

Imagining the beat: causal evidence for dorsal premotor cortex (dPMC) role in beat imagery via transcranial magnetic stimulation (TMS)

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ABSTRACT

The ability to internally generate and maintain a rhythmic pulse, i.e., beat imagery, is a fundamental aspect of musical cognition. While recent theories propose that premotor regions support internal temporal predictions during rhythm perception and imagery, direct causal evidence remains limited. In this study, we investigated the specific contributions of the dorsal premotor cortex (dPMC) and the supplementary motor area (SMA) to beat imagery using transcranial magnetic stimulation (TMS). Forty-two non-musicians listened to rhythmic musical excerpts and judged whether a probe tone, presented after a short silent period, was temporally aligned with the imagined beat. TMS (three pulses at 10 Hz) was delivered over dPMC, SMA, or a sham control site (coil tilted 90° over M1) immediately before the imagery phase. Participants also completed the Bucknell Auditory Imagery Scale (BAIS) to assess individual differences in auditory imagery abilities. Results showed that TMS over the dPMC significantly modulated beat imagery performance, particularly in individuals with lower auditory imagery scores. No effects were observed following SMA stimulation. These findings provide causal evidence for the involvement of the dPMC in the endogenous generation of rhythmic structure and suggest a functional dissociation between motor-related areas in beat-based timing. Moreover, the interaction between stimulation effects and individual imagery abilities indicates that the neural response to TMS is shaped by individual functional states. Collectively, these results highlight the flexible and context-dependent nature of rhythm imagery mechanisms and support a predictive role for the dPMC, and more broadly, the dorsal auditory stream, in internally guided beat processing.

1. Introduction

Humans possess a remarkable ability to extract temporal structure from complex auditory environments, allowing us to perceive, anticipate, and even imagine rhythmic patterns in the absence of explicit sensory input. One of the most compelling examples of this capacity is the perception and mental simulation of the musical beat. Unlike many other perceptual phenomena, beat perception does not depend on a fixed mapping between acoustic features and the resulting percept. Rather, it is shaped by internal, top-down processes that construct and maintain a sense of temporal regularity (Cannon and Patel, 2021; Okawa et al., 2017; Gelding et al., 2019). For instance, listeners can impose different metrical interpretations, such as a waltz or a march, onto the same rhythmic sequence, underscoring the role of cognitive inference

and imagery in structuring rhythmic experience. Within this framework, beat imagery emerges as a fundamentally predictive process, wherein listeners internally generate and maintain a sense of the beat in the absence of corresponding external cues. This aligns with the notion of active perception, whereby auditory experience is continuously shaped by internally generated predictions based on temporal regularities (Morillon et al., 2015; Gelding et al., 2019).

According to neurocomputational models, both beat perception and beat imagery arise from the entrainment of neural populations to a rhythmic structure, producing synchronized oscillatory activity at the beat frequency and its subharmonics, which support the perception of meter (i.e., the hierarchical structuring of beats; Large and Kolen, 1994; Large, 2008; Spiech et al., 2023; van Noorden and Moelants, 1999). For instance, when participants listened to a tone sequence and mentally

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imposed either a binary or ternary meter (i.e., a march or a waltz) results revealed sustained periodic electroencephalography (EEG) responses aligned not only with the beat frequency but also with the imagined metrical structure, indicating that both beat and meter can be internally simulated and are indexed by entrained neural signals (Nozaradan et al., 2011; see also Fujioka et al., 2015; Nozaradan et al., 2016). Further supporting the idea that purely imagined rhythmic structures can give rise to measurable neural entrainment, Okawa et al. (2017) found similar EEG patterns even in the absence of auditory stimulation. These results highlight the flexibility of internal representations in shaping rhythmic experience and reinforce the idea that rhythm processing is not solely stimulus-driven but is also deeply influenced by top-down temporal predictions, with beat imagery being at the core of this mechanism.

Recent evidence indicates that such temporal predictions likely originate in motor regions of the brain (Arnal and Giraud, 2012; Schroeder et al., 2010; Schubotz, 2007; Grahn and Rowe, 2013; Cheng et al., 2022; Morillon et al., 2015; Cannon and Patel, 2021). Using high-density EEG, Cheng et al. (2022) demonstrated that, even in the absence of overt movement or explicit acoustic cues, endogenous neural oscillations in both auditory and motor regions reflected the internal simulation of binary and ternary metrical structures. Crucially, directional connectivity analyses revealed a predominant flow of information from motor to auditory areas at the beat frequency, pointing to a top-down influence of the motor system in shaping the imagined rhythmic structure. The study also identified bidirectional causal interactions between auditory and motor cortices, suggesting a tightly coupled auditory–motor system that supports the hierarchical organization of internally generated rhythms. These findings reinforce the idea that the motor system actively contributes to the construction and maintenance of temporal predictions during rhythm imagery. They provide additional evidence in favor of motor-based models of beat perception, such as the Action Simulation for Auditory Prediction (ASAP) hypothesis (Patel and Iversen, 2014). According to this framework, motor planning regions like the PMC and SMA generate internal temporal predictions that are sent back to the auditory system to guide perception (Arnal, 2012; Ross et al., 2016; Morillon and Baillet, 2017; Araneda et al., 2017; Cannon and Patel, 2021). While it is well established that regions such as PMC and SMA contribute to beat-based timing during perception (Merchant et al., 2015; Cannon and Patel, 2021; Patel and Iversen, 2014; Proksch et al., 2020; Emerick et al., 2025; Grahn and Rowe, 2009; Leow et al., 2022), the causal role of motor planning areas in beat imagery remains untested. In a recent study, we used transcranial magnetic stimulation (TMS) to examine the causal role of SMA and dPMC in beat perception (Lazzari et al., 2025). We delivered online triple-pulse stimulation while participants judged whether a metronome was aligned with the beat of the underlying musical tracks. We found that stimulation of the right caudal dPMC selectively disrupted beat perception, whereas stimulation of the SMA, pre-SMA, and left dPMC had no significant effect. These findings provide causal evidence for the selective involvement of the right dPMC in detecting beats embedded in auditory sequences, corroborating previous research on the role of the premotor cortex in beat-based timing and rhythm processing (Merchant et al., 2015; Patel and Iversen, 2014; Proksch et al., 2020). However, whether this region plays a similar role when the rhythmic structure is internally generated, in the absence of external temporal cues, remains an open and important question. Addressing this gap is crucial to better understand the common and distinct neural mechanisms underlying beat perception and rhythm-based imagery.

Importantly, musical imagery is a highly variable phenomenon, both within and between individuals. On the one hand, subjective vividness can fluctuate from trial to trial, reflecting dynamic changes in engagement or context. On the other hand, individual differences in auditory imagery ability appear to represent stable cognitive traits, which can be reliably assessed using instruments like the Bucknell Auditory Imagery Scale (BAIS; Halpern, 2015). Interestingly, both state-like fluctuations

and trait-like differences in vividness appear to be linked to the structure and function of motor planning regions. At the trial level, higher vividness ratings during imagery tasks involving familiar melodies have been associated with increased activation in both the premotor cortex (Leaver et al., 2009) and the SMA (Zvyagintsev et al., 2013), suggesting that more vivid auditory imagery engages motor simulation mechanisms more strongly. These functional findings are complemented by structural evidence: for example, gray matter volume in the SMA has emerged as the most robust anatomical predictor of auditory imagery vividness, both in whole-brain analyses and in ROI-based studies informed by meta-analytic data (McNorgan, 2012). At the trait level, higher BAIS scores have been linked to increased gray matter volume in the SMA, as well as in the parietal cortex, medial superior frontal gyrus, and middle frontal gyrus (Lima et al., 2015). These findings are consistent with functional imaging studies showing that individuals with high BAIS scores exhibit greater activation in right prefrontal and temporal regions during auditory imagery tasks (Herholz et al., 2012).

Based on the evidence outlined above, in this study, we used TMS to causally investigate the contribution of motor planning areas to beat imagery. First, in Experiment I, we tested whether the clicking noise produced by the TMS coil could affect performance on the Beat-Drop Alignment Test (BDAT; Cinelyte et al., 2022). Participants listened to musical excerpts in which the music was intentionally removed for a short segment and were asked to judge whether a probe sound (a beep) was aligned with the imagined beat. The probe occurs during a short break in the rhythmic components of the music when no rhythmic events are present, thus forcing participants to judge beat alignment relative to an internal pulse maintained in the absence of local acoustic timing cues. This procedure allowed us to control for the potential auditory interference associated with TMS clicks, ensuring that such effects were accounted for in the subsequent Experiment II. In Experiment II, we delivered online TMS to the right dPMC and SMA, with sham stimulation included to control for nonspecific TMS effects, using a within-subject design. Stimulation was applied during the imagery phase of the BDAT to directly investigate the causal role of these motor regions in internally generating the beat in the absence of external timing cues. We also administered the Bucknell Auditory Imagery Scale (BAIS; Halpern, 2015) to assess individual differences in auditory imagery ability, given prior evidence linking such differences to variability in the engagement of motor and premotor regions during imagery tasks (e.g., Herholz et al., 2012; Lima et al., 2015). In this context, it is plausible to hypothesize that the effects of TMS may vary depending on individual differences in auditory imagery abilities. Furthermore, building on evidence linking rhythmic abilities and music reward sensitivity (Zatorre, 2024; Fiveash et al., 2022, 2023; Lazzari et al., 2024; Fullone et al., under review; Lazzari et al., 2025), we administered the extended Barcelona Music Reward Questionnaire (eBMRQ; Cardona et al., 2022) as an index of individual sensitivity to music reward. This allowed us to explore whether reward sensitivity plays a modulatory role in beat imagery, possibly through enhanced engagement or motivation.

2. Experiment I: behavioral validation and control of TMS-induced noise

2.1. Methods

The present Experiment I was designed to verify that the clicking noise produced by the TMS coil does not interfere with performance in the Beat-Drop Alignment Test (BDAT; Cinelyte et al., 2022). For this purpose, participants were tested in a classical TMS setting under a sham protocol, in which no active stimulation was delivered but the TMS clicks were still audible. This control condition mimicked the auditory component of TMS without actual stimulation, thereby allowing us to account for potential confounding auditory effects in Experiment II. Moreover, the original BDAT (Cinelyte et al., 2022) employed an

adaptive procedure, in which stimulus difficulty was adjusted dynamically based on participant performance, thus each participant performs an individualized number of trials. Since Experiment II was designed as a within-subject TMS protocol in which each participant would be tested under stimulation of three sites, we develop a shorter version with a fixed set of stimuli presented uniformly across all participants, thus allowing for consistent comparisons (see also Lazzari et al., 2025). Thus, the main objective of Experiment I was to assess whether performance on the modified BDAT remained comparable to the original version in the presence of coil-related noise. In line with previous findings, we expected the probability of judging the probe as aligned with the imagined beat to decrease as the temporal misalignment of the probe increased, reflecting sensitivity to beat-phase deviations. Additionally, we explored whether individual differences in auditory imagery ability (measured with the BAIS) and music reward sensitivity (measured with the eBMRQ) were related to performance on the BDAT. Lastly, we included only non-musician participants to avoid potential confounds related to musical expertise, consistent with research demonstrating differences in both behavioral performance (Spiech et al., 2023; Repp and Doggett, 2007; Chen et al., 2008; Skaansar et al., 2019; Grahn and Schuit, 2012) and neural activity (Grahn and Rowe, 2009; Grahn and McAuley, 2009; Chen et al., 2008; Grahn and Schuit, 2012; Pando-Naude et al., 2021; Criscuolo et al., 2022; Lumaca et al., 2024) between musicians and non-musicians during rhythmic processing. To balance sample homogeneity with control over expertise, we included only participants with less than three years of formal musical training (Vaquero et al., 2018; Bidelman et al., 2013; Mankel and Bidelman, 2018). The same criterion was applied in Experiment II.

2.1.1. Participants

To determine the required sample size, we conducted a power analysis based on the results of our previous study (Experiment I in Lazzari et al., 2025), which tested an adapted version of the task subsequently used in the TMS experiments. Using the R^2 from the main model effect, with a target power of 80 % and an alpha level of 0.05, the analysis indicated that 36 participants would be sufficient to detect the

critical effect. Accordingly, 37 University of Pavia students participated in the study in exchange for course credits. We removed one participant because only the responses of 33 trials over the total (180, 18.3 %) were recorded. Thus, our sample consists of 36 participants (6 males, mean age = 23.81 ± 3.05 years). All participants were non-musicians, having received less than three years of formal or informal musical training ($M = .88$, $SD = 1.09$), with 18 participants having 0 years of musical training (50 % of the sample). The entire protocol was approved by the local ethical committee of the University of Pavia (Department of Brain and Behavioral Sciences, Ethical Committee Prot. 132/23) and participants were treated in accordance with the Declaration of Helsinki.

2.1.2. Stimuli

Stimuli were selected from the Beat-Drop Alignment Test (BDAT; Cinelyte et al., 2022; online repository provided by the authors at <https://osf.io/jpc29/>). In this task, participants listen to short musical excerpts and are asked to identify and imagine the beat. After the first 3 bars, the music fades out and a probe tone that is either on or off the expected beat is played (see Fig. 1). Participants are then asked to judge whether the tone is on-beat or off-beat. The stimuli are 30 musical tracks without any vocals, in contemporary electronic dance music (EDM) style, which consisted of 6 bars (11000 ms, see Fig. 1): in the first three bars the music plays, in the 4th the music fades out (5800 ms) and, right after, participants heard a probe tone (i.e. a 120 ms woodblock pitch at F2). The probe tone can be on either the 3rd or 4th beat of the 4th bar and is either timed to fall on-beat or off-beat by a variable displacement (i.e., Probe Displacement, PD). There are 7 PDs, at equally distant points along the nonlinear correlation between physical probe displacement and perceived difficulty (15 %, 18 %, 20 %, 23 %, 26 %, 31 %, 45 %; see Cinelyte et al., 2022, equation 1). The on-beat probe has a displacement of 0 %. After the probe, participants are asked to respond whether it was on or off the imagined beat. The music then restarts for 2 final bars.

For the current experiment, and in order to make it suitable for non-musicians, we modified the original BDAT (Cinelyte et al., 2022) in a few points: (1) We selected only tracks where the probe falls on the 3rd beat. This was based on the original study which showed that participants

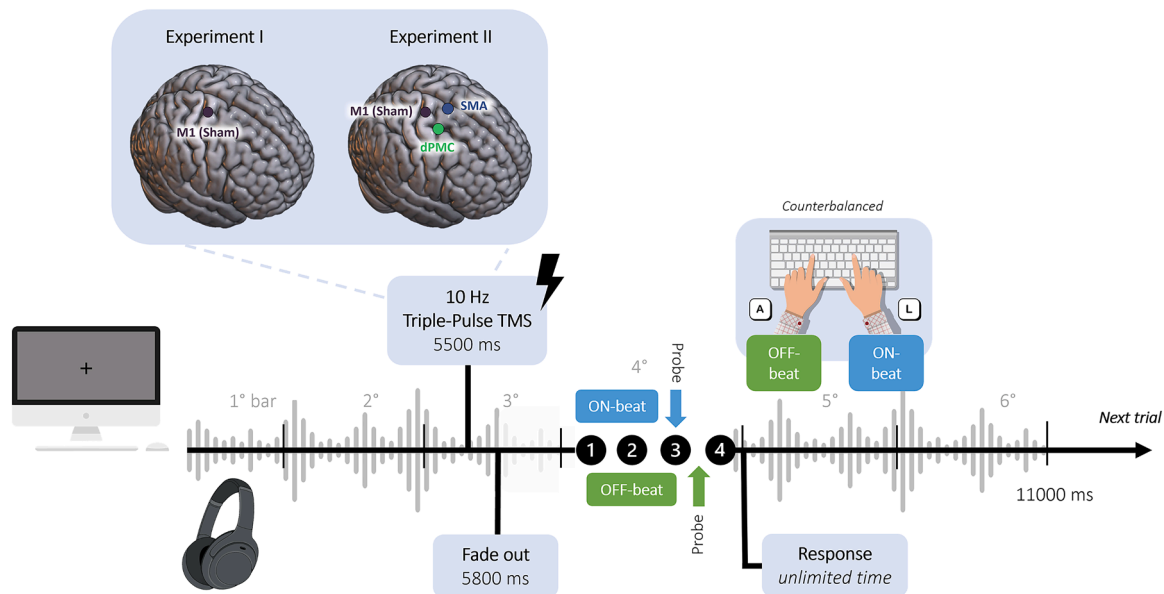


Fig. 1. Schematic representation of the task procedure. After the fixation cross, the musical track began. Participants were instructed to imagine the beat of the track. TMS pulses were delivered at 5500 ms, just before the track faded out at 5800 ms. Participants were then asked to categorize a probe sound, which occurred on the 3rd beat of the 4th bar, as either “on-beat” or “off-beat” relative to the imagined beat. After the 4th silent bar—which contained the probe—the track restarted and continued until 11000 ms. The figure includes two cortical surface renderings of the MNI-152 template: *Experiment I*. M1 is shown as the sham site, where only auditory stimulation mimicking real TMS was applied (no brain stimulation). *Experiment II*. dPMC and SMA are shown as the active stimulation sites, with an additional sham site over M1 used for control.

were 20 % more accurate in detecting the target on the 3rd beat - in a strong and accented position - compared to the 4th beat, which is in the weak, last position of the bar. (2) We selected only off-beat PDs that fall *after* the beat. We made this choice because off-beat probes that preceded the beat have been previously shown to be globally more difficult (Harrison and Müllensiefen, 2018; Manning and Schutz, 2016; Manning et al., 2017). (3) We selected only 6 PDs: 0 %, 15 %, 20 %, 26 %, 31 %, 45 %, ensuring a minimum gap of 5 % between displacement. This gave us a total of 180 stimuli (30 tracks x 6 PDs).

2.1.3. Procedure

Each participant was seated in front of a computer screen (57 cm from the monitor, LCD, 1280×1024 Pixel) in a quiet, lighted room and wearing headphones. Each trial started with a fixation cross of 2000 ms, after which the auditory stimulus was presented. To assess potential effects of TMS noise on task performance, we adopted a standard sham protocol in which the coil was positioned perpendicularly at a 90° angle over the primary motor cortex (M1), with the stimulating surface facing outward so that the pulse and its associated noise were produced without delivering actual stimulation (Lisanby et al., 2001). We applied the same TMS protocol planned for the Experiment II: an online 10 Hz triple-pulse (100 ms inter-pulse interval) delivered via a Magstim Rapid2 stimulator (Magstim Co. Ltd, Whitland, UK) connected to a 70 mm butterfly coil. The auditory pulses were administered at 5500 ms of each musical track, in the way that the end of the third pulse coincides with the starting of the fade out of the tracks (5800 ms), as reported in Fig. 1. In this condition, participants were not exposed to real TMS stimulation but experienced auditory input mimicking actual TMS. This design allowed us to test whether coil clicks interfered with task performance and thereby validate the TMS protocol for Experiment II.

On each trial, participants were asked to categorize the beep sound (i.e. the probe) as “on-beat” or “off-beat” compared to the imaged musical rhythm, as accurately as possible, by pressing the “A” or “L” keys on the keyboard. The response keys were counterbalanced across participants, meaning that odd participants were instructed to press “A” for “on-beat” answers and “L” for “off-beat” ones, while even participants received the opposite key mapping. Stimuli were binaurally delivered using headphones. Six practice trials were included at the beginning of the task, with the feedback “incorrect” displayed only after wrong responses. These trials featured both the on-beat (PD = 0 %) and the most off-beat (PD = 45 %) versions of tracks 5, 9, and 27. To prevent familiarization effects, we selected alternative off-beat versions in which the probe occurred *before* the on-beat position, differing from those used in the main task. During the practice, we adjusted the volume for each participant. After the practice, the experiment started. Short breaks were incorporated every 60 trials, with the order of presentation of stimuli randomized. The software E-Prime 3.0 (Psychology Software Tools, Pittsburgh, PA) was used for stimuli presentation, TMS triggering and data recording.

After completing the BDAT task, participants filled in the *Bucknell Auditory Imagery Scale* (BAIS, Halpern, 2015): this questionnaire comprises the Vividness (BAIS-V) and Control (BAIS-C) scales. Both scales have 14 questions with a 7-point Likert scale answer: participants have to answer how vivid is the image of the sound from (1) “No image present at all” to (7) “As vivid as the actual sound” (BAIS-V), and how easy is to change from imaging one sound to another, from (1) “No image present at all” to (7) “Extremely easy to change the image” (BAIS-C). In line with Zatorre et al. (2010), we calculated the overall score by summing the two subscales (min = 28, max = 196). Additionally, participants filled in the *extended-Barcelona Music Reward Questionnaire* (eBMRQ; Cardona et al., 2022): this questionnaire comprises 24 questions categorized into 6 sub-factors: music-seeking, emotion evocation, mood regulation, sensorimotor, social reward and musical absorption. Participants are asked to rate their level of agreement with each statement on a 5-point Likert scale, from (1) “Fully

disagree” to (5) “Fully agree”. An overall score (min = 24, max = 120) was derived by summing up the individual sub-factor scores.

The entire experiment lasted approximately 2 hours, including instructions, the beat imagery task, short breaks, and questionnaires.

2.1.4. Statistical analysis

Consistent with our previous TMS study on beat perception, we used the probability of responding on-beat as dependent variable, as it provides a more sensitive measure of individual rhythmic processing than binary accuracy alone (Lazzari et al., 2025; see also Manning and Schutz, 2013). However, for completeness, we report all the analyses using the accuracy as dependent variable in the Supplementary Materials (section S1 and S2).

Because there were more off-beat than on-beat probes, we explored if participants responses shifted over time. Thus, we predicted the binary response (0 = off-beat, 1 = on-beat) from the trial number (rescaled between 0 and 1 to ensure convergence). As the main analysis, we predicted the binary response by Probe Displacement (PD, 6 levels: 0 %, 15 %, 20 %, 26 %, 31 %, 45 %).

In addition, we performed two analyses to explore whether individual differences in (1) auditory imagery (BAIS) and (2) music reward (eBMRQ) were related to the participants’ sensitivity to the displacement. To facilitate interpretation of the main effects, questionnaire scores were standardized ($M = 0$, $SD = 1$) before being entered into the model. The Figures therefore display three illustrative lines showing predicted performance at the mean (M), one standard deviation above the mean ($M + 1 SD$), and one standard deviation below the mean ($M - 1 SD$). These lines do not represent participant groups, but they are plotted to help visualize how performance changes across different levels of eBMRQ scores. To account for the binary dependent variable and the nested structure of the data (within participant and within trial), we fitted multilevel logistic regression models (Gelman and Hill, 2006) using package *lme4* (Bates et al., 2015) in the R statistical language (R Core Team, 2023). All the models included random intercepts per participant and per musical track, to take into account both individual differences in response styles and stimulus characteristics. Post-hoc tests were carried out using *phia* (De Rosario-Martinez, 2015) and *emmeans* (Lenth, 2025) packages, applying Holm’s correction for multiple comparisons (Holm, 1979). To provide an estimate of the magnitude of the effects, we reported R^2 for multilevel models (package *performance*; Lüdtke et al., 2021; Nakagawa and Schielzeth, 2013), as well as regression coefficients on the odds-ratio scale (e^b), indicating odds of responding “on-beat” multiplied by e^b for each unit increase in the predictor. We reported all the models with accuracy as dependent variable in the Supplementary Materials (section S1 and S2).

2.2. Results

Participants’ response patterns linearly increased over the trials, as showed by the significant linear effect of trial number ($b = 8.23$, $z = 3.85$, $p < .001$, $e^b = 3763.29$), indicating a growing tendency to report the probe as “on-beat” over time. To control for this shift in responding, trial number was included in the subsequent models. As expected, we found a significant effect of PD ($\chi^2(5) = 503.59$, $p < .001$; Marginal $R^2 = .106$, Conditional $R^2 = .157$), indicating that, as PD increased, the probability of responding that a stimulus is on-beat decreased (from $e^b_{(PD=15\%)} = 0.91$ to $e^b_{(PD=45\%)} = 0.16$; see Fig. 2A). Post-hoc tests using the Holm correction showed significant differences between every PD (all $ps < .024$, all $\chi^2 > 7.05$), except for the pairing 0–15 % ($\chi^2(1) = .76$, $p = .383$) and 15–20 % ($\chi^2(1) = 3.18$, $p = .149$).

When investigating individual differences in *auditory imagery abilities*, the BAIS scores was added into the model ($M = 142.03$, $SD = 19.71$; Marginal $R^2 = .108$, Conditional $R^2 = .160$) and revealed a significant PD x BAIS interaction ($\chi^2(5) = 22.79$, $p < .001$). Post-hoc comparisons showed a significant difference only at PD = 26 % between the $M_{(BAIS)}$

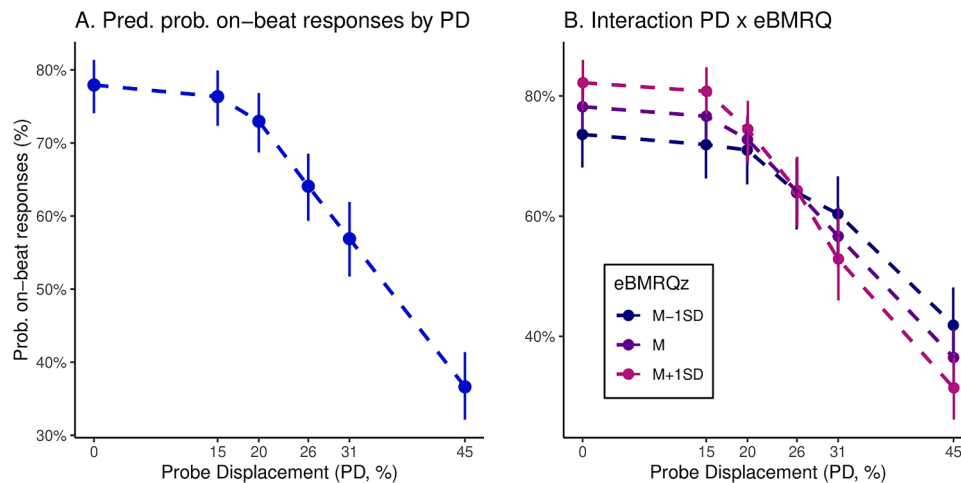


Fig. 2. (A) Visualization of the marginal predicted values in terms of probability of on-beat responses (%) as a function of (A) Probe Displacement (PD) and (B) PD and musical reward (eBMRQ) scores. The three colored lines illustrate predicted performance at the mean (M), one standard deviation above the mean ($M + 1$ SD), and one standard deviation below the mean ($M - 1$ SD) of eBMRQ scores, exemplifying how performance varies across higher, medium, and lower questionnaire levels.

and the $M + 1$ SD ($b = .22, z = 2.72, p = .019$), between M and $M - 1$ SD ($b = -.22, z = -2.72, p = .019$) and between $M + 1$ SD and $M - 1$ SD ($b = -.45, z = -2.72, p = .019$). None of the other comparisons resulted statistically significant (all p s $> .078$). There was also a significant main effect of PD ($\chi^2(5) = 497.75, p < .001$), but no main effect of BAIS score ($\chi^2(1) = 1.04, p = .307$).

When the *music reward sensitivity* (eBMRQ) scores were entered into the model, we found a significant interaction between PD and eBMRQ ($M = 98.33, SD = 11.04; \chi^2(5) = 41.08, p < .001$; Marginal $R^2 = .113$, Conditional $R^2 = .165$), meaning that participants with higher eBMRQ scores reported that the probe was on-beat more frequently at PD = 0 % and PD = 15 %, and that this pattern reversed at higher PD levels (31 % and 45 %), as shown in Fig. 2B. Indeed, we observed a significant difference at PD = 0 % between the $M_{(eBMRQ)}$ and the $M + 1$ SD ($b = -.25, z = -2.89, p = .013$), between M and $M - 1$ SD ($b = .25, z = 2.89, p = .013$) and between $M + 1$ SD and $M - 1$ SD ($b = .51, z = 2.89, p = .013$), and the same for PD = 15 % (M and $M + 1$ SD: $b = -.25, z = -2.84, p = .014$; M and $M - 1$ SD: $b = .25, z = 2.84, p = .014$; $M + 1$ SD and $M - 1$ SD: $b = .49, z = 2.84, p = .014$), with an opposite trend at PD = 45 % (M and $M + 1$ SD: $b = .23, z = 2.76, p = .018$; M and $M - 1$ SD: $b = -.23, z = -2.76, p = .018$; $M + 1$ SD and $M - 1$ SD: $b = -.45, z = -2.76, p = .018$). None of the other comparisons were statistically significant (all p s $> .272$). There was a significant main effect of PD ($\chi^2(5) = 489.21, p < .001$), but no main effects of eBMRQ score ($\chi^2(1) = .22, p = .637$).

Finally, when comparing our results with the original BDAT validation study (Cinelyte et al., 2022), we can qualitatively observe that (I) the changes in the stimuli and the presence of the TMS click did not affect the overall performance range (45–75 % in the original study vs. 32–78 % in the current study), and (II) the pattern of decreasing probability of on-beat responses with increasing PD remains consistent with the original findings. These results support the validity of our modified version of the BDAT to be used in Experiment II.

3. Experiment II: causal role of dPMC and SMA

The objective of Experiment II was to investigate the specific causal involvement of the right dPMC and SMA in beat imagery. Based on our previous TMS study on beat perception, which revealed a clear right-lateralized effect of stimulation (Lazzari et al., 2025), we focused stimulation on right-hemisphere. Additionally, we wanted to investigate whether individual differences in rated imagery ability or music reward sensitivity influenced beat imagery performance or modulated the effects of TMS.

3.1. Methods

3.1.1. Participants

To determine the number of participants required for the experiment we conducted a power analysis based on the results of our previous TMS study, which employed a similar protocol with three sites of stimulation (Experiment III in Lazzari et al., 2025). All parameters were set to the values emerged from the previous study, but we increased the power to 90 %. The results suggested that $N = 41$ participants would be sufficient to detect the crucial effect. To have the same number of counterbalanced orders of stimulation sites (6 possible combinations), we recruited 42 University of Pavia students (11 males, mean age = 22.8 ± 2.57 years). Following data analysis, it was revealed that 2 participants had more than 3 years of formal musical training. However, as the results were consistent regardless of their inclusion (see Supplementary Materials, section S3), and to preserve the full counterbalancing, these participants were retained in the final analysis. The overall sample reported an average of 1.57 years of musical training ($SD = 1.83$) with 17 participants (40.5 % of the total) with no musical training (0 years). All participants provided written informed consent and completed a TMS safety questionnaire (Rossi et al., 2018). The protocol was approved by the local ethical committee of the University of Pavia (Department of Brain and Behavioral Sciences, Ethical Committee Prot. 132/23). Participants were treated in accordance with the Declaration of Helsinki.

3.1.2. Stimuli

To maximize the power of a within-subjects design, each set of BDAT trials had to be repeated for the three TMS conditions (SMA, dPMC and Sham). Therefore, we further adapted the task based on the results of the preceding behavioral study. First, we removed two of the PD (15 % and 26 %), ensuring a 10 %-distance between all consecutive PDs for a total of 4 PDs (0 %, i.e. the “on-beat”, and 20 %, 31 % and 45 % as the “off-beat”). Moreover, we removed the tracks with the lowest accuracy rate (< 42.5 %) for a total of 18 tracks. Each musical track was presented once for each PD, in a randomized order, for a total of 72 trials (18 musical tracks \times 4 BTAs).

3.1.3. Localization of dPMC and SMA stimulation sites

dPMC and SMA were located by stereotaxic navigation obtained through a 3D deformation procedure by fitting a high-resolution Magnetic Resonance Imaging (MRI) model with the participant’s scalp

model and craniometric points (Softaxic®, EMS, Bologna, Italy). This method creates an accurate scalp model without requiring an MRI, achieving localization accuracy of approximately 5 mm, which is close to that obtained using individual MRI (Carducci and Brusco, 2012). The coordinates of the active targets were obtained from our previous TMS study targeting the same regions (Lazzari et al., 2025: dPMC: $x = 30, y = -5, z = 72$, SMA: $x = 5, y = -4, z = 78$). If the stimulation on these coordinates elicited a motor-evoked potential (MEP), we systematically adjusted the hotspot placement anteriorly until no MEPs were observed. This ensured that stimulation remained outside the primary motor cortex in each participant. As a result, while the targeted sites were highly similar across participants, each individual had a slightly adjusted set of stimulation points. We recorded the exact MNI coordinates of each stimulation site for every participant (see Supplementary Materials, section S4, Table S4) and found that the mean MNI coordinates across the sample were not shifted from the original targets by more than 1.8 mm in any dimension (dPMC: $x = 29.9, y = -6.3, z = 70.2$; SMA: $x = 5.6, y = -4.7, z = 76.2$). These mean coordinates of the stimulated areas are illustrated on a surface render of the MNI-152 template in Fig. 1. M1 was selected as the sham site and was localized to the primary hand motor area, which was identified by applying single pulses of TMS, and recording muscle responses from the left hand (see details below). 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 during the whole experiment to monitor coil position for every stimulation location (Lega et al., 2019, 2020a; 2020b; Lazzari et al., 2025).

3.1.4. Transcranial magnetic stimulation (TMS)

TMS stimulation was delivered at 100 % of the individual motor threshold (average intensity of stimulation $M = 54.3$ %, $SD = 4.88$ %). To determine the appropriate stimulation level for each participant, the resting motor threshold was measured from the first dorsal interosseous muscle of the left hand as determined using the Motor Threshold Assessment Tool®, Version 2.0 (www.clinicalresearcher.org/software.htm). The active electrode was positioned on the first dorsal interosseous muscle of the left hand, and the reference electrode was put on the metacarpophalangeal joint of the index finger. The EMG signal was sampled and amplified 1000 times (1000x) using a Digitimer D360 amplifier (Digitimer®) and digitized by an analog-to-digital converter (Power 1401, Cambridge Electronic Design) at a sampling rate of 5 kHz, bandpass filtered from 10 Hz to 2 kHz, then stored using Signal (Cambridge Electronic Design) software. A MEP with a peak-to-peak amplitude of 50 mV was returned to the software as a valid response. We checked in each participant whether stimulation over the defined sites evoked any motor-evoked potential and reassessed the points if this was the case. EMG recordings were performed with 10 mm Ag/AgCl surface electrodes. For dPMC and SMA sites, the coil was oriented with an angle of 45° from the nasion-inion line and the handle pointing outwards. For the sham condition, the coil was positioned over M1, held perpendicularly in a 90° angle to ensure the magnetic field did not stimulate the target areas, as done in Experiment I. This procedure has been successfully used in previous studies on sensorimotor processes (Lega et al., 2020a, 2020b; Lazzari et al., 2025).

3.1.5. Procedure

The procedure and questionnaires are the same as in Experiment I. Each session consisted of a total of three blocks (2 active sites, i.e., dPMC and SMA, and 1 sham condition), with short breaks in between. The order of the blocks (i.e., the TMS sites) was counterbalanced across participants. The experiment – stimuli presentation, data collection and TMS triggering – was run by means of the E-Prime 3.0 Software (Psychology Software Tools, Pittsburgh, PA). In total, the entire

experimental session lasted about two hours.

3.1.6. Statistical analysis

Statistical analysis mirrors the one of Experiment I. Firstly, we predicted the binary response (0 = off-beat, 1 = on-beat) by Probe Displacement (PD, 4 levels: 0 %, 20 %, 31 %, 45 %) and TMS sites (3 levels: dPMC, SMA, Sham). Then, we added (1) auditory imagery (BAIS) and (2) music reward (eBMRQ) to the previous model, to investigate if these measures were related to PD sensitivity and TMS stimulation. All models included random intercepts per participant and per musical track, to account for both individual differences in response styles and track characteristics. We reported all the models with accuracy as dependent variable in the Supplementary Materials (section S1 and S2).

3.2. Results

When predicting on-beat responses by PD and TMS sites (Marginal $R^2 = .103$, Conditional $R^2 = .155$), we found a significant effect of PD ($\chi^2(3) = 477.59, p < .001$), confirming that the probability of indicating that the probe was on-beat significantly decreased at increasing PDs (from $e_{PD=20\%}^b = 0.93$ to $e_{PD=45\%}^b = 0.47$). Post-hoc analysis using the Holm correction showed significant differences between every PD (all $ps < .001$, all $\chi^2 > 47.57$), except for the pairing 0–20 ($\chi^2(1) = .12, p = .723$). Crucially, we also found a significant main effect of TMS sites ($\chi^2(2) = 12.97, p = .002$): post-hoc analysis showed a significant difference between dPMC and Sham ($\chi^2(1) = 14.06, p < .001$), but not between SMA and Sham ($\chi^2(1) = 3.12, p = .098$) or SMA and dPMC ($\chi^2(1) = 3.87, p = .098$), as illustrated in Fig. 3A. Indeed, after the dPMC stimulation, the relative odds of responding “on-beat” increased of 1.24 compared to the Sham (with $e_{SMA}^b = 1.10$). Lastly, the effect of the interaction PD x TMS sites was not statistically significant ($\chi^2(6) = 5.36, p = .498$), see Fig. 3B.

When adding the auditory imagery abilities (BAIS) scores ($M = 137.67$, $SD = 18.51$) in the PD x TMS sites' model (Marginal $R^2 = .071$, Conditional $R^2 = .163$), we found a significant PD x BAIS interaction ($\chi^2(3) = 10.72, p = .013$). However, none of the comparisons between PDs $M_{(BAIS)} : M + 1 SD, M : M - 1 SD, M + 1 SD : M - 1 SD$ were statistically significant (all $ps > .363$). Additionally, we found main significant effects of PD ($\chi^2(3) = 473.85, p < .001$) and TMS sites ($\chi^2(2) = 13.26, p = .001$). Notably, a significant interaction between TMS sites and BAIS ($\chi^2(2) = 6.48, p = .039$) emerged. As depicted in Fig. 3C, we observed a significant difference between dPMC and Sham at BAIS scoring two SD below the mean ($b = -.49, z = -3.86, p < .001$) and equal to the mean ($b = -.22, z = -3.84, p < .001$). None of the other comparisons were statistically significant (all $ps > .064$). This interaction indicates that the effect of the TMS stimulation over dPMC was greater in individuals with low or mean auditory imagery abilities (see Fig. 3C). None of the other main effects or interactions were statistically significant (all $ps > .309$, all $\chi^2 < 7.12$, see Table 1 for the complete statistics).

When adding the music reward sensitivity (eBMRQ) scores ($M = 93.02$, $SD = 11.69$) to the PD x TMS sites' model (Marginal $R^2 = .077$, Conditional $R^2 = .169$), we found a main effect of PD ($\chi^2(3) = 463.55, p < .001$) and TMS sites ($\chi^2(2) = 13.11, p = .001$). Crucially, a significant interaction PD x eBMRQ ($\chi^2(3) = 45.97, p < .001$, see Fig. 3D) emerged indicating that participants with higher music reward sensitivity demonstrated greater accuracy in judging the probe as off-beat at PD levels of 31 % and 45 %, consistent with the findings from Experiment I. Significant differences were found at PD = 45 % between $M_{(eBMRQ)}$ and $M + 1 SD$ ($b = .32, z = 3.61, p = .002$), $M_{(eBMRQ)}$ and $M - 1 SD$ ($b = -.33, z = -3.61, p = .002$) and between $M + 1 SD$ and $M - 1 SD$ ($b = -.64, z = -3.61, p = .002$). None of the other comparisons were statistically significant (all $ps > .837$). None of the other main effects or interactions were statistically significant (all $ps > .070$, all $\chi^2 < 5.49$).

Accuracy analyses (see Supplementary Materials, section S1 and S2) are in line with the analyses reported here. Namely, dPMC stimulation

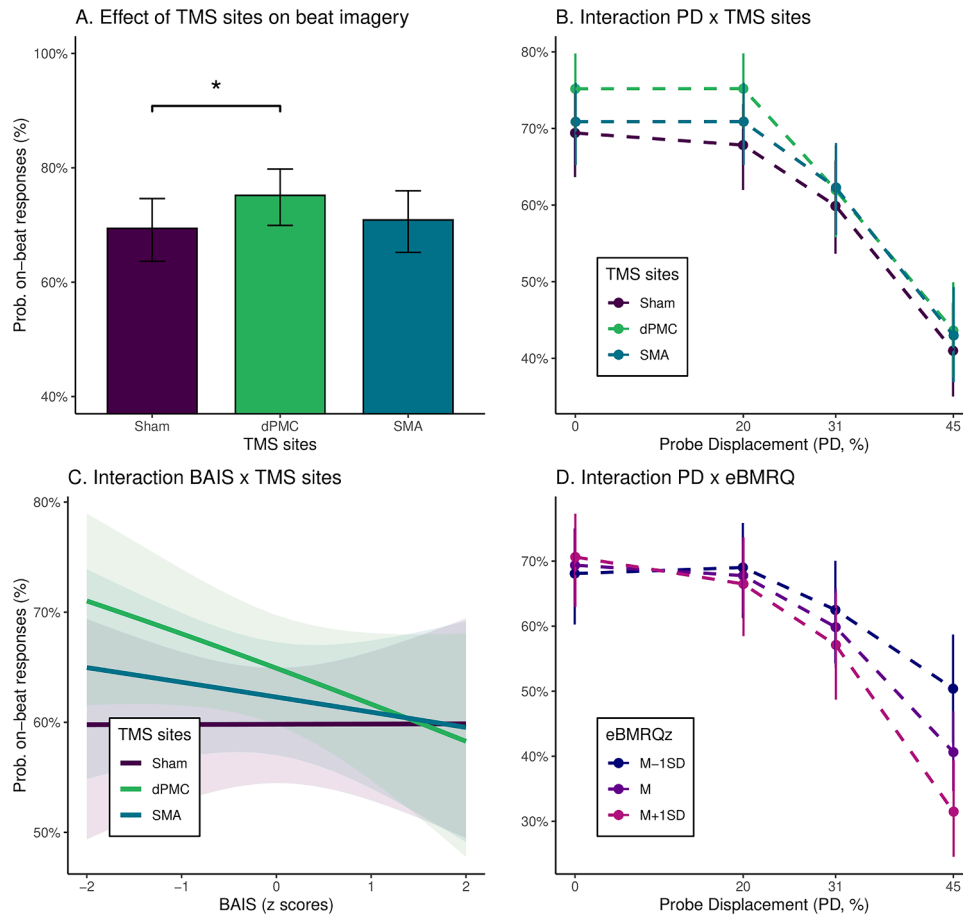


Fig. 3. Visualization of the marginal predicted values in terms of probability of on-beat responses (%) as a function of: (A) TMS sites; (B) Interaction Probe Displacement (PD) x TMS sites. The three colored lines represent TMS sites; (C) Interaction auditory imagery abilities (BAIS; z scores) x TMS sites. The three colored lines represent TMS sites; (D) Interaction Probe Displacement (PD) x music reward (eBMRQ). The three colored lines illustrate predicted performance at the mean (*M*), one standard deviation above the mean (*M* + 1 SD), and one standard deviation below the mean (*M* - 1 SD) of eBMRQ scores, exemplifying how performance varies across higher, medium, and lower questionnaire levels.

Table 1

Global questionnaires scoring, *R*² and statistics of the models with questionnaires (music reward sensitivity, eBMRQ and auditory imagery abilities, BAIS), Probe Displacement (PD) and TMS sites as predictors of the probability of on-beat responses (%).

		eBMRQ	BAIS
Scoring	<i>Mean</i>	93.03	137.67
	<i>SD</i>	11.69	18.51
Models	<i>Marginal</i>	.077	.071
	<i>Conditional</i>	.169	.163
Questionnaire	χ^2 (1)	.94	.695
	<i>p</i>	.332	.405
PD	χ^2 (3)	463.55	473.05
	<i>p</i>	<.001*	<.001*
TMS	χ^2 (2)	13.11	13.26
	<i>p</i>	.001*	.001*
Questionnaire x PD	χ^2 (3)	45.97	10.72
	<i>p</i>	<.001*	.013*
Questionnaire x TMS	χ^2 (2)	5.32	6.48
	<i>p</i>	.070	.039*
PD x TMS	χ^2 (6)	5.49	5.29
	<i>p</i>	.481	.508
Questionnaire x PD x TMS	χ^2 (6)	4.04	7.12
	<i>p</i>	.671	.309

consistently shifted the perception of the probe toward being on-beat across all PD levels. This shift improved the performance for tracks with PD = 0 % (truly on-beat), where participants showed higher accuracy, but it became a disadvantage when the probe was slightly off-beat (PD = 20 %), leading to a drop in accuracy following dPMC stimulation (see Figure S1B). All the other results remain consistent regardless of whether accuracy or on-beat responses were used as dependent variables.

4. Discussion

The endogenous generation of rhythm has long been theorized to rely on motor and premotor regions. Recent models (Patel and Iversen, 2014; Cannon and Patel, 2021) emphasize the role of motor planning regions, such as PMC and SMA, in generating internal temporal predictions during beat perception and imagery, but their causal involvement had remained largely unexplored. A previous study from our laboratory demonstrated a causal and selective role of the right dPMC in beat perception when the beat was physically present in the auditory signal (Lazzari et al., 2025). Therefore, in this study, we used TMS to test the causal contribution of the same right dPMC region during beat imagery compared to right SMA and Sham. Results showed that stimulation of the dPMC, but not SMA, significantly modulated performance on the beat imagery task. Importantly, this effect interacted with participants' auditory imagery abilities, as measured by the BAIS, with greater TMS effect in individuals with lower imagery scores. These findings

support the view that the premotor cortex plays a causal role in the endogenous generation and maintenance of rhythmic structure and are consistent with previous evidence highlighting its role in auditory–motor interactions for beat-based temporal predictions (Zatorre et al., 2007; Fujioka et al., 2015; Iversen et al., 2009; Nozaradan et al., 2011; Cheng et al., 2022; Morillon et al., 2015; Morillon and Baillet, 2017). More broadly, our results underscore the importance of accounting for individual variability in rhythm processing, suggesting that the dPMC involvement in beat imagery is not fixed, but rather dynamically shaped by each individual's functional resources, highlighting the brain's capacity to flexibly engage the auditory-motor pathway to support internal timing.

The current findings build upon theories highlighting the motor system's role in the internal generation of the beat. According to these theories (e.g., Patel and Iversen, 2014; Schubotz, 2007; Arnal, 2012; Morillon et al., 2015; Friston, 2013; Koelsch et al., 2019; Proksch et al., 2020), the motor system plays a key role in the active perception or sensing of time, exerting top-down influences on the auditory system to guide temporal predictions and structure auditory perception. In previous work (Lazzari et al., 2025), we identified the right dPMC as a crucial node in beat-based timing perception, supporting the idea that this region contributes to simulated action planning that enhances the perception of upcoming beats. The current results further demonstrate that dPMC is causally involved in generating an internal model of the beat and forming beat-based timing predictions with or without an external explicit metrical structure. In other words, the dPMC is crucial to the active perception process, by which predictions are continuously updated in response to incoming rhythmical patterns (Friston, 2013; Koelsch et al., 2019; Proksch et al., 2020). In particular, extending previous findings on beat perception (Lazzari et al., 2025), we found that applying TMS to the dPMC immediately before the imagery phase led participants to more frequently judge the probe as temporally aligned with the imagined beat. One possible interpretation is that dPMC stimulation altered the balance between sensory input and top-down temporal expectations, thus disrupting beat-based predictions (Morillon et al., 2015; Friston, 2013; Koelsch et al., 2019; Proksch et al., 2020). As a result, participants may have become less sensitive to subtle temporal deviations, and more inclined to categorize the probe as on time. This interpretation aligns with the view that the dPMC is critically involved in generating and maintaining top-down temporal predictions that guide both perceptual and imagery-based beat processing via structural and functional connections with the auditory system (Arnal, 2012; Ross et al., 2016; Morillon and Baillet, 2017; Araneda et al., 2017; Cannon and Patel, 2021; Patel and Iversen, 2014). Supporting this hypothesis, previous TMS studies have shown that interfering with motor-related frontal areas affects internally timed actions in predictive tasks (Cattaneo and Parmigiani, 2021; Tagliaferri et al., 2023). In these experiments participants performed anticipatory movements based on learned expectations rather than reacting to external signals, demonstrating a reliance on internally simulated temporal structure, conceptually similar to what is required during beat imagery. Additionally, a multimodal imaging study identified five subregions within the premotor cortex, each with distinct connectivity profiles and functional associations (Genon et al., 2017). The coordinates of the dPMC region in our study lie at the junction of two of these subregions, central and dorsal, which they found to be associated with motor and cognitive functions supporting imagined movements and rhythm processing. Taken together, these findings suggest that this sector of the dPMC may support a domain-general mechanism for coordinating top-down, internally generated predictions with bottom-up, externally triggered input.

We did not find evidence for a causal involvement of the SMA in beat imagery, despite its frequent identification, alongside the dorsal striatum, as a core region in models of beat maintenance and neural time-keeping (Cannon and Patel, 2021). Importantly, many of these models are based on non-human primate data (Merchant and Honing, 2014;

Merchant et al., 2015; Merchant and Averbeck, 2017) and thus may not fully capture the functional neuroanatomy of rhythm processing in humans. In particular, species-specific differences in the organization of the motor timing network (Merchant et al., 2015; Patel and Iversen, 2014) raise the possibility that temporal prediction and internally generated rhythmic structures may rely more heavily on lateral premotor regions, such as the dPMC, in humans. An alternative explanation is that the SMA–basal ganglia circuit supports implicit timing processes that operate without focused attention (Grahn and Rowe, 2009, 2013), while our task required explicit attention to the beat and deliberate temporal tracking. Under such conditions, activity in lateral premotor areas like the dPMC may become more prominent. Indeed, Schubotz (2007, 2000) showed that the premotor cortex is selectively engaged when attention is actively directed toward temporal prediction. Conversely, basal ganglia and SMA activity can occur even when regularities are processed passively or implicitly, suggesting a division of labor depending on attentional demands. This interpretation is further supported by recent studies examining the SMA's role in musical groove (Spiech et al., 2025), showing that TMS-induced disruption of SMA activity reduces the precision of beat-based prediction errors, prompting the dorsal striatum to prioritize input from other regions such as the dPMC. Importantly, neuroimaging evidence shows that SMA and dPMC are frequently co-activated during beat perception and rhythmic prediction (Grahn and Brett, 2007; Chen et al., 2008; Grahn and Rowe, 2009, 2013), implying that these regions function as part of an integrated network. Our null result should therefore be interpreted with caution: it may reflect task-specific or attentional factors, or the fact that SMA alone is not sufficient to disrupt this network's functioning when targeted in isolation. In this context, hierarchical models of auditory–motor integration suggest that SMA is positioned at a higher-order level, with more indirect access to auditory inputs (Zatorre et al., 2007). While the dPMC shares direct anatomical connections with auditory regions such as the superior temporal gyrus (STG), connectivity between STG and SMA is mediated by the premotor cortex. Therefore, TMS over dPMC may have disrupted top-down predictions more directly by interfering with the transmission of auditory timing information, while stimulation of SMA may not have impacted these feedforward connections as effectively. Finally, the role of SMA may be more prominent in motor rehearsal or subvocalization imagery, particularly with familiar, structured, or linguistically coded material. Indeed, SMA and pre-SMA are often engaged during vocal or musical imagery involving familiar melodies, singing, or imagined movement (Halpern and Zatorre, 1999; Olshansky et al., 2015; Lima et al., 2016), but not necessarily during imagery of unfamiliar, non-verbal instrumental rhythms (Halpern, 2001). Given that our task required participants to internally maintain the beat of novel instrumental sequences without any vocal or motor rehearsal, it is plausible that SMA's contribution was minimal in this context.

The accuracy analysis (see Supplementary Materials) indicates that the effect of dPMC TMS during rhythm imagery is stronger when the timing deviations are small, indicating a dPMC role in detecting finer temporal differences. Specifically, the interaction between stimulation condition and probe displacement (Sham vs. dPMC in the 0–20 PD pairing) shows that dPMC stimulation enhanced performance when the probe was precisely on-beat (PD = 0 %), resulting in higher accuracy. However, this facilitation turned into a disadvantage when the probe was slightly off-beat (PD = 20 %), leading to reduced accuracy. This pattern aligns with previous interpretations, suggesting that dPMC TMS consistently biases perception toward perceiving the probe as on-beat, particularly within narrow temporal windows (PD = 0–20 %), while its influence diminishes for larger temporal deviations. A limitation of our study is the unbalanced distribution of biological sex in our sample. However, previous research has not reported consistent sex differences in rhythmic abilities (Sergeant and Himonides, 2014; Mastrolalou and Hatziharistos, 2007; Pollatou et al., 2005), suggesting that this imbalance is unlikely to have influenced the present results. Future studies

could nonetheless examine whether factors such as sex and age, in addition to individual differences in reward sensitivity and imagery abilities, modulate rhythmic performance.

We found that the effect of TMS on dPMC was stronger in individuals with lower imagery scores. A possible interpretation of this interaction is that individuals with weaker auditory imagery rely more heavily on motor planning regions, such as the dPMC, to support the internal generation of rhythm. When dPMC activity is transiently inhibited, their internal simulation of temporal structure may become less precise, leading to a higher likelihood of perceiving misaligned probes as on beat. In contrast, individuals with stronger auditory imagery abilities may rely more on auditory or higher-order associative regions, making them less susceptible to motor disruption. This interpretation aligns with previous neuroimaging findings showing that individuals with high BAIS scores engage prefrontal and temporal regions more strongly during auditory imagery tasks (Herholz et al., 2012). The current pattern of results suggests a compensatory role for motor areas in individuals with weaker auditory imagery, in line with the idea that beat processing engages flexible and distributed neural strategies depending on individual cognitive profiles (Herholz et al., 2012; Lima et al., 2015). Further indirect support for this interpretation comes from behavioral studies showing that auditory imagery ability correlates with sensorimotor synchronization performance (Colley et al., 2018; Whitton et al., 2024), suggesting that the sensorimotor system is differentially recruited depending on individual imagery skills. More broadly, these results are consistent with the idea that stronger predictive models of the beat lead to greater precision (Vuust et al., 2022). They are also consistent with the theoretical framework of state-dependent TMS effects, which posits that the neural impact of stimulation depends not only on the TMS parameters but also on the pre-existing activation state of the targeted region. According to this view, neural populations in different functional states at the time of stimulation may be differentially susceptible to TMS interference (Silvanto and Pascual-Leone, 2008; Silvanto and Cattaneo, 2014; Hartwigsen and Silvanto, 2023). In our study, it is plausible that the dPMC was in a more active state in low-BAIS individuals during beat imagery, thus rendering it more sensitive to perturbation. Another, not mutually exclusive, explanation is that participants with lower auditory imagery abilities may have more room for modulation by TMS, making them more susceptible to behavioral effects. In contrast, individuals with higher imagery skills may already perform near ceiling at baseline, leaving less opportunity for TMS to further enhance or disrupt performance. This interpretation aligns with findings from psychopharmacological studies, which have shown that the effects of certain drugs (i.e. risperidone) on memory and music reward processing depend on individual sensitivity to music. Specifically, pharmacological modulation was observed primarily in individuals with low sensitivity to music, while high-sensitivity individuals showed little to no effect (Ferreri et al., 2019).

Finally, we demonstrate that higher music reward sensitivity, as indexed by eBMRQ scores, predicts better beat imagery performance at the trial level. These results align with recent research highlighting the connection between reward sensitivity and rhythmic processing (Zatorre, 2024; Fiveash et al., 2022, 2023). Prior work has shown that both musical pleasure experienced during music listening and trait-level musical hedonia influence rhythm-related tasks, at both the individual (Fullone et al., under review; Lazzari et al., 2025) and interpersonal level (Lazzari et al., 2024). We extend these findings by showing that music reward sensitivity is also linked to beat imagery, a core component of rhythm processing. The observed relationship between music reward sensitivity and beat imagery performance underscores the interplay between affective-motivational systems and cognitive processes in shaping rhythm-related abilities, suggesting that emotional engagement with music can enhance internal timing mechanisms (Fiveash et al., 2023).

In conclusion, our findings confirm the causal role of the right dPMC in the endogenous generation and maintenance of temporal structure

even in the absence of acoustic timing cues, extending motor theories of active perception to the domain of internal rhythm simulation. Together with previous findings (Lazzari et al., 2025), the selective involvement of the dPMC, contrasted with the absence of a causal role for the SMA in this context, suggests a functional specialization within motor-related areas, where the dPMC may primarily support top-down temporal predictions necessary for internal rhythm generation. This result deepens our understanding of the neural mechanisms underlying beat imagery and active perception and provides valuable insights into the shared and distinct neural substrates of beat perception and imagery within the human premotor cortex. Moreover, the interaction with individual auditory imagery abilities highlights how neural mechanisms underlying rhythm perception and imagery are flexible and modulated by individual cognitive resources and functional states, reflecting a dynamic interplay between sensory and motor networks that can be differentially recruited depending on individual profiles. Such flexibility underscores the brain's remarkable ability to adaptively engage diverse neural strategies to support complex cognitive functions like internal timing, suggesting promising avenues for personalized interventions and training aimed at enhancing rhythmic skills across populations.

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CRedit authorship contribution statement

Giorgio Lazzari: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Laura Ferreri:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Luigi Cattaneo:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Virginia Penhune:** Writing – review & editing, Supervision, Project administration, Investigation, Conceptualization. **Carlotta Lega:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors do not declare any competing interests.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2025.121593.

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