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This is the author's manuscript

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1847635> since 2022-03-09T10:58:51Z

Published version:

DOI:10.1016/j.neubiorev.2022.104588

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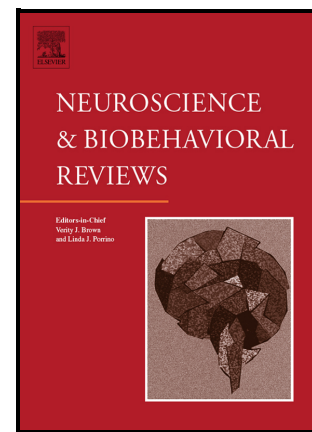
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PII: S0149-7634(22)00077-X

DOI: <https://doi.org/10.1016/j.neubiorev.2022.104588>

Reference: NBR104588

To appear in: *Neuroscience and Biobehavioral Reviews*

Received date: 25 August 2021

Revised date: 31 January 2022

Accepted date: 14 February 2022

Please cite this article as: Anna V. Kasdan, Andrea N. Burgess, Fabrizio Pizzagalli, Alyssa Scartozzi, Alexander Chern, Sonja A. Kotz, Stephen M. Wilson and Reyna L. Gordon, Identifying a brain network for musical rhythm: A functional neuroimaging meta-analysis and systematic review, *Neuroscience and Biobehavioral Reviews*, (2021)
doi:<https://doi.org/10.1016/j.neubiorev.2022.104588>

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Identifying a brain network for musical rhythm: A functional neuroimaging meta-analysis and systematic review

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Abstract

We conducted a systematic review and meta-analysis of 30 functional magnetic resonance imaging studies investigating processing of musical rhythms in neurotypical adults. First, we identified a general network for musical rhythm, encompassing all relevant sensory and motor processes (*Beat-based, rest baseline*, 12 contrasts) which revealed a large network involving auditory and motor regions. This network included the bilateral superior temporal cortices, supplementary motor area (SMA), putamen, and cerebellum. Second, we identified more precise loci for beat-based musical rhythms (*Beat-based, audio-motor control*, 8 contrasts) in the bilateral putamen. Third, we identified regions modulated by beat based rhythmic complexity (*Complexity*, 16

contrasts) which included the bilateral SMA-proper/pre-SMA, cerebellum, inferior parietal regions, and right temporal areas. This meta-analysis suggests that musical rhythm is largely represented in a bilateral cortico-subcortical network. Our findings align with existing theoretical frameworks about auditory-motor coupling to a musical beat and provide a foundation for studying how the neural bases of musical rhythm may overlap with other cognitive domains.

Keywords: rhythm; music; beat; fMRI; meta-analysis

Abstract

We conducted a systematic review and meta-analysis of 30 functional magnetic resonance imaging studies investigating processing of musical rhythms in neurotypical adults. First, we identified a general network for musical rhythm, encompassing all relevant sensory and motor processes (*Beat-based, rest baseline*, 12 contrasts) which revealed a large network involving auditory and motor regions. This network included the bilateral superior temporal cortices, supplementary motor area (SMA), putamen, and cerebellum. Second, we identified more precise loci for beat-based musical rhythms (*Beat-based, audio-motor control*, 8 contrasts) in the bilateral putamen. Third, we identified regions modulated by beat based rhythmic complexity (*Complexity*, 16 contrasts) which included the bilateral SMA-proper/pre-SMA, cerebellum, inferior parietal regions, and right temporal areas. This meta-analysis suggests that musical rhythm is largely represented in a bilateral cortico-subcortical network. Our findings align with existing theoretical frameworks about auditory-motor coupling to a musical beat and provide a foundation for studying how the neural bases of musical rhythm may overlap with other cognitive domains.

Keywords: rhythm; music; beat; fMRI; meta-analysis

Introduction

Humans spontaneously and effortlessly move to and perceive musical rhythms from the earliest days of infancy (Cirelli et al., 2016; Phillips-Silver & Trainor, 2005; Winkler et al., 2009) and in every human culture across the globe (Jacoby et al., 2021; Jacoby & McDermott, 2016; Polak et al., 2018). Rhythm – the pattern of time intervals in a sequence – is often perceived in the context of a musical beat (i.e., a regular pulse that one can tap to) which can be hierarchically organized into different meters (e.g., a waltz meter in three or a duple meter in two). Musical rhythms are ubiquitous and integral to the human experience, and one need only observe a baby listening to a television theme song or a group of wedding guests on the dance floor to be convinced.

Studies of the neural bases of musical rhythm have been approached from multiple methodologies including functional magnetic resonance imaging (fMRI), electroencephalography (EEG), magnetoencephalography (MEG), voxel-based morphometry, animal studies, and human lesion and cognitive neuropsychology studies (see Merchant et al., 2015 for a review). Across these methodologies, it has been well established that coupling/connectivity between cortical auditory and motor regions is integral to musical rhythm during both active rhythm production and passive rhythm perception (Cannon & Patel, 2020; Chen et al., 2008a; Patel & Iversen, 2014; Schubotz et al., 2000). This cortical auditory-motor coupling is situated within a larger cortico-subcortical network implicated in rhythm processing that, broadly, includes the basal ganglia (BG), cerebellum, supplementary motor area (SMA), premotor cortex (PMC), and temporal and parietal cortices (Damm et al., 2020; S. Kotz et al., 2018; Patel & Iversen, 2014).

Functional imaging studies in particular have provided significant information about the spatial functional organization of musical rhythm processing in the brain. As the literature continues to grow, it is important to determine which findings converge robustly across studies, circumventing methodological constraints from a) small samples and b) individual studies that vary considerably in their specific stimuli, task demands, and experimental procedures. Neuroimaging meta-analyses provide one way

to synthesize results across individual studies that may be limited by underpowered sample sizes and/or lenient statistical thresholding (Müller et al., 2018). To this end, we conducted a systematic review and meta-analysis of carefully selected fMRI studies of musical rhythm to identify networks important for processing beat-based musical rhythms. Our meta-analysis will provide important information about which brain regions are central for rhythm processing, converging across studies with different designs.

Evidence from functional neuroimaging (Teki et al., 2011), transcranial magnetic stimulation (TMS) (Grube, Lee, et al., 2010), and neuropsychological populations (Breska & Ivry, 2018; Grahn & Brett, 2009; Grube et al., 2010) suggests that two different timing mechanisms – beat-based and duration-based timing – may be dissociated in the brain. Beat-based timing, which encodes temporal intervals relative to the other intervals in a pattern, leading to the percept of a stable pulse, is thought to engage the SMA and BG, specifically the putamen bilaterally (Grahn & Brett, 2007; Grahn & Rowe, 2013). The putamen is active for beat prediction and maintenance and works in tandem with the SMA. On the other hand, duration-based timing, which encodes temporal intervals as a series of single, absolute durations (Merchant, 2014), largely relies on the cerebellum. The cerebellum establishes temporal predictions (i.e., comparing an expected signal with an outcome), stores absolute durations, and is important for quick and automatic error detection (Andersen & Dalal, 2020; Coull et al., 2011; Grahn, 2012; Grube, Lee, et al., 2010). However, these two timing mechanisms, which have been applied to the context of musical rhythm more specifically, are not mutually exclusive (Penhune & Zatorre, 2019). Multiple frameworks assert a unified and interactive account for beat-based and duration-based timing, supported by functional and anatomical connections between the cerebellum and striato-thalamo-cortical circuits (Bostan & Strick, 2018; Koch et al., 2009; Petter et al., 2016; Schwartz & Kotz, 2013; Teki et al., 2012). Additionally, dependent on the task, there can be individual differences in the extent to which these two timing mechanisms are employed (Grahn & McAuley, 2009). In addition to these regions and primary auditory and motor areas, parietal regions, which serve as a sensorimotor integration zone between cortical motor and auditory regions along the dorsal auditory pathway (Hickok & Poeppel, 2007), are involved in temporal expectations (Coull et al., 2011) and are a key component of the ASAP hypothesis for musical beat perception (Patel & Iversen, 2014).

Here we aimed to identify a brain network for auditory musical rhythm by conducting a meta-analysis and systematic review of fMRI studies. The goals of our meta-analysis were three-fold:

- 1) to identify a network involved in performing musical rhythm tasks, encompassing all the relevant basic sensory and motor processes, here termed *Beat-based (rest baseline)* meta-analysis. We hypothesized that this general network for musical rhythm would encompass a broad, bilateral network, including primary auditory and motor regions, BG, SMA, and cerebellum.

2) to identify a more precise network for processing beat-based musical rhythms, above and beyond basic sensory and motor processes, here termed *Beat-based (audio-motor control)* meta-analysis. We hypothesized that including contrasts with more carefully controlled baseline conditions would reveal neural activation in the BG and SMA bilaterally, highlighting a set of regions more specific to processing beat-based musical rhythms.

3) to identify brain regions modulated by beat-based rhythmic complexity (i.e., more complex rhythms such as syncopated rhythms vs. less complex rhythms, such as isochronous rhythms), here termed *Complexity* meta-analysis. We hypothesized that this analysis would reveal activations in several core regions identified in unified frameworks for timing (cerebellum, SMA, BG), along with additional regions important for musical rhythm in frontal and parietal regions. We predicted that there would be potentially greater activation of the cerebellum compared to the BG, as this analysis controlled for simpler, beat-based processes in the baseline condition.

These three research questions were possible to address with the available data and led us to bin relevant fMRI contrasts into the two umbrella categories of Beat-based and Complexity. We then conducted meta-analyses separately for each category. It is important to note that all of the stimuli within the Complexity category involved rhythms with a beat structure, though the stimuli varied in how strong or weak the respective beat structure was. We conducted quantitative fMRI meta-analyses using the Seed-based *d* mapping software (SDM-PSI) (Albajes-Eizagirre et al., 2019) and descriptively categorized study variables (e.g., descriptions of stimuli, tasks, fMRI scanning paradigm) to obtain a full picture of the types of studies in this field.

In addition to identifying brain regions modulated by rhythmic complexity, we also sought to understand how the Complexity network was modulated by formal musical training. Across multiple methodologies, some work suggests different patterns of neural activity between musicians and non-musicians during rhythm-based tasks (Celma-Miralles & Toro, 2019; Chen et al., 2008b; Habibi et al., 2014; Herdener et al., 2014; Limb et al., 2006; Pollok et al., 2017; Vuust et al., 2005) as well as structural differences between these two groups in brain regions important for rhythm (Baer et al., 2015; Chaddock-Heyman et al., 2021; Gaser & Schlaug, 2003; Hutchinson et al., 2003). However, not all work suggests differences between musicians and non-musicians when processing musical rhythms (Foster & Zatorre, 2010; Geiser et al., 2009; Stupacher et al., 2017). We wanted to understand the robustness of a musical experience and rhythmic complexity relationship using a meta-analytic approach.

Critically, we separated studies within the Beat-based category based on the choice of baseline condition. Studies either had a) a “rest/silence” baseline or b) an auditory/motor control baseline. Separating studies in the meta-analysis by these two quite different baseline conditions is essential for delineating a more representative set of brain regions for musical rhythm processing, beyond the individual contributions of

basic auditory, motor, attentional, or other cognitive processes. Several meta-analyses in the language domain have found that baseline conditions are critical for identifying precise brain networks for a specific cognitive/linguistic process (Adank, 2012; Binder et al., 2008; Price et al., 2005). Our second and third main analyses (Beat-based audio-motor control analysis and the Complexity analysis, respectively) thus provide two important ways to narrow in on regions belonging to a more precise or specialized brain network for musical rhythm, over and above the hypothesized contributions of basic auditory processing and motor actions.

Methods

2.1 Inclusion of Studies

A literature search was conducted in PubMed using the following search criteria: (Brain OR neur*) AND (rhythm* OR beat OR meter) AND (music*) AND (fMRI OR functional connectivity OR functional magnetic resonance imaging). This yielded 146 papers on May 15, 2019. Exclusion criteria at the abstract level included the following:

- 1) not about music
- 2) not an fMRI study (e.g., positron emission tomography (PET), voxel-based morphometry (VBM), etc.)
- 3) study on a clinical population (e.g., amusia, Parkinson's Disease)
- 4) not an empirical study (i.e., a review paper)

Of the 146 papers, 84 were excluded based on the abstract. The 62 remaining records were then screened at the full-text level. Full-text exclusion criteria included the same ones mentioned above (sometimes not clear from the abstract) along with:

- 1) study about children or comparison between children and adults
- 2) region of interest (ROI) or small volume correction (SVC) fMRI analysis only (not permissible in fMRI meta-analytic software)
- 3) fMRI contrasts only comparing musicians to non-musicians (i.e., the manipulation of interest was musical experience)
- 4) fMRI studies with only resting state, psychophysical interaction (PPI), or independent component analysis (ICA) analyses (i.e., analyses of connectivity rather than voxel-wise activation analyses)
- 5) coordinate tables not available or could not be obtained from authors
- 6) study had less than eight subjects

- 7) fMRI contrasts were not in the auditory modality or only compared auditory rhythms to another modality (e.g., vision)
- 8) miscellaneous confounding experimental designs

Miscellaneous confounding experimental designs including the following: rhythm processing during sleep (Lewis et al., 2011), interactions between rhythm, consonance/dissonance, and visual cues (Trost et al., 2014), and aesthetic and tempo judgments of rhythm (Kornysheva et al., 2010). Additionally, there was a family of studies that investigated Pulse Clarity using techniques such as acoustic feature extraction often paired with kernel PCA or decoding techniques (Alluri et al., 2012; Burunat et al., 2016; Toiviainen et al., 2014; Tsatsishvili et al., 2018). Though these studies with more complex analyses provide complementary evidence to studies with more traditional fMRI analyses (contrasts or parametric manipulations), they were deemed too heterogeneous compared to the other studies and were thus not included in the meta-analysis. Studies that solely investigated interval/duration-based timing outside of the context of musical rhythms (e.g., Teki & Griffiths, 2016) or only made comparisons between externally triggered and self-initiated rhythmic movements (Cunnington et al., 2002) were also not included in the meta-analysis.

Of note, we only focus on studies with auditory rhythms in the present meta-analysis. While some work indicates overlapping brain networks between auditory rhythms and rhythms in the visual and tactile domains (Araneda et al., 2017; Karabanov et al., 2009), other work suggests BG activity is greater (Hove et al., 2013) and movement/beat detection is stronger for auditory compared to visual rhythms (Grahn et al., 2011; Repp & Penel, 2004). In general, the auditory system is more tightly coupled with the motor system compared to the visual system (Comstock et al., 2018), which facilitates, for example, better sensorimotor synchronization to auditory rhythms. Additionally, music is experienced primarily in the auditory domain, so we restrict our analyses to fMRI contrasts explicitly looking at auditory rhythmic stimuli.

Twenty-five papers fit our inclusion criteria and a forwards and backwards citation search in Google Scholar was conducted on each one. Six additional papers from the citation search were included (Araneda et al., 2017; De Pretto & James, 2015; Geiser et al., 2012; Konoike et al., 2015; Lewis et al., 2004; Teki et al., 2011), for a total of 31 unique papers in the final analysis. The two papers by Vuust et al. (2006, 2011) were considered as one paper in the meta-analysis, as they were conducted in the same participants with the same stimulus, albeit slightly different tasks. Thus, the total number of papers is effectively 30 (Tables 1 and 2). Coding of all studies was conducted independently by multiple authors (AK, AC, AS, AB) and other authors (RLG, SMW, FP) were consulted for ambiguous cases. We conducted our meta-analysis following PRISMA guidelines (Moher et al., 2009; Page et al., 2021) and neuroimaging

meta-analysis recommendations (Müller et al., 2018). See Figure 1 for a flow chart of eligible studies.

2.2 *Beat-based category*

The goals of our meta-analysis were first to identify brain regions important for beat-based musical rhythm processing and second to identify brain regions modulated by rhythmic complexity. Due to these experimental questions of interest, as well as the heterogeneity of stimuli and experimental questions across studies, relevant fMRI contrasts within papers were divided into two, macroscopic categories: “Beat-based vs. Non-beat-based Rhythm” (Beat-based) and “More vs. Less Complex Rhythm” (Complexity).

A note of importance: We describe stimuli in this paper as beat-based and non-beat-based. These terms, however, should not be equated with the timing mechanisms/frameworks of similar names (duration-based timing and beat-based timing). That is, the timing mechanisms used to process beat-based stimuli (blue section of Figure 2) may involve both kinds of timing (as unified frameworks mentioned in the *Introduction* hypothesize) and the same applies to non-beat-based stimuli (red section of Figure 2).

Separate meta-analyses were conducted for contrasts in the Beat-based category depending upon the type of baseline condition. Studies either had a) an auditory/motor control baseline of non-beat based or scrambled rhythms (e.g., Grahn & Rowe, 2009, 2013; Kornysheva & Schubotz, 2011) or b) a rest/silence baseline (e.g., Chen et al., 2006; Grahn & McAuley, 2009). We did not include contrasts that exclusively probed tempo changes (e.g., McAuley et al., 2012) or beat salience via volume manipulations *only* without additionally varying durational patterns (e.g., Chen et al., 2006, see more details in section 2.3 and Figure 2). These contrasts reflected constructs that were inconsistent with our Beat-based and Complexity categories (see Table S1 in the Supplement for contrasts not included in the present meta-analyses, and the rationale for these decisions).

Within the Beat-based category, three studies (Araneda et al., 2017; De Pretto & James, 2015; Grahn & Rowe, 2009) reported contrasts with *both* “rest/silence” as a baseline, as well as a more appropriate control task (e.g., non-beat based rhythms). Because the goal of the Beat-based analysis was to compare “beat-based” to “non-beat-based” rhythms, and two of these three studies (De Pretto & James, 2015; Grahn & Rowe, 2009) pooled stimuli across both of these broad categories (see Figure 2) and compared them to rest, those contrasts were excluded from the analysis. Only the study by Araneda et al., 2017 had two eligible contrasts for the Beat-based analysis (“auditory-motor control” baseline: beat vs. no-beat rhythms; “rest” baseline: beat rhythms vs. rest). Meta-analyses were conducted separately for the “auditory control” and “rest” baseline groups within Beat-based, so this was not a problem of repeated measures.

2.3 Complexity category: terminology and selection of contrasts

The word “complexity” has various meanings across studies of timing and rhythm. Here, we define complexity as the degree of “beat-based-ness” of a rhythm. As an example, syncopated rhythms (e.g., displacement of regular accents¹ as is often used in jazz/folk music such as *Maple Leaf Rag* by Scott Joplin) are classified as “more complex” and isochronous rhythms (e.g., a steady metronome beat) are classified as “less complex”. See Figure 2 for a graphical depiction and nuanced explanation of these terms. Our interpretation of complexity relates to the degree of beat/pulse saliency as generally driven by durational patterns in sequences rather than intensity manipulations. As an example, Chen et al., 2006 used all isochronous rhythms that only differed in how loud the beat was. Thus, this manipulation of beat saliency did not fit with our definition of complexity. Contrasts in the Complexity category included, for example, parametric increases in the level of beat-based complexity (Chen et al., 2008b), syncopated deviations compared to regular rhythmic patterns (Herdener et al., 2014), or metric and non-metric rhythmic sequences compared to isochronous rhythms (Bengtsson et al., 2009).

Critically, rhythmic complexity should be considered on a continuum, and this continuum may not be linear (Matthews et al., 2019, 2020). We acknowledge there is a subjective component to how we categorized specific fMRI contrasts for the Beat-based and Complexity meta-analyses (more details in Discussion) but we aimed to make our decisions agnostic to the individual interpretations that authors had made about their own papers in order to find some common ground across studies. As an example, we categorize the term “non-metric” as a weak, complex beat-based stimulus, rather than a stimulus that has no detectable beat whatsoever, though individual studies have differed in how this term is used, and thus the construct it represents (Bengtsson et al., 2009; Grahn & Brett, 2007).

We included some fMRI contrasts that were slightly inhomogeneous with others in the analysis to achieve a well-powered analysis. For example, Lewis et al., 2004 define complexity based on the *number* of intervals in a sequence (2-interval sequences being less complex than 6-interval sequences) and while our definition of complexity differs from that of Lewis et al., 2004, we still included this contrast in our Complexity analysis.

2.4 fMRI contrast inclusion

Several studies had different fMRI contrasts eligible for both the Beat-based and Complexity categories. fMRI meta-analyses were conducted separately for each category both to avoid repeated measures (multiple relevant experiments with the same subject group) and to address the experimental aims of the meta-analysis most appropriately. Papers that reported data from the same participants (i.e., Vuust et al.,

¹ Source: Britannica Encyclopedia.

2006; Vuust et al., 2011) were considered one experiment while papers with two separate subject cohorts (Chen et al., 2008b, 2008a) were considered separate experiments (Turkeltaub et al., 2012). Additionally, several papers had multiple relevant contrasts (e.g., “polyrhythmic vs. no movement [listen to isochronous rhythms]” and “polyrhythmic vs. isorhythmic tapping” in Thaut et al., 2008) and in these cases, we chose to include the single “best-fitting” contrast in our analysis (Müller et al., 2018). For studies investigating rhythm working memory (Chapin et al., 2010; Konoike et al., 2012, 2015), we chose to include only the “encoding” phase, where participants were listening to a rhythm, rather than the “maintenance” or “reproduction” phase where no stimulus was present and participants were instructed to reproduce the rhythm from memory (potential working memory and self-initiated timing confounds). See Table S1 in the Supplement for contrasts not included in the present meta-analyses, and the rationale for these decisions.

If authors provided a conjunction analysis table for the relevant contrasts (e.g., Kung et al., 2013) or a “condensed” version of our construct of interest (e.g., Grahn & Rowe, 2009), we used this. For example, in Grahn & Rowe 2009 we used the contrast [volume beat + duration beat – volume nonbeat + duration nonbeat] rather than choosing either [volume beat-volume nonbeat] or [duration beat-duration nonbeat]).

Because our analysis was already limited by sample size due to the size of the overall literature, we included studies that used masks and conjunction analyses (mentioned above) and studies that did not report deactivations. Excluding studies based on these criteria would have resulted in too few studies remaining to conduct meaningful meta-analyses.

2.4.1 Justification for combined analysis of production and perception contrasts

In our analyses, we pooled perception and production paradigms for two reasons. First, nodes for rhythm perception and production are in close proximity to one another – these nodes lie along an anterior/posterior dimensionality. Evidence for this comes from diffusion tensor imaging (DTI) work in humans and non-human primates. In the SMA, the anterior pre-SMA is linked with sensory/perceptual functions, while the posterior SMA-proper is linked with production (Schwartz et al., 2012). This organization of temporal processing is also true for the basal ganglia and its connections with the SMA (Draganski et al., 2008; Lehericy et al., 2004). Other evidence from patient populations corroborates that these nodes are in close proximity. Patients with Parkinson’s Disease (Bégin et al., 2018; Grahn & Brett, 2009), focal BG lesions (Schwartz et al., 2011), focal cerebellar lesions (Ivry & Keele, 1989), or beat deafness (Tranchant et al., 2021) show deficits in both rhythm perception and production. Second, a separation by perception/production for each of our three main analyses would have been too underpowered and thus is not warranted. In light of these reasons, if authors provided a conjunction analysis of perception and production

contrasts, we used the conjunction analysis instead of choosing either the perception or production contrast. Table 3A (Beat-based contrasts with rest baseline), Table 3B (Beat-based contrasts with an audio-motor control baseline) and Table 4 (Complexity) provide a comprehensive description of the fMRI contrasts included in each meta-analysis category.

2.5 Descriptive variables

We extracted several variables of interest for each study in the meta-analysis, including 1) musician/non-musician status of the participants, 2) stimulus category (e.g., sound sequences or real excerpt of music), 3) type of task/rhythm construct (e.g., passive listening or rhythm working memory), 4) whether the tasks in each study involved perception or production of rhythm, and 5) fMRI scanning protocol (i.e., sparse sampling or not). We operationally defined “musician” based on the number of years of formal musical training, with the minimum being about five years of formal training based on included studies (see Table S4 in the Supplement for details on each study’s definition/criteria for musicians and non-musicians). Regarding fMRI scanning protocol, we chose to specifically focus on the use of sparse sampling designs because of the inherent rhythmicity of fMRI scanner noise, which could confound the processing of auditory rhythmic stimuli presented during experiment blocks. The unit of analysis for the descriptive categorization of study manuscript, while the unit of analysis for the coordinate-based fMRI meta-analysis was the fMRI contrast.

IDENTIFICATION

SCREENING

INCLUDED

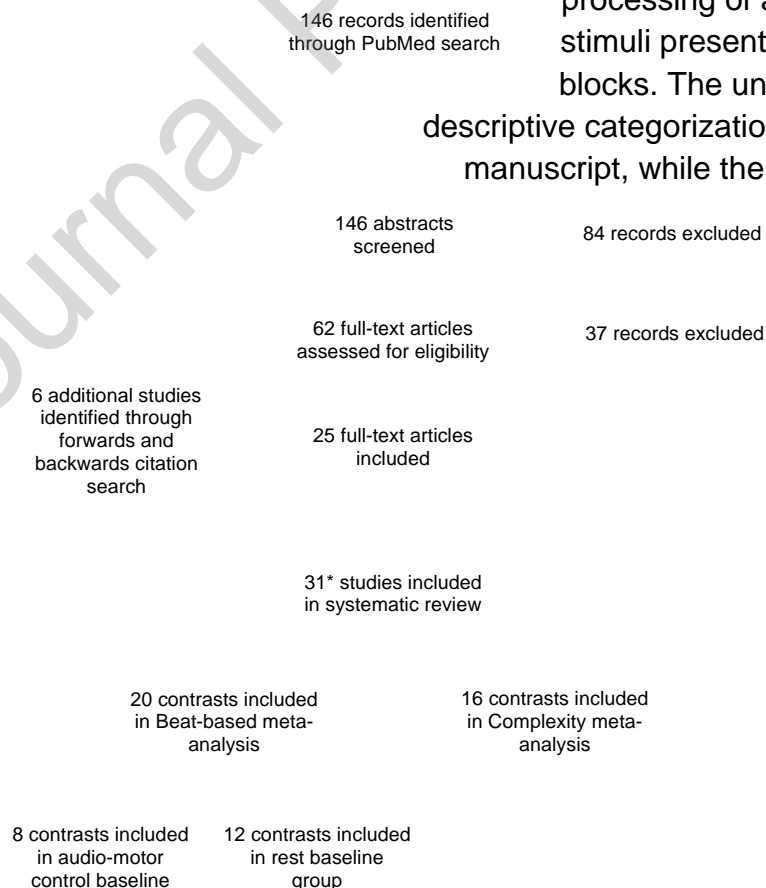


Figure 1. PRISMA flowchart (Page et al., 2021), modified for our specific use of selection procedures for studies included in the meta-analysis. Three studies had eligible contrasts for both the Beat-based and Complexity analyses (Grahn & Brett, 2007; Konoike et al., 2012; Kung et al., 2013). One study had eligible contrasts for both the Beat-based audio-motor control and rest baseline analyses (Araneda et al., 2017). The 12 contrasts included in the Beat-based “rest” baseline group included two from (Chen et al., 2008a) and the 16 contrasts in the Complexity analysis included two from (Chen et al., 2008b). In both cases, the contrasts involved data from non-overlapping participant samples.

* The total number of studies included in the systematic review and meta-analysis was 30. The two papers by Vuust et al., (2006, 2011) were considered as one paper as they were conducted in the same sample of participants with the same stimulus, albeit with slightly different tasks.

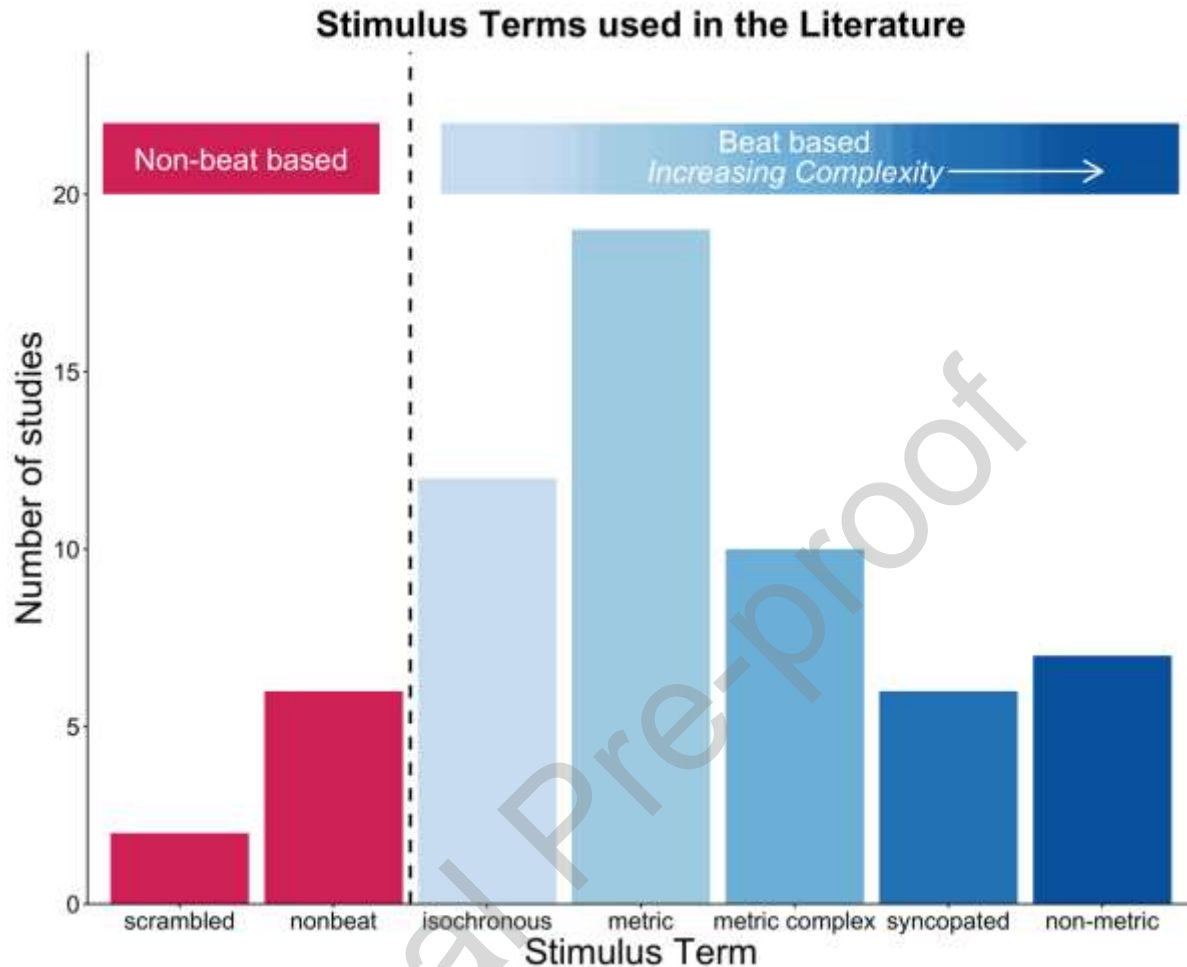


Figure 2. Complexity of rhythm stimuli descriptions from studies included in the meta-analysis. Please see the Supplement for a fun, interactive version of this figure. Non-beat stimulus terms are in red and Beat-based stimulus terms are in blue, with less complex rhythms (strong beat structure) in lighter shades and more complex (weak beat structure) rhythms in darker shades. This figure reflects a dimensionality reduction of terms, as across papers authors used many terms to describe their stimuli. In some instances (e.g., McAuley et al., 2012), authors did not assign a term to their stimuli but rather described them in terms of durations, interonset intervals, etc. In these instances, a stimulus term was assigned based on the description the authors provided. Only terms that were used in the contrasts for the fMRI meta-analyses are included in this figure (e.g., Limb et al 2006 included a “randomized” rhythm condition but this condition was not included in the coordinate-based meta-analyses and is thus not reflected in this figure). If contrasts included multiple terms/conditions (e.g., isochronous, metric, and non-metric conditions as in Bengtsson et al., 2009), each of these terms are reflected in the count; thus, a single paper can be represented multiple times in this figure. Synonyms for stimuli included in each bin are as follows:

Non-beat: irregular, nonperiodic, jittered

Isochronous: metronomic, periodic, regular, isorhythmic

Metric: metric simple, simple, beat, regular, quantized, participant improvisation (Berkowitz & Ansari, 2008), perfectly metric, strongly metric, naturalistic music (pop/rock music, Fedorenko et al., 2012)

Metric complex: complex, regular, main meter (see note on Vuust et al., 2011 below), participant improvisation (Berkowitz & Ansari, 2008), metric (Kung et al., 2013 musical notation of this condition more closely matched with our “metric complex” category, while their perfectly and strongly metric conditions were more in line with our “metric” category)

Syncopated: synchronous syncopated drumming, polyrhythmic, counter meter

Non-metric: ambiguous, irregular, weakly metric

About Thaut et al., 2008: All stimuli in this study were isochronous (2 or 3 Hz beeps). However, participants were required to tap asynchronously in a polyrhythmic pattern in some conditions. Though the stimuli themselves were not syncopated, participants were interacting with them in a syncopated manner, thus Thaut et al., 2008 is counted in both the “isochronous” and “syncopated” categories above and was included in our Complexity meta-analysis.

About Vuust et al., 2011: A metrically complex stimulus was presented to participants, and they were required to tap to the main meter (i.e., isochronous taps) or the counter meter (i.e., syncopated taps). That is, the stimulus stayed the same while participant task demands changed (like above Thaut et al., 2008 study). For this study, the terms “metric complex” and “syncopated” are represented in the figure, as the isochronous taps were always made in the presence of a complex stimulus (these terms also align with the stimulus used in Vuust et al., 2006). This study was also included in our Complexity meta-analysis.

2.6 Meta-Analysis Using SDM-PSI

We used the Seed-based d mapping software (SDM-PSI) (Albajes-Eizagirre et al., 2019), version 6.12, to conduct coordinate-based meta-analyses (CBMA). SDM aims to recreate the original activation maps (“study image”) at the group level of the individual experiments before they are combined into a meta-analytic map by imputing a 3D effect size image for each study. First, SDM generates Hedge’s g effect size and variance from the t values for each activation peak for each study. During this preprocessing step, each peak is convolved with a Gaussian kernel, and upper and lower bound estimates of effect size are calculated. Second, the most likely effect size and variance for each study are estimated using maximum likelihood estimation. Third,

SDM conducts imputation of the subject images via multiple imputations (Rubin, 1987). The maps from each imputation dataset are combined for the meta-analysis which is fit with a standard random-effects model. Fourth, the meta-analytic maps resulting from the different imputation datasets are combined using Rubin's rules (Rubin, 1987). Finally, subject-based permutation testing is conducted to control for the familywise error rate (FWER).

For each contrast of interest (as identified in Tables 3 and 4), the peak coordinates of activity (in either Montreal Neurological Institute (MNI, Evans et al., 1993) or Talairach space (Talairach, 1988) and the corresponding t -value, along with participant sample size and the t -threshold for each study, were entered as input for the SDM meta-analyses. Before conducting the meta-analyses, coordinates reported in Talairach space were converted to MNI space by the SDM software. In some instances, statistical significance was reported as z -values, in which case values were converted to t using the "convert peaks" function in SDM. In studies where no t or z value was reported, a 'p' or an 'n', denoting positive or negative direction of activation, was entered, as recommended by SDM.

Only studies that reported activations at the whole-brain level were included. When studies reported whole brain *and* small volume correction (SVC) or *a-priori* ROI activations, we only included coordinates that met the whole brain threshold and excluded coordinates that did not meet this threshold or were reported with a different threshold. We also excluded contrasts where one experiment was used as a functional localizer for another (e.g., experiment 2 of Grahn & Rowe, 2009).

SDM-PSI offers some advantages over other fMRI coordinate-based meta-analytic software, including ALE (Eickhoff et al., 2009). Specifically, SDM allows for the inclusion of peak coordinate deactivations (in addition to activations) as well as measures of effect size (t or z values) for each peak. Thus, SDM assesses the effect size of activation/deactivation for each voxel (i.e., whether effects are null or not in a given voxel), while ALE measures the degree of overlap, or convergence, in peak activations (i.e., whether activation in one voxel is more common/above chance level than in another voxel). The SDM software can also conduct meta-regressions and analyses with covariates.

All meta-analyses in the current study were conducted with 50 imputations of study images and 1000 permutations of subject images for familywise error (FWE) correction for multiple comparisons. Preprocessing was conducted within a full brain mask and peaks were convolved with an anisotropic Gaussian kernel of 20 mm full width half maximum (FWHM) and a 2mm voxel size. The use of full anisotropy (anisotropy=1) and the FWHM size were based on standard SDM guidelines and recommendations from Radua et al., 2014. Thresholds for all results were set using threshold-free cluster enhancement (TFCE) statistics (Smith & Nichols, 2009) with corrected $p < 0.05$. To assess publication bias for the Beat-based and Complexity meta-

analyses, we report results of the Egger test as implemented in SDM. The Egger test for funnel plot asymmetry should be taken as an exploratory assessment of publication bias as it is only conducted on the peak coordinate of a given cluster. Additionally, it is not recommended to conduct this test with less than 10 studies (Chandler et al., 2020) and our Beat-based “audio-motor control” analysis had 8 contrasts. Thus, we did not conduct the Egger test for this analysis. For all analyses, we report measures of effect size (Hedge’s g) and heterogeneity (I^2 , which should also be interpreted cautiously in small studies (Von Hippel, 2015)) in the Supplement.

2.7 Planned analyses

The goals of the meta-analysis were three-fold: 1) identify a general network involved in performing musical rhythm tasks (Beat-based, rest baseline), 2) identify a more precise network for processing beat-based musical rhythms, above and beyond basic sensory and motor processes (Beat-based, auditory control baseline), and 3) identify regions modulated by rhythmic complexity (Complexity). Critically, isolating the studies within the Beat-based category that used a low-level auditory/motor control as a baseline condition should reveal a more specific and representative rhythm network beyond the contribution of basic auditory and motor processes.

We also sought to understand how the musical experience of participants impacted the processing of complex rhythms. To this end, we conducted an additional meta-analysis in SDM with musician/non-musician as a covariate. Only the Complexity subset of contrasts had an equivalent number of contrasts with musician and non-musician participants. We did not run a covariate analysis with musicians and non-musicians for the Beat-based studies because it did not relate directly to our experimental question (rhythm complexity and musical experience relationship). Additionally, the number of studies in each category would not have been appropriate for such an analysis.

Table 1. Participant characteristics of papers included in the Beat-based meta-analysis.

Study DOI	Number of Participants	Sex	Age	Musicians?
Araneda et al. (2017) 10.1111/ejn.13349	27	Not specified	mean age + SD: 26 + 7.02 yrs	
Chapin et al. (2010) 10.3389/fpsyg.2010.00224	13	7 M, 5 F - one participant unaccounted for	range: 20-46 yrs; mean: 28.83 yrs	both (m)

Chen et al. (2006) 10.1016/j.neuroimage.2006.04.207	11	6 M, 6 F - one excluded in final analyses	range: 19-39 yrs; mean: 27 yrs	
Chen et al. (2008a)^a 10.1093/cercor/bhn042	24 (12/experiment)	Experiment 1 - 6 M, 6 F; Experiment 2 - 6 M, 6 F	Experiment 1 - range: 20-32 yrs; mean: 23.83 yrs; Experiment 2 - range: 19-34 yrs; mean: 24 yrs	
De Pretto & James (2015) 10.1037/pmu0000122	14	8 M, 8 F - two excluded in final analyses	mean: 28.1 yrs; SD: 4.3 yrs	
Fedorenko et al. (2012) 10.1152/jn.00209.2012	12	6 M, 6 F	range: 18-50 yrs	
Geiser et al. (2012) 10.1523/JNEUROSCI.5153-11.2012	17	9 M, 8 F	mean age: 25.1 + 4.4 yrs	
Grahn & Brett (2007) 10.1162/jocn.2007.19.5.893	27	19 M, 8 F	range: 19-38 yrs; mean: 24.5 yrs	both (s/m)
Grahn & McAuley (2009) 10.1016/j.neuroimage.2009.04.039	35	23 M, 12 F	range: 22-46 yrs; mean: 29.9 yrs; SD: 7.2 yrs	
Grahn & Rowe (2009) 10.1523/JNEUROSCI.2018-08.2009	36	21 M, 15 F	range: 18-41 yrs; mean: 29 yrs	both (m)
Grahn & Rowe (2013) 10.1093/cercor/bhs083	24	11 M, 13 F	range: 22-44 yrs; mean: 27 yrs	both (s/m)
Kokal et al. (2011) 10.1371/journal.pone.0027272	18	18 F	range: 19-30 yrs; mean: 23 yrs	
Konoike et al. (2012) 10.1016/j.neuroimage.2012.07.002	16	10 M, 7 F - one excluded in final analyses	range: 18-28 yrs; mean: 21.9 yrs	
Kornysheva et al. (2011) 10.1371/journal.pone.0021421	16	8 M, 8 F	range: 22-29 yrs; mean: 24.8 yrs	
Kung et al. (2013) 10.1162/jocn_a_00325	11	6 M, 5 F	range: 20-38 yrs; mean: 24.73 yrs; SD: 5.18 yrs	✓
Limb et al. (2006) 10.1002/ar.a.20298	24	musicians - 9 M, 3 F; non-musicians - 9 M, 3 F	musicians - mean age: 31+6.52 yrs; non-musicians - mean age: 34 + 14.9 yrs	both (s)
McAuley et al. (2012) 10.1111/j.1749-6632.2011.06433.x	15	3 M, 12 F	range: 18-52 yrs	
Teki et al. (2011) 10.1523/JNEUROSCI.5561-10.2011	18	9 M, 9 F	range: 18-46 yrs; mean: 22.17 yrs	

Notes. Checkmarks indicate the full sample of participants in a given study were categorized as musicians. Blank entries in the “Musician” column indicate there were no musicians in the sample (i.e., only non-musicians in the study). (m)=mixed musician and non-musician participants together. (s)=separated musician and non-musician participants in analyses. (s/m) = musicians and non-musicians either mixed or separated, depending on the specific analysis.

^a Experiment 1 participants were the same non-musician participants as in Chen et al., 2008b. This was not a problem of repeated measures/overlapping subjects because the Chen et al., 2008b study was used in the Complexity meta-analysis, rather than the Beat-based meta-analysis. Experiments 1 and 2 from this study were both included in the meta-analysis as they were conducted in non-overlapping participant samples.

Table 2. Participant characteristics of papers included in the Complexity meta-analysis.

Study DOI	Number of Participants	Sex	Age	Musicians?
Bengtsson & Ullén (2006) 10.1016/j.neuroimage.2005.09.019	11	11 M	range: 23-41 yrs; mean: 33 yrs	✓
Bengtsson et al. (2009) 10.1016/j.cortex.2008.07.002	17	14 M, 3 F	range: 20-36 yrs; mean: 23.6 yrs	
Berkowitz & Ansari (2008) 10.1016/j.neuroimage.2008.02.028	12	5 M, 8 F - one excluded in final analyses	mean age: 21.9 yrs	✓
Chen et al. (2008b)^b 10.1162/jocn.2008.20018	24	12 M, 12 F "balanced for sex"	musicians - range: 19-28 yrs, mean: 23.17 yrs; non-musicians - range: 20-32 yrs; mean: 23.83 yrs	both (s)
Danielsen et al. (2014) 10.1016/j.neuroscience.2014.06.029	19	11 M, 8 F	range: 23-49 yrs; mean: 35.2 yrs; SD: 6.2 yrs	
Foster & Zatorre (2010) 10.1093/cercor/bhp199	20	musicians - 4 M, 5 F; non-musicians - 5 M, 6 F	musicians - mean: 27 yrs; non-musicians - mean: 24 yrs	both (s/m)
Grahn & Brett (2007) 10.1162/jocn.2007.19.5.893	27	19 M, 8 F	range: 19-38 yrs; mean: 24.5 yrs	both (s/m)
Herdener et al. (2014) 10.1093/cercor/bhs367	22	22 M	range: 20-50 yrs	both (s/m)
Jungblut et al. (2012) 10.3233/RNN-2011-0619	28	17 M, 13 F - two excluded from study	range: 21-41 yrs; mean: 26.3 yrs	
Konoike et al. (2012) 10.1016/j.neuroimage.2012.07.002	16	10 M, 7 F - one excluded in final analyses	range: 18-28 yrs; mean: 21.9 yrs	
Konoike et al. (2015) 10.1371/journal.pone.0130120	23	14 M, 15 F - six excluded in final analyses	range: 18-25 yrs; mean: 21.4 yrs	
Kung et al. (2013) 10.1162/jocn_a_00325	11	6 M, 5 F	range: 20-38 yrs; mean: 24.73 yrs; SD: 5.18 yrs	✓
Lewis et al. (2004) 10.1016/j.neuropsychologia.2004.03.001	10	5 M, 5 F	mean age: 27 yrs	
Thaut et al. (2008) 10.1371/journal.pone.0002312	12	9 M, 3 F	range: 20-36 yrs; mean + SEM: 26.1 + 1.8 yrs	✓
Vuust et al. (2006) Vuust et al. (2011)^c 10.1016/j.neuroimage.2005.12.037 10.1016/j.neulet.2011.03.015	18	14 M, 4 F	mean: 29 yrs; SE: 1 yr	✓

Notes. Refer to Table 1 captions for more details.

^b Same non-musician subject cohort, but different data, as Experiment 1 of Chen, Penhune, & Zatorre, 2008a.

^c Same subjects and stimuli, albeit different tasks, across the two studies.

Table 3A. fMRI contrasts included in the Beat-based meta-analysis with rest baseline.

Study	Contrast analyzed/type of analysis	Experimental conditions included in contrast, if multiple	Perception or production contrast	Deactivations reported?	Other notes
Araneda et al. (2017) ^a	auditory beat vs. rest		perception	no	inclusive mask of all conditions vs. rest
Chapin et al. (2010)	“attend 2” rhythms vs. rest		perception	yes	
Chen et al. (2006)	isochronous vs. silence		production	no	
Chen et al. (2008a) Experiment 1	conjunction: listen with anticipation and tap vs. silence	simple, complex, ambiguous (nonmetric) rhythms	perception & production	no	different group of participants than Experiment 2
Chen et al. (2008a) Experiment 2	conjunction: passive listen, listen with anticipation and tap vs. silence	Simple, complex, ambiguous (nonmetric) rhythms	perception & production	no	different group of participants than Experiment 1
Grahn & Brett (2007)	all rhythms vs. rest	metric simple, metric complex, nonmetric	perception	no	
Grahn & McAuley (2009) ^d	all stimuli vs. rest	test and control sequences	perception	no	
Kokal et al. (2011)	synchronization to a syncopated rhythm vs. random pauses		production	no	
Konoike et al. (2012)	rhythm vs. silence, encoding phase		perception	no	used an inclusive mask of rhythm vs. baseline (silent fixation) to exclude deactivations in number working memory task
Kung et al. (2013)	tap isochronous vs. silence		production	no	varying interonset intervals based on participant

					performance in "Tap Beat" condition
Limb et al. (2006)	conjunction of musicians and non-musicians for [quantized rhythms vs. rest]		perception	no	
McAuley et al. (2012) ^d	600ms tempo vs. rest	test and control sequences	perception	no	

Table 3B. fMRI contrasts included in the Beat-based meta-analysis with auditory/motor control baseline.

Study	Contrast analyzed/type of analysis	Experimental conditions included in contrast, if multiple	Perception or production contrast	Deactivations reported?	Other notes
Araneda et al. (2017) ^a	auditory beat vs. no-beat rhythms		perception	yes, none significant	inclusive mask of all conditions vs. rest
De Pretto & James (2015) ^b	regular-1 vs. irregular-1		production	yes, none significant	
Fedorenko et al. (2012) ^c	[intact music + pitch scrambled] vs. [rhythm scrambled + both scrambled]		perception	yes, none significant	statistical parametric map (SPM) obtained directly from the first author
Geiser et al. (2012)	periodic vs. non-periodic sequences		perception	yes	
Grahn & Rowe (2009) ^c	beat vs. nonbeat	[volume beat + duration beat – volume nonbeat + duration nonbeat]	perception	no	only used data from Exp. 1 - activations from Exp. 1 were used as a functional localizer for Exp. 2
Grahn & Rowe (2013)	beat vs. nonbeat		perception	yes	
Kornysheva et al. (2011) ^c	synchronization vs. random/scrambled rhythms	[PMv TMS] + [PMv no TMS] + [AG TMS] + [AG no TMS]*	production	no	Participants completed two TMS-fMRI sessions, with two fMRI scans per session.
Teke et al. (2011) ^e	regular vs.		perception	yes	

	irregular sequences				
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Notes for Tables 3A ad 3B. * Abbreviations: PMv = left ventral premotor cortex. AG = left angular gyrus/parieto-occipital lobe. TMS = transcranial magnetic stimulation. Though this study included a TMS manipulation, the authors performed a conjunction analysis for the contrast we included in our study, which should account for effects related to the TMS.

Contrasts categorized as perception are those where participants were listening to music, while production contrasts are those where participants were actively producing rhythms (see Figure 3D for more details).

^a All conditions for the inclusive mask consisted of {[auditory beat + auditory no beat + vibrotactile beat + vibrotactile no beat + visual beat + visual no beat] – rest}

^b The reported contrast, irregular vs. regular rhythms, reflects non-beat-based vs. beat-based rhythm. As an approximation for beat-based vs. non-beat-based rhythms, we flipped the direction of the *t*-values for this contrast.

^c Scrambled rhythms sound different (e.g., white noise) than non-beat rhythms (e.g., jittered clicks) but to have enough studies in our analyses, we did not distinguish studies based on this level of granularity.

^d Test and control sequences were both considered “metric simple”.

^e The “regular vs. irregular” contrast was considered as beat-based vs. non-beat-based (positive *t*-values), while the “irregular vs. regular” contrast was considered as non-beat-based vs. beat-based (negative *t*-values). The authors align “regular vs. irregular” with relative, beat-based timing and “irregular vs. regular” with absolute, duration-based timing.

Table 4. fMRI contrasts included in the Complexity meta-analysis.

Study	Contrast analyzed/type of analysis	Experimental conditions included in contrast, if multiple	Perception or production contrast	Deactivations reported?	Other notes
Bengtsson & Ullén (2006)	contrast for main effect of rhythm	{[Combined (rhythm + melody) + rhythm] – [melody + isochronous]}	production	no	
Bengtsson et al. (2009)	metric + non-metric rhythms vs. isochronous	isochronous, metric, non-metric	perception	yes	

Berkowitz & Ansari (2008)	rhythmic improvisation vs. metronome		production	yes, none significant	
Chen et al. (2008b) ^a (musician group)	parametric covariation with rhythm complexity	metric simple, metric complex, nonmetric	production	yes, none significant	behavioral measures (%ITI deviation scores) regressed against brain activity across all conditions
Chen et al. (2008b) ^a (non-musician group)	parametric covariation with rhythm complexity	metric simple, metric complex, nonmetric	production	yes, none significant	behavioral measures (%ITI deviation scores) regressed against brain activity across all conditions
Danielsen et al. (2014)	transitions (drum breaks) vs. continuous (repetitive drum groove)		perception	yes, none significant	
Foster & Zatorre (2010)	rhythm task vs. auditory control (isochronous)		perception	yes	
Grahn & Brett (2007) ^b	metric simple vs. metric complex + nonmetric rhythms	metric simple, metric complex, nonmetric	perception	yes, none significant	
Herdener et al. (2014)	syncopated deviations vs. regular rhythmic pattern compared to rest		perception	no	
Jungblut et al. (2012)	regression for rhythm complexity	regular groupings, regular groupings with rests, irregular groupings	production	no	unclear from Methods section if/how a mask was used
Konoike et al. (2012)	rhythm (metric) vs. number (isochronous) working memory control, encoding phase		perception	no	used an inclusive mask of rhythm vs. baseline (silent fixation) to exclude deactivations in number working memory task
Konoike et al. (2015)	rhythm (metric) vs. number (isochronous) working memory control, encoding phase	conjunction across 4 effectors (right finger, left finger, right foot, mouth)	perception	no	used an inclusive mask of rhythm vs. baseline (silent fixation) to exclude deactivations in number working memory task
Kung et al.	Conjunction of [find	collapsed across	perception	no	varying inter-onset-

(2013)	beat – listen isochronous] + [tap beat – tap isochronous]	perfectly metric, strongly metric, metric, weakly metric levels, two tempi (fast, slow) and meter (duple or triple meter)	and production		intervals for isochronous condition based on participant performance in “Tap Beat” condition
Lewis et al. (2004)	parametric analysis for synchronize phase	2, 4, 6 interval rhythms	production	no	
Thaut et al. (2008)	polyrhythmic vs. isorhythmic	2 Hz and 3 Hz stimulus and tapping rates	production	yes	
Vuust et al. (2006) Vuust et al. (2011)	tap counter meter vs. tap main meter		production	yes, none significant	we chose to include only the contrast from the 2011 paper to avoid issues of repeated subjects in the same analysis

Notes. Contrasts categorized as perception are those where participants were listening to music, while production contrasts are those where participants were actively producing rhythms (see Figure 3D for more details).

^a %ITI (inter-tap-interval) deviation is a behavioral measure of synchronization ability. Increases in %ITI deviation indicate worse synchronization performance. Across the three levels of rhythm complexity for both musicians and non-musicians, %ITI increased (lowest %ITI deviation in metric simple condition, highest deviation in non-metric condition). Thus, %ITI deviation was taken as a measure of rhythm complexity for the parametric analyses. Brain regions that show increased activity relate to worse tapping performance, while brain regions that show decreased activity relate to better tapping performance (none found).

^b This contrast was considered “Less vs. More Complex”, so the direction of the *t*-values was reversed to reflect “More vs. Less Complex”.

Results

3.1 Descriptive study characteristics

Across all papers included in the meta-analysis, we sought to characterize 1) musical experience of participants, 2) presence of sparse sampling method, 3) type of stimulus, and 4) type of task participants completed in the fMRI scanner. Data and figures presented here reflect studies pooled across the Beat-based and Complexity meta-analyses (i.e., manuscript is the unit of analysis, rather than fMRI contrast) because some papers were included in both the Beat-based and Complexity meta-analyses.

First, we extracted information about the musical experience of the participants (Figure 3A). We defined “musician” based on the number of years of formal musical

training, which was about a minimum of 5 years. However, the specific definition of “professional musician” varied across papers, consistent with variability in how musicianship is reported in the field (see Table S4 in the Supplement). Across the total 30 papers, 5 included professional musician participants, 17 included non-musician participants, and 8 included both musician and non-musician participants. Though not our main question of interest, we noted 6 papers made direct comparisons between musician and non-musicians participants for processing of rhythm (or processing of melody in the case of Foster & Zatorre, 2010) (see Tables 1, 2, and S4).

Second, we categorized whether papers employed a sparse sampling method (Figure 3B). The sparse sampling method involves silent delay periods between fMRI volume acquisitions such that the loud, rhythmic noise of the scanner does not contaminate the presentation of auditory stimuli (Hall et al., 1999; Perrachione & Ghosh, 2013). Few studies ($n=8$) used sparse sampling.

Third, we categorized the type of stimulus across studies (Figure 3C). Most commonly, studies used a “simple sound sequence” - a sequence of sounds (usually presented as a pure tone, piano note, or woodblock sound) with varying inter-onset-intervals, level of complexity (e.g., isochronous, metric), and sequence length (e.g., 11 notes, 5 seconds, etc.). Studies also used naturalistic music (e.g., “real” music not designed for a laboratory setting such as Sting’s “The Lazarus Heart” (Vuust et al., 2006; Vuust et al., 2011), naturalistic music with manipulations, or multi-timbre percussion sequences (e.g., layers of snare drum, bass drum, hi-hat as in (Herdener et al., 2014). One study used scripted sheet music, where the participant read off of a visual musical score while listening in real time to what they were playing (Bengtsson & Ullén, 2006). Another study used scripted sheet music with improvisation, where the participant was required to improvise along one dimension (melodic or rhythmic) while following a visual musical score, also while listening to what they were playing (Berkowitz & Ansari, 2008).

Fourth, we characterized the type of tasks participants completed in the fMRI scanner (Figure 3D). Several studies required participants to engage in two or three different tasks; each of these separate “task phases” are represented in the figure (i.e., the denominator for this plot is not 30 (total number of studies), but rather 36, for studies that had multiple task phases). For example, several studies had participants complete a “passive listening” and a “tapping” (i.e., synchronize with a rhythm) task (Chen et al., 2008b, 2008a; Kung et al., 2013; Thaut et al., 2008; Vuust et al., 2006; Vuust et al., 2011). In Berkowitz & Ansari, 2008, participants had to improvise rhythms on the piano as well as follow a musical score. Overall, there was quite a diverse range of tasks employed across the studies included in the meta-analysis, with the most common being tapping ($n=10$) and passive listening tasks ($n=10$).

Most tasks involved rhythm perception (i.e., passive listening, beat/meter judgments, non-beat musical judgments, music attention task, same/different rhythm

discrimination). Non-beat musical judgments included tasks involving intensity discrimination (Geiser et al., 2012) and judgments about tempo (Grahn & McAuley, 2009; McAuley et al., 2012) and interval length (Teki et al., 2011). The two studies using beat/meter judgments either had participants rate on a Likert scale “How much did the most recent rhythm have a beat?” (Grahn & Rowe, 2013) or had participants complete a “beat vs. no-beat” discrimination task (Araneda et al., 2017). In the music attention task, participants performed a pitch change detection, though they were also told by the experimenter to focus on “feeling the beat” when listening to the stimuli (Grahn & Rowe, 2009).

Production tasks included tapping, improvisation, and scripted piano playing. Studies varied in whether they asked participants to synchronize *with* the stimulus, tap to a beat, or drum a rhythm. All these variations are considered under the “tapping” task category. Tasks that explicitly involved both perception and production of rhythm included working memory (with attend/encode and reproduce phases) and the singing recall tasks. Most production tasks required participants to use their right hand or right index finger to execute the rhythms (Bengtsson & Ullén, 2006; Berkowitz & Ansari, 2008; Chapin et al., 2010; Chen et al., 2006, 2008a, 2008b; Konoike et al., 2012; Lewis et al., 2004; Thaut et al., 2008; Vuust et al., 2006; Vuust et al., 2011), while only two studies had participants alternate between using their left and right index fingers (Kokal et al., 2011; Kornysheva & Schubotz, 2011). One study required participants to use multiple effectors to produce rhythms (right and left index fingers, right foot, mouth (Konoike et al., 2015)), one study involved singing (i.e., effector was the mouth, (Jungblut et al., 2012)) and two studies did not specify which effector participants used to produce rhythms (De Pretto & James, 2015; Kung et al., 2013).

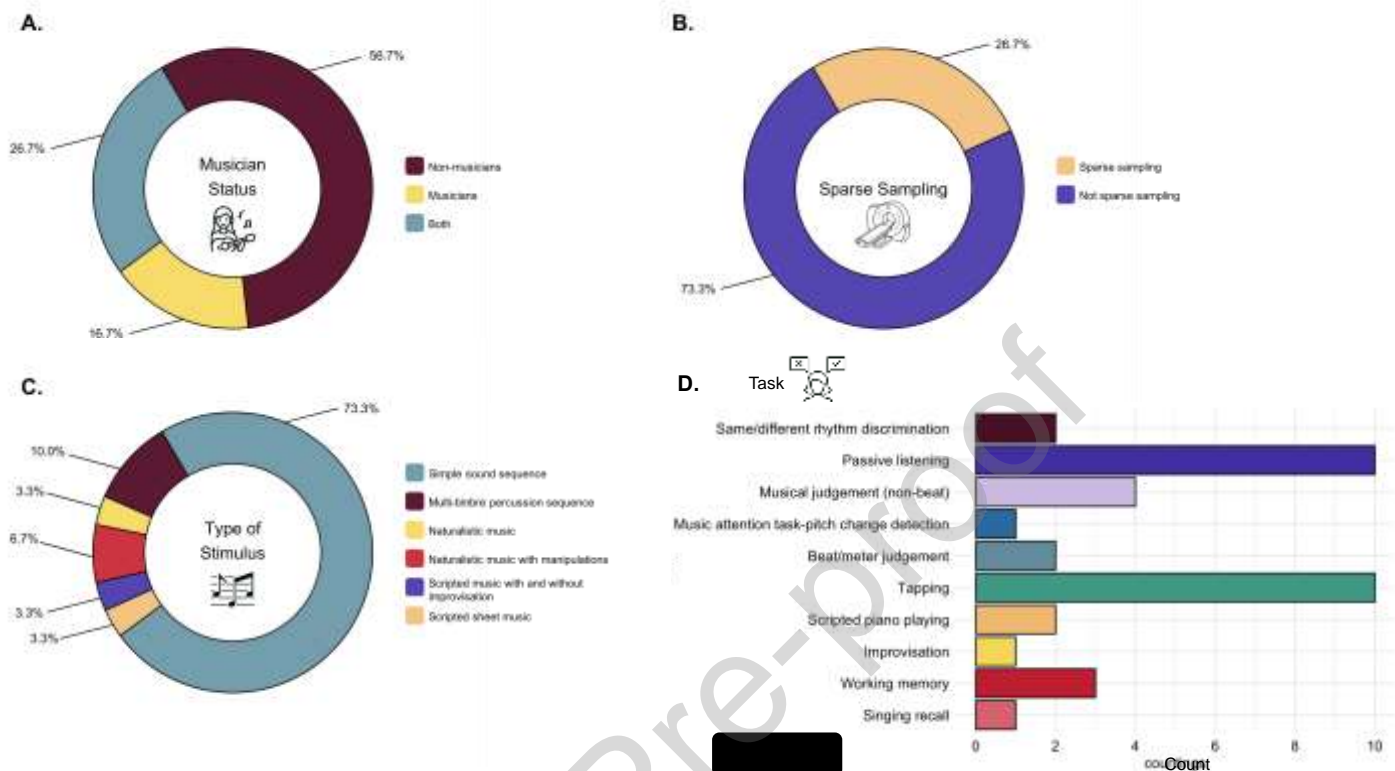


Figure 3. Donut/horizontal bar plots of study characteristics: A) musician status; B) scan protocol (sparse sampling); C) type of stimulus; D) type of task. Visualizations were created using the inauguration package (C. Bedford-Petersen, 2021).

Notes. One study (Chen et al., 2008b) had a “passive listening” component in their task (reflected in the above plot), however the authors did not analyze data from this task for the fMRI experiment.

3.2 Beat-based contrasts with a rest baseline

Twelve contrasts (221 participants, 266 activation foci) compared beat-based rhythms to a rest/silence baseline. This analysis revealed 6 significant clusters that encompassed large activations in the left and right temporal lobes (including the striatum and surrounding areas) bilateral cerebellum, bilateral supplementary motor area (SMA), the right middle frontal gyrus (MFG), and the left anterior thalamus (Table 5A, Figure 4). There were no significant clusters for the reverse contrast (i.e., rest > beat-based rhythm). Heterogeneity was low for all peak coordinates ($I^2 < 40\%$) (Deeks et al., 2021) and the Egger test indicated no evidence of publication bias (see Table S2 in the Supplement). Anatomical labelling of cerebellar activations was completed using the atlas from Diedrichsen and colleagues (Diedrichsen et al., 2009).

3.3 Beat-based contrasts with an audio-motor control baseline

Eight contrasts (164 participants, 140 activation foci) had an auditory/motor control baseline condition (e.g., scrambled rhythms or non-beat-based auditory stimuli). This analysis revealed 4 significant clusters in the putamen bilaterally, left rolandic operculum, and left ventral precentral sulcus (Table 5B, Figure 4). There were no significant clusters for the reverse contrast (i.e., non-beat-based > beat-based rhythm). Heterogeneity was low for all peak coordinates. See Table S2 in the Supplement.

Table 5. Significant clusters for Beat-based studies with a rest/silence baseline and an audio-motor control baseline.

Region	Center of Mass (MNI)	Peak Coordinate (MNI)	Z Value	p	Extent (mm ³)
A. Rest baseline					
Left superior temporal cortex and adjacent regions: STG, insula, pIFG, PrC, PoC, SMG, BG (caudate, putamen, pallidum)	-47, -18, 18	-56, -30, 4	10.069	<0.001	96864
Right superior temporal cortex and adjacent regions: STG, insula, pIFG, PrC, PoC, SMG, BG (caudate, putamen, pallidum)	49, -17, 16	54, -16, -6	9.439	<0.001	92752
Bilateral cerebellum*	2, -62, -31	-26, -70, -24	7.583	<0.001	59936
Bilateral SMA	-1, -2, 61	2, 2, 60	8.628	<0.001	15256
Left anterior thalamus	-12, -18, 6	-12, -18, 0	5.618	0.022	1008
Right MFG	41, 36, 27	42, 36, 28	5.299	0.022	528
B. Audio-motor control baseline					
Right putamen	28, 1, 3	32, -10, 6	5.651	<0.001	8656
Left putamen	-27, -2, 2	-26, 0, 2	4.868	<0.001	4688
Left rolandic operculum	-52, 4, 5	-54, 2, 6	4.438	<0.001	1472
Left ventral precentral sulcus	-53, 10, 20	-48, 6, 22	3.538	0.041	552

Notes. *The cerebellum cluster encompasses the following areas: left lobule I_IV, left lobule V, left lobule VI, left Crus I, left Crus II, left dentate, right lobule I_IV, right lobule V, right lobule VI, right Crus I, right Crus II, right lobule VIIb, right lobule VIIa, right dentate, vermis lobule VI. Abbreviations: STG=superior temporal gyrus; pIFG=posterior inferior frontal gyrus; PrC=precentral gyrus; PoC=postcentral gyrus;

SMG=supramarginal gyrus; BG=basal ganglia; SMA= supplementary motor area;
MFG= middle frontal gyrus.

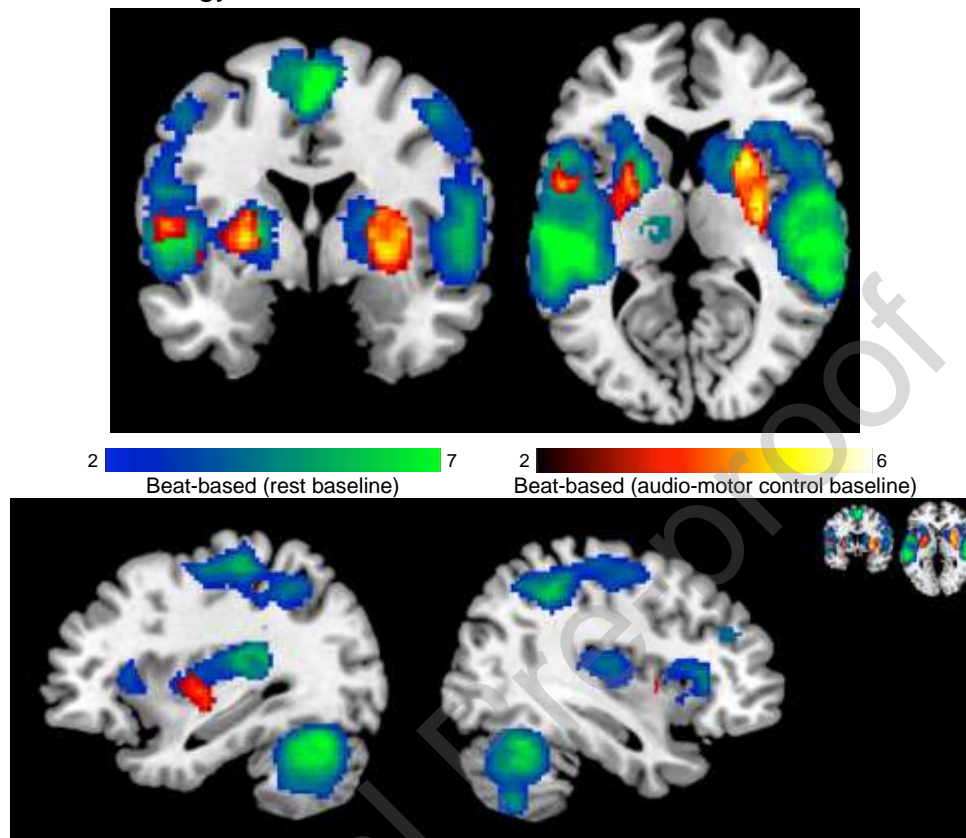


Figure 4. Results for studies with “rest/silence” as a baseline (cool colors) and studies with an auditory/motor control baseline (warm colors). Results are overlaid on the Colin27 template brain (Holmes et al., 1998). Threshold free cluster enhancement (TFCE) map contains SDM-z values, thresholded at $p < 0.05$.

3.4 Rhythm complexity

The Complexity analysis consisted of 16 contrasts (270 participants, 165 activation foci). This analysis revealed 6 significant clusters for more compared to less complex rhythms in the bilateral SMA/pre-SMA region, bilateral cerebellum, right supramarginal gyrus and ventral precentral gyrus/sulcus, left precentral gyrus, left intraparietal sulcus, and right STG/MTG (Table 6 and Figure 5). There were two significant clusters for the reverse contrast (i.e., less complex vs. more complex rhythms) in the left STG and left putamen. Heterogeneity was low for all peak coordinates and the Egger test indicated no evidence of publication bias (see Table S2 in the Supplement). Anatomical labelling of cerebellar activations was completed using the atlas from Diedrichsen and colleagues (Diedrichsen et al., 2009).

Table 6. Significant clusters for the main Complexity meta-analysis.

Region	Center of Mass	MNI Coordinates (peak)	Z Value	p Value	Extent (mm ³)
<i>More vs. Less Complex</i>					
Bilateral cerebellum*	-5, -66, -32	-2, -60, -24	5.665	<0.001	42960
Right SMG, PrC, ventral precentral sulcus	45, -20, 44	50, -34, 44	5.423	<0.001	25648
Bilateral SMA region (SMA-proper and pre-SMA)	-1, 14, 51	4, 32, 44	5.070	<0.001	18136
Left precentral gyrus	-27, -6, 51	-30, -6, 56	5.932	<0.001	4448
Right STG, MTG	64, -31, 7	66, -26, 4	5.528	<0.001	3792
Left intraparietal sulcus	-37, -52, 41	-38, -50, 38	5.460	<0.001	1680
<i>Less vs. More Complex</i>					
Left STG	-49, -7, -1	-54, -8, 0	-3.898	0.026	480
Left putamen	-31, -9, 5	-32, -8, 4	-4.196	0.022	184

Notes. *The cerebellum cluster encompasses the following areas: left lobule V, left lobule VI, left Crus I, left Crus II, left lobule VIIb, left dentate, left interposed nucleus, right lobule I_IV, right lobule V, right lobule VI, right Crus I, right Crus II, right lobule VIIb, right lobule VIIa, right lobule VIIb, right dentate, right interposed nucleus, vermis lobule VI. Abbreviations: SMG=supramarginal gyrus; PrC=precentral gyrus; SMA=supplementary motor area; STG=superior temporal gyrus; MTG=middle temporal gyrus.

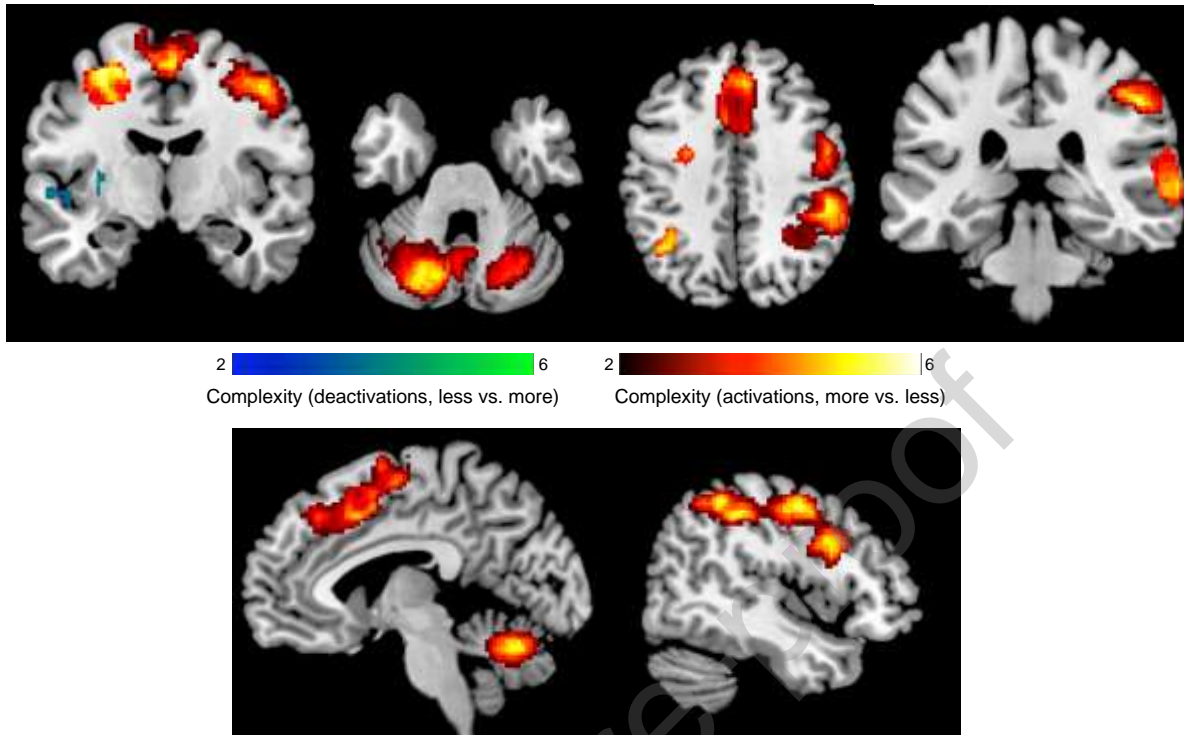


Figure 5. Results of Complexity meta-analysis. Warm colors are activations (more vs. less complex rhythm) and cool colors are deactivations (less vs. more complex rhythm). TFCE map contains SDM-z values, thresholded at $p < 0.05$.

3.5 Relationship between musicianship and rhythmic complexity

To assess the relationship between rhythm processing and musicianship, we ran an additional meta-analysis for the Complexity subset of studies, with musicianship as a covariate (“musician” studies coded as 1 and “non-musician” studies coded as 0). This analysis included 13 experiments. We excluded the studies by Herdener et al., 2014, Foster & Zatorre, 2010, and Grahn & Brett, 2007 because they pooled professional musician and non-musician participants in our contrasts of interest (we only had musicianship information at the level of study, rather than at the level of individual participants). Of the 13 experiments, 6 investigated musicians (76 participants) and 7 investigated non-musicians (125 participants). This analysis yielded several significant activations in similar regions to the main Complexity meta-analysis (Figure 6). These findings indicate that musical experience does not greatly influence the brain basis of rhythm processing for more compared to less complex beat-based musical rhythms. The Coordinate table for the covariate analysis is presented in Table S3 in the Supplement.

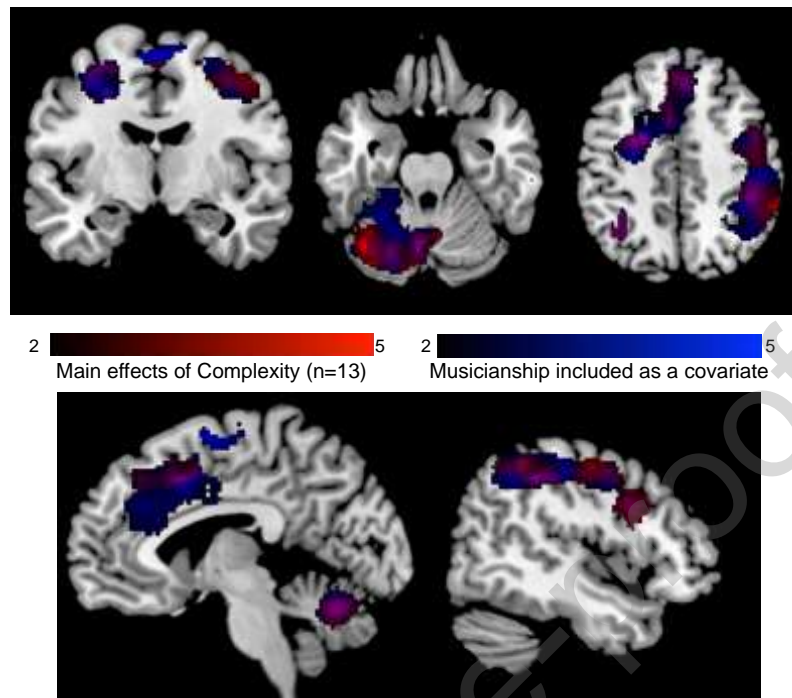


Figure 6. Results of the Complexity meta-analysis with musicianship as a covariate (blue) and main Complexity analysis with the same 13 studies (red). Overlap between the two maps is shown in purple. TFCE map contains z values, thresholded at $p < 0.05$.

Discussion

We conducted a systematic review and meta-analysis of fMRI studies investigating the perception or production of musical rhythm in neurotypical adults. First, we aimed to identify a general network involved in performing musical rhythm tasks, encompassing all the relevant basic sensory and motor processes. We found in this analysis (Beat-based, rest baseline) a large, symmetrical cortico-subcortical network that included auditory and motor regions. Second, we asked which regions were more narrowly implicated in processing beat-based musical rhythms, above and beyond basic sensory and motor processes (Beat-based, audio-motor control). This contrast, which notably included the bilateral putamen, involved a smaller and more restricted network than the Beat-based (rest baseline) meta-analysis. Third, we further narrowed in on a network for musical rhythm by investigating more compared to less complex rhythms (e.g., syncopated vs. isochronous sequences). Regions activated in the Complexity meta-analysis included the bilateral SMA-proper/pre-SMA, cerebellum, inferior parietal regions, and right temporal regions. These second and third analyses provide two different levels of granularity for characterizing a brain network for musical rhythm. Lastly, a descriptive characterization of studies included in the meta-analysis highlighted

substantial heterogeneity in the types of stimuli and tasks used across studies. Our results suggest that musical rhythm engages a largely bilateral cortico-subcortical network of brain regions, with the choice of a baseline condition crucial for accurately and precisely characterizing a brain network that supports musical rhythm processing.

4.1 A wide network of brain regions emerges when rest is used as a baseline

A large and symmetrical cortico-subcortical network emerged when we contrasted beat-based rhythms to a rest baseline. This network encompassed large bilateral clusters in the superior temporal cortex and surrounding regions (i.e., the basal ganglia, insula, supramarginal gyri), bilateral cerebellum, bilateral SMA region, the right middle frontal gyrus, and the left anterior thalamus. The Beat-based (rest baseline) analysis provides information about all the regions involved in performing musical rhythm tasks, including relevant basic sensory and motor processes. It is important to note that some of these activations are related to processing not unique to rhythm, as auditory and motor processes were not controlled for in any of these contrasts.

Previously identified core nodes in the rhythm network – the striatum, SMA, and cerebellum – emerged as significant activations when comparing beat-based rhythms to rest. The striatum, specifically the putamen, and sometimes the caudate, is a central hub in the striatal-beat frequency model of timing (Matell & Meck, 2004). The striatum works in tandem with the SMA, also an important region for beat-based timing. The SMA provides cortical input to the striatum and is a key component of cerebellar and cortico-subcortical networks for temporal processing (Cannon & Patel, 2020; Kotz et al., 2009; Schwartz et al., 2012). The role of the SMA in musical rhythm is discussed in more detail in section 4.3.

We also found activation of the cerebellum bilaterally. While some functional neuroimaging (Teki et al., 2011) and neuropsychological studies (Breska & Ivry, 2018; Grube et al., 2010) suggest dissociations between striatal/SMA and cerebellar roles for beat-based and duration-based timing respectively, multiple frameworks propose an integrated account of these two timing mechanisms (Petter et al., 2016; Schwartz & Kotz, 2013; Teki et al., 2012). The neural circuits subserving beat-based and duration-based timing likely function as a unified system rather than segregated operations. The anatomical architecture of these systems supports such an account. The cerebellum outputs signals to cortico-striatal circuits through the thalamus, and the striatum receives input from multiple cortical regions including the SMA and prefrontal cortex (Bostan & Strick, 2018; Petter et al., 2016; Schwartz & Kotz, 2016). The anatomical integration of these structures naturally supports their functional relationship. For example, a recent MEG study found that the cerebellum, putamen, and thalamus show similarly timed beta-band power fluctuations in response to rhythmic stimuli (Andersen & Dalal, 2020) - beta-band power is an important oscillatory marker of beat processing (Fujioka et al., 2012; Fujioka et al., 2009; Iversen et al., 2009). Additionally, the

cerebellum and pre-SMA show functional connectivity during a rhythm improvisation task (de Manzano & Ullén, 2012). One model compellingly proposes that the cerebellum and striatum differ in their relative contribution to four stages of temporal processing: initiation, continuation, adjustment, and termination (Petter et al., 2016). This model posits that these two structures can perform similar timing functions despite having different neural architecture, a concept known as degeneracy (Petter et al., 2016). Our meta-analysis results maintain that, while the striatum and cerebellum do exhibit some attunement to specific aspects of musical rhythm processing (most apparent in the Complexity meta-analysis discussed in section 4.3) we should principally consider them within an integrated framework as this first analysis revealed activations in both subcortical structures.

The large bilateral temporal clusters in the Beat-based (rest baseline) contrast align with other literature and theoretical accounts about musical rhythm strongly engaging auditory-motor networks in the brain (Kotz et al., 2018; Patel & Iversen, 2014) and provide some support for the now well-established tenet that passive beat perception, even in the absence of movement, engages motor areas of the brain (Cannon & Patel, 2020; Chen et al., 2008a; Gordon et al., 2018; Kung et al., 2013; Patel & Iversen, 2014). Beat saliency modulates functional connectivity between auditory areas (e.g., planum temporale and posterior STG) and the dorsal premotor cortex (Chen et al., 2006, 2008b; Kung et al., 2013). Additionally, the left arcuate fasciculus, a white matter pathway connecting frontal and temporal regions, is associated with performance on a sensorimotor synchronization task (Blecher et al., 2016). While these large temporal clusters did not appear in our subsequent analysis with an auditory/motor control baseline, it is possible that with a larger sample size of studies, some temporal areas (albeit more restricted than in the rest baseline group) would emerge, even with basic auditory processing demands commensurate between conditions. Taken together, our Beat-based (rest baseline) analysis reveals a network for musical rhythm that includes subcortical (BG, cerebellum) and cortical (auditory, motor) regions. However, it is likely that the large temporal activations in this analysis are due, at least in part, to unmatched auditory and motor demands and thus include activations due to the comparison with the silent baseline (i.e., not specific to rhythm). We now turn to this topic specifically.

While our first analysis using contrasts with a rest baseline was designed to reveal a network for musical rhythm including all the relevant basic sensory and motor processes, it is worth now considering this choice of a baseline condition. In many cases, rest is a non-optimal baseline condition for several reasons (Binder et al., 2008; Price et al., 2005). In its most basic form, the baseline condition of rest fails to control activation that is not the activation of interest. Baseline conditions should ideally only differ from the experimental condition in one regard (i.e., the key experimental manipulation/question of interest), and rest conditions typically do not meet this

criterion. It has been suggested to use acoustically matched baseline conditions in studies of speech/language (Adank, 2012; Scott et al., 2000), and ideally these types of designs should also be the case for fMRI studies of music.

During short periods of rest in event-related fMRI designs, significant cognitive activity has been observed that can be even greater than during simple auditory perceptual task conditions (Binder et al., 1999; Stark & Squire, 2001). In the language domain, a thorough study investigating varying speech comprehension paradigms found large, bilateral activations in the superior temporal gyrus (STG) for “passive words vs. rest”. The authors concluded that this activity was primarily capturing “prelinguistic auditory stage[s] of processing,” rather than activations specific to word recognition (Binder et al., 2008). Instead, the authors determined that a task contrasting “semantic decision vs. tone decision” was a much more appropriate, robust, and consistent contrast for mapping speech comprehension. Though this specific study we have highlighted is in the language domain, similar considerations about baseline conditions should apply to studies of musical rhythm. Notably, a recent fMRI meta-analysis on rhythm and syntax excluded experiments with a rest baseline (Heard & Lee, 2020), and a meta-analysis on internally-based and externally-cued timing only included studies with a “visuo-perceptual/motor control condition to exclude all activations that were not directly connected to timing” (Teghil et al., 2019). Thus, while these studies accounted for rest conditions as a limitation by simply not including these contrasts in their analyses, our meta-analysis explicitly explored how this type of (popular) baseline condition impacted results. While rest baselines may not be the most ideal choice, they can still be informative about brain networks at some level, particularly when conducting novel/exploratory analyses or when there is a need to capture all the components of a network (e.g., the non-specific sensory, motor, or attentional aspects of perceiving or synchronizing to a musical beat). Our next two subsequent analyses have more carefully matched baseline conditions that allow us to narrow in on a more precise network for musical rhythm.

4.2 Beat-based rhythms activate the putamen bilaterally

Beat-based compared to non-beat-based rhythms activated the putamen bilaterally, the left rolandic operculum, and the left ventral precentral sulcus. Controlling for basic auditory processes and motor processes, this analysis revealed a more precise network for processing beat-based musical rhythms, above and beyond basic sensory and motor processes. All contrasts in this analysis had an active auditory control baseline, and production contrasts also matched motor activity across conditions.

As discussed previously, the striatum is a canonical brain region for processing beat-based musical rhythms and for perception of predictable sensory cues (Cannon & Patel, 2020; Grahn & Rowe, 2009; Grahn & Brett, 2007; Kotz et al., 2009). Past work

has shown that the striatum is most active for internal generation of the beat and beat prediction/continuation, where the beat percept has already been established, compared to when a beat must be found or adjusted (e.g., when a temporal sequence gets faster or slower) (Chapin et al., 2010; Grahn & Rowe, 2009; Grahn & Rowe, 2013). Additionally, lesions to the right striatum (putamen and caudate) are significantly related to rhythm amusia following stroke, providing more causal evidence that the basal ganglia are integral structures for musical rhythm (Sihvonen et al., 2016).

The basal ganglia have been conceptualized as internal pacemakers. Patients with focal lesions to the basal ganglia are a) more variable in tapping in a spontaneous motor tapping task compared to their neurotypical counterparts (Schwartz et al., 2011) and b) indifferent to manipulations of temporal regularity (beat vs non-beat based stimulus categorization), as measured by EEG (Schwartz et al., 2015). Individuals with Parkinson's Disease (PD), a neurodegenerative disease caused by the progressive loss of dopaminergic neurons in the substantia nigra of the basal ganglia, exhibit difficulties in discriminating beat-based rhythms, but not rhythms with a less clear beat structure (Grahn & Brett, 2009). Patients with PD performed just as well as neurotypical controls in discriminating metrically complex rhythms (i.e., the more difficult condition), corroborating the basal ganglia's role in processing rhythms with a strong and clear beat structure. The basal ganglia are also not general "music" regions, as they were not activated in an fMRI meta-analysis of general music listening (Gordon et al., 2018). The bilateral putamen thus seems to be an important region for beat-based musical rhythms.

Of note, we did not observe a (hypothesized) SMA cluster in this analysis, likely due to the small number of contrasts. However, the SMA *did* emerge as a significant cluster in our other two analyses.

In addition to the bilateral putamen, our beat-based vs. non-beat-based meta-analysis revealed activation of the left rolandic operculum and left ventral precentral sulcus. The rolandic operculum has been identified in complementary fMRI studies of musical rhythm, although in the right hemisphere (Alluri et al., 2012; Toivainen et al., 2014). The precentral region is integral for control of movement and previous studies have reported activations in the adjacent gyrus for many aspects of music and language processing (for a sample of relevant meta-analyses, see: Adank, 2012; Gordon et al., 2018; Heard & Lee, 2020; LaCroix et al., 2015; Tagarelli et al., 2019). It is also possible that the precentral activity we observe here, and also in the Complexity analysis, may relate to the "multiple demand" system (Fedorenko et al., 2013). The putative roles of the rolandic operculum and precentral region could align with the sensorimotor integration demands involved in listening to and producing musical rhythms.

4.3 Rhythmic complexity activates the SMA, cerebellum, regions in the inferior parietal lobes

We found that more compared to less complex beat-based rhythms (e.g., syncopated vs. isochronous rhythms) activated the SMA bilaterally (SMA-proper and pre-SMA regions), large clusters in the cerebellum bilaterally, the left precentral gyrus and intraparietal sulcus, and areas in the right parietal and temporal lobes. We also found two areas of activation for the reverse contrast (i.e., less vs. more complex beat-based rhythms) in the left STG and left putamen. This analysis not only controls for simple auditory processing and motor activity, but also controls for simpler beat-based processes in the baseline conditions (i.e., what is “left over” is the effect of rhythmic complexity).

The dissociation between putamen and cerebellum activation in our Complexity results do suggest at least some degree of specialized timing functions between the two structures (the former canonically associated with beat-based timing and the latter with duration-based timing). As discussed previously (section 4.1), however, these two timing networks are highly integrated anatomically and functionally. The cerebellar activation in the Complexity analysis could indicate that the cerebellum may be important for tracking/processing rhythms with a less predictable (i.e., more syncopated) beat structure, while the putamen (the deactivation in this analysis, less vs. more complex beat-based rhythms) is engaged for processing rhythms with a stronger, more “on-beat” structure (as discussed in sections 4.1 & 4.2). This account aligns with our original hypothesis about greater cerebellum compared to putamen activation for this analysis. Evidence from other methodologies supports these findings. Gray matter volume of the cerebellum has been linked to discrimination tasks for more complex rhythms (Paquette et al., 2017) and individuals with focal lesions in the cerebellum exhibit reduced amplitude in tracking the beat frequency of rhythmic sequences only when they are presented at fast tempi (Nozaradan et al., 2017). However, individuals with focal basal ganglia lesions (in that same study) exhibited more variable responses for complex rhythms (which may require greater internal generation of the beat). These results suggest some specialization in function between the basal ganglia and cerebellum, albeit within an integrated framework for musical rhythm processing, which aligns with our meta-analysis findings.

We also observed both bilateral SMA-proper and pre-SMA activation in this analysis, as in our Beat-based (rest baseline) analysis. These two structures have distinct anatomical and functional differences despite both receiving cerebellar and basal ganglia input (with basal ganglia input predominating) (Akkal et al., 2007). The SMA-proper has dense connections with the primary motor cortex (M1), while the pre-SMA has dense connections with prefrontal areas (and is not densely connected with M1). Functionally, the SMA-proper is involved in sensorimotor and sequential temporal processing, while the pre-SMA is more associated with sensory and non-sequential processing (Schwartz et al., 2012). Regarding musical rhythm specifically, the SMA region has been labelled as a “motor planning region” activated not only during beat

production but also during beat perception when no overt movements are required (Patel & Iversen, 2014). While our results do not allow us to make any conclusions about differences in SMA-proper/pre-SMA involvement in musical rhythm, both components close a key cortico-subcortical loop for rhythm processing. The robust nature of this analysis (baseline conditions controlling for motor, auditory, simple beat processing demands) positions the SMA-proper and pre-SMA as important structures for processing complex rhythms.

Our clusters of activation in the bilateral inferior parietal lobes complement a recent study finding similar activations for processing of “medium complexity” musical rhythms (Matthews et al., 2020). The parietal cortex serves as a sensorimotor integration zone (Hickok & Poeppel, 2007) linking auditory and premotor regions along the dorsal auditory pathway, an integral component of the ASAP hypothesis for musical beat perception (Patel & Iversen, 2014). The ASAP (action simulation for auditory prediction) hypothesis posits that motor planning regions provide top-down information to auditory regions to predict the timing of upcoming beats, relying on connections between these regions via the parietal cortex. Parietal regions are involved in temporal expectations and in orienting attention in time for perception and production demands (Bueti & Walsh, 2009; Coull et al., 2011; Coull & Nobre, 1998; Sakai et al., 1999). The left inferior parietal cortex in particular exhibits increased functional connectivity with the SMA, cerebellum, and sensory areas during a meter perception task (Bolger et al., 2012), indicating its involvement in a cortico-subcortical network for rhythm. Evidence from other methodologies including MEG and TMS, respectively, suggests that rhythmic deviations activate parietal and superior temporal regions (Lappe et al., 2016) and down-regulation of the left parietal cortex interferes with the ability to detect phase shifts of the beat (Ross et al., 2018). However, parietal regions, including the intraparietal sulcus specifically, are a core component of the multiple demand network and are activated for various kinds of hard vs. easy tasks (e.g., mathematical or spatial working memory paradigms) (Fedorenko et al., 2013). While task difficulty in our Complexity meta-analysis was not manipulated *per se* (rather, we categorized *stimuli* based on complexity), it could be the case that complex rhythms are more difficult to process and thus activate parietal multiple demand areas that are more related to task difficulty rather than rhythm specifically. Thus, a “multiple demand” explanation could in part account for the inferior parietal activations we observe for more vs. less complex beat-based rhythms. Taken together, these various proposed roles of the inferior parietal lobe position it as a potentially important structure for processing complex musical rhythms.

Overall, the network of brain regions involved in processing complex rhythms is more extensive than both the a) deactivations found for this same analysis and b) the Beat-based (auditory control baseline) analysis. Our results align well with findings from Jantzen et al., 2004 who found a much broader network of activity for syncopated

tapping compared to synchronization (i.e., isochronous rhythmic pacing) (Jantzen et al., 2004), which may be considered analogous to our more vs. less complex stimulus categorization. It is important to note that this more extensive network could also be due to the fact that there were more contrasts in this analysis compared to the other two analyses (i.e., Complexity analysis included 16 contrasts, while Beat-based audio-motor control included only 8).

4.4 Musical experience does not substantially influence a brain network for rhythmic complexity

We found that the meta-analysis with musical experience as a covariate did not substantially modulate the main Complexity network results. This analysis should be taken as exploratory, as the number of studies in each group was small and likely underpowered (6 with musicians, 7 with non-musicians). Processing more compared to less complex beat-based rhythms seems to activate, overall, similar brain regions in musicians and non-musicians, with some slight differences (as the two maps, analyses with and without the covariate, did not show complete overlap).

A group of studies included within our meta-analysis reported secondary analyses comparing neural processing of rhythm in musicians and non-musicians. One study found no interaction between group (musicians and non-musicians) and rhythm type (Grahn & Brett, 2007), paralleling a more recent fMRI study that explored rhythmic complexity and group relationships (Matthews et al., 2020).

In contrast, other work has found that professional musicians compared to non-musicians exhibit greater activation in left hemisphere regions including the SMG, MFG, IFG, and MTG when listening to musical rhythms (Herdener et al., 2014; Limb et al., 2006) and non-musicians exhibit greater activation in the bilateral STG, right parietal cortex, and other regions (Limb et al., 2006). Musicians and non-musicians have been shown to exhibit differences in coupling (i.e., functional connectivity) between cortical auditory and motor regions (Chen et al., 2008b). More generally, a consensus has yet to be reached on the relationship between musical experience and neural correlates of rhythm or even processing other musical features such as melody. Beat perception and synchronization occur spontaneously in most people, regardless of musical experience, and this behavioral ability may be paralleled by activation of roughly similar brain networks across individuals.

One potentially important factor influencing the above set of findings is the varying ways in which “musician” is defined in the literature. Even within the small subset of fMRI studies in this meta-analysis, the definition of musician varied widely from individuals who a) began musical training between 3 and 10 years old and were pursuing (or had already obtained) a degree in music (Chen et al., 2008b), b) practiced their instrument for at least one hour per day and were in professional/semi-professional music ensembles (Thaut et al., 2008), and c) were trained musicians with a range of 8-

18 years of training (Kung et al., 2013) (Table S4). Given the wide range of musical experience in the population, future studies might approach the challenge of characterizing musicianship by using continuous measures of musical engagement (e.g., Gold MSI, Müllensiefen et al., 2014) to avoid artificially placing individuals in dichotomous categories. It would also be informative to see if these results on a rhythmic complexity x musical experience relationship hold in a larger sample.

4.5 Laterality: what is the evidence for bilateral processing of rhythm?

We found that musical rhythm is largely represented bilaterally in the brain. The Beat-based (audio-motor control baseline) analysis revealed activation of the bilateral putamen and the Beat-based (rest baseline) analysis revealed a symmetrical brain network encompassing the superior temporal cortices, SMA, basal ganglia, and cerebellum. The Complexity analysis also revealed bilateral clusters of activation in the SMA, cerebellum, and inferior parietal cortices (with some right hemisphere bias here). These bilaterality findings a) parallel another recent fMRI meta-analysis on rhythm (Heard & Lee, 2020) and b) align with brain networks for music listening in general, which show bilateral, widespread activations in neurotypical individuals (Alluri et al., 2012; Gordon et al., 2018).

Cognitive neuropsychology and lesion-deficit studies provide another line of evidence with which to consider the laterality of musical rhythm. Double dissociation studies have found that individuals with left hemisphere (LH) lesions are impaired on rhythm tasks, while individuals with right hemisphere (RH) lesions are impaired on pitch tasks (Alcock et al., 2000; Murayama et al., 2004; Peretz, 1990). Other studies report rhythm or meter deficits in *both* LH and RH lesion patients compared to controls (Ayotte et al., 2000; Liégeois-Chauvel et al., 1998; Peretz, 1990; Schuppert et al., 2000), indicating no strong evidence for a rhythm/meter laterality effect. Though findings are mixed within and across studies, potentially due to lesion etiology, task demands, and other factors, evidence from lesion studies seems to indicate that both hemispheres can support various aspects of rhythm and meter processing.

In general, the laterality of musical rhythm processing is significantly less well-studied than other cognitive domains such as language. The aphasiology literature overwhelmingly supports the left hemisphere-lateralization of language – aphasia, an acquired communication disorder resulting from damage to regions of the brain that support language, almost always results from injury to the left hemisphere, and very rarely from injury to the right hemisphere (Berthier, 2005; Pedersen et al., 1995). However, it is important to consider that claims about the laterality of language may be influenced by methodology. Functional imaging studies of language tend to highlight bilaterality more so than lesion studies (Scott et al., 2000) and certain aspects of language processing are not strictly left-lateralized (Huth et al., 2016). Thus, while we observe a mostly bilateral network for rhythm processing in our fMRI meta-analysis, it is

possible that lesion-deficit studies characterizing rhythm abilities in large participant cohorts would yield a more lateralized network. More studies that integrate functional neuroimaging with lesion-deficit approaches, as has been done in memory and language (Oedekoven et al., 2019; Cathy J. Price & Friston, 2002; Schneck et al., 2021; Streese & Tranel, 2021) will advance our understanding of the laterality of musical rhythm and its relationship with speech/language (Kotz et al., 2018).

4.6 A heterogeneous literature: Recommendations for future fMRI studies of musical rhythm

Our descriptive characterization of the studies included in the meta-analysis highlights vast differences in the type and description of stimuli and tasks. Despite these design differences, however, results converge across studies to reveal brain networks for musical rhythm that align with previous literature on timing frameworks (Merchant, 2014; Petter et al., 2016; Schwartz & Kotz, 2013; Teki et al., 2011, 2012). The interesting heterogeneity brought to light by our meta-analysis provides new directions for the design and implementation of future fMRI studies of musical rhythm.

First, we recommend that authors both make examples of their auditory stimuli publicly available and clearly illustrate the musical and temporal structure of the stimuli. Fewer than half of the studies included in our meta-analysis made audio clips of their stimuli available, either as supplemental information published with the paper or as proprietary content on a lab/academic website. Often, studies presented schematics of their rhythms (for example, figures of dots and dashes or tables of a series of durations) that could be difficult to parse and were subject to flexible interpretation. Sometimes studies represented their rhythm stimuli through musical notation. When studies do not represent their stimuli in musical notation, it makes comparisons of stimuli across studies inherently difficult when descriptions and terms varied (e.g., polyrhythmic, syncopated, ambiguous, etc.). We thus suggest that the stimuli material are represented in multiple formats and modalities (sound files, musical notation, and additional intuitive visualizations) and that authors make examples of their stimuli used in studies of musical rhythm publicly available on free and accessible open-source platforms such as Open Science Framework (www.osf.io) (McKiernan et al., 2016). Even for studies that have used stimuli from prior work (e.g., Araneda et al., 2017), using beat and non-beat sequences from Grahn & Rowe, 2009), publishing a select few stimulus examples would be helpful to the research community. Ideally, any researcher publishing on music should host their auditory stimuli on an open-source platform. Additionally, we might also recommend, due to our discussion of the heterogeneous literature above (section 4.6), that authors consider using standardized terms to describe stimuli of varying levels of rhythmic complexity, such as the terms we present in this paper as one option (see Figure 2).

Second, future fMRI studies of musical rhythm must carefully consider the choice of a baseline condition. Our results show that the type of baseline condition is key to pinpointing a more specific and representative set of brain regions for musical rhythm. Depending on their exact research question, researchers could employ various baseline conditions that control basic auditory, motor, attentional, or other cognitive processes (e.g., non-beat-based rhythms) rather than a baseline of rest/silence (see Section 4.2). Additionally, contrasts and the conditions going into such contrasts should be informed by the literature (see Tables 3 and 4) such that specific findings can be replicated in the future.

Third, we observed that most studies did not use sparse sampling scanning paradigms for studies of auditory musical rhythms. As we did not conduct a specific meta-regression or covariate SDM meta-analysis with this variable, we cannot conclude how this design choice specifically influences a brain network for musical rhythm, nor can we offer recommendations for the use of sparse sampling fMRI designs based on our data. However, sparse sampling has several advantages over continuous imaging for studies of auditory processing (“no technical advance has had a greater impact on the field [of auditory cognitive neuroscience] than *sparse-sampling*,” Perrachione & Ghosh, 2013). We think it is especially important for studies of auditory *rhythms* to consider using this technique. Sparse sampling ensures that activation is not the result of an interaction between the stimulus and scanner noise (Hall et al., 1999). Particularly in the case of rhythm, the concurrent sounds of the regular rhythmicity of the scanner and the actual rhythm stimuli could very likely interfere with one another, potentially leading to “complexity confounds” and/or activations related to effortful listening/increased attentional demands. However, sparse sampling may not be suitable for all designs (e.g., studies of rhythm working memory that may use long audio clips that cannot be interrupted by volume acquisition). We also echo the considerations outlined by Adank, 2012, namely that decisions about sparse sampling and continuous designs are a trade-off between experiment duration and BOLD signal quality (Adank, 2012).

Last, most studies included in our meta-analysis were conducted in small samples (all but two studies had $N < 30$ participants). These task-based fMRI studies necessitate replication and extension in larger participant cohorts (Turner et al., 2018) which may be made easier through collaborative efforts and international consortia.

4.7 Limitations of our work

There are several limitations regarding our quantitative fMRI meta-analyses. First, our sample size of studies for each SDM meta-analysis was smaller than the recommended 17 studies for coordinate-based fMRI meta-analyses (Müller et al., 2018). We had to make a trade-off between including contrasts even more heterogeneous than those already included in our meta-analyses and most effectively

evaluating our construct of interest (Beat-based or Complexity). The small number of fMRI studies on musical rhythm at the outset made these decisions even more difficult.

Second, and related to the issue of sample size, we would have been underpowered to conduct sub-meta-analyses parsing perception and production contrasts; thus, contrasts of perception and production tasks were pooled. We acknowledge that the issue of perception and production is integral to understanding rhythm in the brain, and hope that publication of additional fMRI studies on musical rhythm in the future will make such meta-analyses possible.

Third, we included contrasts that used masks (e.g., Araneda et al., 2017) or conjunctions (e.g., Chen et al., 2008a). Analyses that use masks or conjunctions are debatable, yet acceptable, for inclusion in meta-analyses (Müller et al., 2018). SDM also recommends only including studies that report both activations and deactivations. We included studies (most of which were in the Beat-based rest baseline category) that did not report deactivations. If we had excluded studies that used masks/conjunctions and did not report deactivations, we would not have had enough studies to develop meaningful brain maps, when we were already limited by sample size based on the extant literature (the Beat-based control baseline analysis only had 8 contrasts). Müller et al., 2018 recommend that researchers are transparent in reporting these choices. In Tables 3 and 4, we report the use of masks, conjunctions analyses, and reported/significant deactivations and believe we have been transparent in reporting the rationale for each of our decisions.

Fourth, we chose the “best-fitting” contrast per paper for each meta-analysis. This is preferred over pooling coordinates across all relevant contrasts, especially given that SDM aims to recreate original subject activation maps (Albajes-Eizagirre et al., 2019). We accept that our choices about the “best-fitting” contrast may be different than what other researchers may have deemed the “best-fitting” contrast.

A last limitation of this meta-analysis and systematic review is the unavoidable subjective nature in which we categorized some of the fMRI contrasts within the Beat-based or Complexity categories. These categorization decisions were difficult. We sometimes had to veer from the original research goals/constructs that the authors of individual papers purported, to find some common ground across the heterogeneous studies. For example, Grahn & Brett, 2007 consider “metric complex” and “non-metric” stimuli as “non-beat-inducing rhythms”, while Bengtsson et al., 2009 considered their “metric” rhythms (which most likely would have fallen under the “metric complex” category in Grahn & Brett, 2007) as low complexity rhythms and “non-metric” rhythms as more complex rhythms. In our meta-analysis, we chose to consider “metric complex” and “non-metric” rhythms as beat-based rhythms and recognize that there is no ideal solution for dimensionality reduction of the various stimulus terms/constructs in this literature. The stimulus from Danielsen et al., 2014 presented another such tricky decision: their stimulus was a repetitive drum groove with drum breaks inserted at

uneven intervals. We considered these drum breaks, or transitions, as more complex than the surrounding continuous groove music, though the authors note “there was no increase in syntactic complexity, measured as [an] increase in syncopation... in the breaks as compared to the continuous parts” (Danielsen et al., 2014). With our macroscopic categories of Beat-based and Complexity, we would have needed to exclude the contrast from Danielsen et al., 2014 based on their description, and this would have been the case for many contrasts across studies.

Importantly, our Beat-based and Complexity categories should be considered on a continuum, rather than as clearly delineated black-and-white categories. It is quite possible we would have seen deactivations in the Beat-based auditory control baseline meta-analysis (perhaps in the cerebellum) if we had considered some of the contrasts manipulating “more vs. less complex rhythms” as “non-beat-based vs. beat-based” rhythms. Additionally, rhythmic complexity in ecological real-world music may be modeled as an inverted-U shape (Matthews et al., 2019), and we were not able to capture this nonlinearity in our analyses.

Even within studies, the terms “beat” and “nonbeat” exist on a flexible scale, as evidenced by behavioral ratings for “nonbeat” stimuli (Grahn & Rowe, 2009). In the behavioral component of this study, participants provided a range of ratings on a scale from “no beat” to “definitely has a beat” for nonbeat stimuli, indicating that some participants may have felt a sense of a musical beat in stimuli designed not to have one. Variations in ratings both within and across studies may relate to task instructions. It could be the case that task instructions may influence participants to enter a particular perceptual mode where they are more or less likely to perceive/attend to a musical beat, regardless of the stimulus. For example, a metric complex rhythm may be perceived differently (and thus activate a potentially different set of brain regions) depending upon whether participants are told to either a) pay attention to if a rhythm has a beat or not or b) passively listen to rhythms while completing a distractor task. Our meta-analysis did not address this issue, which would not be possible to address thoroughly without methods such as participant self-reports or control conditions bearing on task instruction manipulations.

As with any meta-analysis, our results are only as good as the studies available in the extant literature. Studies reporting null or unexpected results often are not published (though this is rapidly changing, see: Franco et al., 2014; “The Importance of No Evidence,” 2019). Despite this “file-drawer” problem, meta-analyses that include “non-headline” results, as we have done, have been shown to diminish publication bias and validate meta-analytic results (Mathur & VanderWeele, 2021).

4.8 Summary and conclusions

In summary, our meta-analysis findings revealed that the extant literature on musical rhythm processing converges on a largely bilateral cortico-subcortical network

of brain regions. First, the Beat-based rhythm vs. rest comparison revealed a network for musical rhythm tasks that captured broad cortical auditory-motor networks in addition to subcortical nodes for rhythm – the basal ganglia and cerebellum. Given this broad network of auditory and motor areas, we conducted two further analyses to narrow in on a more representative set of brain regions for processing beat-based musical rhythms over and above basic auditory and motor processing. The Beat-based (audio-motor control baseline) contrast demonstrates that musical rhythms with a clear beat versus non-beat-based temporal structure activated the putamen bilaterally in addition to the left ventral precentral sulcus and rolandic operculum. Finally, the Complexity meta-analysis demonstrated a brain network for rhythmically complex musical sequences (i.e., syncopated rhythms) compared to simple metrical beat-based stimuli. The findings from this meta-analysis were discussed in the context of complementary evidence (behavioral, neurophysiological, and neuropathological findings), together highlighting the neural circuitry underlying musical beat perception and production. This study creates a foundation for other biological investigations into the human ability to perceive and synchronize to a musical beat (i.e., future work with clinical, theoretical, genetic, behavior, other neuroimaging methods).

4.9 Future directions

In addition to our suggestions on the design and implementation of future fMRI studies of musical rhythm, our meta-analysis provides a foundation for understanding how the brain basis of rhythm relates to other cognitive functions, including language. Behavioral and neural evidence indicate robust relationships between musical rhythm and language skills in neurotypical adults and children (Chern et al., 2018; Gordon et al., 2015; Magne et al., 2016; Ozernov-Palchik & Patel, 2018; Swaminathan & Schellenberg, 2019; Tierney et al., 2021; Woodruff Carr et al., 2014) and individuals with speech and language impairments, including dyslexia (Canette et al., 2020; Fiveash et al., 2020; Huss et al., 2011) and developmental language disorder (Corriveau & Goswami, 2009; Ladányi et al., 2021; Przybylski et al., 2013). Additionally, evidence from second language learners suggests that mastering two languages with different rhythmic properties enhances musical rhythm perception, indicating a domain-general role of rhythm (Roncaglia-Denissen et al., 2013). Our meta-analysis revealed some regions that overlap with potential language regions, in particular the ventral precentral cortex which is implicated in phonological encoding (Price et al., 1997). However, the brain networks for rhythm and language by no means largely overlap (and recent evidence suggests music processing does not rely on language regions (Chen et al., 2021)). Future neuroimaging and lesion symptom-mapping studies directly comparing musical rhythm and language are needed to clarify their relative overlap/dissociation in the brain. In addition to language, social cognition/communication is linked with musical rhythm in behavioral studies (Endedijk et

al., 2015; Kirschner & Tomasello, 2009; Lense & Dykens, 2016; Trainor & Cirelli, 2015), and “social brain” networks show overlap with timing networks (Schirmer et al., 2016). Our meta-analysis can provide a starting place for advancing our understanding of how the brain bases of rhythm overlap with various cognitive domains.

Acknowledgments

The research reported in this publication was supported by the Office of the Director of the National Institute of Health (NIH) under Award No. DP2HD098859 (to RLG), National Institute on Deafness and Other Communication Disorders award No. 1F31DC020112-01 (to AK), and a National Science Foundation Graduate Research Fellowship Program award (to AK). The use of REDCap was made possible by Grant No. UL1 TR000445 from the National Center for Advancing Translational Sciences (NCATS)/NIH. We also thank the Department of Otolaryngology – Head & Neck Surgery at Vanderbilt University Medical Center for their support. The content is solely the responsibility of the authors and does not necessarily reflect the official views of the funders.

We thank Dr. Joaquim Radua for methods feedback. The authors report no conflicts of interest.

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Highlights

- Musical rhythm engages a bilateral cortico-subcortical network involving auditory and motor regions
- Beat-based musical rhythms activate the bilateral putamen
- The bilateral SMA, cerebellum, and other regions are modulated by rhythmic complexity
- Findings converge with other methodologies and align with existing theoretical frameworks