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MASTER THESIS

THE CAUSAL ROLE OF RIGHT VS. LEFT dPMC IN RHYTHM
PERCEPTION: a TMS study

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Abstract

This study explored the role of the dorsal premotor cortex (dPMC) in how we perceive beats in music, using a targeted transcranial magnetic stimulation (TMS) approach. Specifically, we examined how this stimulation affected their ability to judge whether a musical stimuli was "on beat" or "off beat."

Our results showed that stimulating the right dPMC made participants more likely to perceive a rhythm as "on beat." This effect was not observed when the left side was stimulated, suggesting that rhythm perception may be more specialized to the right hemisphere of the brain, aligning with theories that this area has a unique role in processing time-related information. Additionally, we found that individuals with higher musical sensitivity, as measured by the Barcelona Music Reward Questionnaire (BMRQ), were more accurate in rhythm perception. This implies that emotional and motivational factors can influence the neural networks involved in recognizing rhythms.

These findings add to our understanding of how different sides of the brain handle music-related cognitive functions. They also support models like the Action Simulation for Auditory Prediction (ASAP), which suggest that simulating movement is crucial for predicting timing in auditory perception. On a practical level, our study points to potential applications in therapies for individuals with difficulties in motor coordination and rhythm perception, and in enhancing brain-computer interfaces (BCIs) for music and cognitive rehabilitation. Future research should delve deeper into how the right dPMC interacts with other parts of the brain, using advanced imaging techniques to map the neural pathways that support rhythm perception.

Index

Abstract	iii
1. Contextualization of Rhythm Perception.....	7
1.1 The Importance of Rhythm Perception in Humans	7
1.2 Contemporary Models of Rhythm Perception	11
2. Neural Correlates of Rhythm Perception	14
2.1 Sensorimotor Integration in Rhythm Perception.....	14
- Auditory-Motor Integration in Rhythm Perception.....	15
- The Specific Role of the dPMC in Rhythmic Synchronization	18
- Influence of Premotor Cortex Activation on Rhythm Perception.....	19
- Modulation of Cortical Activity by rhythmic Complexity	20
- Comparing Simple and Complex Rhythms in Rhythmic Synchronization	21
2.2 The Role of the Dorsal Premotor Cortex in Rhythm Perception.....	22
- Activation of the Dorsal Premotor Cortex During Rhythm Listening	22
- Passive versus Active Listening Conditions	25
- Rhythm Complexity and dPMC Activation.....	26
- Theoretical Implications and Connections to Existing Models.....	26
2.3 Involvement of Other Cortical Areas in Rhythm Perception	28
- Activation of the SMA, preSMA, and Lateral Cerebellum	28
- Activation of the SMA in Rhythm Perception.....	29

- Role of the preSMA in Rhythm Processing	30
- Involvement of the Lateral Cerebellum in Rhythm Perception.....	31
- Interaction Between the SMA, preSMA, and Lateral Cerebellum.....	33
3. Lateralization	34
3.1 Lateralization of the dorsal auditory stream in auditory-motor integration in musical context	34
- The Dorsal Auditory Stream and Its Role in Rhythm Perception.....	35
- Hemispheric Differences in the Dorsal Auditory Stream	36
3.2 Hemisphere Differences in the dPMC during Rhythm Perception.....	38
- Hemispheric Specialization in the dPMC.....	39
- The Role of the Left dPMC in Rhythm Perception.....	40
- The Role of the Right dPMC in Rhythm Perception	41
- Functional Implications of Lateralization in Rhythm Perception	42
- Interplay Between the Hemispheres in the dPMC During Rhythm Perception.....	43
- Neurophysiological Evidence for Hemispheric Differences in the dPMC	44
- Impact of Rhythm Complexity on Hemispheric Activation in the dPMC	45
4. The Causal Role of Right vs Left dPMC in Rhythm Perception: a TMS Study	46
4.1 Materials and methods.....	47
- Participants	47

- Stimuli and tasks	48
- Procedures	49
- Neuronavigation	51
- Transcranial Magnetic Stimulation	51
- Data Analysis	53
4.2 Results	54
4.3 Discussion.....	56
5. General Conclusion	58
References	63

1. Contextualization of Rhythm Perception

1.1 The Importance of Rhythm Perception in Humans

Music perception and performance are a natural human activity, present in every culture and religion. A fundamental aspect of music cognition is the perception of a regular pulse (or beat) in rhythmic auditory patterns, which is often associated with the natural tendency of actively synchronizing body movements to the musical sequence. Whereas many animals can encode temporal intervals, humans have the unique ability to flexibly and proactively extract a regular beat from complex auditory patterns, such as music.

It is intrinsic to human nature to move in response to pleasurable sequences of sound, often attempting to synchronize foot-tapping to a song, whether consciously or not. This common behavior is a distinctive human trait, characterized by the ability to "feel" the beat, which triggers neural mechanisms of reception, analysis, and response to auditory stimuli. In music cognition, beat perception refers to the capacity to detect a regular pulse (or beat) in rhythmic auditory patterns, which spontaneously elicits a motor activation in humans (Honing, 2013; Damm et al., 2020). The ability to perceive and motorically entrain to the beat of musical rhythms does not need a special training, it is present in every culture and emerges spontaneously even in young infants (Savage et al., 2015; Winkler et al., 2009). Despite the spontaneous nature of this behavior, beat perception and production require a fine level of abstractness in the internal representation of periodicities and a temporally precise coupling between auditory perception and motor action. Proksch et al. (2020, p. 2) also propose that "cross-cultural perceptual priors may

exist for some aspects of rhythm perception and production.” Nevertheless, every human culture integrates a beat into its music, with this detectable regular pulse being perceived and utilized by listeners and performers to coordinate their movements (Patel and Iversen, 2014).

Rhythm appears to imply "movement in time," a concept encompassing multiple aspects such as "pulse, phrasing, harmony, and meter" (Large and Palmer, 2002, p. 3). In this context, we adopt the definition of rhythm provided by Fiveash et al. (2022, pp.1-2), which describes it as "the serially ordered pattern of time intervals in a stimulus sequence (i.e., time spans marked by event onsets)." The ability to detect regularities in auditory sequences seems to be directly linked to the origins of music, as well as to activities such as dancing, speech, or collective music production—actions that involve the influence of auditory stimuli on perceptual and motor domains (Winkler et al., 2009; Merchant et al., 2015). This fundamental nature of rhythm has emerged as a critical principle in the organization of cerebral function (Patel and Iversen, 2014).

Rhythmic entrainment appears to be an intuitive action that does not require specialized training. It is a common human ability, characterized by the capacity to discern the pulse in auditory sequences with equally distributed points and to align physical movements with that beat or pulse (Merchant et al., 2015; Merchant and Honing, 2014). The perception of this beat and the intervals of time is interpreted by the listener as a unique sequence, composed of multiples or subdivisions of the beat, rather than as isolated intervals (Grahn and Rowe, 2009). Additionally, research involving newborn infants suggests that this ability is innate or spontaneous (Winkler et al., 2009; Araneda, 2017), demonstrating a precise aptitude present early in development (Bengtsson et al., 2009). This supports the idea that rhythm

perception is an essential tool not only for music but from the very beginning of human life.

However, the fact that this is an innate ability does not imply simplicity. Recent scientific studies have begun to reclassify rhythmic ability as multilayered, indicating that rhythm processing is a complex skill that may encompass various layers of competencies (Damm et al., 2020). For example, considering the subprocesses required in rhythm perception—such as pulse extraction, attention, and working memory—it is plausible to hypothesize that diverse biological bases are likely involved, beyond the evolutionary accounts that shape different abilities.

Given the multifaceted nature of rhythm processing and the various underlying competencies it may involve, it becomes essential to differentiate between rhythm perception and rhythm production tasks. A review of the literature reveals a variety of tasks used to assess these skills, including rhythm pattern discrimination, rhythm reproduction, timing, beat alignment, and tapping, each of which is based on different components, such as memory-based or beat-based processes. Hence, recognizing these distinctions is crucial, as they may involve different neural mechanisms (Fiveash et al., 2022).

Rhythmic entrainment in humans relies on complex cognitive aspects, in which we can identify a dynamic interplay between auditory and motor systems (Merchant and Honing, 2014), and refers to the capacity to align movements of the body to an outer rhythm (Giovanelli et al., 2014). An improved functional interaction has been observed among auditory and motor regions during beat perception (Patel and Iversen, 2014), and neuroimaging evidence also endorse this connection (Grahn and Rowe, 2009). Even though in absence of motoric behavioral responses, rhythm is suited to evoke activity in auditory and motor domains (Cameron and Grahn,

2016). Literature confirms the powerful link among rhythm perception and movement through studies that investigated the activation of (pre)motor areas in the brain while only listening to rhythmic patterns (Grahn and Brett, 2007). Another important feature for rhythmic entrainment is the relationship between sequential and temporal mechanisms in the auditory context. Sequential mechanisms are responsible for organizing events in a specific order along a given time. This allows an individual to synchronize their movements with the rhythm, supporting in the auditory system the perception and adjustment to these events, by the integration of these information (Merchant and Honing, 2014).

In addition to the complex interplay between auditory and motor systems, which facilitates the alignment of body movements to an external rhythm, emotional engagement and reward mechanisms also play a crucial role in rhythm perception. Given the rewarding nature of music, a review by Fiveash et al. (2023) identified a gap in the literature regarding the link between reward and rhythm, suggesting possible directions for future research. As we saw before, following a rhythm relies on making temporal predictions; this means that the subject exposed to a rhythm has its own temporal expectations that could match or not with the auditory excerpt. Hence, we assume that to be able to synchronize with an external auditory stimuli might result in a rewarding response for the individual (Fiveash et al. 2023). Reward seems to be one of the layers that can help to explain the human ability to adjust in period and phase to different types of rhythm, within various levels of complexity, regulating rhythmic action in diverse range and change of tempi and music signals (Merchant and Honing, 2014). Curiously, human beings are flexible enough to synchronize at rates both integer multiples or basic beat fractioned (Merchant and Honing, 2014), which is in line with the idea about statistical universals in human

music proposed by Savage et al. (2015), an observation that music often employs an isochronous beat structure grouped into metrical hierarchies typically based in multiples of two or three beats; it suggests that the human rhythmic flexibility could be due to adaptations to the prevalent musical structure.

1.2 Contemporary Models of Rhythm Perception

Rhythm perception is a fundamental aspect of human cognition, present in various daily activities such as speech, dance, music, and general cognitive processing. Rhythm is defined by the structured organization of sounds and silences into temporal sequences, providing a framework within which humans can anticipate and respond to auditory patterns (Fiveash et al., 2023). This ability is not only essential for coordinating movements and actions but is also closely linked to emotional responses and the brain's reward systems, particularly in the context of musical experiences (Trost et al., 2017; Fiveash et al., 2023). As research in these areas grows, understanding the mechanisms behind rhythm perception has become increasingly important.

Several contemporary models have been proposed to explain how humans perceive and synchronize with rhythmic stimuli, often referred to as "entrainment models." These models conceptualize rhythm perception as the alignment of internal neural processes with external rhythmic stimuli, facilitating coordination and prediction in a dynamic environment. For instance, Merchant and Honing (2014) define rhythmic entrainment as the ability to perceive regularities in auditory stimuli or music and synchronize motor actions to these auditory signals. Temporal

expectations play a crucial role in this process, shaping how we perceive, attend to, and interact with rhythmic sequences or musical patterns (Fiveash et al., 2023).

One prominent model is the Dynamic Attending Theory (DAT), proposed by Jones and Boltz (1989). DAT suggests that attention is modulated over time by the synchronization of intrinsic neural oscillations with external temporal patterns. According to this theory, the brain's internal rhythms align with external stimuli, enhancing the processing of expected events and aiding in the perception of rhythmic structures (Fiveash et al., 2023). This model highlights the active role of attention in rhythm perception, proposing that our ability to track and predict rhythmic patterns is rooted in these synchronized neural oscillations.

Another influential framework is the Action Simulation for Auditory Prediction (ASAP) Hypothesis by Patel and Iversen (2014), which proposes that beat perception involves the brain's ability to simulate action to predict auditory events. This simulation allows for the maintenance of a perceived beat within the brain, even in the absence of external cues, demonstrating the tight coupling between auditory prediction and motor action (Cannon and Patel, 2021). The "Action Simulation for Auditory Prediction" (ASAP) hypothesis suggests that motor planning regions utilize a shared neural network for simulating actions to generate temporal predictions regarding beat times. That information is then transferred from motor to auditory regions where it provides temporal predictive signals for upcoming beats, therefore shaping the perceptual interpretation of musical rhythms. At the neural level, the ASAP hypothesis posits that communication between motor and auditory areas during beat perception relies on a dorsal auditory pathway, involving specifically the dorsal PMC. A recent extension of this model proposes that the motor system contributes to the accuracy of auditory predictions by providing a periodic temporal

framework through oscillatory connections between SMA and the dorsal striatum, making this circuit crucial to beat maintenance and to auditory expectations (Cannon & Patel, 2021). The ASAP hypothesis underscores the interplay between sensory and motor processes, suggesting that our understanding of rhythm is deeply tied to the brain's ability to anticipate and prepare for action. Oscillator models offer another perspective by focusing on the brain's oscillatory processes in rhythm perception.. For example, Large and Jones (1999) introduced the Neural Resonance Theory, which builds on the neural mechanisms proposed by DAT. This theory posits that neural oscillators in the brain resonate with rhythmic stimuli, enabling the perception of rhythm (Patel and Iversen, 2014). However, the theory's reliance on phase coupling to explain rhythm perception has limitations, particularly in accounting for the natural variations in tempo observed in live musical performances. To address these limitations, Large and Palmer (2002) proposed the Sine Circle Map model, which suggests that a single internal oscillator aligns with an external regular signal, allowing for greater flexibility in adapting to changes in tempo. This model provides a more nuanced understanding of how the brain accommodates the fluidity of real-world rhythmic experiences.

Additional approaches, such as Neural Network Models, emphasize the importance of sensory-motor integration in rhythm perception. These models suggest that the correlation between sensory and motor areas of the brain is crucial for synchronization and rhythm processing (Merchant and Averbeck, 2017). Similarly, dynamic systems techniques have been used to represent neural patterns of beat at an algorithmic level. While these techniques have shown promise, they still require improvements to incorporate more realistic neurobiological details, such as accounting for the unique properties of individual neurons, microcircuit organization,

and the dynamic interactions between cortical and subcortical areas (Merchant et al., 2015).

While computational and algorithmic models have significantly contributed to our understanding of rhythm perception, there is still a need for further refinement. Advancing these models to better represent the computational properties of neural circuits at an operational level is crucial for a more comprehensive understanding of how neural mechanisms support rhythmic processing (Merchant et al., 2015). Such progress will deepen our knowledge of the complex interplay between perception, cognition, and motor control in rhythm perception, shedding light on the fundamental nature of rhythm in human cognition.

2. Neural Correlates of Rhythm Perception

2.1 Sensorimotor Integration in Rhythm Perception

The human capacity to perceive and synchronize with rhythmic patterns, such as those found in music, involves intricate coordination between the auditory and motor systems. At the heart of this process we have the auditory and the premotor cortex (PMC), particularly the dorsal premotor cortex (dPMC). These areas collaborate to interpret rhythmic cues and orchestrate corresponding motor responses. This chapter examines the interaction between these brain regions, with a particular emphasis on the PMC and dPMC, and how their activities are influenced by rhythmic complexity. Additionally, we explore how activation within these motor regions impacts rhythm perception. The chapter aims to shed light on the key

mechanisms of sensorimotor integration in rhythm perception, focusing on the crucial role of the PMC, particularly the dPMC, in these processes.

- Auditory-Motor Integration in Rhythm Perception

Rhythm perception and synchronization require the coordinated activity of several brain regions, especially the auditory cortex and the PMC, including the dPMC. Research indicates that these regions interact dynamically to decode rhythmic patterns and guide motor actions, such as tapping a foot or clapping hands (Grahn & Brett, 2007; Grahn & Rowe, 2009).

The PMC, particularly the dPMC, is vital within this auditory-motor network. For instance, Hadley et al. (2015) showed that the right dPMC is actively involved in temporal prediction during musical interactions, suggesting that motor simulation processes play a crucial role in rhythm perception. Giovanelli et al. (2014) demonstrated that disrupting the right dPMC with repetitive transcranial magnetic stimulation (rTMS) hampers synchronization with complex rhythms, underscoring the importance of the dPMC in auditory-motor integration.

Merchant et al. (2015) further highlighted the role of the PMC and the supplementary motor area (SMA) in rhythm perception, revealing their involvement in a neural network responsible for beat perception and synchronization across both human and non-human primates. This network includes the motor cortico-basal ganglia-thalamo-cortical (mCBGT) circuit, where the SMA and putamen function as key nodes. Oscillatory activity in the delta and beta bands connects motor and auditory areas, supporting the idea that these regions work together to generate predictive timing for musical rhythms.

The interaction between auditory and motor areas is thought to be facilitated by beta-band oscillations (13-25 Hz), which synchronize neural excitability with rhythmic events, enabling predictive timing (Arnal, 2012; Morillon & Baillet, 2017). Recent theories propose that rhythm perception relies on the interplay between auditory and motor systems to predict the timing of rhythmic events. The Action Simulation for Auditory Prediction (ASAP) hypothesis suggests that the motor system mimics periodic movements to forecast beat timing, even without actual movement (Patel and Iversen, 2014). This simulation is supported by neural circuits that connect auditory and motor areas, such as the dorsal auditory pathway.

Complementary to this, the Gradual Audiomotor Evolution (GAE) hypothesis presents an evolutionary perspective, positing that human rhythmic abilities evolved gradually through increasingly sophisticated interactions between auditory and motor systems (Proksch et al., 2020). According to the GAE hypothesis, these capabilities developed progressively, driven by evolutionary pressures that favored synchronized behaviors such as music, dance, and vocal communication.

Together, these hypotheses highlight two interrelated processes: motor action simulation for predicting rhythmic events (ASAP) and the evolutionary refinement of audiomotor pathways that underpin these predictive mechanisms (GAE). Both models emphasize the fundamental role of the motor system in rhythm perception, which goes beyond mere motor planning to encompass our capacity to engage with musical rhythms (see Figure 1).

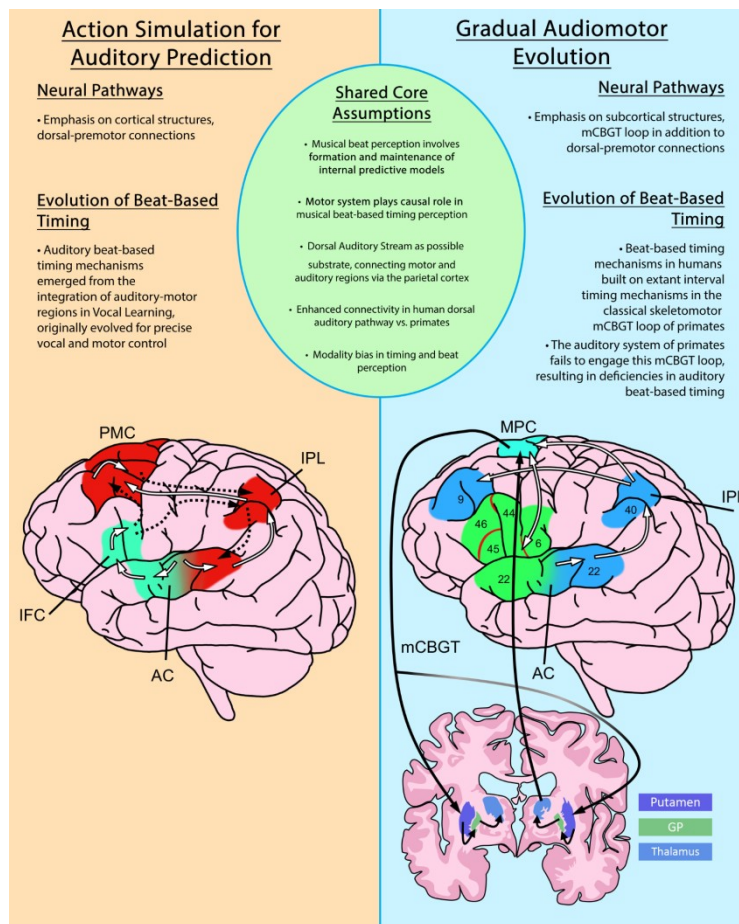


Figure 1 *Theoretical Models of Musical Rhythm Perception.*

This figure illustrates two main models that explain the mechanisms of beat-based timing in the human brain. The "Action Simulation for Auditory Prediction" (ASAP) model emphasizes the integration of cortical structures, such as the dorsal premotor cortex (dPMC), and auditory-motor connections that are thought to have evolved for precise vocal and motor control. In contrast, the "Gradual Audiomotor Evolution" (GAE) model suggests that beat-based timing mechanisms developed from subcortical circuits, like the cortico-basal ganglia-thalamo-cortical (mCBGT) loop, gradually adapting to support rhythmic synchronization in humans. Both models share core assumptions about the formation and maintenance of internal predictive models and the causal role of the motor system in musical beat-based timing perception (Adapted from Proksch et al., 2020).

Cannon and Patel (2021) further expanded on this idea by proposing that beat perception involves action-like processes within the supplementary motor area

(SMA) and dorsal striatum, which provide temporal predictions and facilitate beat-based anticipation. According to their model, the SMA generates precise firing rate dynamics aligned with beat intervals, organized by dorsal striatum activity, highlighting the significance of motor neurophysiology in covert rhythm perception.

- The Specific Role of the dPMC in Rhythmic Synchronization

The dorsal premotor cortex (dPMC) plays a crucial role in rhythm perception by contributing to motor planning and cognitive processes, such as anticipating and predicting auditory events. Merchant and Averbeck (2017) showed that the medial premotor cortex (MPC) in macaques represents time intervals during rhythmic tasks through mechanisms aligned with drift-diffusion models (DDM). This finding supports the idea that similar mechanisms may be active in the human dPMC to aid temporal prediction and synchronization.

Ross et al. (2016) examined the role of motor planning and simulation in rhythm perception, focusing on the dPMC's significance in both beat-based and interval-based timing. Their study demonstrated that dPMC activity is essential for accurate beat perception, underscoring its involvement in forming and maintaining temporal predictions, consistent with motor simulation theories of beat perception.

Human studies also support the dPMC's role in rhythmic synchronization. Lega et al. (2016) found that the dPMC is pivotal in learning new auditory-motor associations, indicating its function in integrating sensory inputs and motor outputs. This aligns with evidence suggesting the dPMC is critical for adapting to complex rhythmic structures (Ross et al., 2018a).

Further, Lega et al. (2020a) revealed that distinct regions within the human dPMC handle contralateral and ipsilateral sensorimotor processes, indicating a specialized role in coordinating motor actions across both sides of the body. This specialization is particularly relevant for synchronizing movements with rhythms that require intricate bilateral coordination.

- Influence of Premotor Cortex Activation on Rhythm Perception

Activation of the PMC, particularly the dPMC, directly affects rhythm perception and synchronization capabilities. Studies using TMS to manipulate cortical excitability have provided insights into the causal roles of these regions. For instance, Parmigiani et al. (2015) found that TMS over the left dPMC disrupts inhibitory control over motor actions, suggesting the dPMC's critical role in adjusting motor responses during rhythm synchronization.

Lega et al. (2020b) further demonstrated that dPMC stimulation alters neural representations of rhythmic patterns, especially under conditions requiring complex temporal integration, supporting the role of the PMC in adapting to dynamic rhythmic environments.

Proksch et al. (2020) highlighted the role of the motor system in developing and maintaining internal predictive models for rhythm perception, consistent with the Active Inference framework. Both the ASAP hypothesis (Patel and Iversen, 2014) and the Gradual Audiomotor Evolution (GAE) hypothesis propose that motor regions, including the dPMC, are fundamental for predicting rhythmic events and maintaining synchronization.

- Modulation of Cortical Activity by rhythmic Complexity

Rhythmic complexity, characterized by the variability in timing and structure of patterns, has a notable impact on neural activity in the PMC, dPMC, and other cortical regions. Simple rhythms, with regular and predictable intervals, utilize a limited range of neural resources. In contrast, complex rhythms, which involve irregular or syncopated patterns, demand greater cognitive effort and more extensive cortical engagement (Grahn & Rowe, 2009; Hadley et al., 2015).

Research has shown that the brain dynamically adjusts its neural connectivity in response to rhythmic complexity. For example, Hadley et al. (2015) observed increased activation in the right dPMC during synchronization with complex rhythms, indicating that this region helps manage the cognitive load associated with these tasks. Similarly, Parmigiani and Cattaneo (2018) showed that TMS over the dPMC specifically hinders the inhibition of inappropriate motor responses during complex rhythmic tasks, underscoring its role in refining motor control.

Leow et al. (2022) investigated the role of the supplementary motor area (SMA) in rhythm perception, finding that increased SMA excitability enhances rhythm discrimination, while decreased excitability impairs performance. These findings suggest that the SMA and dPMC work in tandem to facilitate synchronization with complex rhythms, likely through the formation of forward temporal predictions and adjustments in motor output.

Araneda et al. (2017) provided evidence for a supramodal network involved in beat processing across multiple sensory modalities (auditory, visual, and tactile). They demonstrated that regions like the putamen and SMA are consistently engaged

in beat detection, regardless of the sensory input, emphasizing their central role in rhythm perception across different sensory domains.

- Comparing Simple and Complex Rhythms in Rhythmic Synchronization

Simple and complex rhythms engage the PMC and dPMC differently. Simple rhythms, which are easier to predict, activate the auditory cortex and PMC more directly, facilitating efficient synchronization with minimal cognitive effort. In contrast, complex rhythms, which require decoding irregular temporal patterns, lead to heightened activation in motor areas such as the dPMC and SMA (Grahn & Brett, 2007; Grahn & Rowe, 2009).

Ross et al. (2018a) found that the dPMC exhibits increased beta-band activity during synchronization with complex rhythms, reflecting greater demands on motor planning and temporal prediction. This suggests that the dPMC adjusts its activity based on rhythmic complexity to optimize performance.

Amiez et al. (2006) further demonstrated that local morphology predicts functional organization within the human dPMC. The involvement of this region in complex rhythmic synchronization may be influenced by its anatomical structure, which supports specific motor planning and sensorimotor integration functions.

Understanding rhythm perception and synchronization in the human brain hinges on the dynamic integration between auditory and motor areas, particularly through mechanisms involving the premotor cortex. Neurophysiological and theoretical models, such as the ASAP and GAE hypotheses, suggest that circuits linking the auditory and motor systems facilitate temporal prediction and rhythmic synchronization. Beta-band oscillations and functional connectivity between these

areas are critical for modulating neural responses to rhythmic complexity, enabling accurate anticipation and reaction to rhythmic events.

However, the specific function of regions like the dorsal premotor cortex (dPMC) warrants further investigation. As a crucial subregion of the premotor cortex, the dPMC is central to mediating rhythmic synchronization and temporal prediction, significantly influencing how the brain processes and responds to rhythmic stimuli. In the following section, we will explore the role of the dPMC in rhythm perception in greater detail, focusing on its contributions to auditory-motor integration and its impact on cortical activity modulation in response to diverse rhythmic patterns.

2.2 The Role of the Dorsal Premotor Cortex in Rhythm Perception

- Activation of the Dorsal Premotor Cortex During Rhythm Listening

The dorsal premotor cortex (dPMC) is crucial in rhythm perception, expanding its role beyond motor planning to encompass significant functions during rhythm listening. Numerous studies have demonstrated that the dPMC is actively engaged even without overt motor activity, supporting processes such as predictive timing, sensorimotor integration, and rhythm anticipation (Arnal, 2012; Morillon and Baillet, 2017; Hadley et al., 2015). This section examines the experimental methods used to identify dPMC activation during rhythm listening, investigates the differences in activation between passive and active listening, and analyzes the impact of rhythm complexity on dPMC engagement. Furthermore, we will relate these findings to theoretical models, including the Action Simulation for Auditory Prediction (ASAP)

hypothesis (Patel and Iversen, 2014), and discuss their implications for understanding the role of the dPMC in rhythm perception.

Studies using neuroimaging techniques, such as functional magnetic resonance imaging (fMRI) and magnetoencephalography (MEG), consistently demonstrate dPMC activation during rhythm listening. For instance, Bengtsson et al. (2009) utilized fMRI to reveal significant dPMC activation when participants anticipated rhythmic patterns during listening tasks. This suggests that the dPMC is involved in creating internal models of rhythmic sequences, allowing the brain to synchronize with external auditory stimuli.

Araneda et al. (2017) further expanded this understanding by examining the supramodal nature of the neural networks involved in beat detection across various sensory modalities, such as hearing, vision, and touch. Their findings indicate that the dPMC is part of a broader network that is consistently activated during beat detection, regardless of the sensory modality, supporting the view that the dPMC plays a fundamental role in processing temporal patterns beyond the auditory domain. This supramodal activation underscores the dPMC's importance in integrating temporal information from multiple sensory inputs, thereby reinforcing its role in rhythm perception (see Figure 2).

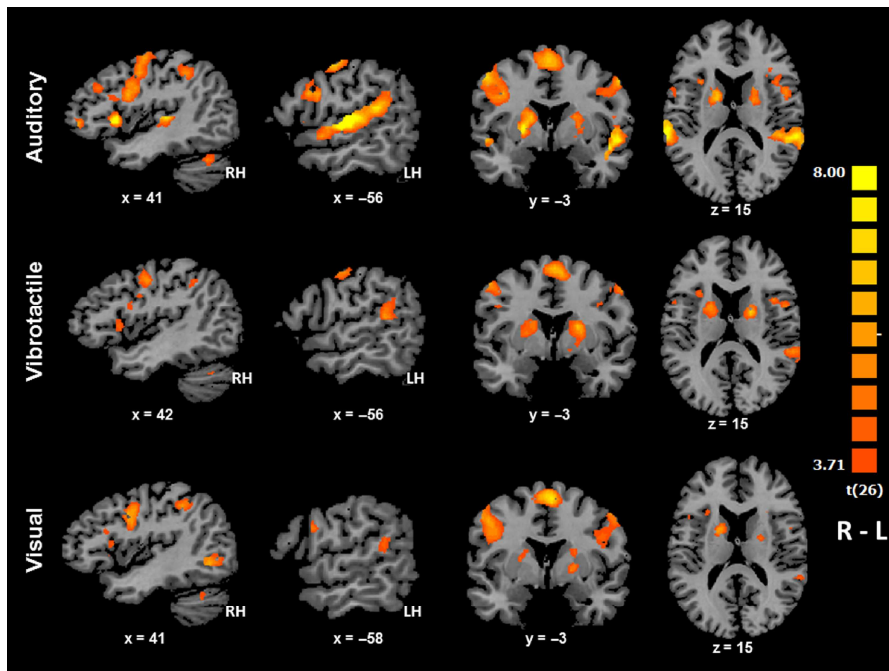


Figure 2 *Supramodal Neural Network Involving the Dorsal Premotor Cortex in Beat Detection Across Multiple Sensory Modalities .*

Supramodal network for beat detection involving the dorsal premotor cortex (dPMC) across auditory, visual, and tactile modalities. The figure demonstrates the dPMC's participation in a broader neural network activated during beat detection, regardless of the sensory modality, emphasizing its role in integrating temporal information from multiple sensory inputs (Adapted from Araneda et al., 2017).

Additionally, Genon et al. (2017) employed advanced imaging techniques to explore the connectivity patterns associated with the dPMC during rhythm perception tasks. Their research showed that the dPMC has extensive connections with both motor and sensory regions, indicating its function as a central hub in the brain's rhythm processing network. The connectivity between the dPMC and auditory areas during rhythm listening suggests that it facilitates the integration of sensory inputs with motor planning, even in the absence of overt movements. This finding aligns with the expanding literature emphasizing the dPMC's role in sensorimotor integration beyond explicit motor tasks (Amiez et al., 2006; Arnal, 2012; Hadley et al., 2015; Ross et al., 2016; Morillon and Baillet, 2017).

- *Passive versus Active Listening Conditions*

Several studies have explored the variation in dPMC activation between passive and active listening conditions. Lega et al. (2016) used repetitive transcranial magnetic stimulation (rTMS) to demonstrate the causal role of the dPMC in learning and applying auditory-motor associations. Their findings indicate that disruption of dPMC activity significantly impairs the ability to learn new auditory-motor associations, particularly under active listening conditions that require explicit engagement. This suggests that the dPMC is crucial for integrating sensory inputs with motor planning during active listening tasks.

Ross et al. (2018a) provided further evidence by showing that the left dPMC has a more prominent role in tasks that involve active synchronization and tempo monitoring compared to passive listening tasks. This differential engagement supports the hypothesis that dPMC involvement in rhythm processing is modulated by task demands and levels of cognitive engagement, highlighting its importance in both passive and active listening scenarios.

Cattaneo and Parmigiani (2021) also examined the distinction between passive and active rhythm listening by investigating neural activation patterns in the dPMC and other related regions. Their findings show that, while the dPMC is consistently activated in both conditions, the extent and intensity of its activation are influenced by the level of attention and cognitive load required. This suggests that dPMC activation is not merely a function of sensory processing but also involves higher-order cognitive processes that vary with task demands.

- Rhythm Complexity and dPMC Activation

The complexity of rhythmic patterns also affects the degree of dPMC activation. Giovanelli et al. (2014) found that the right dPMC is more actively engaged when participants synchronize with complex rhythmic sequences, as shown in rTMS studies. These findings indicate that the dPMC is involved not only in motor planning but also in the cognitive processes needed to interpret and anticipate complex rhythmic structures.

Lega et al. (2020a) provided additional insights into how the dPMC's involvement varies with task demands and rhythm complexity. Their research highlights that the dPMC comprises multiple areas that contribute differently depending on the task's complexity and predictability. This multifocal representation suggests that the dPMC is crucial in internal simulations of rhythmic patterns, especially when rhythms are complex and less predictable.

Parmigiani et al. (2015) observed that the dPMC's influence on motor areas depends on the complexity of the rhythmic sequence. They found that disrupting dPMC activity affects the ability to synchronize with complex rhythms but has little impact on simpler, more predictable patterns. This suggests that the dPMC is engaged in both cognitive and motor functions that adapt to the demands of rhythm complexity, reinforcing its role in managing the internal representations of complex rhythmic sequences.

- Theoretical Implications and Connections to Existing Models

The evidence of dPMC activation during rhythm listening aligns with several theoretical models of rhythm perception, such as the ASAP hypothesis proposed by Patel and Iversen (2014). This hypothesis posits that beat perception involves precise communication between auditory and motor planning regions, even without overt movement. Arnal (2012) and Morillon and Baillet (2017) have shown that the dPMC is active during rhythm perception tasks that do not require physical movements, suggesting that it contributes to predicting beat timing through internal movement simulation.

Ross et al. (2016) and Ross et al. (2018a) further support motor simulation theories by demonstrating that the dPMC's role in rhythm perception is crucial for shaping perceptual processes rather than merely reflecting unexecuted motor plans. This is consistent with the idea that the dPMC serves as a central hub for coordinating sensory inputs and motor outputs, enabling the brain to effectively anticipate and respond to rhythmic patterns.

Araneda et al. (2017) provided a broader context by showing that the dPMC is part of a supramodal network involved in rhythm perception across different sensory modalities. This reinforces the idea that the dPMC plays a pivotal role in integrating temporal information, suggesting that its function extends beyond specific sensory modalities and provides a unifying framework for understanding rhythm perception across various contexts.

Genon et al. (2017) further elucidate this understanding by highlighting the dPMC's extensive connectivity with other brain areas involved in rhythm processing. Their findings suggest that the dPMC's role is not only to integrate sensory and motor information but also to facilitate communication across a distributed network,

which is essential for maintaining accurate temporal predictions and motor adjustments during rhythm listening.

The findings discussed here emphasize the intricate role of sensory-motor integration outlined in the previous chapter, focusing on the specific mechanisms underlying dPMC activation during rhythm listening. The reviewed studies suggest that the dPMC plays a multifaceted role in rhythm perception, contributing to motor and cognitive processes involved in anticipating, detecting, and synchronizing with rhythmic patterns. The evidence indicates that the dPMC is not only engaged during active listening conditions but also plays a critical role in passive listening, where it supports predictive timing and sensory integration.

By aligning these findings with current theoretical models, such as the ASAP hypothesis and motor simulation theories, this discussion reinforces the importance of the dPMC in rhythm perception and highlights its dynamic role in shaping how rhythms are processed and understood in the brain. In the next section, we will discuss other cortical areas involved in rhythm perception, such as the supplementary motor area (SMA), pre-SMA, and lateral cerebellum.

2.3 Involvement of Other Cortical Areas in Rhythm Perception

- Activation of the SMA, preSMA, and Lateral Cerebellum

Rhythm perception relies on a complex network of cortical and subcortical areas that facilitate the integration of auditory and motor processes. While significant emphasis has been placed on the premotor cortex (PMC) and its role in rhythm synchronization, other brain regions, such as the supplementary motor area (SMA),

pre-supplementary motor area (preSMA), and the lateral cerebellum, are equally important to the neural network underlying rhythm perception. These regions contribute to various aspects of rhythmic processing, including motor planning, sensorimotor integration, and the prediction and adjustment of timing in response to rhythmic stimuli. A thorough understanding of the roles played by these areas is essential for a comprehensive view of the neural mechanisms of rhythm perception.

The SMA and preSMA, though traditionally associated with motor planning and execution, are also crucial in tasks requiring temporal prediction and coordination (Leow et al., 2022; Ross et al., 2018a; Chen et al., 2008b). The lateral cerebellum, which is well known for its involvement in motor control and timing, also plays a key role in processing temporal sequences, including rhythm perception and synchronization (Matthews et al., 2020; Schubotz et al., 2000). This section explores the specific contributions of the SMA, preSMA, and lateral cerebellum to rhythm perception, highlighting their functional roles, the effects of rhythmic complexity on their activation, and their interactions with other regions involved in rhythm processing.

- Activation of the SMA in Rhythm Perception

The supplementary motor area (SMA) is a critical component of the motor network involved in rhythm perception. It is active during both the planning and execution of rhythmic movements and plays a significant role in rhythm perception even when no overt motor actions are performed (Grahn & Brett, 2007; Grahn & Rowe, 2009). The SMA is believed to facilitate rhythm perception by generating and maintaining internal representations of rhythmic patterns, which are essential for

predicting and synchronizing movements with external beats (Cannon & Patel, 2021; Grahn, 2009).

Several studies have highlighted the involvement of the SMA in rhythm perception tasks. For instance, Leow et al. (2022) used transcranial direct current stimulation (tDCS) to modulate SMA excitability and found that increased SMA activity enhanced rhythm discrimination, while decreased activity impaired rhythm perception. These findings suggest that the SMA is critical for the neural mechanisms underlying beat-based timing, supporting the idea that it contributes to forward temporal predictions during rhythm perception.

Research by Araneda et al. (2017) showed that the SMA is consistently activated during beat detection across different sensory modalities, indicating that it is part of a supramodal network that integrates temporal information from multiple sensory domains, further emphasizing its role in rhythm perception. The SMA's involvement in rhythm perception is also affected by rhythmic complexity. Ross et al. (2018a) demonstrated that the SMA exhibits greater activation when participants are required to synchronize with complex rhythms, suggesting that it helps manage the cognitive and motor demands of intricate rhythmic structures. Neuroimaging studies support this, showing that the SMA is part of a network including the premotor cortex and basal ganglia, which are engaged in processing complex rhythmic patterns (Grahn & Rowe, 2009; Matthews et al., 2020; Chen et al., 2008a).

- Role of the preSMA in Rhythm Processing

The pre-supplementary motor area (preSMA) is another region implicated in rhythm perception. While the preSMA is primarily known for its role in higher-order

motor control functions, such as planning and voluntary action initiation, recent research indicates that it also contributes to the cognitive processes underlying rhythm perception (Ross et al., 2018b; Zalta et al., 2023). The preSMA appears to be involved in the temporal organization of motor responses, particularly when internal timing mechanisms must be adjusted to accommodate external rhythmic cues (Limb et al., 2006).

Studies have shown that the preSMA is activated during tasks that require synchronization of movements with rhythmic stimuli, even in the absence of overt motor actions (Ross et al., 2018b). This suggests that the preSMA supports internal simulations of rhythmic patterns, enabling the brain to predict and adjust to beat timing without physical movement. The involvement of the preSMA in rhythm perception aligns with theories such as the Action Simulation for Auditory Prediction (ASAP) hypothesis, which posits that beat perception involves the brain's capacity to simulate action to predict auditory events (Patel & Iversen, 2014; Cannon & Patel, 2021).

The preSMA's role in rhythm perception is also modulated by the complexity of rhythmic patterns. Research has shown that preSMA activation increases with the complexity of rhythmic tasks, suggesting its involvement in processing intricate temporal structures that require fine-tuning internal models of rhythmic sequences (Lega et al., 2020b; Morillon & Baillet, 2017). This aligns with the view that the preSMA plays a role in the flexible adjustment of temporal predictions based on the variability of auditory input.

- Involvement of the Lateral Cerebellum in Rhythm Perception

The lateral cerebellum, traditionally associated with motor control and coordination, is also critical for temporal processing, especially in tasks demanding precise timing, such as rhythm perception (Matthews et al., 2020; Kung et al., 2013). The cerebellum is thought to support synchronization with external auditory cues by providing a temporal framework for accurate timing and coordination (Teki et al., 2011; Merchant et al., 2015).

Studies have found that the lateral cerebellum is activated during rhythm perception tasks, particularly when rhythmic events are unpredictable or irregular (Grahn & Brett, 2007; Bengtsson et al., 2009; Gordon et al., 2018). This suggests that the cerebellum plays a role in processing the temporal aspects of rhythm by comparing predicted and actual timing intervals to detect discrepancies and adjust motor responses accordingly (Schubotz et al., 2000).

Neuroimaging evidence supports the idea that the cerebellum contributes to rhythm perception by working in conjunction with other motor areas, such as the SMA and dPMC. For example, Matthews et al. (2020) found that the lateral cerebellum shows increased activation during the perception of groove-based rhythms, which have medium complexity and elicit a strong urge to move. This activation is linked to regions associated with beat perception and reward, such as the basal ganglia, suggesting that the cerebellum plays a role in both the affective and motor aspects of rhythm perception.

The cerebellum's involvement in rhythm perception also varies with rhythmic complexity. Studies show that cerebellar activation intensifies when participants synchronize with more complex rhythms, which require greater cognitive and motor effort (Grahn & Rowe, 2009; Hadley et al., 2015). This indicates that the cerebellum

helps manage the demands of rhythmic complexity by supporting the precise timing and coordination necessary for accurate synchronization.

- Interaction Between the SMA, preSMA, and Lateral Cerebellum

The SMA, preSMA, and lateral cerebellum interact dynamically to facilitate rhythm perception and synchronization. These regions form a network that integrates motor planning, temporal prediction, and sensory feedback, enabling accurate perception and synchronization of rhythmic patterns (Matthews et al., 2020; Leow et al., 2022). The SMA and preSMA are involved in generating and adjusting internal models of rhythmic sequences, while the cerebellum provides a temporal framework for coordinating movements with external beats.

Research suggests that this network operates hierarchically, with the preSMA and SMA contributing to higher-order cognitive processes related to temporal prediction and the lateral cerebellum managing more precise motor control functions (Cannon & Patel, 2021; Merchant & Averbeck, 2017). For instance, Leow et al. (2022) demonstrated that increasing SMA excitability improves rhythm discrimination, highlighting its importance in beat-based timing. Similarly, the lateral cerebellum's role in rhythm perception appears vital for handling the demands of rhythmic complexity, as it aids in the precise timing and coordination required for synchronization (Grahn & Brett, 2007; Matthews et al., 2020).

In summary, the SMA, preSMA, and lateral cerebellum each play distinct but complementary roles in rhythm perception. The SMA and preSMA are essential for generating and maintaining internal representations of rhythmic patterns, facilitating the prediction and synchronization of movements to external beats. The lateral

cerebellum is crucial for the precise timing and coordination of these movements, particularly in response to complex or unpredictable rhythms. Together, these regions form an integrated network that supports rhythm perception and synchronization through motor planning, temporal prediction, and sensory feedback.

These findings align with theoretical models like the ASAP hypothesis, which proposes that beat perception involves motor simulation processes that predict auditory events (Patel & Iversen, 2014). The dynamic interplay between the SMA, preSMA, and lateral cerebellum underscores their importance in enabling the brain to anticipate and respond to rhythmic stimuli, allowing humans to engage effectively with music and other rhythmic activities.

The next chapter will explore the concept of lateralization in rhythm perception, examining the contributions brain hemispheres to rhythmic pattern processing and the implications of this lateralization for our understanding of rhythm cognition.

3. Lateralization

3.1 Lateralization of the dorsal auditory stream in auditory-motor integration in musical context

The lateralization of brain function, particularly within the dorsal auditory stream, is crucial for understanding how humans perceive and synchronize with musical rhythms. This process relies on a dynamic network that interconnects auditory processing regions with motor planning areas, thereby enabling the prediction and execution of movements in synchrony with rhythmic patterns in music.

The dorsal auditory stream, which connects auditory regions in the temporal cortex to motor planning areas in the frontal cortex, exhibits distinct patterns of lateralization that are essential for comprehending rhythm perception in a musical context.

Recent research highlights differential contributions of the left and right hemispheres to auditory-motor integration during rhythm perception. The left hemisphere is primarily associated with fine temporal resolution, sequential processing, and precise motor control, whereas the right hemisphere is more involved in processing global rhythmic structures and complex temporal patterns (Hickok and Poeppel, 2004; Kasdan et al., 2022). This chapter will explore the lateralization of the dorsal auditory stream, integrating findings from recent neuroimaging and neurophysiological studies to clarify the contributions of each hemisphere to auditory-motor integration in music.

- The Dorsal Auditory Stream and Its Role in Rhythm Perception

The dorsal auditory stream is a key pathway linking the posterior auditory cortex to motor regions, including the dorsal premotor cortex (dPMC) and the supplementary motor area (SMA). This pathway plays a fundamental role in integrating auditory inputs with motor planning, thereby facilitating beat perception and synchronization with musical rhythms (Hickok and Poeppel, 2004; Araneda et al., 2017). The lateralization of this stream is thought to underpin the distinct ways each hemisphere processes rhythmic information, with the left hemisphere being more involved in fine temporal processing and the right hemisphere contributing to the handling of complex rhythmic patterns (Kasdan et al., 2022; Rauschecker, 2011).

Rauschecker (2011) discusses the hierarchical organization and specialization within the auditory pathways, emphasizing that the dorsal stream is not only lateralized but also functionally distinct in how it supports auditory-motor integration. The left dorsal stream, which extends into frontal regions such as the dPMC, is particularly implicated in tasks that demand precise temporal control and sequencing, which are critical for rhythm perception and synchronization. Conversely, the right hemisphere is more engaged in integrating complex auditory patterns, reflecting its specialization in processing broader temporal and spectral aspects of music.

- Hemispheric Differences in the Dorsal Auditory Stream

The dorsal auditory stream in the left hemisphere has been shown to be particularly effective in tasks that require precise timing and fine temporal resolution. According to Hickok and Poeppel (2004) and Rauschecker (2011), this stream facilitates the rapid processing of auditory information and the coordination of motor responses, such as tapping to a beat or synchronizing movements with a regular pulse (see figure 3a and 3b). Functional magnetic resonance imaging (fMRI) studies have demonstrated greater activation in the left dPMC during tasks that involve predicting and maintaining rhythmic sequences, suggesting its role in supporting temporally precise motor actions (Chen et al., 2008a; Junemann et al., 2023).

In contrast, the right hemisphere is more actively involved in processing complex and less predictable rhythmic patterns. Araneda et al. (2017) showed that regions within the right dorsal auditory stream, including the right dPMC, are more engaged when participants process irregular or syncopated rhythms, which require

higher cognitive effort and temporal integration (see figure 3c). This finding is consistent with the research by Giovanelli et al. (2014), which demonstrated that disruption of the right dPMC impairs the ability to synchronize with complex rhythms, underscoring the specialized role of the right hemisphere in managing rhythmic complexity.

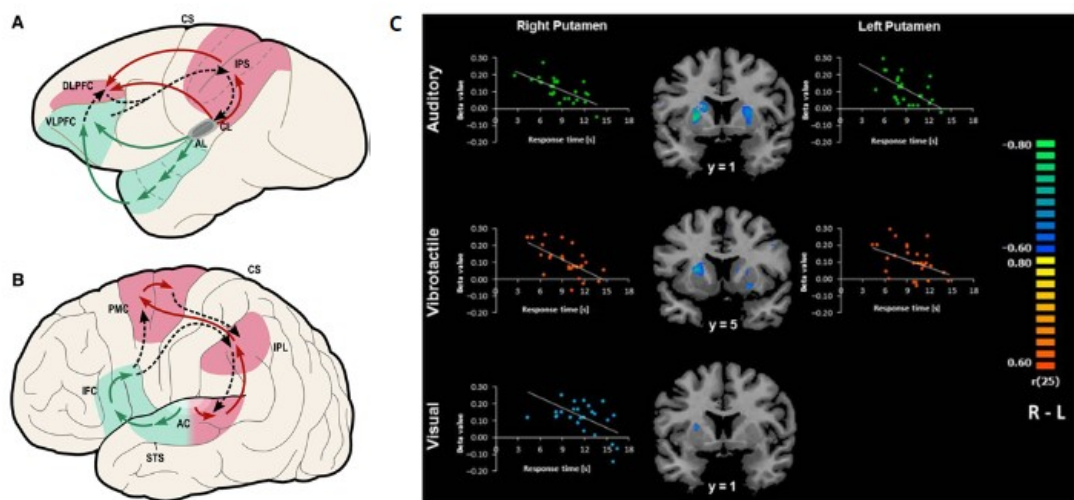


Figure 3. Representation of the neural bases and models of sensorimotor integration involved in rhythm perception.

(A and B) Theoretical models of the dorsal auditory stream (in red), in both non-human primates (A) and humans (B), illustrating how sensorimotor integration between the auditory cortex, motor areas (such as the premotor cortex and SMA), and inferior parietal regions is crucial for speech, language perception, and rhythmic synchronization (Rauschecker, 2011). (C) Brain activation maps in humans during beat detection across different sensory modalities (auditory, vibrotactile, and visual), obtained using functional magnetic resonance imaging (fMRI), showing the activation of a supramodal network involving the dorsal auditory cortex, supplementary motor area (SMA), and putamen, suggesting a key role of the dorsal stream in mediating motor predictions and sensorimotor integration for rhythm perception (Araneda et al., 2017). The combination of figures A, B, and C highlights how the processing of complex rhythms relies on an interconnected network between auditory and motor regions, reinforcing the importance of the dorsal stream in rhythm anticipation and perception

Penhune and Zatorre (2019) further examined the lateralization of the dorsal auditory stream, proposing that beat-based timing relies on the integration of sensory information with temporal patterns encoded in motor regions, such as the medial premotor cortex (MPC). They suggest that the left hemisphere, particularly the left MPC, is optimized for tasks requiring precise temporal predictions, while the right hemisphere is more suited to tasks involving more complex rhythmic structures due to its broader integration across sensory modalities.

The next section will further explore hemispheric differences in the dorsal premotor cortex (dPMC) during rhythm perception and production, examining how each hemisphere supports distinct aspects of rhythmic processing and contributes to the overall coordination of rhythmic behaviors.

3.2 Hemisphere Differences in the dPMC during Rhythm Perception

Rhythm perception is an intricate cognitive function that needs the coordination of multiple brain areas, most notably the dorsal premotor cortex (dPMC). Situated within the premotor cortex, the dPMC is essential for integrating auditory and motor signals, enabling humans to predict and synchronize with rhythmic sequences. However, the roles of the dPMC in rhythm perception differ between the two hemispheres. Recent research highlights significant hemispheric variations in how the left and right dPMC are engaged during rhythm perception, suggesting specialized roles in managing different components of rhythmic information (Kasdan et al., 2022; Moore et al., 2017). This section provides an in-depth examination of these differences by reviewing findings from neuroimaging,

neurophysiological, and lesion studies to better understand the unique contributions of the left and right dPMC to rhythm perception.

- Hemispheric Specialization in the dPMC

The differences between hemispheres in the dPMC's involvement in rhythm perception can be explained by the broader context of lateralized brain functions. Traditionally, the left hemisphere is linked to functions requiring fine temporal resolution, precise motor control, and sequential processing, while the right hemisphere is more adept at integrating complex temporal structures and recognizing global patterns (Junemann et al., 2023; Vaquero et al., 2018). Functional magnetic resonance imaging (fMRI) studies have consistently shown that the left dPMC is more actively engaged in tasks demanding high temporal precision and motor coordination, such as tapping along to a regular beat (Kasdan et al., 2022; Junemann et al., 2023). In contrast, the right dPMC is predominantly activated during tasks that involve interpreting irregular, syncopated, or complex rhythmic patterns, which require broader temporal integration and greater cognitive flexibility (Giovanelli et al., 2014; Vaquero et al., 2018). This division of labor reflects a specialization where the left hemisphere supports tasks that require temporal accuracy, while the right hemisphere facilitates the processing of more intricate rhythmic structures.

The complexity of rhythmic patterns significantly influences the degree of lateralization within the dorsal auditory stream. Vaquero et al. (2018) found that complex rhythms, such as those involving syncopation or polyrhythms, tend to increase activation in the right hemisphere, particularly in the right dPMC and associated motor areas. This suggests that the right hemisphere is better equipped

to handle the cognitive demands associated with processing intricate rhythmic patterns, while the left hemisphere is more engaged with simpler, regular rhythms that require precise timing and synchronization.

Siman-Tov et al. (2022) demonstrated that as rhythm complexity increases, there is greater reliance on the right hemisphere's dorsal auditory stream. Their study indicated that the right dPMC and SMA are involved in managing the additional cognitive load required for processing complex rhythms, highlighting a hemispheric specialization that reflects the nature of the rhythmic task. In contrast, tasks involving simpler rhythms, which demand less cognitive effort, tend to engage the left hemisphere more robustly, consistent with its specialization for fine temporal resolution (Chen et al., 2008a; Junemann et al., 2023).

Penhune and Zatorre (2019) also note that beat-based timing mechanisms, particularly those relying on internal motor simulations, exhibit a degree of lateralization depending on the complexity of the rhythmic pattern. The left hemisphere tends to dominate in simpler, more predictable rhythms due to its specialization in precise motor control, whereas the right hemisphere is recruited for more complex rhythms that require integration across multiple sensory and motor areas.

These distinct specializations imply that each hemisphere's dPMC has a unique role in rhythm perception, influenced by the complexity and predictability of the rhythmic stimuli.

- The Role of the Left dPMC in Rhythm Perception

The left dPMC is primarily involved in tasks that demand precise temporal prediction and synchronization with a consistent beat. For instance, Moore et al. (2017) found that the left dPMC is crucial when participants maintain a steady tempo during rhythm production tasks, highlighting its role in coordinating motor actions with temporal precision. This aligns with the left hemisphere's specialization in sequential processing, indicating that the left dPMC aids in executing rhythmic movements by preserving an internal representation of the beat.

Furthermore, the left dPMC integrates auditory and motor information vital for rhythm perception. Genon et al. (2017) demonstrated that the left dPMC has extensive connectivity with both auditory and motor regions, supporting its function in aligning motor responses with auditory signals. This connectivity is essential for tasks involving regular rhythms, where precise coordination between auditory inputs and motor outputs is required. Consequently, the left dPMC acts as a hub for sensory-motor integration, ensuring accurate beat synchronization and rhythm production.

Additional evidence from Kasdan et al. (2022) indicates that disrupting the left dPMC through transcranial magnetic stimulation (TMS) significantly impairs the ability to synchronize with a regular beat, whereas tasks involving complex rhythms remain relatively unaffected. This suggests that the left dPMC is particularly critical for maintaining regular temporal patterns, emphasizing its specialization in fine temporal processing.

- The Role of the Right dPMC in Rhythm Perception

Conversely, the right dPMC is more engaged in processing complex and irregular rhythmic patterns that involve greater cognitive demands and flexibility. Research by Giovanelli et al. (2014) showed that the right dPMC is crucial for synchronizing with rhythms that include syncopation or irregular timing. When repetitive TMS was used to disrupt right dPMC activity, participants exhibited a significant reduction in their ability to synchronize with complex rhythms, while performance on simpler rhythms remained largely unaffected. This underscores the right dPMC's specialized role in handling the cognitive and motor demands of rhythm complexity.

The right dPMC is also involved in integrating broader temporal and spectral aspects of rhythm perception. Vaquero et al. (2018) reported that tasks involving intricate rhythms, such as polyrhythms or syncopated patterns, resulted in higher activation in the right dPMC compared to the left. This suggests that the right dPMC is adept at managing more variable rhythmic information, requiring adaptive responses to unexpected changes in rhythm, aligning with the right hemisphere's specialization for global processing of complex patterns.

Moreover, the right dPMC's role in rhythm perception extends beyond purely auditory stimuli. Warrier and Zatorre (2004) found that the right auditory cortex and related regions, including the right dPMC, are essential for using melodic context in pitch constancy tasks. This suggests that the right dPMC plays a broader role in integrating rhythmic and melodic information, reflecting its comprehensive involvement in music cognition.

- Functional Implications of Lateralization in Rhythm Perception

The lateralization of the dorsal auditory stream has significant implications for understanding how the brain integrates auditory and motor information during rhythm perception. The distinct roles of the left and right hemispheres suggest that the brain utilizes a division of labor strategy, optimizing performance by leveraging the unique strengths of each hemisphere. For instance, the left hemisphere's specialization in fine temporal processing and sequential organization supports the precise timing needed for musical performance and dance, where synchronization with a steady beat is crucial (Hickok and Poeppel, 2004; Kasdan et al., 2022; Rauschecker, 2011).

Conversely, the right hemisphere's capacity for processing complex rhythmic structures enhances the brain's ability to integrate diverse and dynamic musical patterns, thereby facilitating a broader range of musical experiences (Vaquero et al., 2018; Araneda et al., 2017). This hemispheric specialization likely reflects evolutionary adaptations that enable humans to navigate and respond to the complexities of musical rhythm, balancing the needs for both precision and flexibility in rhythmic behaviors (Penhune and Zatorre, 2019).

- Interplay Between the Hemispheres in the dPMC During Rhythm Perception

Although the left and right dPMC have distinct functions, they do not operate independently. Rhythm perception involves a dynamic interaction between both hemispheres, allowing for a flexible and adaptive response to varying rhythmic contexts. Amiez et al. (2006) highlighted the significance of bilateral dPMC activity in coordinating movements and integrating sensory information across hemispheres. Their findings suggest that while the left dPMC is primarily involved in precise

temporal control, the right dPMC offers contextual support for interpreting more complex rhythmic patterns.

This bilateral cooperation is especially evident in tasks that require simultaneous processing of both regular and irregular rhythms. Cattaneo and Parmigiani (2021) found that mixed rhythmic tasks, incorporating predictable and unpredictable elements, engaged both the left and right dPMC and increased connectivity between these regions. This suggests a collaborative effort where the left dPMC manages predictable rhythmic elements, while the right dPMC handles the more complex and variable aspects.

- Neurophysiological Evidence for Hemispheric Differences in the dPMC

Neurophysiological research further supports the notion of hemispheric differences in the dPMC's role in rhythm perception. Johnsrude et al. (2000) found that patients with lesions in the right temporal lobe, including areas connected to the dPMC, exhibited impairments in processing complex auditory patterns, while simpler rhythms remained unaffected. This finding underscores the right dPMC's importance in managing rhythm complexity, consistent with its role in processing irregular or syncopated rhythms.

Conversely, Limb et al. (2006) demonstrated that the left dPMC is essential for tasks that require rapid and precise motor responses to rhythmic cues. Disruptions in the left dPMC led to a notable decline in performance on tasks involving synchronization to a regular beat, underscoring its role in fine motor control and temporal precision.

- Impact of Rhythm Complexity on Hemispheric Activation in the dPMC

The complexity of rhythmic patterns substantially influences the level of activation in each hemisphere's dPMC. Vaquero et al. (2018) found that increasing rhythmic complexity, such as through syncopation or polyrhythms, resulted in greater activation in the right hemisphere, particularly within the right dPMC. This indicates that the right hemisphere is more suited to manage the cognitive demands of complex rhythms due to its specialization in integrating temporal and spectral information.

In contrast, simpler rhythmic patterns, which demand less cognitive effort but require precise timing, predominantly engage the left hemisphere (Kasdan et al., 2022; Junemann et al., 2023). This division of labor allows the brain to efficiently process a wide range of rhythmic stimuli, adapting to various rhythmic contexts by balancing precision and complexity.

The observed hemispheric differences in the dPMC during rhythm perception highlight a specialized division of labor between the left and right hemispheres, each contributing uniquely to the processing of rhythmic information. While the left dPMC is crucial for tasks requiring fine temporal precision and motor synchronization, the right dPMC is more involved in handling complex and irregular rhythms, reflecting its specialization in broader temporal and spectral processing.

Together, these insights underscore the importance of hemispheric specialization in rhythm perception, offering a nuanced perspective on how the brain integrates auditory and motor information for musical cognition. This lateralization enables humans to flexibly adapt to diverse rhythmic contexts, balancing the demands of both precision and complexity in rhythmic processing.

Based on this understanding of hemispheric specialization, the subsequent chapter will further investigate the causal roles of the left and right dPMC in rhythm perception. By applying transcranial magnetic stimulation (TMS), we aim to elucidate the specific contributions of each hemisphere to rhythm perception and processing, providing direct evidence of the distinct functions of the left and right dPMC. This approach will enhance our understanding of the neural mechanisms underpinning rhythm perception, offering a more detailed depiction of how the brain orchestrates the interplay between auditory and motor systems in musical contexts.

In summary, the lateralization of the dorsal auditory stream plays an important role in auditory-motor integration during rhythm perception. The left hemisphere specializes in fine temporal resolution and precise motor timing, whereas the right hemisphere is more involved in processing complex and irregular rhythmic patterns. These findings underscore the significance of hemispheric specialization in optimizing rhythm perception and synchronization within musical contexts (Rauschecker, 2011; Penhune and Zatorre, 2019).

4. The Causal Role of Right vs Left dPMC in Rhythm Perception: a TMS Study

This is one of three experiments conducted as part of a more general study on the functional organization of rhythm perception within the human premotor cortex. The results indicated that selective activation of the most caudal part of the right dorsal premotor cortex was effective in influencing subjects' performance for predictions involving the presence of a beat in the sequence. Specifically, the present experiment tested whether the effect of caudal dPMC on beat perception was right-hemisphere specific. Secondly, it sought to replicate the original finding

using an independent sample. Using the same task, stimulation procedure, and analyses as the previous experiment, stimulation was targeted only at right and left dPMC and a sham site. This experiment was preregistered on the AsPredicted platform (https://aspredicted.org/D7B_9CK).

4.1 Materials and methods

- Participants

Power was estimated for the main effect of right dPMC TMS (vs. Sham), which was deemed most critical to detect in this experiment, using the simulation approach as implemented in the R package *simr* (Green & MacLeod, 2016). The simulation was based on the results of the prior experiment. To test the robustness of the effect experimentally, we set all parameters at the values that emerged in the previous experiment, except for the crucial effect for which we used a safeguard power approach (Perugini et al., 2014). Rather than powering the study to detect the original effect ($b = .216$, see Table 1), we powered it to detect a smaller one, corresponding to the lower bound of the 60% confidence interval ($b = .167$). The results suggested that $N = 42$ participants would provide 82.5% power to detect the crucial effect.

Therefore, 42 neurologically healthy volunteers participated in the study (17 males, mean age = 23.5 ± 2.61 years). All were non-musicians and had not had more than three consecutive years of formal music instruction. Before the experiment with TMS, the participants read and signed an informed consent form and filled out a questionnaire that evaluated their eligibility to receive TMS

(adaptation from Rossi et al., 2021). None of them had any history of neurological problems or epileptic attacks, and no contraindications for TMS application were identified.

- Stimuli and tasks

This task is adapted from the Computerized Adaptive Beat Alignment Test (CA-BAT) developed by Harrison and Müllensiefen (2018a). In this task, participants listened to short musical excerpts, taken from a variety of musical genres, with an overlaid, auditory metronome beat track. These tracks were either on-the-beat or off-the-beat, with the latter also varying in degree of displacement. In the original version of the task, off-beat tracks could precede or follow the true beat of the stimuli. In line with the fact that off-beat tracks that precede the beat are universally harder (Harrison & Müllensiefen, 2018a; Manning & Schutz, 2016; Manning et al., 2017), we included only off-beat tracks that followed the beat.

Furthermore, there were a fixed set of stimuli to use due to the adaptive paradigm of the original task, wherein, as soon as the participants could discriminate the off-beat intervals, they would progressively be made smaller. Moreover, given the two-alternative forced-choice paradigm used in the original study, and in view of our research interest in beat perception for the sake of the TMS study, we used an on-off categorization of responses.

We accessed the stimuli used in the Harrison and Müllensiefen study from an online repository (Harrison and Müllensiefen, 2018a, 2018b). This bank contains 25 tracks taken from a range of musical styles and meters, approximately five seconds in duration apiece. Each track is overlaid with a metronome track consisting of a 20

ms sine tone with frequency 1000 Hz and a 10 ms fade-out. The displacement level is measured by the beat-track accuracy (BTA), an index between 0 and 1 (Harrison & Müllensiefen, 2018a). Small values mean more displacement; a maximal value of 1 gives a perfect metronome-beat alignment.

For the current experiment, we had two conditions—on-beat (1.0 BTA) and off-beat (BTAs of .50, .60). Each musical track was presented once for each BTA, for a total of 80 trials (20 musical tracks x 4 BTAs) per block, corresponding to each of the stimulation sites. In particular, the experiment consisted of three stimulation sites: right dPMC, left dPMC, and Sham.

We also tested information related to the sensitivity of the subjects to musical reward using the Barcelona Music Reward Questionnaire (BMRQ; Mas-Herrero et al., 2013) as well as a beat perception test. This was done to investigate whether individual differences in reward sensitivity to music, as suggested by studies from our lab, lately, influence beat perception ability.

- Procedures

The participants were seated in front of a computer monitor (LCD, 1280 × 1024 Pixel), at a distance of 57 centimeters, in a quiet and well-illuminated room, and used professional headphones (Sennheiser HD 280 Pro) for the auditory stimuli. Before task performance, all participants answered the Barcelona Music Reward Questionnaire (Mas-Herrero et al., 2013). This task was performed while under the influence of Transcranial Magnetic Stimulation (TMS) in three stimulation conditions: right dorsal premotor cortex (dPMC) stimulation, left dPMC stimulation, and a control condition.

Each trial started with a 3-second fixation cross, followed by the onset of the auditory stimulus. The participants indicated as quickly and accurately as possible whether each excerpt was "on beat" or "off-beat" by pressing the "A" or "L" keys on the keyboard, respectively (see Figure 4). The response keys were counterbalanced across participants. Six practice trials were presented at the start of the task and feedback ("incorrect") was shown after incorrect responses only.. The order of presentation of stimuli was randomized. Stimuli were delivered binaurally.

The whole experiment – stimuli presentation, data collection, and TMS triggering – was controlled by means of the E-Prime 3.0 Software (Psychology Software Tools, Pittsburgh, PA). The experiment lasted in total about two hours, including instructions, short breaks, and questionnaires. The experiment included three pulses of TMS at 10 Hz, delivered just prior to the presentation of the auditory stimulus, with the third pulse coinciding with the onset of the musical one. Each session consisted of three blocks corresponding to the three stimulation conditions: right dPMC, left dPMC, and sham. The blocks were ordered randomly and counterbalanced, to avoid order effects, across the participants.

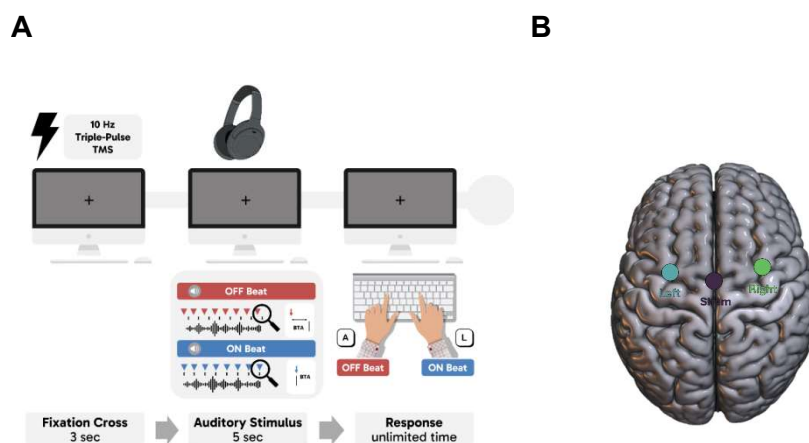


Figure 4. (A) Schematic representation of the task procedure for the behavioral and TMS experiments. After the fixation cross (3 sec), participants listened to the musical track (5 sec). Participants were deemed to categorize each track as 'on-the-beat' or 'off-the-beat' by pressing the "A" or "L" keys on the keyboard (counterbalanced). Triple pulse 10 Hz TMS was delivered immediately before the auditory stimulus, with the third pulse aligned with the musical track onset. (B) Surface render of the MNI-152 template with indication of the average cortical location of the Experiment (right and left dPMC).

- *Neuronavigation*

The active sites of stimulation were located by stereotaxic navigation obtained through a 3D deformation procedure by fitting a high-resolution MRI model with the participant's scalp model and craniometric points (Softaxic®, EMS, Bologna, Italy). This procedure has been proven to ensure a good localization accuracy (5 mm), with a level of precision close to that obtained using individual MRI (Carducci & Brusco, 2012). Mean MNI coordinates for the 2 active sites were $x = 28.9$, $y = -5.8$, $z = 72.9$ for right dPMC and $x = -31.8$, $y = -3.8$, $z = 71.4$ for left dPMC (see Figure 4C). A 3D optical digitizer (Polaris Vicra, NDI) was used in combination with the Softaxic neuronavigation software to co-register in the same virtual space the participant's head, the digitizer pen, and the TMS coil throughout the whole experiment to monitor coil position for each stimulation location (Lega et al., 2019, 2020a, 2020b).

- *Transcranial Magnetic Stimulation*

TMS was delivered using a Magstim Rapid2 stimulator (Magstim Co. Ltd, Whitland, UK) via a 70 mm butterfly coil. The stimulation intensity was set for all subjects following the measurement of the resting motor threshold from the left first dorsal interosseous muscle with the use of the Motor Threshold Assessment Tool®, Version 2.0 (www.clinicalresearcher.org/software.htm). An MEP with a peak-to-peak amplitude of 50 mV was fed back to the software as a valid response.

The EMG electromyographic recordings were carried out using Ag/AgCl surface electrodes (10 mm diameter). The active electrode was placed on the first dorsal interosseous muscle of the left hand, while the reference electrode was placed on the metacarpophalangeal joint of the index finger. The EMG signal was sampled and amplified 1000 times (1000x) using a Digitimer D360 amplifier (Digitimer®), further digitized by an analog-to-digital converter (Power 1401, Cambridge Electronic Design) with a sampling rate of 5 kHz, band-pass filtered from 10 to 2000 Hz, and stored using Signal (Cambridge Electronic Design) software.

Stimulation in this experiment was given at 100% of the individual motor threshold, with an average stimulation intensity of $M = 48.7\%$ ($DS = 4.34\%$). Over the premotor cortex sites, the coil was placed at a 45° angle from the nasion-inion line, with the handle pointed in the latero-inferior direction. For the sham condition, the coil was placed over the vertex perpendicular at an angle of 90° to avoid any stimulation over the lateral and posterior directions of the target sites.

It has been demonstrated that this sham condition does not produce an electric field capable of altering neuronal excitability (Lisanby et al., 2001) and, indeed, it has been used in prior studies employing the same TMS paradigm (Lega et al., 2020a, 2020b).

- Data Analysis

The following statistical analysis was preregistered to examine the main hypothesis, based on the results of previous experiments: We employed multilevel logistic regression models, which are particularly suitable for multilevel structured data, where participants' responses are influenced by multiple factors. These models enabled us to examine the influence of Beat Tracking Accuracy (BTA) and TMS stimulation on participants' responses.

The primary model (Model 1) was designed to predict the binary outcome (0 = off-the-beat, 1 = on-the-beat) based on BTA and TMS effects. BTA was treated as a continuous predictor, ranging from 0.50 to 1.00. To capture potential learning effects over the experiment duration, we included linear, quadratic, and cubic time terms to model changes in participants' responses over time. The model was adjusted using random intercepts at two levels: Participants and Music tracks. Random intercepts were implemented for each participant, allowing the model to account for individual variations in responses, recognizing that different participants might have distinct baseline performances, regardless of the experimental conditions (BTA or TMS). Similarly, random intercepts were assigned to the music tracks to adjust for intrinsic differences between the tracks used in the experiment, ensuring that variability in responses was attributed to the experimental manipulations rather than differences in the music track characteristics.

A second model (Model 2) was developed to explore potential interactions, specifically investigating whether individual differences in musical reward, as assessed by the Barcelona Music Reward Questionnaire (BMRQ), were related to participants' sensitivity to BTA. The BMRQ was standardized to have a mean of 0

and a standard deviation of 1 before being included in the model, facilitating direct comparison of effects between participants.

To analyze the main effects and interactions identified, we conducted post hoc tests using the *phia* package, which allows for a detailed decomposition of interactions in linear mixed models. To control for Type I errors in multiple comparisons, we applied the Holm correction.

4.2 Results

A summary of the Model 1 (Marginal $R^2 = .149$, Conditional $R^2 = .239$) is illustrated in table 1. Confirming previous findings, Model 1 revealed a significant main effect of BTA: the likelihood of producing on-beat responses increased with BTA. The model has, therefore, critically confirmed our main hypothesis: compared to the sham control condition, stimulation of the right dPMC significantly increased the probability of indicating that the musical stimulus is on the beat ($b = 0.136$, $z = 2.443$, $p = .007$).

The effect of stimulating the left dPMC did not significantly differ from the sham control condition in Model 1 (see Figures 5A and 5B and Table 1). Post-hoc tests (Holm correction) confirmed that stimulation of the right dPMC corresponded to a significantly higher probability of considering a stimulus as on-beat compared to both Sham ($\chi^2(1) = 5.96$, $p = .032$) and left dPMC ($\chi^2(1) = 6.47$, $p = .032$). No significant difference was found between Sham and left dPMC stimulation ($\chi^2(1) = 0.009$, $p = .92$; see Figure 5B).

Table 1. Summary of Model 1

Predictor	Estimate	Std. Error	Z value	p-value
(Intercept)	-3.402	0.157	-21.619	< .001
Trial nr linear	-31.332	2.376	-13.184	< .001
Trial nr quadratic	-0.627	2.333	-0.269	0.786
Trial nr cubic	-7.789	2.348	-3.317	< .001
TMS Left	-0.006	0.056	-0.099	0.921
TMS Right	0.136	0.056	2.443	0.007*
BTA	3.907	0.124	31.582	< .001

Note. *Because we preregistered a directional hypothesis (a positive effect of right TMS stimulation), the p-value reported is one-tailed. The two-tailed p-value is $p = .015$

Model 2 expanded upon Model 1 by incorporating the overall BMRQ score and its interactions with BTA and TMS as additional predictors of the binary response. The results confirmed the main effects of BTA ($b = 3.938$, $z = 31.654$, $p < .001$) and the stimulation of the right dPMC ($b = 0.139$, $z = 2.492$, $p = .013$). Furthermore, the model revealed a significant interaction between BMRQ and BTA ($b = 0.740$; $z = 6.135$; $p < .001$).

No statistically significant main effect was observed for BMRQ ($b = -0.062$, $z = -0.826$, $p = .410$), and similarly, no significant interactions were found between BMRQ and right dPMC TMS ($b = 0.021$, $z = 0.378$, $p = .710$) or left dPMC TMS ($b = 0.056$, $z = 1.004$, $p = .320$; Marginal $R^2 = .154$, Conditional $R^2 = .245$). Consistent with previous experiments, the interaction between BMRQ and BTA suggested that participants with higher musical reward scores demonstrated superior performance and enhanced rhythm perceptual abilities (see Figure 5C).

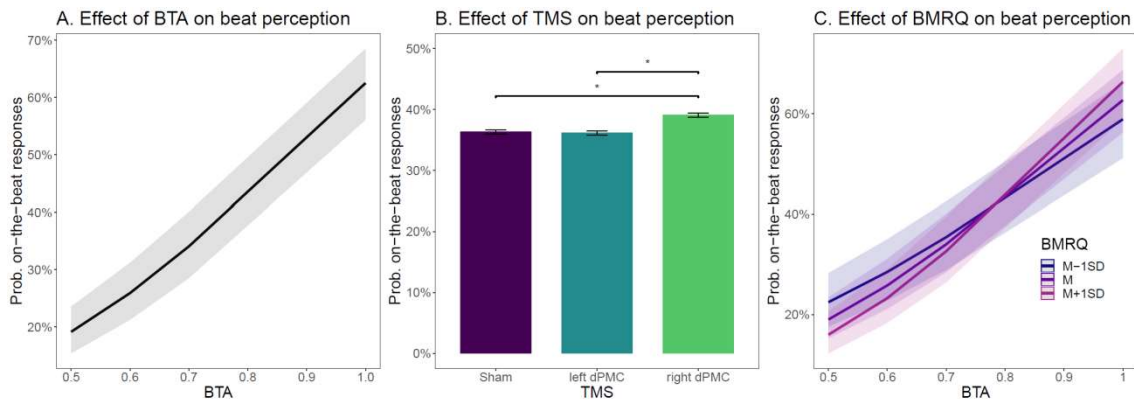


Figure 5. Results of the Experiment

Visualization of the marginal predicted values in terms of on-beat response probabilities as a function of BTA levels and TMS stimulation sites (A), as a function of the TMS stimulation sites (B) and as a function of BTA levels and BMRQ score (C). For ease of interpretation, panel C visualize original BTA in the original scale, instead of centered values.

4.3 Discussion

This study aimed to examine whether selective stimulation of the caudal portion of the dorsal premotor cortex (dPMC) specifically affects beat perception in musical sequences. To do so, we utilized a focal transcranial magnetic stimulation (TMS) protocol to replicate prior findings using a new, independent sample. Additionally, we assessed the impact of stimulating the right and left dPMC, in comparison to a control (sham) condition, on participants' ability to accurately identify whether a beat was "on the beat" or "off the beat" across various temporal displacement scenarios.

Our findings indicate that stimulation of the right dPMC significantly increased the likelihood of participants categorizing musical stimuli as "on beat" relative to the control condition, an effect not observed when the left hemisphere was stimulated. The absence of significant differences between left dPMC stimulation and the control

condition reinforces the idea that beat perception within the dPMC may be lateralized to the right hemisphere (Chen et al., 2008a; Giovanelli et al., 2014; Kasdan et al., 2022; Jünemann et al., 2023).

These results align with previous studies that underscore the importance of the right hemisphere in tasks involving temporal and rhythmic perception (Zatorre & Belin, 2001; Johnsrude et al., 2000; Patterson et al. 2002; Warrier & Zatorre, 2004; Vaquero et al. 2018; Moore et al., 2017; Lega et al., 2016; Siman-Tov et al., 2022; Jünemann et al., 2023; Chen et al., 2008a). The replication of earlier experimental outcomes with this new sample further strengthens the argument that right, but not left, dPMC activation plays a crucial role in rhythm perception. This lateralization is likely linked to specialized temporal processing mechanisms in the brain (Morillon & Baillet, 2017; Cannon & Patel, 2021; Proksch et al., 2020; Ross et al., 2018a). Additionally, our findings lend support to the hypothesis that the right dPMC is more actively involved in integrating temporal information crucial for rhythm perception (Schubotz & von Cramon, 2002; Arnal, 2012; Hadley et al., 2015; Ross et al., 2016; Morillon & Bailley, 2017; Araneda et al., 2017), and contribute to the broader body of research on the lateralization of cognitive functions in musical and temporal perception tasks (Hickok and Poeppel, 2004; Rauschecker, 2011; Kasdan et al., 2022; Araneda et al., 2017; Giovanelli et al., 2014; Vaquero et al., 2018; Siman-Tov et al., 2022; Chen et al., 2008a; Junemann et al., 2023; Penhune & Zatorre, 2019).

A noteworthy observation from our study is the interaction between musical sensitivity and rhythm perception. According to Model 2, musical sensitivity—as measured by the Barcelona Music Reward Questionnaire (BMRQ)—significantly interacts with beat tracking accuracy (BTA). Participants with higher BMRQ scores demonstrated superior performance in rhythm perception, suggesting that an

individual's sensitivity to musical reward may influence their ability to perceive rhythm. This points to the potential role of motivational and emotional factors in modulating the neural networks responsible for rhythm perception (Fiveash et al., 2022, 2023; Mas-Herrero, 2013; Janata et al., 2012; Matthews et al., 2020; Vuust & Witek, 2014, Witek et al., 2014).

In sum, our findings underscore the significance of the right dorsal premotor cortex's (dPMC) lateralization in rhythm perception, highlighting its pivotal role in the integration of temporal information essential for musical processing. By replicating previous research and uncovering the interaction between musical sensitivity and rhythm perception accuracy, we also point to the influence of emotional and motivational factors in shaping the neural networks governing these functions. These insights pave the way for a broader discussion on the theoretical and practical ramifications of our results, an acknowledgment of the study's limitations, and an exploration of future research directions. Specifically, we agree for further investigation into the contributions of the right dPMC, as well as other cortical and subcortical circuits, to musical cognition and rhythmic rehabilitation.

5. General Conclusion

Our study maintains a high methodological standard, replicating a rigorous approach previously employed in an earlier experiment with a new participant sample. However, we acknowledge certain limitations. Notably, we did not collect data on the participants' musical backgrounds. Given that prior research has identified a correlation between musical training and BMRQ scores (Mas-Herrero, 2013), this omission may have influenced the observed relationship between BMRQ

scores and rhythm perception performance in our sample, which comprised non-musicians.

The findings of this study have several theoretical implications for understanding the lateralization and functional roles of the motor system in rhythm perception, sensory-motor integration in musical cognition, and neural plasticity.

Firstly, our results provide evidence that rhythm perception may be lateralized to the right hemisphere, particularly in the caudal region of the dPMC. This finding adds to the body of research on functional brain lateralization, particularly in relation to tasks involving temporal and rhythmic processing, suggesting that the right hemisphere plays a specialized role in coordinating auditory and motor processes (Zatorre & Belin, 2001; Chen et al., 2008a; Giovanelli et al., 2014, Kasdan et al., 2022; Jünemann et al., 2023).

Moreover, the results support theories proposing that the motor system is actively engaged in perceiving musical beats, even in the absence of overt movement (Grahn & Brett, 2007; Chen et al., 2008a, 2008b; Gordon et al., 2018; Patel & Iversen, 2014; Ross et al., 2016; Cannon & Patel, 2021; Morillon & Baillet, 2017; Araneda et al., 2017). Our study reinforces models such as the ASAP (Action Simulation for Auditory Prediction), which argues that action simulation is vital for temporal prediction in auditory perception (Patel & Iversen, 2014; Cannon & Patel, 2021; Merchant & Averbeck, 2017; Merchant et al., 2015). Given the right dPMC's role in sensory-motor integration during rhythm perception, these findings suggest that musical cognition involves complex, multimodal interactions between cortical and subcortical areas, providing deeper insight into the mechanisms underlying beat perception tasks (Merchant & Honing, 2014; Merchant et al., 2015; Morillon & Baillet, 2017; Cannon & Patel, 2021; Schubotz et al., 2000).

Additionally, this research offers new perspectives on neural plasticity in the context of rhythm perception, particularly regarding how musical experience and sensitivity to musical reward shape the organization and functioning of the neural networks involved (Fiveash et al., 2022, 2023; Mas-Herrero, 2013). These findings hold significance for theories of neuroplasticity and functional brain adaptation.

From a practical standpoint, the study's findings have several applications. For example, rhythm-based therapeutic interventions could be developed for patients with brain injuries or neurodegenerative diseases (such as Parkinson's disease) that affect motor coordination and rhythm perception (Dalla Bella, 2020; Janzen et al., 2022; Koshimori and Thaut, 2018). Understanding the specific function of the right dPMC could help refine targeted stimulation and training strategies for these areas. The findings also suggest avenues for improving brain stimulation techniques like TMS or tDCS to enhance temporal perception in individuals with rhythmic deficits. Our results demonstrate that focal stimulation of the right dPMC can modulate rhythm perception, underscoring its importance (Giovanelli et al., 2014; Kasdan et al., 2022; Junemann et al., 2023).

Additionally, our findings can inform more effective music teaching methods that leverage brain function lateralization, helping to design educational programs that maximize activation of the right dPMC, especially for students facing rhythmic challenges (Limb et al., 2006; Grahn, 2009; Vaquero et al., 2018). Understanding the role of the right dPMC in rhythm perception may also guide the creation of assistive and rehabilitation devices, such as auditory and visual prostheses, that utilize rhythmic stimuli to facilitate sensorimotor integration in individuals with perceptual difficulties (Hadley et al., 2015; Giovanelli et al., 2014; Araneda et al., 2017; Proksch et al., 2020). Similarly, our results could be applied to optimize brain-computer

interfaces (BCIs) by calibrating algorithms to more accurately interpret brain signals related to rhythm, enhancing their efficiency in musical and cognitive rehabilitation contexts (Jeunet et al., 2019; Pichiorri et al., 2011).

Building on the findings of this study, several future research directions could further elucidate the role of the right dPMC in rhythm perception. For example, additional studies could explore how other cortical and subcortical regions, such as the auditory cortex, basal ganglia, and cerebellum, interact with the right dPMC (Grahn & Rowe, 2013; Matthews et al., 2020; Fiveash et al., 2023; Leow et al., 2022, Coull & Nobre, 2008). Techniques like fMRI, EEG, or functional connectivity studies could provide a clearer understanding of these neural networks.

Moreover, replicating this study in different populations, including professional musicians and patients with neurological deficits affecting rhythm (Chen et al., 2008a; Limb et al., 2006; Grahn et al., 2009; Fiveash et al., 2022), would help to determine whether the role of the right dPMC is influenced by musical experience or specific neurological conditions. This could offer new insights into brain plasticity in response to both musical training and pathological changes.

Future research could also focus on varying brain stimulation protocols, such as altering the frequency, intensity, or duration of TMS, or using tDCS for longer-lasting effects, to identify optimal conditions for enhancing rhythm perception and therapeutic interventions (Thut et al., 2011; Janzen et al., 2022; Dalla Bella, 2020; Schön and Tillmann, 2015). Longitudinal studies could track changes in neural organization over time in response to rhythm-based interventions. Integrating sensory and motor feedback using technologies like virtual reality, tactile feedback, or BCIs could further advance our understanding of how the brain processes multiple sensory inputs during rhythm perception tasks (Janzen et al., 2022).

Finally, studies that combine brain stimulation techniques like rTMS or tDCS with brain imaging methods such as fMRI or EEG could shed light on the causal connectivity between the right dPMC and other regions involved in rhythm perception (Grahn & Rowe, 2009, 2013; Ross et al., 2018a; Cannon & Patel, 2021; Leow et al., 2022; Morillon & Baillet, 2017). These investigations could clarify the specific neural pathways supporting rhythm perception, providing a foundation for developing new therapeutic and educational interventions.

In conclusion, this study offers new perspectives on the lateralization and functional role of the right dorsal premotor cortex (dPMC) in rhythm perception, reinforcing the notion that specialized temporal processing in this brain region is vital for musical cognition. While our findings are consistent with existing theories and suggest potential therapeutic applications, they also reveal areas needing further investigation, particularly the role of integrating sensory and motor feedback in rhythm-based interventions. Although the study has certain limitations, such as the absence of detailed data on participants' musical backgrounds, it adds valuable evidence to the growing research on the neural mechanisms of rhythm perception and proposes practical uses in fields like education, rehabilitation, and the development of brain-computer interfaces. Future research should continue to investigate these themes, utilizing diverse methods and participant groups to enhance our understanding of the brain's capacity for rhythm processing and its flexibility in adapting to various sensory inputs.

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