlate of mirroring activity, mu suppression has the unique opportunity to support or counter simulation theories of beat perception, though investigations yielding favorable evidence should be accompanied by a broader investigation into the computations underpinning simulation as a mechanism for perception.

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References