

# The Role of the Motor System in the Processing of Rhythmic Complexity: A Critical Review

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## Abstract

The desire to move to music appears to be a human universal. This behavioral response seems to be supported by a tight coupling of auditory and motor networks, even in the absence of overt movement. The prevailing theories explain this phenomenon either in terms of passive brain network entrainment to musical periodicity or motor system involvement in predictive coding. Both explanations recognize the role of rhythmic complexity in modulating motor activity. However, the precise nature of the relationship between rhythmic complexity and motor activity remains unclear. In this work, we conducted an fMRI literature review to examine this relationship. Out of 110 screened articles, 24 met inclusion criteria, reporting findings ranging from non-existent to linear or inverted-U-shaped. Underlying these findings, we encountered significant heterogeneity in the measurement and conceptualization of rhythmic complexity. We provide a summary of the relationships found, the approaches to measuring rhythmic complexity and the different types of tasks and stimuli used. We conclude that, in order to move forward, more agreement is needed regarding measures and notions of complexity.

**Keywords:** beat perception; action-perception coupling; rhythmic complexity; music cognition.

## Introduction

The urge to move seems to be a universal psychological response to music (Singh & Mehr, 2023). Ethnographic studies have found dancing to music in every examined society (Mehr et al., 2019). Moreover, the development of musical rhythm perception follows a similar pattern across various cultures (Hannon, Nave-Blodgett & Nave, 2018). For instance, the perception of musical rhythms demonstrates perceptual narrowing. At 12 months old, infants exhibit culture-specific responses to musical rhythms, in contrast to their culture-agnostic responses observed at 6 months of age (Hannon & Trehub, 2005). Additionally, children aged 5-24 months show considerably more movement in response to rhythmically periodic stimuli

compared to speech, with some level of tempo flexibility (Zentner & Eerola, 2010).

This behavioral response to rhythmic sound indicates a tight coupling between auditory and motor networks (Cannon & Patel, 2021; Kasdan et al., 2022). This connection is reflected in a facilitation effect on tracking the timing of sound events through periodic movement. For example, pianists demonstrate better prediction of the timing of the final sound in a sequence when they actively move to the beat of that sequence (Manning, Siminoski, & Schutz, 2020). Importantly, this type of enhancement provided by synchronizing movement to the beat is also present in non-musicians (Manning & Schutz, 2013).

Neuroimaging studies have provided evidence that sensorimotor synchronization relies on functional connectivity between the motor and auditory areas of the brain as shown in fMRI during beat tapping experiments (Toiviainen et al., 2020; Siman-Tov et al., 2022). Additionally, patient studies show that children at risk for developmental coordination disorder encounter more difficulties than neurotypical controls in both duration and rhythmic perception tasks (Chang et al., 2021). Similarly, Parkinson's patients have shown poorer rhythmic discrimination abilities than healthy controls (Grahn & Brett, 2009), but they can benefit from music or dance interventions for gait rehabilitation (Pereira et al., 2019).

These behavioral, neuroimaging and lesion studies are further complemented by the finding that motor areas of the brain are active during passive perception of rhythm, that is, when no overt movement is being performed (Chen, Penhune & Zatorre, 2008b; Gordon, Cobb & Balasubramaniam, 2018). Although this covert tracking of temporal regularity by the motor system could be the result

of frequent associations between music and movement, some have argued that the motor system plays a causal role in rhythm perception (Grahn & Rowe, 2009; Patel & Iversen, 2014; Schubotz, 2007; Zatorre, Chen & Penhune, 2007). However, the precise functional role of the motor system during the perception of musical rhythm remains unclear.

The prevailing theories explain this activity as some combination of bottom-up and top-down processes (Large et al., 2023, Vuust & Witek, 2014). Theoretical approaches explaining this activity recognize the role of rhythmic complexity in modulating auditory-motor coupling (Vuust & Witek, 2014). Rhythmic complexity is often defined in terms of how a discrete pattern of durations (the rhythm itself) fits within a particular temporal hierarchical structure, such as the *meter* or *beat* (Tichko, Kim & Large, 2022; Vuust & Witek, 2014). The percept of the beat and meter is a subjective abstraction created by the listener. For example, the *beat* defines periodically relevant moments in time and the *meter* adds hierarchy to them, making some more important than others. Together, they provide a type of temporal scaffolding that allows the listener to organize the perception of rhythmic information and generate expectations about future events (Vuust & Witek, 2014). Definitions and measures of complexity vary widely, ranging from the number of different time intervals present in a rhythm (Lewis et al., 2004); to accounts of motor accuracy, such as the precision with which participants perform polyrhythms (Thaut, Demartin & Sanes, 2008). Here, we define complexity as *beat strength*, or the degree to which a particular rhythm allows for the perception of a relatively stable organizing beat. This understanding of complexity is often operationalized as the degree of syncopation, defined as the presence of sound events in weak or less important metrical positions followed by silence in strong or important metrical positions (Witek et al., 2014).

Two main theoretical approaches provide accounts of the relationship between motor areas and rhythmic processing: dynamical systems (DS) and predictive coding (PC). Each one yields different predictions on the relationship between recruitment of motor areas and rhythmic complexity. According to DS, instead of representing time intervals per se, the brain maps timing information to the phase of an oscillator that entrains with rhythmic events (Large et al., 2023). This oscillator drives attentional rhythms that generate top-down expectations about future events. To explain the involvement of the motor area in rhythm perception, Large et al. (2015) proposed a model that includes two interacting heterogeneous-frequency networks, one corresponding to auditory cortex dynamics and a second one for the motor cortex (e.g., SMA). When presented with an isochronous rhythm, both networks synchronize with the frequency present in auditory stimuli, generating both harmonics and subharmonics. However, when presented

with a complex rhythm with high degrees of syncopation, this coupling differs. The auditory network exhibits activity that closely tracks frequencies present in the stimulus, which in very syncopated rhythms will not include the beat. Then, it is the motor network that is predicted to entrain at the beat frequency. Importantly, this suggests that in the case of a beat-based rhythm, motor activity should remain rather constant at the beat frequency, both at low and high levels of complexity (Large et al., 2023).

On the other hand, the predictive coding approach (PC) suggests that the brain is constantly predicting the causes of its own internal states by comparing sensory input to a generative internal model of the world acquired through experience (Friston, 2005). This hierarchical process is formally approximated by Bayesian inference, where top-down predictions provide priors to lower levels in nested neural networks, all the way to sensory information. Conversely, lower level sensory information is contrasted with prior predictions, generating bottom-up prediction error signals that update the internal model. In this sense, the brain is primarily involved in minimizing prediction error. To do so, the brain either actively aligns attention with the predicted information sources or produces the necessary movements to fulfill its predictions, using efference copies as motor commands aimed at generating the expected sensory input (Clark, 2013).

Regarding rhythm, PC posits that beat- or meter-based internal models serve as priors for predicting upcoming sound events (Vuust & Witek, 2014). In the context of syncopation, error signals are produced indicating the absence of sound events at the expected pulse times, which leads to a desire to move to the beat of the music to enact the predicted sound event, thereby fulfilling the prediction made by the model (Witek, 2017). This motor engagement would be significantly reduced in isochronous rhythms, where error signals are absent, and in highly complex rhythms, where beat-based models are not effective at predicting upcoming events. Importantly, previous studies have found a behavioral association between rhythmic complexity and the desire to move to music that follows an inverted-U shape (Cameron et al., 2023; Stupacher, Wrede & Vuust, 2022; Witek et al., 2014).

In short, DS suggests that motor area activity should be similar across the complexity spectrum, as long as it is possible to form a beat-based model of the incoming rhythm. PC predicts that we should observe an inverted-U-shaped association between complexity and motor area activation where low and high complexity rhythms show less motor engagement than medium complexity ones. In this work, we conducted an fMRI literature review to examine the available evidence for the relationship between motor area activation and rhythmic complexity in light of these theoretical predictions. We provide a summary of the reported associations, the

populations tested, the approaches to measuring rhythmic complexity and the different types of tasks and stimuli used. We found significant heterogeneity in how complexity is conceptualized and measured, which made it difficult to compare across studies. We present an ad-hoc, theoretically driven categorization of stimuli aimed at making results comparable.

## Methods

### Literature search

A literature search was conducted on PubMed, Scopus and Web of Science (WoS) using the search string: (rhythm\* OR beat OR meter) AND (complex\* OR syncopat\*) AND (music\*) AND (fMRI OR functional magnetic resonance imaging). This search yielded 168 papers from inception until October 4<sup>th</sup> 2023. After removal of duplicates (n=58), 110 papers were screened at the abstract level with the following exclusion criteria:

- a) not about music.
- b) not on humans
- c) not a research article
- d) not an fMRI study
- e) not related to rhythmic complexity

These criteria were further evaluated during a full text read resulting in 24 final papers. Search flowchart and number of articles removed at each stage can be found in figure 1.

### Complexity recategorization

Complexity definitions and measures varied widely across studies. Only 12 studies (50%) used or referenced some objective measure of complexity (see **Complexity Metric** column in Table 1).

Most studies used two or three categories to define more or less complex stimuli. These categories were mostly different (strongly metric, metrically weak, complex, non-metric, etc.). Aiming to make the stimulus categories comparable between studies, stimuli were recreated when possible (16 studies) and three complexity metrics were applied to all possible categories. This presented a number of challenges since, first, some studies did not rely on the stimuli and used performance measures instead (n=3) (e.g., playing polyrhythms, improvising on the piano), others used segments of natural music (to which most complexity metrics cannot be applied) (n=3) and yet others did not provide clear enough instructions for reproduction (n=2). Secondly, current complexity metrics are designed to either assume some form of metrical structure (i.e., C-score, Fitch and Rosenfeld's Longuet-Higgins-Lee implementation [LHL]) or are completely independent of it and thus poorly represent syncopation based complexity (i.e., normalized Pairwise Variability Index [nPVI]) (Condit-Schultz, 2019). Given these limitations, we first proceeded to sort the stimuli into 4 large categories qualitatively: Rest, when a

silent passive condition was included in the contrasts; Isochronous, the least complex condition, in which subjects heard or tapped to a metronome producing a stable pulse; Complexity, including varying complexity stimuli which were created using some form of metrical structure and in which rhythmic intervals were composed of integer-ratios; and Non-metric, in which stimuli did not conform to any metrical structure and were composed of non-integer ratio intervals. Within the Complexity category, we sought to further divide the stimuli by establishing cutoff points for Low, Medium and High complexity rhythms by using the LHL metric. This proved to be impossible without splitting up the contrasts from the original studies. For example, when scored with LHL, both the *metric simple* (LHL: 2) and *metric complex* (LHL: 3) stimulus from the Chen, Penhune and Zatorre (2006, 2008a, 2008b) fell within the range of the complex condition from Grahn and Brett (2007) (Mean: 4.3, SD: 1.3, min: 2, max: 7). Thus, separating the conditions from Chen, Penhune and Zatorre (2006, 2008a, 2008b) would require splitting a uniform category from Grahn and Brett's study (2007).

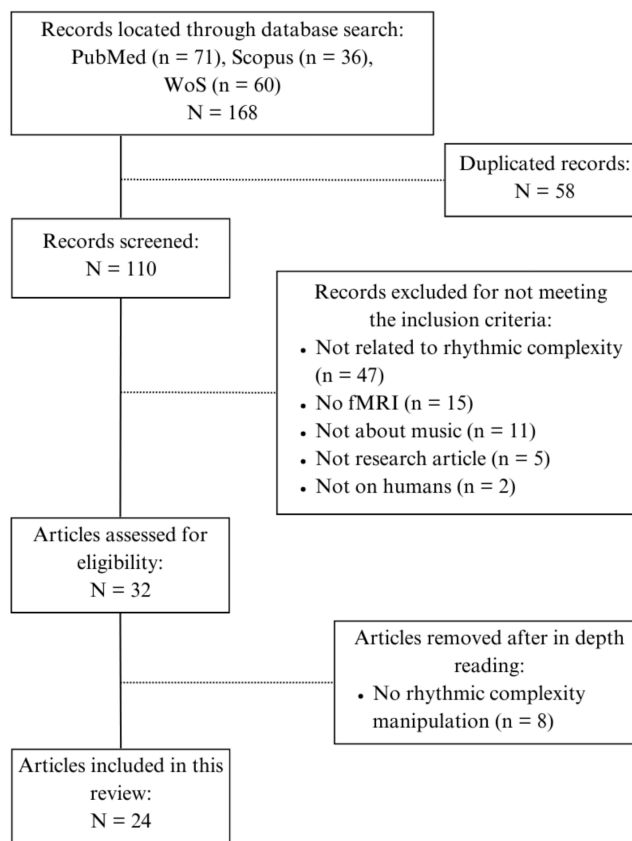


Figure 1: Search flowchart.

In order to preserve the contrasts from original studies and be able to compare across them we proceeded to generate audios based on the stimuli from the Complexity category employed in each of the selected studies. We used the reproduced stimuli to assess the degree of rhythmic

complexity perceptually and provide an ad-hoc categorization by an expert drummer (author 1). This resulted in three further categories: Low complexity, in which machine performed stimuli presented a clear metrical structure with low overall syncopation; Medium complexity, in which machine performed stimuli which presented a higher degree of syncopation with some sound events on less salient metrical positions; High complexity, including machine performed polyphonic stimuli with a high degree of syncopation, with some stimuli presenting little to no sound events aligned with strong metrical positions but still conforming to some metrical structure. This category also included human performed natural music, since these stimuli were polyphonic and presented a wider degree of variability provided by either tempo changes (Vuust et al., 2006; Alluri et al., 2012) or expressive variations, which have been shown to alter the perceived timing of events (Danielsen et al., 2019).

The process of ordering the stimuli for comparison resulted in some between-study conditions being mapped to other categories while respecting the original relation between levels. For example, Grahn and Brett's (2007) *complex* condition was included in our Medium complexity category, while their *simple* condition was included in the Low complexity category. Their highest complexity category, *nonmetric*, was included in our Non-metric category.

## Results

The reviewed literature exhibited significant heterogeneity in the conditions utilized across original studies, precluding the ability to conduct a meaningful meta-analysis. Instead, we organized the reviewed articles according to the previously described complexity levels and activation of areas and contrasts were notated within this framework in order to evaluate the presence of activations relating to particular levels of complexity. Table 1 presents a summary of populations, associations, tasks and metrics.

Associations between complexity and motor area engagement, study populations, stimuli used and complexity metrics varied widely. Table 1 provides an ad-hoc re-ordering of complexity levels based on a categorization of stimuli used for ease of comparison across similar levels. Associations were coded as /, when a positive association between rhythmic complexity and motor activation was found between one lower complexity condition and a higher one; \, when a negative association was found between a lower complexity association and a higher one; -, when no association was found; ∩, in the case of inverted-U-shaped associations; and /, \ when associations were mixed but did not represent an inverted-U-shape. Brain areas are represented in the condition that had the higher activation in the original study and coloured segments of the table indicate what contrast yielded said activation. For example, Sakai et al., (1999) contrasted isochronous stimuli with rhythms with medium complexity and non-integer ratio

rhythms. It found activations for both medium complexity and non-integer rhythms as compared to isochrony.

## Populations

8 studies (33.3%) contrasted musicians and non-musicians, 6 studies included only musicians, 5 (20.8%) exclusively recruited non-musicians, 3 (12.5%) did not control for musical training and 2 (8.3%) studies carried out contrasts between Parkinson's patients and age matched controls. Additionally, we found that almost all studies were conducted by labs in the global north and predominantly on WEIRD populations (96%) (Henrich, Heine, & Norenzayan, 2010).

## Tasks

9 studies (37.5%) described pure passive perception tasks which involved listening to rhythms with no concurrent cognitive instructions (Perception), 6 (25%) involved active conditions (Action). Tasks we considered active when overt movement was required from the participants. Active conditions included rhythm reproduction; metric synchronization and/or continuation with the stimuli at phase, antiphase or a provided ratio (3:2); and improvisation at a piano. Effectors included mostly the hands, except for Jungblut et al., (2012), which required participants to sing the provided written stimuli. 6 studies (25%) included some concurrent attentional or working memory tasks performed at the same time as the passive perception task (e.g. Perception + Attention, Perception + Working Memory, Perception + Distractor), and 3 (12.5%) studies included both passive and active conditions (Perception + Action).

## Complexity

11 studies (45.8%) did not employ any objective complexity metric and organized complexity ad-hoc (None). 5 (20.8%) used or referenced Essens and Povel's C-score (1985) for defining complexity, 3 (12.5%) applied the Pressing model (Pressing, 1999), 2 (8.3%) used both the C-score and Fitch and Rosenfeld's metric (2007), and 2 (8.3%) used Pulse Clarity (Lartillot et al., 2008). These metrics differ in significant ways. The C-score, the Pressing model and Fitch and Rosenfeldt all work with music in symbolic format. However, they measure different aspects of complexity. The C-score developed by Povel and Essens (1985) indicates metricality as the best fit between the rhythms and different "internal clocks", representing a variety of metrical structures. Pressing (1999) uses a theoretical cognitive complexity model that organizes rhythms hierarchically and gives varying weights to different subdivisions, assuming a duple metrical structure. Fitch and Rosenfeld's measure (2007) is an adaptation of the Longuet-Higgins and Lee measure (LHL) (Longuet-Higgins & Lee, 1984) which also assumes a binary metrical structure and assigns weights to different metrical positions to provide a syncopation index. None of these metrics works with non metrical or non-integer ratio rhythms. The Pulse Clarity metric is the

Table 1: Results summary.

Article	Methods				Results					
	Population	Task	Complexity metric	Relation	Rest	Isochronous	Low complexity	Medium complexity	High complexity	Non-metrical
Sakai et al., (1999)	Non-musicians (n=6, 2f)	Action	None	/		-		< PMC, cerebellum		iso < PMC
Ullén, Forssberg & Ehrsson (2003)	Non-musicians (n=17, 3f)	Action	None	/		-		< vPMC, dPMC, CMA, SMA, pre-SMA, cerebellum lobule IV		
Lewis et al., (2004)	Uncontrolled (n=10, 5f)	Action	None	/	-					< SMA, pre-SMA, dPMC positive correlation with number of intervals
Chen, Penhune & Zatorre (2005)	Non-musicians (n=12, 6f)	Perception + action	C-score	/			-	< pre-SMA, dPMC, cerebellum lobule VI covariation with ITI standard deviation, same areas were found to be active during both passive and active conditions		
Vuust et al., (2006)	Musicians (n=18, 4f)	Perception + action	None	/				-	< IFG	
Grahn & Brett (2007)	Musicians (n=14) and non-musicians (n=13) (8f)	Perception + attention	C-score	\			pre-SMA, SMA, caudate, páldido, putamen >	putamen >		-
Thaut, Demartin, & Sanes (2008)	Musicians (n=12, 3f)	Perception + action	None	/	-			< M1, S1, PMC, SMA, pre-SMA		
Bengtsson, et al., (2009)	Uncontrolled (n=17, 3f)	Perception	None	/, \		IFG, pre-SMA >		-	< cerebellum	-
Chen, Penhune & Zatorre (2008a)	Musicians (n=12, 6f) and non-musicians (n=12, 6f)	Action	C-score	/			-	< pre-SMA, SMA, dPMC, vPMC, dIPFC, cerebellum lobule VI covariation with ITI standard deviation		
Chen, Penhune & Zatorre (2008b)	Non-musicians (n=12, 6f)	Perception	C-score	/			-	< right SMA, left pre-SMA, right dPMC, left cerebellum lobule VI and right dIPFC covariation with ITI standard deviation		
Berkowitz & Ansari (2008)	Musicians (n=13, 8f)	Action	None	/	-				< dPMC, IFG	
Grahn & Rowe (2009)	Musicians (n=19) and non-musicians (n=17) (15f)	Perception	Subjective validation	\				putamen >		< no effect
Chapin et al., (2010)	Musicians and non-musicians (n=13, 5f)	Perception + WM	None	/	-				< SMA, caudate	
Jungblut et al., 2012	Non-musicians (n=30, 13f)	Action	None	/			-	< IFG		
Geiser, Nötter & Gabrieli (2012)	Uncontrolled (n=17, 8f)	Perception + distraction	None	\	putamen >					-
Alluri et al., (2012)	Musicians (n=11, 5f)	Perception	Pulse Clarity	\				SMA, putamen negative correlation with complexity		
Kung et al., (2013)	Musicians (n=11, 5f)	Perception + attention	Pilot + C-score	/				vIPFC positive correlation with complexity		
Herdener et al., (2014)	Musicians and non-musicians (n=22)	Perception + distraction	None	/				-	< IFG	
Tsatsishvili et al., (2018)	Musicians (n=11, 5f)	Perception	Pulse Clarity	\				left SMA, IFG negative correlation with complexity		
Vikene, Skeie & Specht (2019a)	PD (n=15, 6f) and controls (n=15, 8f)	Perception	Pressing + subjective validation	-		-			-	
Vikene, Skeie & Specht (2019b)	PD (n=15, 6f) and controls (n=15, 8f)	Perception	Pressing + subjective validation	-		-			-	
Matthews et al., (2020)	Musicians (n=29, 12f) and non-musicians (n=23, 12f)	Perception	C-score + Fitch & Rosenfeld	\				putamen, caudate, pallidum, SMA, pre-SMA, bilateral dorsal PMC and right crus 1 in the cerebellum >	< no effect	

Article	Methods				Results					
	Population	Task	Complexity metric	Relation	Rest	Isochronous	Low complexity	Medium complexity	High complexity	Non-integer ratio/ Random
Færøvik, Specht & Vikene (2021)	Musicians and non-musicians (n=10, 6f)	Perception + attention	Pressing + subjective validation	-		-			-	
Siman-Tov et al., 2022	Musicians and non-musicians (n=71, 41f)	Perception	C-score + Fitch & Rosenfeld	∩		-	< BA55b positive correlation with entropy, ENT standard deviation and LRV <	< BA55b positive correlation with entropy, ENT standard deviation and LRV >	> BA55b positive correlation with entropy, ENT standard deviation and LRV	

*CMA: cingulate motor area; d: dorsal; dl: dorsolateral; v: ventral; PD: Parkinson's Disease; PMC: premotor cortex; SMA: supplementary motor area; IFG: inferior frontal gyrus; M1: primary motor area; SI: primary sensory area; ITI: inter-tap interval; ENT: entropy; LRV: length of resultant vector; WM: working memory.*  
*f indicates numbers of females.*  
*/, a positive association was found between one lower complexity condition and a higher one; \, a negative association was found between a lower complexity association and a higher one; -, no association was found; and ∩, in the case of inverted-U-shaped associations.*  
*Empty cells with a - in the Results columns indicate this condition was included in the original study but not tested, for instance, Sakai et al., (1999) included an Isochronous condition but only found activation when comparing Medium complexity rhythms over Isochronous ones and Non-metrical rhythms over Isochronous ones. They did not test Isochronous over any other condition. When not specified, <> indicates the contrast was applied to the nearest condition marked with -, otherwise, the relevant contrast is included in the cell reporting the activation.*  
*No-effect indicates the contrast was tested and no effect was found.*

only metric which works on audio representations instead of symbolic data (Lartillot et al., 2008). This measure is derived from an onset detection algorithm and an autocorrelation function and is meant to capture the ease with which participants are able to perceive the beat of a musical piece.

### Associations

Out of 24 studies, 13 (54.2%) reported increased motor area activation for more complex rhythms with 8 of these comparisons involving medium complexity versus lower complexity. Six studies (25%) indicated greater activation in motor areas for medium over high complexity rhythms, or negative correlations between complexity and motor area engagement, where more complex rhythms were associated with less activity in motor regions of interest. Three studies (12.5%) showed no significant complexity effect, 1 found a mixed effect, and 1 observed an inverted-U-shaped relationship between sensory-motor synchronization performance and motor area activation, in which the highest correlation between complexity and motor activation was found for medium complexity rhythms with smaller but significant correlations for low and high complexity rhythms. When conditions were arranged by complexity, a pattern emerged in which medium complexity rhythms engaged motor areas significantly more than their low or high contrasts. Main areas involved in the processing of medium complexity rhythms over low or high ones included cortical areas SMA (8 studies, 33%) and PMC (7 studies, 29%) and subcortical areas such as the putamen (4 studies, 16%).

### Conclusions

We conducted a systematic review to assess the association between rhythmic complexity and the recruitment of the motor system. Dynamical systems (DS) models from Large et al., (2023) suggest motor activity should remain rather constant through a wide spectrum of complexity, spanning from isochrony to rhythms with no energy at the beat frequency. In contrast, predictive coding (PC) predicts an inverted-U-shaped interaction, where motor areas are more

engaged in the processing of medium complexity rhythms over low or high complexity ones. Out of 110 reviewed articles, 24 reported findings ranging from non-existent to linear or inverted-U-shaped relations. When contrasts were organized by their level of complexity, over half (54.2%) of the studies reported higher motor area activations for rhythms of medium complexity as opposed to lower or higher complexity ones. Although this pattern of results could be interpreted as evidence for an inverted-U-shape relation between rhythmic complexity and motor area activation, only one study directly reported this finding. Additionally, when studies from the same research group are considered jointly, the number of studies reporting activations for medium complexity rhythms over low or high ones is reduced by half. Regarding DS, 3 patient studies from the same research group found flat associations between complexity and motor area activation (12.5%). In the context of the evidence presented here, it would seem like more support is given to PC than to DS's specific prediction regarding the role of the motor system in the processing of rhythmic complexity. However, it has been shown that oscillators are a highly versatile strategy for modeling other very different types of behavior than those predicted here (Doelling and Assaneo, 2021) and we suggest that in future models, PC's predictions may be accommodated within a DS framework, given that both theories are far from necessarily pitted against each other (Witek & Vuust, 2014; Large et al., 2023).

However, underlying these findings, we encountered significant heterogeneity in the measurement and conceptualization of rhythmic complexity and an overall lack of theoretically driven hypothesis testing, which precluded us from conducting a meaningful meta-analysis. Finally, given the heterogeneity in the methodology of the reviewed papers, we consider the theoretical implications of our findings should be taken with a grain of salt and should be considered only as a first step in answering our question. Future directions should include objective measures of complexity, contrasting theoretical predictions directly and inclusion of natural music.

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