Predictive and Dynamic Mechanisms of Rhythm and Groove

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1. Foreword

Music possesses the peculiar ability to move us emotionally and physically. But why don't all sounds evoke these profound effects? After all, few people enjoy static noise or start nodding their head to the rhythm of a whirring microwave. While musical experiences are vast and varied, music cognition researchers believe that part of the answer to this question lies in our ability to detect and apply structure, and thus meaning, to rhythms. However, while some perceived structure may be necessary, it is not sufficient; otherwise, we'd dance along to all sorts of periodic sounds like car motors, so what makes musical rhythms special? This has generated decades of investigations into how humans find and interact with the beats in music, a trait that appears quite rarely in the animal kingdom.

This work by no means seeks to definitively answer this question in its entirety, but it does aim to shed more light upon the topic and continue the march of progress in rhythm perception and synchronization research. Specifically, it attempts to do this by measuring the pleasurable urge to move to music and the beat perception abilities necessary for producing it. The first two studies do this by manipulating rhythmic complexity while recording changes in pupil size to assess cognitive effort, which is theorized to be necessary for reducing prediction error surrounding the beat. The second study also recorded the variability and intensity of participants' foot taps as a measure of how precisely and confidently they could synchronize to the musical beat, respectively. The third study explored how beat perception ability (which impacted the results of the first two studies) is shaped by experience and expertise. Namely, it examined whether inactive musicians retain the heightened beat perception abilities of their regularly practicing counterparts.

This dissertation first lays out the theoretical background necessary for understanding the three studies, outlining key concepts and definitions before moving into their explanatory frameworks. Afterwards, the motivations for conducting the current work are provided with each study's rationale and results summarized in brief. Subsequently, the outcomes and implications of the entire dissertation are critically assessed and its overall contribution to the broader scientific community are discussed. Finally, the papers comprising this work are furnished in full for readers to make their own judgments. With that, let's keep things groovin' forward.

2. Abstract

This dissertation investigates the predictive and dynamic mechanisms underlying rhythm processing and groove. It accomplishes this by measuring the pleasurable urge to move to music (groove) and the beat perception abilities necessary for producing it. The first two studies do this by manipulating rhythmic complexity while recording changes in pupil size to assess cognitive effort, which is theorized to be necessary for reducing prediction error surrounding the beat. The second study additionally recorded the variability and intensity of participants' foot taps as a measure of how precisely and confidently they could synchronize to the musical beat, respectively, to examine their relationship to groove. The third study explored how beat perception ability (which impacted the results of the first two studies) is shaped by experience and expertise. Namely, it examined whether inactive musicians retain the heightened beat perception abilities of their regularly practicing counterparts. In this work, I demonstrate that: 1) the pupil drift rate indexes groove ratings, 2) pickups elicit greater pupil dilations while 3) syncopations elicit greater groove ratings, 4) synchronizing to the beat increases groove ratings and pupil dilations, 5) tapping becomes softer and less precise with increasing complexity, 6) the inverted U-shaped curve between rhythmic complexity and groove is stronger for real music than synthetic drumbeats, and 7) greater beat perception is associated with more musical training, more precise tapping, and more prominent inverted U-shaped curves. In summary, this dissertation contributes a number of novel findings, extensions, and replications to the rich literature on beat perception and groove.

3. List of Papers

Study 1

Spiech, C., Sioros, G., Endestad, T., Danielsen, A., & Laeng, B. (2022). Pupil drift rate indexes groove ratings. *Scientific Reports*, *12*(1), 1-13.

Study 2

Spiech, C., Hope, M., Schmidt Câmara, G., Sioros, G., Endestad, T., Laeng, B., & Danielsen, A. (2022). Sensorimotor Synchronization Increases Groove.
https://doi.org/10.5281/zenodo.6908099

Study 3

Spiech, C., Endestad, T., Laeng, B., Danielsen, A., & Haghish, E.F. (2022). Practice Makes Perfect: Beat Perception is Enhanced by Musical Training Not Active Music Playing. Submitted.

4. Theoretical Background

3.1 Groove

Groove is a musical concept that has fascinated researchers from a variety of disciplines ranging from musicology and phenomenology to psychology and neuroscience more recently. It should come as no surprise then that ‘groove’ as such has been defined in a number of related, but different, ways. Câmara and Danielsen (2018) have proposed three different understandings: 1) groove as a type of rhythmic pattern and performance style, primarily used by musicologists; 2) groove as the pleasurable urge to move, most commonly adopted by music psychologists and neuroscientists; and 3) groove as a pleasing, effortless, and timeless state of playing music described mostly by phenomenologists. For the sake of this dissertation, only the second understanding of groove as the pleasurable urge to move to music will be used.

Madison first broadly operationalized groove as “wanting to move some part of the body in relation to some aspect of the sound pattern” (2006) and Janata, Tomic, and Haberman expanded this definition to include its connection to pleasure in a series of perceptual and tapping studies (2012). Both studies stress the importance of rhythmic features like having a clear or strong beat on which to base one’s movements, which has been substantiated by a large number of subsequent groove studies (Burger et al., 2013; Cirelli & Trehub, 2019; Madison et al., 2011; Madison & Sioros, 2014; Stupacher, Hove, et al., 2016; Stupacher, 2019). This has led many groove researchers to manipulate rhythmic features to investigate how they relate to groove. These features include syncopation (Matthews et al., 2022; Sioros et al., 2014; Skaansar et al., 2019; Witek et al., 2014, 2017), pickups (Sioros et al., 2022), microtiming (Davies et al., 2013; Frühauf et al., 2013; Senn et al., 2016; Skaansar et al., 2019), and pulse clarity (Gonzalez-Sanchez et al., 2018; Stupacher, Hove, et al., 2016; Stupacher, Wrede, et al., 2022). What seems to connect all of these different rhythmic features is that they all impact the predictability, certainty, or complexity of the rhythm, where groove tends to exhibit an inverted U-shaped relationship (Matthews et al., 2019, 2022; Sioros et al., 2014; Stupacher, Wrede, et al., 2022; Witek et al., 2014). Before discussing why groove exhibits this pattern, it is important to elaborate how these different rhythmic features relate to rhythmic complexity and expectations.

3.2 Rhythmic Complexity

As already noted, many different rhythmic features associated with groove seem to relate to complexity and indeed many of these studies discuss rhythmic complexity as interchangeable with the feature being manipulated. According to Pressing, complexity is multifaceted and can be defined and quantified in a number of (not mutually exclusive) ways (Pressing, 1999) so it isn't surprising that its application to rhythm would be composed of multiple auditory features. Central themes that emerge time and again deal with structure and order that incur some sort of cognitive cost either in terms of perceptual processing or behavioral production, with greater complexity incurring greater costs (Pressing, 1999). This can, for example, be the "cognitive costs incurred in maintaining the metrical framework" (Pressing, 1999) which leads to the first, and perhaps most popular way of quantifying rhythmic complexity, syncopation.

To understand syncopation, one must first have a basic grasp of musical meter. At its simplest, meter is the hierarchical organization of strongly and weakly accented notes (Lerdahl & Jackendoff, 1983). Key to this is the idea that the meter is an internal structuring of expectations about when musical notes will occur. In Justin London's words, "meter involves *our initial perception as well as subsequent anticipation of a series of beats* that we abstract from the rhythmic surface of the music as it unfolds in time" (emphasis mine) (London, 2012). So in light of this, syncopations have been defined as "rhythmic events which violate metric expectations…when onsets occur on metrically weak accents and rests or tied notes occur on metrically strong accents" (Vuust & Witek, 2014). Thus, syncopations derive their rhythmic complexity directly from their more unexpected nature, at least until the point that they violate the meter so much that the listener can no longer perceive it (the upper end of rhythmic complexity). However, some researchers have claimed that syncopations can, perhaps paradoxically, *reinforce* the meter through their violations by making listeners "even more aware of the 'missing' beat" (Câmara & Danielsen, 2018). This leads to the next rhythmic feature: pickups.

Pickups, like syncopations, occur at metrically weak timepoints but differ in that the subsequent strong beat is present rather than omitted (Kennedy & Kennedy, 2013; Sioros et al., 2018, 2022). This has the effect of directly cueing that subsequent strong beat, perhaps even making it sound illusorily louder in the process (Irwin & Zwislocki, 1971; Scharf, 1978). So in contrast to syncopations which can subvert metric expectations or indirectly draw attention to strong metric locations, pickups fulfill metric expectations. This may potentially reduce the overall amount of rhythmic complexity by directly reinforcing strong beats.

The next rhythmic feature, microtiming, also plays with our metric expectations but in a more subtle way. Rather than shifting a musical event all the way to the next strong or weak metric position, microtiming deviations are typically only shifted by tens of milliseconds where they may not even be consciously noticed by the untrained ear (Câmara & Danielsen, 2018; Senn et al., 2016). This can make a rhythm more complex by introducing variability to metric locations, especially if the goal is to precisely synchronize one's movements to those locations. This is perhaps why perceptual experiments with microtiming tend to report decreases in groove (Davies et al., 2013; Frühauf et al., 2013; Skaansar et al., 2019), although this may differ depending on the musical style (like jazz where microtiming is more expected), degree of microtiming, and listeners' musical experience (Davies et al., 2013; Senn et al., 2016).

If microtiming muddies one's perception of a steady rhythmic structure, pulse clarity can be thought of as the opposite, instead reflecting "how easily…listeners can perceive the underlying rhythmic or metrical pulsation" (Lartillot, Eerola, et al., 2008). As one might guess from the name, high pulse clarity implies a predictable rhythmic structure (and thus, less rhythmic complexity) (Alluri et al., 2012; Stupacher, Wrede, et al., 2022; Toussaint & Trochidis, 2018). Unsurprisingly and most related to groove, this has been shown to facilitate more synchronous movements (Kantan et al., 2021; Stupacher, Hove, et al., 2016) and more movement overall (Burger et al., 2013; Cirelli & Trehub, 2019; Gonzalez-Sanchez et al., 2018). Computationally, pulse clarity can be estimated with a single line of code in the MIRToolbox in Matlab (Lartillot, Toiviainen, et al., 2008). This algorithm works by first detecting the onsets of different musical events in the audio file. Depending on the settings, pulse clarity can then be directly computed from this information (e.g., the *'ExtremEnvelope'* estimates the total amplitude variability of the onset detection curve). However, more commonly researchers use one of the settings based on the autocorrelation of this curve which measures the periodicity of the detected rhythms (i.e., how repetitive or regular the detected musical events are). One of these settings, the *'EntropyAutocor'* heuristic, calculates the entropy of the autocorrelation curve which has been used to quantify uncertainty (or predictability) in a wide variety of domains (Shannon, 1948).

In information theory, Shannon entropy is a mathematical estimation of uncertainty (Shannon, 1948). Put simply, entropy measures how surprising an event is based on the probabilities of all possible outcomes for that event given some sequence of events. When flipping a coin, for example, a fair coin with equal odds of heads or tails would have greater entropy than a biased coin that has a greater probability for heads; when flipping the fair coin, the outcome is more random (or uncertain). Because music is structured sound, entropy can be used to calculate just how structured it is. This has therefore made entropy a useful tool for quantifying the predictability or complexity of many different aspects of music (Daikoku, 2018; De Fleurian et al., 2014; de Fleurian et al., 2017; Eerola et al., 2006; Gold et al., 2019; Hansen & Pearce, 2014; Lumaca et al., 2019; Margulis & Beatty, 2008; Milne & Herff, 2020; Quiroga-Martinez et al., 2019; Quiroga‐Martinez et al., 2020; Quiroga-Martinez et al., 2021; Temperley & others, 2007). Applied to rhythm, a completely uniform, isochronous sequence of tones would have low entropy while a sequence of randomly occurring tones would have high entropy. Under this quantification then, greater entropy is associated with higher rhythmic complexity.

Regardless of how it is quantified, increased rhythmic complexity is generally assumed to result in less predictability, at least for the purposes of this thesis. As hinted at throughout this section, some predictability is necessary to both perceive the beat structure and synchronize our movements to it. The next section discusses this in more detail.

3.3 Sensory Precision and Sensorimotor Synchronization

The ability to synchronize our movements to external rhythms is critical for interacting with music (Repp, 2005; Repp & Su, 2013). In order to accurately synchronize our movements to music, it is generally assumed that we first need to perceive the rhythmic structure of the music (an ability known as beat perception) to base our movements on (although this may not always be the case, see Bégel et al., 2017 and Fiveash et al., 2022). If the structure is less clear to us because it is too complex, then our movements will be less precise; they will be less stable or more variable. This has been replicated in multiple labs (Chen et al., 2008; Franěk et al., 1987, 1988; Mathias et al., 2020; Skaansar et al., 2019; Snyder et al., 2006) and may explain why musicians, who are presumably better at extracting rhythmic structures from music, tend to be more stable synchronizers (Fiveash et al., 2022; Franěk et al., 1991; Repp, 2010; Repp &

Doggett, 2007). These results have been explained in terms of two popular theories: dynamic attending theory and predictive coding theory.

3.4 Dynamic Attending Theory

Dynamic attending (or dynamic systems) theory posits that internal oscillators in the brain synchronize to external rhythms, enhancing attention at the peaks of these oscillations and effectively structuring our perception of the music (Jones, 2018; Jones & Boltz, 1989; Large, 2008; Large & Jones, 1999; Large & Snyder, 2009). While there is some debate about whether these oscillatory enhancements are a boost in attention (Large et al., 2015) or a reduction due to processing fluency (O'Connell et al., 2015), these are not necessarily incompatible since they could both be context- and/or task-dependent. These oscillators need not be linear; indeed, nonlinear oscillator models have been able to account for such complex phenomena as metric hierarchies and natural music performances without the need for explicit, top-down predictions (Large & Palmer, 1996, 2002; Palmer & Demos, 2022). However, these oscillators have a limit and their synchronization grows increasingly worse with increasing rhythmic complexity (Henry & Herrmann, 2014; Large & Jones, 1999; Nozaradan et al., 2016; Snyder et al., 2006). This seems to be due, at least in part, to these oscillators' endogenous nature.

Because these synchronized oscillators are internal, their activity continues to briefly "resonate" at the same synchronized frequencies through periods of silence even when the external rhythm is not present (Tal et al., 2017). This has been used to explain why, among other things, people are able to continue steadily tapping at the rate they had synchronized to for a short while before returning to their natural rate (Bégel et al., 2022; Stupacher, Witte, et al., 2016; Tranchant et al., 2022). Importantly for this thesis, the properties of these internal oscillators seem capable of adaptation, particularly with musical experience (Bigand, 1997; Drake et al., 2000; Jones & Yee, 1997; Matthews et al., 2016; Scheurich et al., 2018; Tranchant et al., 2022).

3.5 Predictive Coding Theory

Predictive coding takes a different but not mutually exclusive approach to explaining sensory precision and sensorimotor synchronization (Palmer & Demos, 2022). As the name suggests, predictive coding asserts that the brain is constantly generating and updating predictive models comparing expected sensory inputs to the actual sensory inputs it is receiving (Clark, 2015; Friston, 2010; Hohwy, 2013), first represented with computational models of the human visual cortex by Rao & Ballard in 1999 (Rao & Ballard, 1999). These models are hierarchical, with lower level perceptual information being compared and fed forward (along with error information) to higher levels that assess, for example, how reliable (or certain) this information is based on prior predictions. These models are quite flexible with more weight being placed on the importance of either the incoming perceptual information or the top-down prior predictions depending on the context, quality of the incoming information, and past experience, among other factors.

To better illustrate this, imagine being at a noisy concert that's about to begin. In this scenario, the brain is exposed to lots of auditory information like other attendees' conversations, people shuffling towards the stage, and speaker buzz from the overhead monitors. Most of this information is too unpredictable and behaviorally irrelevant to warrant updating top-down predictions, especially because past experience has proven it to be uninformative. Now imagine the first note of the opening act ringing out. This very clear and loud auditory information immediately stands out among the background noise, generating a large prediction error between top-down predictions which expected more uninformative background noise and the new lower level percept for the music beginning. This signals an update to top-down predictions, shifting them from expecting background noise to expecting higher fidelity musical input.

This general process can be applied to musical rhythms as well (Lumaca et al., 2019; Vuust et al., 2009). Simple, isochronous rhythms cultivate strong top-down predictions about when the next beat will occur (after the same amount of time has passed since the last beat). Because these expectations are so strong, even a small deviation from isochrony can result in a large prediction error signal. For highly complex rhythms, this effect is reversed; since the rhythm is too complex, top-down predictions are quite weak and so small deviations are more expected, resulting in little prediction error.

There are situations, however, when these top-down predictions cannot be tuned by simply adjusting perceptual expectations. In these cases, predictive coding theorists argue that the brain can utilize another strategy – changing the sensory inputs themselves by moving in a process called active inference (Friston, 2010). This is postulated to be optimal at moderate levels of rhythmic complexity where top-down predictions expect when their violations will occur since they can then be suppressed by moving one's body to match the top-down predictions. In this way, action and perception are viewed as two sides of the same coin, where the prediction errors between expected and perceived sensations during both action and perception propagate bidirectionally through the nervous system so that the resulting errors can be minimized. In perception, the precision of sensory information (i.e., how informative it is) regulates how much the internal model should be adjusted; in more variable conditions, perception is informed more by top-down predictions rather than the noisier sensory inputs whose effects are dampened due to low precision. On the flip side, action spurs us to move such that our ensuing sensory inputs are exactly what we predicted, enhancing precision in a self-fulfilling prophecy.

At this point, it should be stressed that minimizing prediction error could be achieved by an oscillatory process of dynamic attending since predictive coding is rather agnostic about how exactly this is implemented in the brain. For instance, large updates to top-down predictions about the meter could realign internal oscillators to better process rhythms after a time signature change. Indeed, when movement is used to guide oscillations in the dynamic attending framework, it has been termed 'active sensing' which seems analogous to predictive coding's 'active inference' (Morillon et al., 2014, 2015). Similarly, the internal model of top-down predictions could *itself* be oscillatory. This is, however, less parsimonious; see Palmer & Demos (2022) for a more detailed comparison of the two theories (Palmer & Demos, 2022). In any case, using movement to reduce prediction error forms the basis of groove under predictive coding.

3.6 How Rhythmic Complexity Relates to Groove

As briefly noted in Section 3.1, the literature reports an inverted U-shaped relationship between rhythmic complexity and groove where the highest ratings of groove are in response to moderately complex musical rhythms (Matthews et al., 2019, 2022; Sioros et al., 2014; Stupacher, Wrede, et al., 2022; Witek et al., 2014). Since 2014 when this relationship was first reported, a number of papers have explained this result in terms of predictive coding (Foster Vander Elst et al., 2021; Gebauer et al., 2015; Koelsch et al., 2019; Stupacher, Matthews, et al., 2022; Vuust, 2018; Vuust et al., 2014, 2018, 2022; Vuust & Witek, 2014). The general argument is as such: rhythmic complexity introduces commensurate amounts of uncertainty to our sensory systems and consequently, we make more errors trying to predict when the next musical note will occur. Concurrently, as rhythmic complexity increases, our sensory precision (and thus our ability to very accurately perceive and move to the rhythm's structure) decreases. However, moderate amounts of rhythmic complexity strike a sweet spot where there are prediction errors (unlike at very low levels of rhythmic complexity), but not so many that we can't make sense of them (like at very high levels of rhythmic complexity). That is to say, the prediction errors in moderately complex contexts are highly precise; these prediction errors are expected (through both repetition and enculturation) and can thus be corrected. This correction is carried out primarily by using our internal model of the rhythm's structure to guide movements which simultaneously reinforce the moments where movements occur, directing attention away from deviant events that occur between movements and suppressing their influence on the model. Through the lens of predictive coding, *groove is merely active inference at work while listening to moderately complex rhythms*. The pleasurable aspect is theorized to follow from either participatory affordances (Witek, 2017) or by the rewarding value of the prediction itself because it is (speculated to be) evolutionarily adaptive (Clark, 2015; Huron, 2006). A visual depiction summarizing the assumptions of the theory is shown in Figure 1 (adapted from Koelsch, Vuust, & Friston (2019).

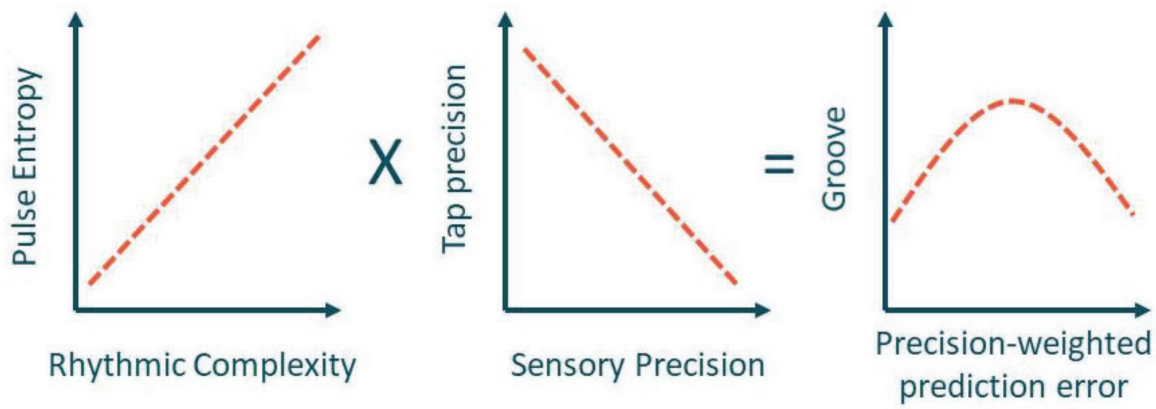

Figure 1. Schematic illustrating the predictive coding model of groove. The x-axis labels describe the abstract mental processes theorized to be occurring while the y-axis labels represent measurable variables that have been ascribed to them.

While the predictive coding account makes a compelling case, it is not without its shortcomings. Supporters of this view concede that its explanation of pleasure is rather weak (Vuust & Witek, 2014) and more general critics of predictive coding in music have argued that predictive coding alone is probably insufficient to account for the variety of pleasures derived from music (Schaefer et al., 2013). Some researchers take it a step further and argue that humans actually prefer *novelty* rather than the familiarity that predictive coding depends upon, an account that can also be modeled computationally (Schmidhuber, 2009).

The other major critique deals with stylistic enculturation and familiarity, both of which highly correlate with groove (Senn et al., 2018, 2021). Most Western music employs moderately complex rhythms and this could have arisen for reasons unrelated to prediction that subsequently became encultured and preferred over time. In line with this, recent work has demonstrated that similarly complex rhythmic patterns randomly generated by an algorithm evoke less groove pleasure than their human-composed counterparts (Sioros et al., 2022). The critique most relevant for this work, however, is the scant neurophysiological evidence.

3.7 Attention Modulation and Pupil Dilation

Both dynamic attending and predictive coding hinge on attention modulation, differing primarily on the mechanisms and goals of these modulations. While attention and its modulation could be a dissertation on its own, it's still important to have a working definition. For this purpose, no thesis from a psychology department would be complete without the classic definition from William James: "Every one [sic] knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others, and is a condition which has a real opposite in the confused, dazed, scatterbrained state which in French is called *distraction*, and *Zerstreutheit* in German." (James, 1890). The reason why this definition is so often quoted today is because it succinctly captures so many of the important aspects of attention that continue to be studied today. Namely, it explains how attention enhances the processing of our environment and that certain things are selected over others, implying that its capacity is limited (see Posner & Boies, 1971 and Posner & Petersen, 1990 for a more detailed discussion of these components of attention). In the context of groove, attention is directed toward (or away from) different rhythmic features to enhance (or suppress) their influence on internal models of the temporal structure. Thus, to elucidate the neural mechanisms underlying groove, it's useful to measure how attention changes over time in variously complex musical contexts.

One useful and convenient way to achieve this is by measuring changes in the pupil size, pupillometry. The pupil dilates with sympathetic nervous system arousal which is mediated by acetylcholine and, more importantly, norepinephrine (Laeng & Alnaes, 2019). It should come as no surprise then that pupil dilation is highly correlated with locus coeruleus activity since the small brainstem nucleus is the brain's chief producer of norepinephrine (Alnæs et al., 2014; Endestad et al., 2020; Joshi et al., 2016; Murphy et al., 2014). Thus, pupillometry offers researchers a quick, non-invasive way to track noradrenergic mental processes like cognitive effort (Kahneman, 1973; Kahneman & Beatty, 1966; Laeng et al., 2012; Laeng & Alnaes, 2019), attention deployment (Dahl et al., 2020; Grueschow et al., 2020; Mather et al., 2016; Oliva, 2019), physiological arousal (Joshi et al., 2016; Wang et al., 2018), and cognitive surprise (Kloosterman et al., 2015; Lavín et al., 2014; Preuschoff, 2011). Furthermore, because music does not possess luminance properties that confound dilation responses via the pupillary light reflex, pupillometry is particularly well-suited for measuring attention modulations while listening to music. Indeed, this has already proved fruitful with studies demonstrating greater dilations for syncopated (and groovy) rhythms (Bowling et al., 2019), music with larger microtiming asynchronies (Skaansar et al., 2019), and melodies that were more liked and predictable (Bianco et al., 2019). Therefore, pupillometry seemed the best tool to investigate the predictive and dynamic mechanisms of rhythm and groove.

5. Research Questions and Goals

The main goals of this thesis were to investigate whether groove is a product of predictive processes and to better understand human beat perception more broadly. This was accomplished over the course of three studies. The first study attempted to find neurophysiological evidence that supports the theory, namely that the pupil dilation response would exhibit the same inverted U-shaped relationship with rhythmic complexity as groove. Given the pupil's established relation to cognitive effort (Kahneman, 1973; Kahneman & Beatty, 1966), it could reflect the active process of correcting prediction errors said to occur when participants experience feelings of groove. The second study sought to directly test one of predictive coding's primary assumptions – that movement corrects prediction errors and thus, should increase feelings of groove relative to passively listening to the music without movement. The final study explored the factors relevant to sharpening the beat perception skills that influenced the other studies.

4.1 Pupil Drift Rate Indexes Groove Ratings

The first study found neurophysiological evidence for the predictive coding of groove by recording changes in participants' pupil sizes while they listened to drumbeats of varying rhythmic complexity. The pupil dilates with sympathetic nervous system arousal mediated primarily by norepinephrine (Alnæs et al., 2014; Laeng & Alnaes, 2019). Thus, it should come as no surprise that pupil dilation has been highly correlated with the activity of the locus coeruleus, the brain's primary producer of norepinephrine, in both invasive studies of primates (Joshi et al., 2016) and functional studies of humans (Alnæs et al., 2014; Endestad et al., 2020). This seems of particular relevance for this study since norepinephrine has recently been hypothesized to encode the precision of sensory predictions (Yon & Frith, 2021).

Therefore, if the predictive coding account is correct, then changes in noradrenergic arousal indexed by the pupil should correspond to groove ratings along an inverted U-shaped curve with rhythmic complexity. We found that the pupil drift rate (e.g., the rate that the pupil size changed over time) did precisely that, indicating that groovier (moderately complex) rhythms sustained attention longer. This effect appeared more prominent in participants with higher beat perception ability scores.

Furthermore, this study also characterized rhythmic complexity not just in terms of syncopation (as is common with drumbeat stimuli) but also pickups to independently explore the effects of both on groove. We found distinct roles for each rhythmic feature. Pickups were associated with greater pupil dilations, likely in a process of priming attention toward the strong beats relevant for establishing the meter. Notably, pickups had no direct effect on groove ratings. Syncopations, on the other hand, elicited greater feelings of groove but did not influence pupil dilation alone.

4.2 Sensorimotor Synchronization Increases Groove

As discussed in Sections 3.5 and 3.6, predictive coding posits that groove is an embodied correction of sensory prediction errors arising from rhythmic complexity. Thus, it stands to reason that if this is true, *actual* movement should increase feelings of groove relative to passive listening where movement can only, at best, be mentally simulated. This second study tested this by asking subjects to either tap their foot to the beat or passively listen to clips of real music that varied in rhythmic complexity (quantified as pulse entropy) while we recorded their pupil sizes. They then rated each musical clip in terms of groove.

We found support for predictive coding's assumption that synchronous movements increase feelings of groove, and possibly by reducing prediction errors as evidenced by greater pupil dilations while synchronizing. Extending past findings of the inverted U-curve of groove from simplified auditory stimuli to more ecologically-relevant music clips, we also showed that both tap stability and intensity decreased with increasing rhythmic complexity, indicating that participants became less confident in their less precise movements.

4.3 Use It or Lose It: Actively Playing Music Increases Beat Perception Ability

The final study explored how beat perception is impacted by individual differences. We aggregated psychoacoustic and demographic data collected from three different experiments (two of which are presented here in Sections 3.1 and 3.2) and analyzed whether musicians who regularly practiced their instrument(s) exhibited better beat perception than their counterparts who no longer practiced. Put another way, we investigated whether fine-grained beat perception is a use-dependent ability that degrades with neglect.

Beat perception abilities were assessed using the Computerised Adaptive Beat Alignment Test (CA-BAT), a reliable and validated psychoacoustic test (Harrison & Müllensiefen, 2018b, 2018a). The CA-BAT presents subjects with pairs of short musical clips with overlaid beep tracks, one of which is on the beat and one that is misaligned. Participants must report which beep track was aligned to the beat and depending on the correctness of their response, the difference in beep tracks becomes smaller (if the response was correct) or larger (if the response was incorrect). This adaptive design allows the CA-BAT to obtain an estimate of beat perception ability in just 25 trials, lasting around 10 minutes.

We found that musicians who actively practiced their instruments scored higher on the CA-BAT than both musicians who no longer practiced weekly and nonmusicians. However, our groups differed in their years of musical training and so we attempted to control for this with both traditional linear as well as several non-parametric, nonlinear, machine learning-based regression analyses. This revealed that once years of musical training were accounted for, regular rehearsal no longer had any impact on beat perception ability. This suggests that beat perception is *not* a use-dependent ability but rather remains stable once sufficiently trained.

6. General Discussion

This work has lent support to the predictive coding model of groove and expanded the study of use-dependent plasticity in musical expertise to beat perception. That said, it *does not* definitively rule out alternative explanations or influences on our work, chiefly dynamic attending for the first two studies and the role of genetic predispositions in the third.

While the study designs in the first two experiments did not allow nonlinear oscillator models to be fit to the data in order to directly test this, it remains possible that the stimuli drove some endogenous entrainment processes that gave rise to our groove findings. The relative sluggishness of the pupil dilation response and uncertainty about how its peak latency changes in more repetitive environments like music, combined with the overall short length of our pupil recordings (particularly the second study) all prevented us from exploring this possibility more fully. That said, the sensorimotor synchronization results in the second study are perfectly consistent with a mental process of dynamic attending and past work has indeed validated linear oscillatory mechanisms in the pupil (Fink et al., 2018). A critical next step could employ longer trials and additionally collect electroencephalography (which has finer temporal resolution) to address this possibility.

Similarly, the third study was not suited to answer questions relating to the influence of genetic predisposition on beat perception because no genetic data was collected from our participants. That said, a genome-wide association study confirmed that there are many genes that factor into rhythmic abilities like beat perception and synchronization (Niarchou et al., 2022). It would thus be interesting to investigate whether certain genes interact with both neural plasticity and musicians' playing habits. For instance, one could examine whether some genes encode more enduring neural plasticity or if certain genes predispose one to stick to more routine rehearsal over the lifespan. So despite these limitations, this work has extended past findings and provided a basis for continued progress in rhythm research.

Specifically, the work has broadened the scope of rhythmic complexity to be more inclusive in both theoretical and practical ways. While the overwhelming trend for groove research in music psychology is to manipulate or measure syncopation, this work highlights the importance of accounting for pickups since they play a different (and perhaps even counteractive) role to syncopations. Future research could manipulate pickups and more directly investigate their effects on both perceived complexity and groove. Finally, calculating pulse entropy using the MIRToolbox offers a convenient way to quantify the rhythmic complexity of real musical clips, opening the door for researchers to use a massive library of ecological stimuli in future studies. In fact, when comparing the pupil responses of the first two studies, this work has demonstrated that more ecologically-relevant clips of real music (widely held to be too noisy and uncontrolled for psychology and neuroscience research) actually produce *more* robust results than the simplified rhythmic stimuli typically regarded as the gold standard in the lab.

Regarding methodology, the first study contributes to the wider pupillometry literature by illustrating the useful role of a different aspect of the pupil time series analysis, the pupil drift rate. Drift measures could yield promising results when traditional approaches averaging the entire time series either don't work or aren't appropriate. Similarly, the second study emphasizes the importance of recording not just the timing of taps when subjects are synchronizing to movement, but the forcefulness of their taps as well, something often neglected in both the sensorimotor synchronization and groove literature. In our case, analyzing tap intensity yielded interesting insights related to subjects' certainty. More generally, this work exemplifies the rewards of adopting a plurality of methodologies since supplementing our ratings task with pupillometry, psychoacoustics, and sensorimotor synchronization yielded such comprehensive findings.

Building off of this last point, this work should also encourage researchers to embrace a plurality of disciplines and engage in interdisciplinary work. Without the crucial support of musicologists and music technologists, the stimuli used throughout this work may have been severely limited in terms of confounds and interpretation. Similarly, without the cognitive psychology methodologies and computational modeling analyses, the work's theoretical arguments would have suffered equally. To develop a truly critical perspective, one needs to reach across conventional epistemological boundaries in academia.

7. References

Alluri, V., Toiviainen, P., Jääskeläinen, I. P., Glerean, E., Sams, M., & Brattico, E. (2012). Large-scale brain networks emerge from dynamic processing of musical timbre, key and rhythm. *NeuroImage*, *59*(4), 3677–3689. https://doi.org/10.1016/j.neuroimage.2011.11.019

Alnæs, D., Sneve, M. H., Espeseth, T., Endestad, T., Pavert, S. H. P., & Laeng, B. (2014). Pupil size signals mental effort deployed during multiple object tracking and predicts brain activity in the dorsal attention network and the locus coeruleus. *Journal of Vision*, *14*(4), 1–1.

Bégel, V., Benoit, C.-E., Correa, A., Cutanda, D., Kotz, S. A., & Dalla Bella, S. (2017). “Lost in time” but still moving to the beat. *Neuropsychologia*, *94*, 129–138. https://doi.org/10.1016/j.neuropsychologia.2016.11.022

Bégel, V., Demos, A. P., Wang, M., & Palmer, C. (2022). Social Interaction and Rate Effects in Models of Musical Synchronization. *Frontiers in Psychology*, *13*, 865536. https://doi.org/10.3389/fpsyg.2022.865536

Bianco, R., Gold, B. P., Johnson, A. P., & Penhune, V. B. (2019). Music predictability and liking enhance pupil dilation and promote motor learning in non-musicians. *Scientific Reports*, *9*(1), 1–12.

Bigand, E. (1997). Perceiving musical stability: The effect of tonal structure, rhythm, and musical expertise. *Journal of Experimental Psychology: Human Perception and Performance*, *23*(3), 808–822. https://doi.org/10.1037/0096-1523.23.3.808

Bowling, D. L., Graf Ancochea, P., Hove, M. J., & Fitch, W. (2019). Pupillometry of Groove: Evidence for Noradrenergic Arousal in the Link Between Music and Movement. *Frontiers in Neuroscience*, *12*, 1039.

Burger, B., Thompson, M. R., Luck, G., Saarikallio, S., & Toiviainen, P. (2013). Influences of Rhythm- and Timbre-Related Musical Features on Characteristics of Music-Induced Movement. *Frontiers in Psychology*, *4*. https://doi.org/10.3389/fpsyg.2013.00183

Câmara, G. S., & Danielsen, A. (2018). Groove. In A. Rehding & S. Rings (Eds.), *The Oxford Handbook of Critical Concepts in Music theory*. Oxford University Press.

Chen, J. L., Penhune, V. B., & Zatorre, R. J. (2008). Moving on Time: Brain Network for Auditory-Motor Synchronization is Modulated by Rhythm Complexity and Musical

Training. *Journal of Cognitive Neuroscience*, *20*(2), 226–239. https://doi.org/10.1162/jocn.2008.20018

Cirelli, L. K., & Trehub, S. E. (2019). Dancing to Metallica and Dora: Case Study of a 19-Month-Old. *Frontiers in Psychology*, *10*, 1073. https://doi.org/10.3389/fpsyg.2019.01073

Clark, A. (2015). *Surfing uncertainty: Prediction, action, and the embodied mind*. Oxford University Press.

Dahl, M. J., Mather, M., Sander, M. C., & Werkle-Bergner, M. (2020). Noradrenergic responsiveness supports selective attention across the adult lifespan. *Journal of Neuroscience*, *40*(22), 4372–4390.

Daikoku, T. (2018). Neurophysiological Markers of Statistical Learning in Music and Language: Hierarchy, Entropy, and Uncertainty. *Brain Sciences*, *8*(6), 114. https://doi.org/10.3390/brainsci8060114

Davies, M., Madison, G., Silva, P., & Gouyon, F. (2013). The Effect of Microtiming Deviations on the Perception of Groove in Short Rhythms. *Music Perception*, *30*(5), 497–510. https://doi.org/10.1525/mp.2013.30.5.497

De Fleurian, R., Ben-Tal, O., Müllensiefen, D., & Blackwell, T. (2014). Comparing Perceptual and Computational Complexity for Short Rhythmic Patterns. *Procedia - Social and Behavioral Sciences*, *126*, 111–112. https://doi.org/10.1016/j.sbspro.2014.02.333

de Fleurian, R., Blackwell, T., Ben-Tal, O., & Müllensiefen, D. (2017). Information-Theoretic Measures Predict the Human Judgment of Rhythm Complexity. *Cognitive Science*, *41*(3), 800–813. https://doi.org/10.1111/cogs.12347

Drake, C., Jones, M. R., & Baruch, C. (2000). The development of rhythmic attending in auditory sequences: Attunement, referent period, focal attending. *Cognition*, *77*(3), 251–288. https://doi.org/10.1016/S0010-0277(00)00106-2

Eerola, T., Himberg, T., Toiviainen, P., & Louhivuori, J. (2006). Perceived complexity of western and African folk melodies by western and African listeners. *Psychology of Music*, *34*(3), 337–371. https://doi.org/10.1177/0305735606064842

Endestad, T., Godøy, R. I., Sneve, M. H., Hagen, T., Bochynska, A., & Laeng, B. (2020). Mental Effort When Playing, Listening, and Imagining Music in One Pianist's Eyes and Brain. *Frontiers in Human Neuroscience*, *14*, 576888.

https://doi.org/10.3389/fnhum.2020.576888

Fink, L. K., Hurley, B. K., Geng, J. J., & Janata, P. (2018). A linear oscillator model predicts dynamic temporal attention and pupillary entrainment to rhythmic patterns. *Journal of Eye Movement Research*, *11*(2), 12.

Fiveash, A., Bella, S. D., Bigand, E., Gordon, R. L., & Tillmann, B. (2022). You got rhythm, or more: The multidimensionality of rhythmic abilities. *Attention, Perception, & Psychophysics*, *84*(4), 1370–1392. https://doi.org/10.3758/s13414-022-02487-2

Foster Vander Elst, O., Vuust, P., & Kringelbach, M. L. (2021). Sweet anticipation and positive emotions in music, groove, and dance. *Current Opinion in Behavioral Sciences*, *39*, 79–84. https://doi.org/10.1016/j.cobeha.2021.02.016

Franěk, M., Mates, J., Radil, T., Beck, K., & Pöppel, E. (1991). Finger tapping in musicians and nonmusicians. *International Journal of Psychophysiology*, *11*(3), 277–279. https://doi.org/10.1016/0167-8760(91)90022-P

Franěk, M., Radil, T., & Indra, M. (1988). Tracking irregular acoustic patterns by finger tapping. *International Journal of Psychophysiology*, *6*(4), 327–330. https://doi.org/10.1016/0167-8760(88)90020-7

Franěk, M., Radil, T., Indra, M., & Lánsky, P. (1987). Following complex rhythmical acoustical patterns by tapping. *International Journal of Psychophysiology*, *5*(3), 187–192. https://doi.org/10.1016/0167-8760(87)90005-5

Friston, K. (2010). The free-energy principle: A unified brain theory? *Nature Reviews Neuroscience*, *11*(2), 127–138. https://doi.org/10.1038/nrn2787

Frühauf, J., Kopiez, R., & Platz, F. (2013). Music on the timing grid: The influence of microtiming on the perceived groove quality of a simple drum pattern performance. *Musicae Scientiae*, *17*(2), 246–260. https://doi.org/10.1177/1029864913486793

Gebauer, L., Kringelbach, M. L., & Vuust, P. (2015). Predictive coding links perception, action, and learning to emotions in music. *Physics of Life Reviews*, *13*, 50–52. https://doi.org/10.1016/j.plrev.2015.04.023

Gold, B. P., Pearce, M. T., Mas-Herrero, E., Dagher, A., & Zatorre, R. J. (2019). Predictability and Uncertainty in the Pleasure of Music: A Reward for Learning? *The Journal of Neuroscience*, *39*(47), 9397–9409. https://doi.org/10.1523/JNEUROSCI.0428-19.2019

Gonzalez-Sanchez, V. E., Zelechowska, A., & Jensenius, A. R. (2018). Correspondences

Between Music and Involuntary Human Micromotion During Standstill. *Frontiers in Psychology*, *9*, 1382. https://doi.org/10.3389/fpsyg.2018.01382

Grueschow, M., Kleim, B., & Ruff, C. C. (2020). Role of the locus coeruleus arousal system in cognitive control. *Journal of Neuroendocrinology*, *32*(12), 12890.

Hansen, N. Chr., & Pearce, M. T. (2014). Predictive uncertainty in auditory sequence processing. *Frontiers in Psychology*, *5*. https://doi.org/10.3389/fpsyg.2014.01052

Harrison, P. M. C., & Müllensiefen, D. (2018a). Development and validation of the Computerised Adaptive Beat Alignment Test (CA-BAT. *Scientific Reports*, *8*(12395), 1–19. https://doi.org/10.1038/s41598-018-30318-8

Harrison, P. M. C., & Müllensiefen, D. (2018b). https://doi.org/10.5281/zenodo.1415353

Henry, M. J., & Herrmann, B. (2014). Low-Frequency Neural Oscillations Support Dynamic Attending in Temporal Context. *Timing & Time Perception*, *2*(1), 62–86. https://doi.org/10.1163/22134468-00002011

Hohwy, J. (2013). *The predictive mind*. Oxford University Press.

Huron, D. (2006). *Sweet anticipation: Music and the psychology of expectation*. The MIT Press.

Irwin, R. J., & Zwislocki, J. J. (1971). Loudness effects in pairs of tone bursts. *Perception & Psychophysics*, *10*(3), 189–192.

James, W. (1890). *The Principles of Psychology*. London, England: Dover Publications.

Janata, P., Tomic, S. T., & Haberman, J. M. (2012). Sensorimotor coupling in music and the psychology of the groove. *Journal of Experimental Psychology: General*, *141*(1), 54.

Jones, M. R. (2018). *Time will tell: A theory of dynamic attending*. Oxford University Press.

Jones, M. R., & Boltz, M. (1989). Dynamic attending and responses to time. *Psychological Review*, *96*(3), 459.

Jones, M. R., & Yee, W. (1997). Sensitivity to time change: The role of context and skill. *Journal of Experimental Psychology: Human Perception and Performance*, *23*(3), 693–709. https://doi.org/10.1037/0096-1523.23.3.693

Joshi, S., Li, Y., Kalwani, R. M., & Gold, J. I. (2016). Relationships between pupil diameter and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron*, *89*(1), 221–234.

Kahneman, D. (1973). *Attention and Effort* (Vol. 1063). Prentice-Hall.

Kahneman, D., & Beatty, J. (1966). Pupil diameter and load on memory. *Science*, *154*(3756), 1583–1585.

Kantan, P., Alecu, R. S., & Dahl, S. (2021). The Effect of Auditory Pulse Clarity on Sensorimotor Synchronization. In R. Kronland-Martinet, S. Ystad, & M. Aramaki (Eds.), *Perception, Representations, Image, Sound, Music* (Vol. 12631, pp. 379–395). Springer International Publishing. https://doi.org/10.1007/978-3-030-70210-6_25

Kennedy, M., & Kennedy, J. (2013). *The Oxford Dictionary of Music*. Oxford University Press.

Kloosterman, N. A., Meindertsma, T., van Loon, A. M., Lamme, V. A. F., Bonneh, Y. S., & Donner, T. H. (2015). Pupil size tracks perceptual content and surprise. *European Journal of Neuroscience*, *41*(8), 1068–1078. https://doi.org/10.1111/ejn.12859

Koelsch, S., Vuust, P., & Friston, K. (2019). *Predictive Processes and the Peculiar Case of Music. Trends in cognitive sciences*.

Laeng, B., & Alnaes, D. (2019). Pupillometry. In *Eye Movement Research* (pp. 449–502). Springer.

Laeng, B., Sirois, S., & Gredebäck, G. (2012). Pupillometry: A window to the preconscious? *Perspectives on Psychological Science*, *7*(1), 18–27.

Large, E. W. (2008). Resonating to musical rhythm: Theory and experiment. *The Psychology of Time*, 189–231.

Large, E. W., Herrera, J. A., & Velasco, M. J. (2015). Neural Networks for Beat Perception in Musical Rhythm. *Frontiers in Systems Neuroscience*, *9*. https://doi.org/10.3389/fnsys.2015.00159

Large, E. W., & Jones, M. R. (1999). The dynamics of attending: How people track time-varying events. *Psychological Review*, *106*(1), 119–159. https://doi.org/10.1037/0033-295X.106.1.119

Large, E. W., & Palmer, C. (1996). Nonlinear dynamics of rhythm perception in performed music. *The Journal of the Acoustical Society of America*, *99*(4), 2481–2500. https://doi.org/10.1121/1.415575

Large, E. W., & Palmer, C. (2002). Perceiving temporal regularity in music. *Cognitive Science*, *26*(1), 1–37. https://doi.org/10.1207/s15516709cog2601_1

Large, E. W., & Snyder, J. S. (2009). Pulse and meter as neural resonance. *Annals of the New York Academy of Sciences*, *1169*(1), 46–57.

Lartillot, O., Eerola, T., Toiviainen, P., & Fornari, J. (2008). Multi-Feature Modeling of Pulse

Clarity: Design, Validation and Optimization. *ISMIR*, 521–526.

Lartillot, O., Toiviainen, P., & Eerola, T. (2008). A Matlab Toolbox for Music Information Retrieval. In C. Preisach, H. Burkhardt, L. Schmidt-Thieme, & R. Decker (Eds.), *Data Analysis, Machine Learning and Applications* (pp. 261–268). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-78246-9_31

Lavín, C., San Martín, R., & Rosales Jubal, E. (2014). Pupil dilation signals uncertainty and surprise in a learning gambling task. *Frontiers in Behavioral Neuroscience*, *7*. https://doi.org/10.3389/fnbeh.2013.00218

Lerdahl, F. 1943-, & Jackendoff, R. 1945-. (1983). *A generative theory of tonal music*. MIT Press; WorldCat.org. http://www.gbv.de/dms/bowker/toc/9780262120944.pdf

London, J. (2012). *Hearing in time: Psychological aspects of musical meter*. Oxford University Press.

Lumaca, M., Trusbak Haumann, N., Brattico, E., Grube, M., & Vuust, P. (2019). Weighting of neural prediction error by rhythmic complexity: A predictive coding account using mismatch negativity. *European Journal of Neuroscience*, *49*(12), 1597–1609. https://doi.org/10.1111/ejn.14329

Madison, G. (2006). Experiencing groove induced by music: Consistency and phenomenology. *Music perception*, *24*(2), 201–208.

Madison, G., Gouyon, F., Ullén, F., & Hörnström, K. (2011). Modeling the tendency for music to induce movement in humans: First correlations with low-level audio descriptors across music genres. *Journal of Experimental Psychology: Human Perception and Performance*, *37*(5).

Madison, G., & Sioros, G. (2014). What musicians do to induce the sensation of groove in simple and complex melodies, and how listeners perceive it. *Frontiers in Psychology*, *5*, 894.

Margulis, E. H., & Beatty, A. P. (2008). Musical style, psychoaesthetics, and prospects for entropy as an analytic tool. *Computer Music Journal*, *32*(4), 64–78.

Mather, M., Clewett, D., Sakaki, M., & Harley, C. W. (2016). Norepinephrine ignites local hotspots of neuronal excitation: How arousal amplifies selectivity in perception and memory. *Behavioral and Brain Sciences*, *39*, e200. https://doi.org/10.1017/S0140525X15000667

Mathias, B., Zamm, A., Gianferrara, P. G., Ross, B., & Palmer, C. (2020). Rhythm Complexity Modulates Behavioral and Neural Dynamics During Auditory–Motor Synchronization. *Journal of Cognitive Neuroscience*, *32*(10), 1864–1880. https://doi.org/10.1162/jocn_a_01601

Matthews, T. E., Thibodeau, J. N. L., Gunther, B. P., & Penhune, V. B. (2016). The Impact of Instrument-Specific Musical Training on Rhythm Perception and Production. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.00069

Matthews, T. E., Witek, M. A. G., Thibodeau, J. L. N., Vuust, P., & Penhune, V. B. (2022). Perceived Motor Synchrony With the Beat is More Strongly Related to Groove Than Measured Synchrony. *Music Perception*, *39*(5), 423–442. https://doi.org/10.1525/mp.2022.39.5.423

Matthews, T. E., Witek, M. A., Heggli, O. A., Penhune, V. B., & Vuust, P. (2019). The sensation of groove is affected by the interaction of rhythmic and harmonic complexity. *PloS One*, *14*(1), 0204539.

Milne, A. J., & Herff, S. A. (2020). The perceptual relevance of balance, evenness, and entropy in musical rhythms. *Cognition*, *203*, 104233. https://doi.org/10.1016/j.cognition.2020.104233

Morillon, B., Hackett, T. A., Kajikawa, Y., & Schroeder, C. E. (2015). Predictive motor control of sensory dynamics in auditory active sensing. *Current Opinion in Neurobiology*, *31*, 230–238. https://doi.org/10.1016/j.conb.2014.12.005

Morillon, B., Schroeder, C. E., & Wyart, V. (2014). Motor contributions to the temporal precision of auditory attention. *Nature communications*, *5*(1), 1–9.

Murphy, P. R., O'Connell, R. G., O'Sullivan, M., Robertson, I. H., & Balsters, J. H. (2014). Pupil diameter covaries with BOLD activity in human locus coeruleus. *Human Brain Mapping*, *35*(8), 4140–4154. https://doi.org/10.1002/hbm.22466

Niarchou, M., Gustavson, D. E., Sathirapongsasuti, J. F., Anglada-Tort, M., Eising, E., Bell, E., McArthur, E., Straub, P., McAuley, J. D., Capra, J. A., & others. (2022). Genome-wide association study of musical beat synchronization demonstrates high polygenicity. *Nature Human Behaviour*, 1–18.

Nozaradan, S., Peretz, I., & Keller, P. E. (2016). Individual Differences in Rhythmic Cortical Entrainment Correlate with Predictive Behavior in Sensorimotor Synchronization.

Scientific Reports, *6*(1), 20612. https://doi.org/10.1038/srep20612

O'Connell, M. N., Barczak, A., Ross, D., McGinnis, T., Schroeder, C. E., & Lakatos, P. (2015). Multi-scale entrainment of coupled neuronal oscillations in primary auditory cortex. *Frontiers in Human Neuroscience*, *9*, 655.

Oliva, M. (2019). Pupil size and search performance in low and high perceptual load. *Cognitive, Affective, & Behavioral Neuroscience*, *19*(2), 366–376.

Palmer, C., & Demos, A. P. (2022). Are We in Time? How Predictive Coding and Dynamical Systems Explain Musical Synchrony. *Current Directions in Psychological Science*, *31*(2), 147–153. https://doi.org/10.1177/09637214211053635

Posner, M. I., & Boies, S. J. (1971). Components of attention. *Psychological Review*, *78*(5), 391.

Posner, M. I., & Petersen, S. E. (1990). The Attention System of the Human Brain. *Annual Review of Neuroscience*, *13*(1), 25–42. https://doi.org/10.1146/annurev.ne.13.030190.000325

Pressing, J. (1999). Cognitive complexity and the structure of musical patterns. *Proceedings of the 4th Conference of the Australasian Cognitive Science Society*.

Preuschoff, K. (2011). Pupil dilation signals surprise: Evidence for noradrenaline's role in decision making. *Frontiers in Neuroscience*, *5*. https://doi.org/10.3389/fnins.2011.00115

Quiroga‐Martinez, D. R., C. Hansen, N., Højlund, A., Pearce, M., Brattico, E., & Vuust, P. (2020). Musical prediction error responses similarly reduced by predictive uncertainty in musicians and non‐musicians. *European Journal of Neuroscience*, *51*(11), 2250–2269. https://doi.org/10.1111/ejn.14667

Quiroga-Martinez, D. R., Hansen, N. C., Højlund, A., Pearce, M. T., Brattico, E., & Vuust, P. (2019). Reduced prediction error responses in high-as compared to low-uncertainty musical contexts. *Cortex*, *120*, 181–200. https://doi.org/10.1016/j.cortex.2019.06.010

Quiroga-Martinez, D. R., Tillmann, B., Brattico, E., Cholvy, F., Fornoni, L., Vuust, P., & Caclin, A. (2021). Listeners with congenital amusia are sensitive to context uncertainty in melodic sequences. *Neuropsychologia*, *158*, 107911. https://doi.org/10.1016/j.neuropsychologia.2021.107911

Rao, R. P., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, *2*(1), 79–87.

Repp, B. H. (2005). Sensorimotor synchronization: A review of the tapping literature. *Psychonomic Bulletin & Review*, *12*(6), 969–992. https://doi.org/10.3758/BF03206433

Repp, B. H. (2010). Sensorimotor synchronization and perception of timing: Effects of music training and task experience. *Human Movement Science*, *29*(2), 200–213. https://doi.org/10.1016/j.humov.2009.08.002

Repp, B. H., & Doggett, R. (2007). Tapping to a Very Slow Beat: A Comparison of Musicians and Nonmusicians. *Music Perception*, *24*(4), 367–376. https://doi.org/10.1525/mp.2007.24.4.367

Repp, B. H., & Su, Y. H. (2013). Sensorimotor synchronization: A review of recent research (2006–2012. *Psychonomic Bulletin & Review*, *20*(3), 403–452.

Schaefer, R. S., Overy, K., & Nelson, P. (2013). Affect and non-uniform characteristics of predictive processing in musical behaviour. *Behavioral and Brain Sciences*, *36*(3), 226–227. https://doi.org/10.1017/S0140525X12002373

Scharf, B. (1978). Loudness. *Handbook of Perception*, *4*, 187–242.

Scheurich, R., Zamm, A., & Palmer, C. (2018). Tapping Into Rate Flexibility: Musical Training Facilitates Synchronization Around Spontaneous Production Rates. *Frontiers in Psychology*, *9*, 458. https://doi.org/10.3389/fpsyg.2018.00458

Schmidhuber, J. (2009). *Art & Science as By-Products of Search for Novel Patterns. . .*

Senn, O., Bechtold, T. A., Hoesl, F., & Kilchenmann, L. (2021). Taste and familiarity affect the experience of groove in popular music. *Musicae Scientiae*, *25*(1), 45–66. https://doi.org/10.1177/1029864919839172

Senn, O., Kilchenmann, L., Bechtold, T., & Hoesl, F. (2018). Groove in drum patterns as a function of both rhythmic properties and listeners' attitudes. *PloS One*, *13*(6), 0199604.

Senn, O., Kilchenmann, L., von Georgi, R., & Bullerjahn, C. (2016). The Effect of Expert Performance Microtiming on Listeners' Experience of Groove in Swing or Funk Music. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.01487

Shannon, C. E. (1948). A Mathematical Theory of Communication. *Bell System Technical Journal*, *27*(3), 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Sioros, G., Davies, M. E., & Guedes, C. (2018). A generative model for the characterization of musical rhythms. *Journal of New Music Research*, *47*(2), 114–128.

Sioros, G., Madison, G., Cocharro, D., Danielsen, A., & Gouyon, F. (2022). Syncopation and

Groove in Polyphonic Music: Patterns Matter. *Music Perception: An Interdisciplinary Journal*, *39*(5), 503–531.

Sioros, G., Miron, M., Davies, M., Gouyon, F., & Madison, G. (2014). Syncopation creates the sensation of groove in synthesized music examples. *Frontiers in Psychology*, *5*, 1036.

Skaansar, J. F., Laeng, B., & Danielsen, A. (2019). Microtiming and Mental Effort: Onset Asynchronies in Musical Rhythm Modulate Pupil Size. *Music Perception*, *37*(2), 111–133. https://doi.org/10.1525/mp.2019.37.2.111

Snyder, J. S., Hannon, E. E., Large, E. W., & Christiansen, M. H. (2006). Synchronization and Continuation Tapping to Complex Meters. *Music Perception*, *24*(2), 135–146. https://doi.org/10.1525/mp.2006.24.2.135

Stupacher, J. (2019). The experience of flow during sensorimotor synchronization to musical rhythms. *Musicae Scientiae*, *23*(3), 348–361. https://doi.org/10.1177/1029864919836720

Stupacher, J., Hove, M. J., & Janata, P. (2016). Audio features underlying perceived groove and sensorimotor synchronization in music. *Music Perception: An Interdisciplinary Journal*, *33*(5), 571–589.

Stupacher, J., Matthews, T. E., Pando-Naude, V., Foster Vander Elst, O., & Vuust, P. (2022). The sweet spot between predictability and surprise: Musical groove in brain, body, and social interactions. *Frontiers in Psychology*, *13*, 906190. https://doi.org/10.3389/fpsyg.2022.906190

Stupacher, J., Witte, M., Hove, M. J., & Wood, G. (2016). Neural Entrainment in Drum Rhythms with Silent Breaks: Evidence from Steady-state Evoked and Event-related Potentials. *Journal of Cognitive Neuroscience*, *28*(12), 1865–1877. https://doi.org/10.1162/jocn_a_01013

Stupacher, J., Wrede, M., & Vuust, P. (2022). A brief and efficient stimulus set to create the inverted U-shaped relationship between rhythmic complexity and the sensation of groove. *PLOS ONE*, *17*(5), e0266902. https://doi.org/10.1371/journal.pone.0266902

Tal, I., Large, E. W., Rabinovitch, E., Wei, Y., Schroeder, C. E., Poeppel, D., & Zion Golumbic, E. (2017). Neural Entrainment to the Beat: The “Missing-Pulse” Phenomenon. *The Journal of Neuroscience*, *37*(26), 6331–6341. https://doi.org/10.1523/JNEUROSCI.2500-16.2017

Temperley, D. & others. (2007). *Music and probability*. Mit Press.

Toussaint, G. T., & Trochidis, K. (2018). On Measuring the Complexity of Musical Rhythm. *2018 9th IEEE Annual Ubiquitous Computing, Electronics & Mobile Communication Conference (UEMCON)*, 753–757. https://doi.org/10.1109/UEMCON.2018.8796634

Tranchant, P., Scholler, E., & Palmer, C. (2022). Endogenous rhythms influence musicians' and non-musicians' interpersonal synchrony. *Scientific Reports*, *12*(1), 12973. https://doi.org/10.1038/s41598-022-16686-2

Vuust, P. (2018). Groove on the Brain. In M. Aramaki, M. E. P. Davies, R. Kronland-Martinet, & S. Ystad (Eds.), *Music Technology with Swing* (Vol. 11265, pp. 101–110). Springer International Publishing. https://doi.org/10.1007/978-3-030-01692-0_7

Vuust, P., Dietz, M. J., Witek, M., & Kringelbach, M. L. (2018). Now you hear it: A predictive coding model for understanding rhythmic incongruity: Now you hear it. *Annals of the New York Academy of Sciences*, *1423*(1), 19–29. https://doi.org/10.1111/nyas.13622

Vuust, P., Gebauer, L. K., & Witek, M. A. G. (2014). Neural Underpinnings of Music: The Polyrhythmic Brain. In H. Merchant & V. de Lafuente (Eds.), *Neurobiology of Interval Timing* (Vol. 829, pp. 339–356). Springer New York. https://doi.org/10.1007/978-1-4939-1782-2_18

Vuust, P., Heggli, O. A., Friston, K. J., & Kringelbach, M. L. (2022). Music in the brain. *Nature Reviews Neuroscience*, *23*(5), 287–305. https://doi.org/10.1038/s41583-022-00578-5

Vuust, P., Ostergaard, L., Pallesen, K. J., Bailey, C., & Roepstorff, A. (2009). Predictive coding of music – Brain responses to rhythmic incongruity. *Cortex*, *45*(1), 80–92. https://doi.org/10.1016/j.cortex.2008.05.014

Vuust, P., & Witek, M. A. (2014). Rhythmic complexity and predictive coding: A novel approach to modeling rhythm and meter perception in music. *Frontiers in Psychology*, *5*, 1111.

Wang, C.-A., Baird, T., Huang, J., Coutinho, J. D., Brien, D. C., & Munoz, D. P. (2018). Arousal Effects on Pupil Size, Heart Rate, and Skin Conductance in an Emotional Face Task. *Frontiers in Neurology*, *9*, 1029. https://doi.org/10.3389/fneur.2018.01029

Witek, M. A. (2017). Filling in: Syncopation, pleasure and distributed embodiment in groove. *Music Analysis*, *36*(1), 138–160.

Witek, M. A., Clarke, E. F., Wallentin, M., Kringelbach, M. L., & Vuust, P. (2014). Syncopation, body-movement and pleasure in groove music. *PloS one*, *9*(4), 94446.

Witek, M. A., Popescu, T., Clarke, E. F., Hansen, M., Konvalinka, I., Kringelbach, M. L., &

Vuust, P. (2017). Syncopation affects free body-movement in musical groove. *Experimental Brain Research*, *235*(4), 995–1005.

Yon, D., & Frith, C. D. (2021). Precision and the Bayesian brain. *Current Biology*, *31*(17), 1026–1032.

8. Papers 1-3

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Pupil drift rate indexes groove ratings

Connor Spiech[1,2]✉, George Sioros[1,3], Tor Endestad[1,2], Anne Danielsen[1,3] & Bruno Laeng[1,2]

Groove, understood as an enjoyable compulsion to move to musical rhythms, typically varies along an inverted U-curve with increasing rhythmic complexity (e.g., syncopation, pickups). Predictive coding accounts posit that moderate complexity drives us to move to reduce sensory prediction errors and model the temporal structure. While musicologists generally distinguish the effects of pickups (anacruses) and syncopations, their difference remains unexplored in groove. We used pupillometry as an index to noradrenergic arousal while subjects listened to and rated drumbeats varying in rhythmic complexity. We replicated the inverted U-shaped relationship between rhythmic complexity and groove and showed this is modulated by musical ability, based on a psychoacoustic beat perception test. The pupil drift rates suggest that groovier rhythms hold attention longer than ones rated less groovy. Moreover, we found complementary effects of syncopations and pickups on groove ratings and pupil size, respectively, discovering a distinct predictive process related to pickups. We suggest that the brain deploys attention to pickups to sharpen subsequent strong beats, augmenting the predictive scaffolding's focus on beats that reduce syncopations' prediction errors. This interpretation is in accordance with groove envisioned as an embodied resolution of precision-weighted prediction error.

Theoretical background. The peculiar ability for music to enjoyably compel us to move in synchrony with its rhythm has generated considerable academic interest over the years[1–3]. This enjoyable urge to move (hereafter referred to as "groove" for simplicity's sake) to music seems to be linked, at least in part, to the rhythm's complexity[4–7]. Recently, this has been framed within predictive coding models of the mind, positing that groove-induced movements help to resolve sensory ambiguity regarding musical pulse and meter, thus minimizing prediction errors stemming from structural deviations like syncopation[8,9]. This is proposed to occur along an inverted U-shaped curve[10]. At low levels of complexity, there is little prediction error to resolve so movement isn't needed to reinforce our metric model since it is already closely aligned with the rhythm. At more moderate levels of complexity, the body can be moved in synchrony with the basic beats of the groove, allowing proprioceptive inputs to reinforce the perceived pulse and meter of the rhythm and thus eradicate the sensory prediction errors. (Pulse here refers to the tempo in which you would tap your feet to the music, and meter to the way in which you would group these beats). In a more phenomenological approach, this body movement has been suggested to result in "participatory pleasure" by filling in the expected beat[11]. However, in highly complex rhythms, meter may become unclear, the prediction about the timing of notes may be weakened, and synchronous movements hindered[12]. Therefore, the greatest 'precision' in prediction errors (i.e., the most "predictable" prediction errors) occurs at moderate levels of metric complexity where these errors can be corrected by moving in a process of active inference[8].

The above theory is also compatible with dynamic attending theory (DAT) accounts[13] where active sensing (using movement to change sensory inputs) can entrain neural oscillations to relevant parts of the rhythm, selectively enhancing or suppressing their processing with attention[14,15]. While the elegance and plausibility of this account is enticing, strong evidence mapping behavior (i.e., the experience of groove) to neurophysiological processes using musically-relevant stimuli has remained elusive.

Pupillometry of groove. If predictive coding underlies the enjoyable urge to move in response to music, then some neurophysiological marker of precision-weighted prediction errors should be found alongside the experience. One likely candidate is the neurotransmitter norepinephrine which has been hypothesized to encode the reliability (i.e., precision) of sensory predictions and enhance the signal-to-noise ratio of incom-

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ing information[16]. Pupillometry offers a convenient way to investigate this given its tight correlation to locus coeruleus activity, the brain's primary norepinephrine producer[17–19]. Consequently, the pupil dilation response's association with cognitive effort and attention allocation is well-documented[20–22] and previous research shows that the pupil can index the deployment of attentional resources[23–27]. Since actively modulating the precision of prediction errors is likely to require attention[28], it stands to reason that this process—if it is crucial to the experience of groove—could be observed using pupillometry. Initial findings are encouraging. Bowling, Graf Ancochea, Hove, and Fitch recorded greater pupil dilations in response to syncopated (and groovy) rhythms compared to unsyncopated (and less groovy) rhythms[29] while Skaansar, Laeng, and Danielsen found that larger microtiming asynchronies elicited greater pupil dilations[30]. Thus, the question does not seem to be *whether* noradrenergic arousal is related to groove, but rather *how* it is related to groove and if this is consistent with the existing theories.

The present study. We hypothesized that if the experience of groove is associated with an active process of suppressing prediction errors, then it should be reflected in stronger pupillometric arousal at moderate levels of syncopation where precision-weighted prediction error is highest and active inference is needed (and able) to correct it. To accomplish this, we decided to record participants' pupil responses while listening to drumbeats varying in the amount of deviations from isochrony (and thus predictability). They also rated the drumbeats in terms of how much they wanted to move, how much they enjoyed them, and how energetic they were. Unique to our study, we characterized the deviations from isochrony in two orthogonal ways to investigate groove: events on unstressed or weak beats followed by subsequent strong beat events (pickups) and events on unstressed beats *not* followed by subsequent strong beat events (syncopations). The standard musicological definitions of pickups (also called anacruses or upbeats) and syncopation (see definitions in Refs.[31,32]) indicate that each deviation type has a different musical function: (a) pickups cue the following strong beat event and then fulfill it; (b) syncopations break this bond by omitting the strong beat event[32,33]. In other words, or psychological terms, pickups could be analogous to a priming stimulus prior to a temporal event while a syncopation seems more akin to its omission. Such a role of pickups in the experience of groove has been previously hypothesized[5,6] although it was not investigated independently of syncopation. We predicted that pickups would elicit weaker pupil dilations than syncopations because syncopations lack a subsequent strong beat, making them more surprising and requiring more cognitive resources to suppress. For the purposes of this paper, we treat both pickups and syncopation as deviations that increase the rhythmic complexity of our stimuli (relative to rhythms without weak beat events) even if they may do so in different ways.

Many studies in cognitive psychology have employed simple drumbeats (e.g., kick-snare-hihat) to investigate rhythmic properties' relation to groove[4,7,29,34–36]. However, these foundational studies tended to be more exploratory in nature and so several factors and parameters were uncontrolled, like event order, metric levels, perceived musicality, and the potential effect of pickups. To ensure that rhythmic complexity is the driving factor behind groove, the order of rhythmic events needs to be consistent in each condition since a kick-snare and snare-kick sound are qualitatively different and could therefore impact the urge to move. Moreover, the syncopated drumbeats in these studies tend to rely more heavily on faster metric levels whereas their lower or unsyncopated counterparts tend to remain at slower subdivisions, that is, subdivisions that are one level higher in the metric hierarchy. If these variations are systematic, they may introduce additional cognitive demands (e.g., attending to another metrical level) that scale in parallel to the amount of syncopation. Another pitfall is that stimuli sound nonmusical or cease to sound musical after being subjected to rigorous manipulation. If certain rhythmic conditions systematically sound less musical than others, this could affect the experience of groove and create or exaggerate differences that could then falsely be attributed to metric complexity; indeed, experienced familiarity with the music has been shown to play a role in groove[34]. Finally, while prior groove studies rigorously accounted for syncopations, none explicitly examined the predictive role of pickups and its effect on groove.

Because individual differences in beat perception could affect the way subjects model the rhythms, and therefore their experience of groove, we also administered the Computerised Adaptive Beat Alignment Test (CA-BAT)[37,38]. With this information, we hoped to extend previous findings that demonstrated a more prominent inverted U-shaped relationship between groove and syncopation in musicians[39] by directly probing beat perception abilities that have been linked to synchronizing to high- and low-groove music[40], without necessarily identifying such ability with musicianship. Specifically, we expected to find divergent results between high and low beat perception performance at the upper end of rhythmic complexity. Since good beat perception would be necessary to generate a predictive model of the most complex repeating drumbeat, this should result in greater groove ratings for high performers on the CA-BAT but not the low performers.

Methods

Participants. We recruited 30 participants (seven women) with varying degrees of musical experience and expertise as assessed by a custom-made questionnaire and the CA-BAT. All participants provided informed consent in accordance with the Declaration of Helsinki[41] and were compensated with a 100 NOK (~ €10) gift card. Ethical approval was granted by the Department of Psychology's internal research ethics committee at the University of Oslo (reference number 8131575). The average age of our sample was 26.8 (range 18–42, SD 5.07 years) and the average time spent listening to music was 24.03 h per week (range 1–84, median 21). Eleven of our subjects reported no musical training while the remaining 19 had trained for an average of 8.47 years (range 1–20, SD 6.22 years). Of these, 11 of 19 subjects played multiple instruments, with eight playing stringed instruments, four percussion, two brass instruments, seven piano, one voice, and five other/electronic instruments for an average of 5 h per week (range 0–27, standard deviation 6.59 h). A summary of each subject's demographics and performance can be found in Table 1 of the Supplementary Materials.

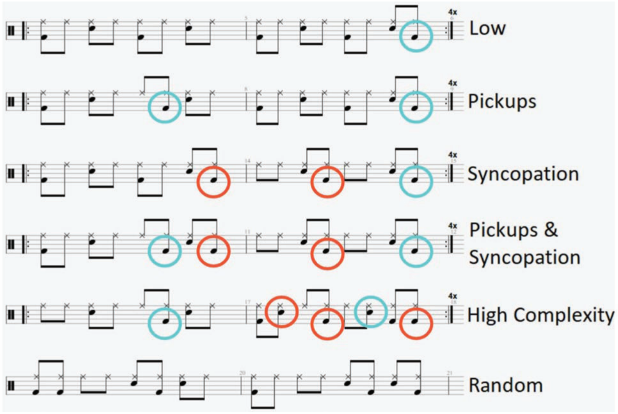

Figure 1. Musical notation for our drumbeat stimuli. Pickups are circled in blue while syncopations are circled in orange.

Stimuli. To ensure that our behavioral and pupillometry results reflected rhythmic complexity, each drumbeat followed the same order of events (alternating kicks and snare hits over a zeitgeber hihat, with an extra kick in the second bar) at the same metric level (that of the quaver) using the algorithm proposed by Sioros et al.[32]. Furthermore, we designed each stimulus with musicality in mind, starting with a standard back-beat rock drumbeat. It should be stressed here that our operationalization of Rhythmic Complexity narrowly treats any deviation from isochrony as an increase in complexity. While differing somewhat from the previously used Syncopation Index[7] in that it distinguishes between pickups and syncopations and avoids assigning scalar weights, it orders our stimuli in the same manner. How this maps onto psychological perceptions of complexity is an open question.

We settled on six different drumbeats: (1) a low complexity pattern with no pickups or syncopations (Low), (2) a pattern made moderately complex with pickups (Pickups), (3) a pattern made moderately complex with syncopation (Syncopation), (4) a pattern made moderately complex with both pickups and syncopation (Pickups and Syncopation), (5) a pattern made highly complex with more pickups and syncopations (High Complexity), and (6) a random condition where the event placements were pseudorandom (meeting our control criteria) and did not loop (Random). Except for the random condition, each drumbeat consisted of four two-bar patterns at 100 beats per minute for a total duration of 19.2 s. At the end of each two-bar pattern a kick drum stroke on the last eighth note position, that is, a pick-up to the first beat in bar 1, signals the start/end of a new pattern. The "random" condition was different from the others in that the pattern was randomly generated and varied with each repetition. Notations of each drumbeat are presented in Fig. 1 and sound files can be found here: https://osf.io/sd5up/?view_only=fa6bd354eb214368b77da9d5f18abcf1.

All stimuli were composed in Ableton Live, using MaxForLive devices for the automation of transformations, and produced in Reaper and then edited to appropriate lengths with Audacity[42].

Procedure. Pupil diameters were continuously sampled at 60 Hz using a SensoMotoric Instruments (SMI) RED250 eye tracker mounted beneath a 22-inch LED monitor in a dimly lit room situated 70 cm away from the subject. After a five-point (arranged in a cross) calibration and validation procedure, participants were instructed to passively listen to each drumbeat and immediately after rate each by how much they felt compelled to move ("I did not want to move at all" vs. "I wanted to move a lot" with movement being specified to include tapping or nodding), how much they liked the drumbeat ("I did not enjoy it at all" vs. "I enjoyed it a lot"), and how energetic the drumbeat sounded ("The drumbeat was very calm" vs. "The drumbeat was very excited") using visual analogue scales that spanned half the width of the monitor with each key press corresponding to a jump of seven pixels. This scale granularity was not visible to the subject and the sensitivity was titrated to feel natural during piloting. The first two questions were used to measure groove while the last acted as a catch question and to control for perceived energetic arousal of the stimuli. During each trial, subjects fixated on a black fixation cross presented on a gray background generated with Psychtoolbox-3 for MATLAB[43]. The first three seconds of fixation were silent, serving as a baseline. Subsequently, a stereo drumbeat stimulus was played at a comfortable volume from two Genelec speakers (model 8030 W) flanking the screen with a subwoofer beneath the desk to enhance the bass since previous research suggests that it plays an important role in groove and establishing the beat for sensorimotor synchronization[44–47]. Each stimulus was presented ten times in a pseudorandom order such that no stimulus could repeat back to back. Thus, all subjects completed 60 trials and were permitted to take self-paced breaks every five trials. After the main portion of the experiment, each participant then completed the CA-BAT with the entire experiment lasting about one hour.

Behavioral analysis. All subjects' ratings of Urge to Move, Enjoyment, and Perceived Arousal were z-scored to control for individual differences in the way that subjects used the visual analog scales. The z-scored ratings of each trial were averaged for each drumbeat for each subject and then summary statistics were calculated at the group level for each drumbeat. To investigate beat perception, we grouped participants into High ($N = 15$)

and Low ($N = 15$) Performance using a median split on their ability scores from the CA-BAT. The distribution of Beat Perception Ability scores as well as its significant correlations with our demographics measures are plotted in Supplementary Figs. 1–3. Differences between the High Complexity and Random drumbeats were compared using a mixed analysis of variance (ANOVA) with Beat Perception Performance group (High or Low) as a between-subjects factor and Rhythmic Complexity (High Complexity or Random) as a within-subject factor.

To replicate past findings of an inverted-U relationship between rhythmic complexity and groove, we fit mixed effects models to our subjects' ratings (Urge to Move, Enjoyment, Perceived Arousal). In keeping with standard practice, we first fit intercepts-only models with random effects of Subject and Stimulus Repetition and compared them to models with Rhythmic Complexity as linear slopes (linear model) as well as linear and quadratic slopes (quadratic model). Model comparison was conducted via likelihood ratio tests and both the Akaike (AIC) and Bayesian information criterions (BIC)[48]. Follow-up t-tests using Satterthwaite's method were carried out for best-fitting significant models.

To explore the possibly different effects of pickups and syncopation on perceived groove, we also organized our first four rhythms in a 2×2 design for a repeated measures ANOVA with factors Pickups (Present or Absent) vs. Syncopation (Present or Absent). The High Complexity and Random patterns were excluded from this analysis because they would unbalance the design. All behavioral plots and analyses were carried out using custom scripts in R (version 3.6.0[49]) and functions from the "dplyr", "readr", "ggplot2", "lme4", "lmerTest", "effsize", and "ez" packages.

Pupillometry analysis. Data were exported using SMI BeGaze™ to a format suitable for preprocessing and analysis using custom scripts in R (version 3.6.0[49]) as well as functions from the "pupillometry" package[50]. First, the pupil time series for the right eye were locked to the stimuli onsets. Blinks were removed along with the preceding and succeeding 100 ms to eliminate edge artifacts resulting from partial occlusions of the pupil. Each trial was then smoothed using a 500 ms Hann window at 60 Hz and gaps smaller than 750 ms were interpolated with cubic splining. Next, the median pupil value from the last 1000 ms of each trial's baseline period was subtracted from the rest of its time series to correct for random trial-to-trial fluctuations in a way that is less contaminated by noise than divisive baseline correction[51]. Finally, trials with more than 33% missing data were excluded and the remaining data was averaged in 100 ms bins for plotting and statistical analysis with the packages "ggplot2" and "ez", respectively. Overall, this left us with 96.94% of valid pupil samples for analysis.

In addition to the pupil traces for individual trials, we were also interested in the rate at which these traces decayed since they could represent "decreasing attentional engagement"[22]. This is of particular importance to us because if norepinephrine is involved with suppressing precision-weighted prediction errors, then its firing would be more sustained while listening to groovier rhythms. Conversely, attention would disengage more rapidly to both simpler rhythms (which do not produce many prediction errors to suppress) and more complex rhythms (where prediction errors cannot be suppressed). Thus, for each of the four stimuli repetitions within a trial, we calculated the slope between the average pupil size in the first and last beats (300 ms) and took this pupil drift rate to represent attentional maintenance (at higher values) or fatigue (at lower values).

Finally, the same repeated measures ANOVA with Pickups (Present or Absent) and Syncopations (Present or Absent) as factors was computed with average Pupil Size as the dependent measure. Significant effects were then localized to time windows corresponding to the rhythmic manipulations of interest (i.e., the moments surrounding the pickups or the syncopations) by repeating the test in those windows.

Results

Behavioral results. As expected, adding slopes for Rhythmic Complexity improved the model fit for all ratings. However, the quadratic slope significantly improved the fit for Urge to Move ($\chi^2(1) = 14.643$, $p < 0.001$) and Enjoyment ($\chi^2(1) = 20.774$, $p < 0.001$) while our control question, Perceived Arousal, only trended toward a significantly better fit ($\chi^2(1) = 3.429$, $p = 0.064$). Follow-up tests revealed significant negative quadratic (i.e., inverted U-shaped) trends for both Urge to Move ($b(29) = -3.167$, 95% CI [-4.643, -1.691]) and Enjoyment ($b(29) = -2.659$, 95% CI [-3.64, -1.675]), but not Perceived Arousal ($b(29) = -0.694$, 95% CI [-1.432, 0.043]). The significant quadratic predictors for Urge to Move and Enjoyment ratings are plotted in Fig. 2a.

Adding Beat Perception group to the mixed effects models yielded similar significant quadratic trends for Urge to Move ($b(28) = -3.738$, 95% CI [-5.804, -1.672]) and Enjoyment ($b(28) = -2.664$, 95% CI [-4.055, -1.27]) that better fit their linear equivalents (Urge to Move: $\chi^2(2) = 15.253$, $p < 0.001$; Enjoyment: $\chi^2(2) = 20.774$, $p < 0.001$). However, Beat Perception did not significantly impact any ratings except as an interaction with Enjoyment's linear trend which thus resulted in a slightly better model fit ($\chi^2(3) = 9.247$, $p = 0.02$). Follow-up tests revealed this was driven by the Low Beat Perception Performance group exhibiting a significant negative linear trend ($b(14) = -3.618$, 95% CI [-6.044, -1.193]) that was absent in the High Beat Perception Performance group. This indicates that while both High and Low Beat Perception groups showed prominent quadratic trends for both Urge to Move and Enjoyment, only the Low Beat Perception Performance group had a significant linear trend that improved model fit for Enjoyment. This is plotted in Fig. 2b.

The mixed ANOVA comparing High and Low CA-BAT Performance groups' Urge to Move ratings to the High Complexity and Random drumbeats yielded a marginally significant interaction between the two factors ($F(1,28) = 4.492$, $p = 0.043$, $\eta^2G = 0.022$) driven by a small effect in the High Beat Perception Performance group ($F(1,14) = 5.189$, $p = 0.039$, $\eta^2G = 0.077$) showing higher ratings for the High Complexity relative to the Random drumbeat that was absent in the Low Beat Perception Performance group ($F(1,14) = 0.115$, $p = 0.740$, $\eta^2G < 0.001$). For Enjoyment, a similarly marginal increase in ratings for the High Complexity compared to the Random drumbeat was found for both High and Low Beat Perception Performance groups ($F(1,28) = 5.490$, $p = 0.026$, $\eta^2G = 0.025$) alongside a slightly larger group difference where High Performers rated both drumbeats somewhat

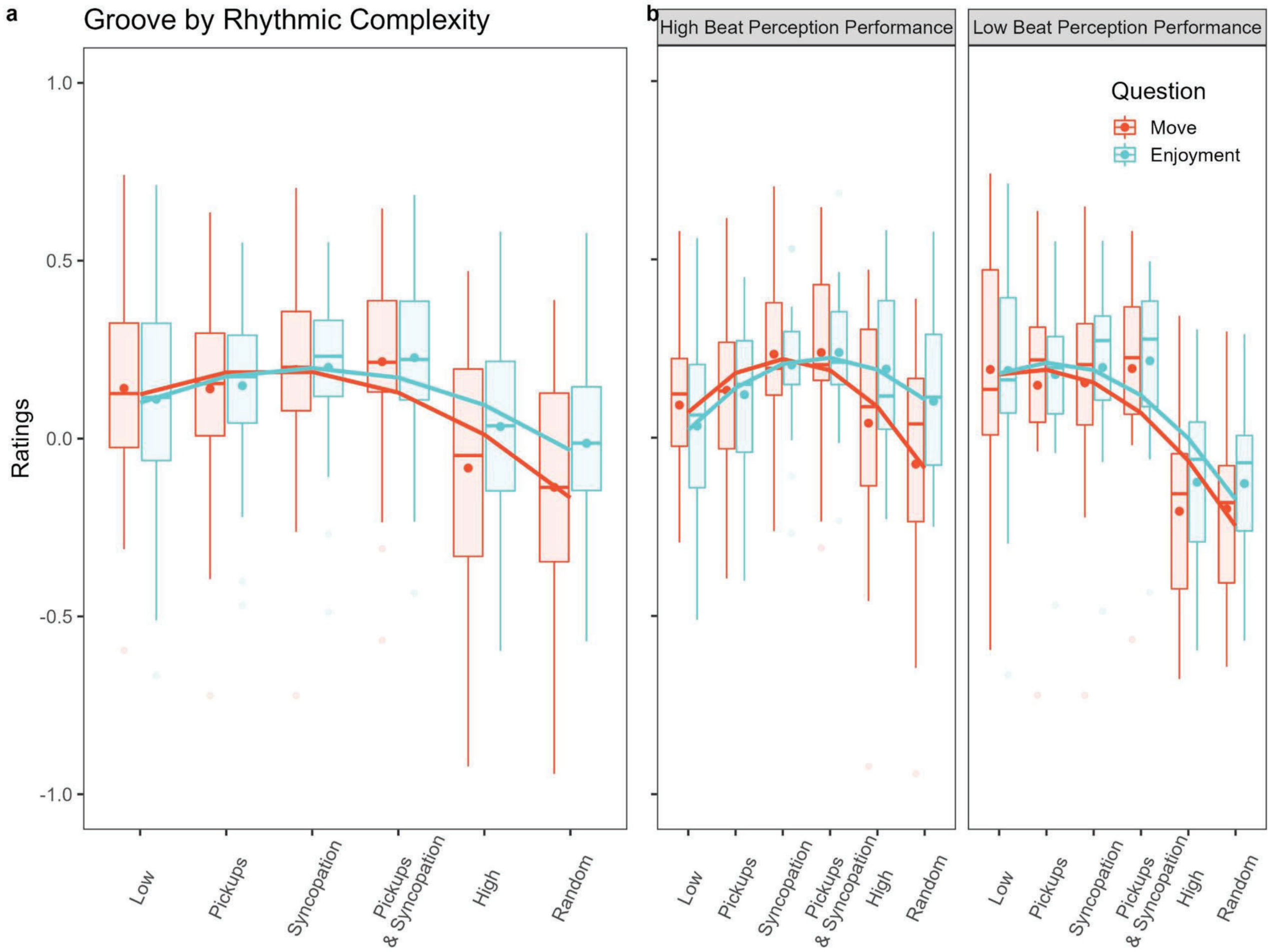

Figure 2. Quadratic models of the behavioral results across Rhythmic Complexity. (**A**) Quadratic models for Urge to Move, Enjoyment, and Perceived Arousal with individual subject predictors. Urge to Move and Enjoyment displayed significant quadratic trends. (**B**) Groove ratings across Rhythmic Complexity split by performance on the CA-BAT. There was a significant interaction between Beat Perception and the linear relationship between Rhythmic Complexity for Enjoyment.

higher than Low Performers ($F(1,28) = 6.108$, $p = 0.020$, $\eta^2G = 0.160$). No significant main effects or interactions were found for Perceived Arousal. Given the inconsistency between Urge to Move and Enjoyment ratings, these results should be taken with some caution.

Using the 2×2 design, a two-way repeated measures ANOVAs with within-subjects factors Pickups and Syncopation revealed that Syncopation, but not Pickups, significantly boosted ratings of Urge to Move ($F(1,29) = 4.781$, $p = 0.037$, $\eta^2G = 0.045$), Enjoyment ($F(1,29) = 10.515$, $p = 0.003$, $\eta^2G = 0.095$), and Perceived Arousal ($F(1,29) = 8.665$, $p = 0.006$, $\eta^2G = 0.085$) with no significant interaction between the two factors. These results are depicted in the boxplots in Fig. 3 below.

Pupillometry results. Binned and averaged pupil traces of each rhythm with within-subject confidence intervals are plotted in Fig. 4. All conditions demonstrate a sudden dilation consistent with the classic stimulus onset effect in the first repetition out of four, potentially masking effects of interest. To ensure that our drift rate results are untainted by such startle effects, this first repetition window was excluded from further analyses.

The pupil size's drift rate, representing the degree of attentional maintenance or fatigue, is plotted over the remaining three repetitions of the drumbeats in Fig. 5. A repeated measures ANOVA on the pupil drift rate with within-subject factors Rhythm and Repetition revealed a significant modest effect of Repetition ($F(1,29) = 26.774$, $p < 0.001$, $\eta^2G = 0.105$) and a smaller but significant interaction between the two factors ($F(5,145) = 2.434$, $p = 0.038$, $\eta^2G = 0.044$). Post-hoc tests revealed this interaction to be driven by a main effect of Rhythm found only in the second repetition ($F(4.517,130.994) = 3.104$, $p = 0.0139$, $\eta^2G = 0.067$, Huynh–Feldt corrected) and a trend in the third repetition ($F(5,145) = 2.009$, $p = 0.081$, $\eta^2G = 0.054$). For this reason and from visual inspection of the entire pupil trace time series, we chose to focus further analyses on the second repetition alone. Remarkably, the pupil's drift rate during the second repetition mirrors the Urge to Move and Enjoyment ratings in the behavioral portion of the experiment. Using the same mixed effects modeling procedure as the behavioral data, we found that a quadratic model fits the pupil drift rate data significantly better than a linear model ($\chi^2(1) = 9.721$,

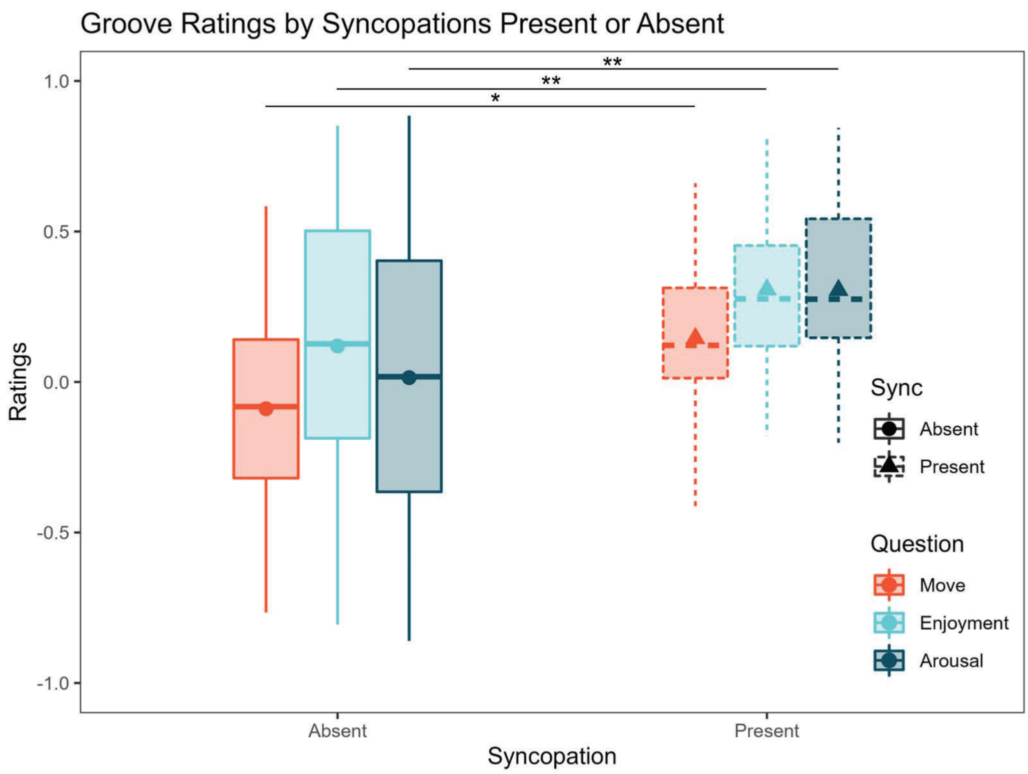

Figure 3. Ratings with pickups (present or absent) and syncopations (present or absent) analyzed orthogonally. The presence of syncopations results in greater ratings of urge to move, enjoyment, and perceived arousal regardless of pickups' presence. Large dots and triangles represent averages. Single asterisk is $p < 0.05$, two asterisks $p < 0.01$.

$p = 0.002$). Follow-up contrasts showed that this quadratic trend for Rhythm was significant ($b(148) = -0.349$, 95% CI [-0.557, -0.140]), demonstrating an inverted U-shape. This is depicted in Fig. 6a.

Adding beat perception as a fixed effect like we did with the behavioral data improved model fit for the pupil drift rates as well ($\chi^2(2) = 15.939$, $p < 0.001$). Follow-up tests revealed a main effect of the quadratic trend ($b(146) = -0.605$, 95% CI [-0.890, -0.321]) and a significant interaction with Beat Perception ($b(146) = 0.513$, 95% CI [0.111, 0.915]). This interaction was driven by a significant quadratic trend that was only present in the High Beat Perception Performance group ($b(14) = -0.428$, 95% CI [-0.619, -0.237]), indicating this group exhibited an inverted U-shape while the Low Beat Perception Performance group did not. This is plotted in Fig. 6b.

Next, we repeated our analysis of pickups vs. syncopations using average pupil size data on the entire time window. Here, a repeated measures ANOVA with the factors pickups (Present or Absent) and syncopation (Present or Absent) revealed a significant main effect of pickups ($F(1,29) = 4.421$, $p = 0.044$, $\eta^2G = 0.011$). To confirm that this effect was indeed driven by the actual presence of the pickups, we ran this analysis on time windows surrounding the pickups. Given the temporal resolution of the pupil dilation response, we chose 1500 ms windows starting with the standard kick and ending 300 ms after the downbeat of the second bar to ensure each window had the same number of events (two kicks and a snare). This is illustrated in Fig. 7a. The repeated measures ANOVA corroborated this suspicion: there was a significant main effect of Pickups ($F(1,29) = 4.626$, $p = 0.040$, $\eta^2G = 0.013$) with no effect of Syncopation or interaction, indicating greater pupil dilations in the two conditions with pickups. This is plotted in Fig. 7b.

Discussion

In this study, we aimed to investigate pupillometric arousal in the context of groove and its relation to rhythmic complexity using a broad range of rigorously controlled drumbeat stimuli with the novel distinction between pickups and syncopations. We replicated previous behavioral results demonstrating an inverted U-shaped relationship between rhythmic complexity and groove, a relationship that seems less linear with rhythmic expertise as assessed by a beat perception test. We found that rhythms rated groovier were associated with more sustained attention as measured by the pupil size's drift rate and that this also mapped onto groove ratings split by beat perception ability. Finally, pickups evoked greater pupil dilations while syncopations did not, whereas syncopations resulted in higher groove ratings while pickups exerted no effect on ratings.

Groove ratings. First and foremost, groove ratings confirmed previous findings[4,5,7,29,34,35]. However, our results also go beyond replication and add nuance by investigating pickups orthogonally to syncopation. While

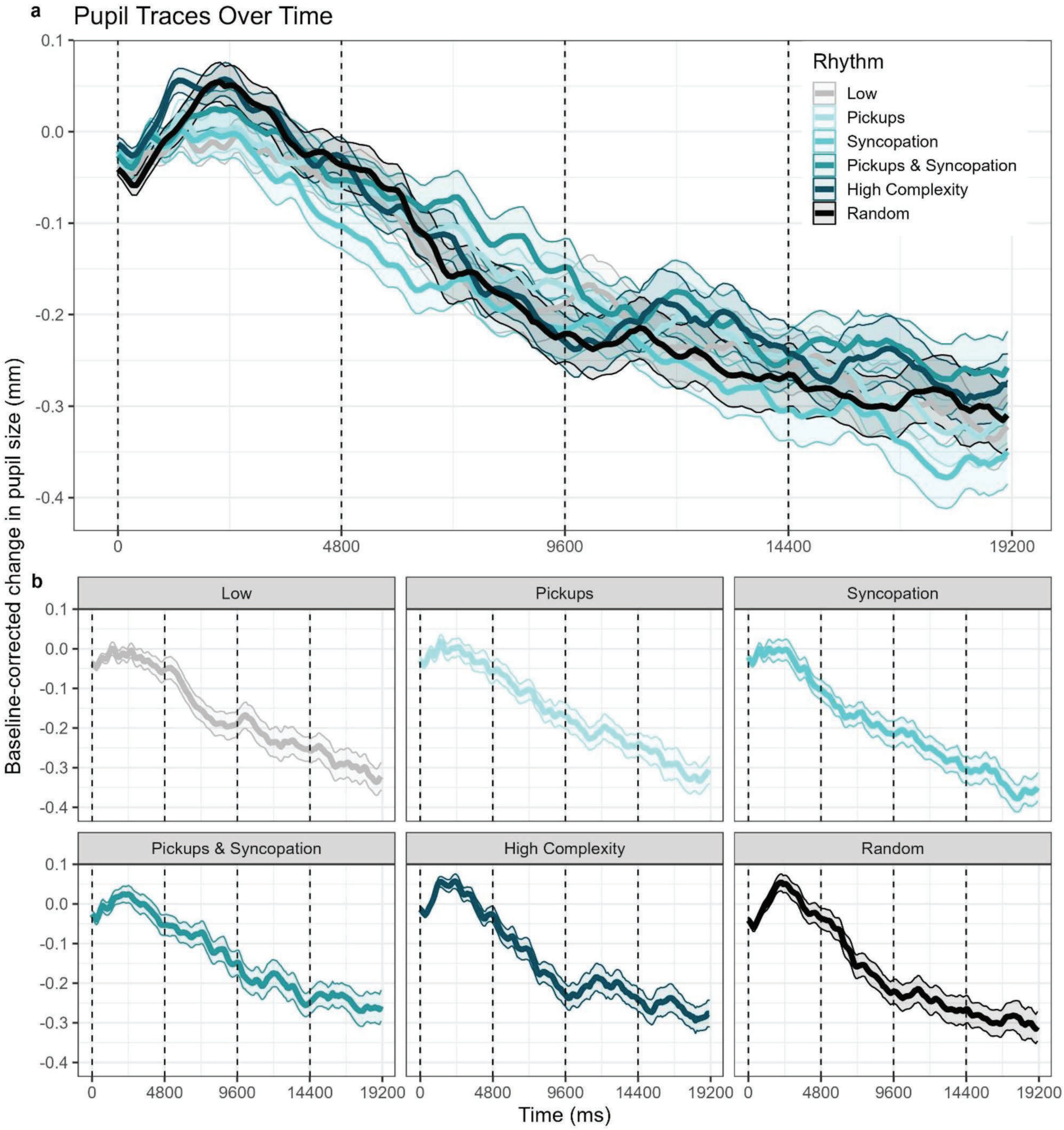

Figure 4. Pupil trace plots for all rhythm conditions over time. Ribbons represent within-subject 95% confidence intervals. Dashed vertical lines represent the boundaries where the first five rhythms looped. (**A**) Pupil traces for all rhythm conditions plotted against each other. (**B**) Pupil traces for each individual rhythm condition plotted separately for better visibility.

syncopation is certainly one way of manipulating rhythmic expectations, we discovered that their combination with pickups, that is, unstressed notes that reinforce the following strong beat (pulse) or the beginning of a new measure (meter)[31], is what produced maximal groove in our sample of drumbeats, as was previously hypothesized by Sioros et al.[5,6]. This characterization of groove is in line with both the descriptive musicological model proposed by Sioros et al.[32] and predictive coding as we will discuss further in the following subsection.

Our analyses using beat perception performance as an individual difference also fit neatly within the predictive coding framework. Qualitatively, High Performers on the CA-BAT displayed inverted-U curves centered closer to the moderate levels of rhythmic complexity whereas ow Performers exhibited a significant negative linear trend that the High Performers did not. At upper levels of complexity, groove ratings are only enhanced by repetition in subjects with high CA-BAT performance, implying that the enjoyable urge to move to rhythms is indeed related to global predictions about their structures should they be perceived. Low Performers also

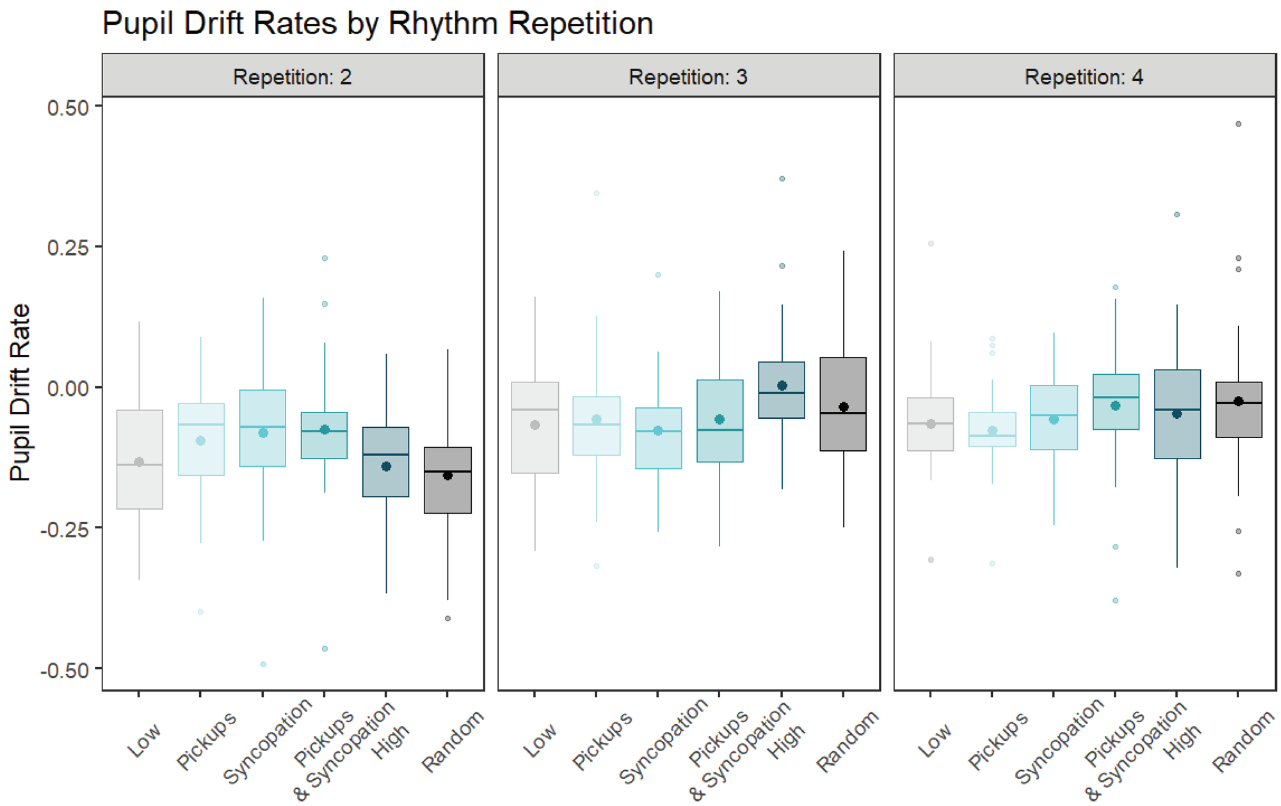

Figure 5. Pupil drift rates by condition across the remaining three within-trial drumbeat repetitions. Drift rates were calculated by averaging the pupil sizes in the first and last three time bins of each repetition with each trial and then computing the slope between these two averages. Large dots represent averages.

appeared to find the Low Complexity rhythm groovier than high performers, likely because our Low Complexity rhythm was still complex enough to produce prediction errors for them to suppress. The high performance group, however, would not have this experience since their global model of the beat is strong enough to automatically suppress these smaller errors without the need for active inference. This is supported by studies like those of Matthews et al.[39] where experienced musicians displayed more pronounced quadratic effects in their groove ratings. These findings, however, should be taken with some caution given the inconsistent and marginal nature of our results, especially when comparing ratings of the High Complexity and Random drumbeats between groups. Further, using the entire distribution of CA-BAT scores as a linear predictor in our models was not significant, likely because our sample size was not particularly large or widely dispersed which may have adversely impacted our effect sizes. Thus, more focused work is needed to definitively support these claims.

Attentional maintenance. Our groove ratings were most closely mirrored by the pupil drift rate, suggesting that more sustained attention is associated with greater groove. This relationship persisted, albeit with similarly small effect sizes, when subjects were split by their CA-BAT performance as well. This is consistent with the hypothesis that an active process of correcting prediction errors with attentional resources underlies the enjoyable urge to move to music. We believe that this better maintenance of attention was the product of the interplay between pickups and syncopations in our stimuli. This drift, however, seems to approach floor with our musical stimuli after around 10 s, indicating that habituation can occur and mask these differences over extended periods of time.

Divergent/complementary roles for pickups and syncopations. Analyzing groove ratings and pupil size data with syncopations and pickups as separate factors exposed a dissociation where syncopations, but not pickups, significantly boosted ratings but pickups, not syncopations, evoked greater pupil dilations. While this may seem puzzling at first, in the context of our stimuli and the predictive contexts they created together, this can be explained by their different musical functions and the information that they feed to higher-order predictions about the metric structure. Syncopations, by generating prediction errors that challenge global predictions of pulse, create the primary tension that compels us to actively correct them with our movement. Pickups, on the other hand, may strengthen global predictions regarding pulse and meter by immediately fulfilling the expectation that events occur on strong beats, that is, they point out important beats by leading up to and anticipating them, in accordance with the previous hypotheses of Sioros et al.[5,6]. This covert deployment of attentional resources to the pickups occurs regardless of the presence of syncopations and is thus reflected in greater pupil size.

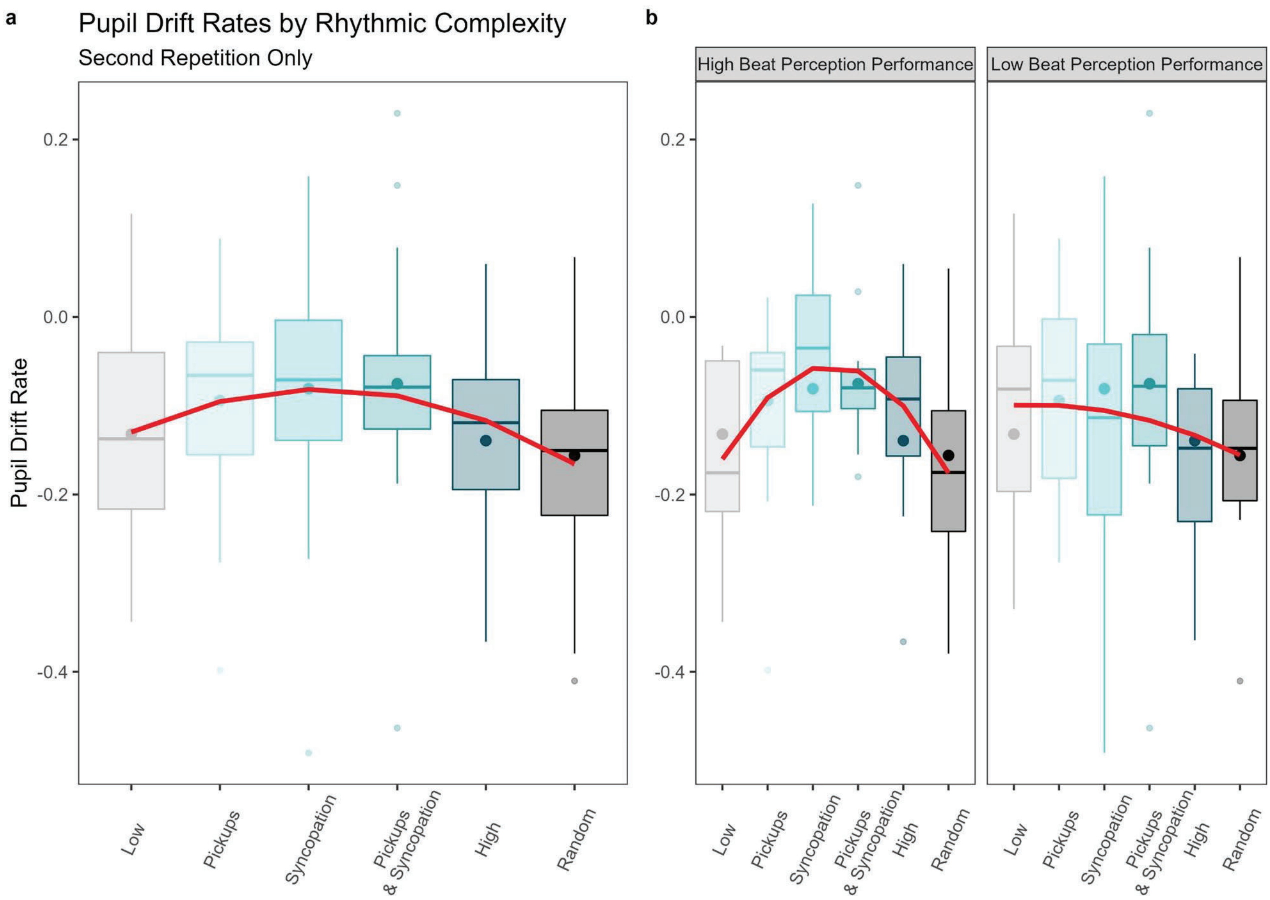

Figure 6. Quadratic fits for the pupil drift rate across rhythmic complexity for Repetition 2 where the significant interaction was found. (**A**) Quadratic predictor of pupil drift rates by rhythm condition during the second repetition of the drum pattern within the trials. Large dots represent averages. (**B**) Pupil drift rates with quadratic predictors by high and low beat perception performance. High performers displayed a significant quadratic relationship with rhythmic complexity while low performers did not.

To support the arguments above, we linked pupil dilations to the specific window where the pickups manipulation occurred in our stimuli; this effect endured through all repetitions within the trials. Because the time window's onset corresponded to 300 ms before the pickup in the Pickups and Pickups and Syncopation rhythms, it seems possible that the pupil may have dilated in anticipation of the beat to strengthen global predictive models of the metric structure. This explanation adds support to the predictive coding literature where the brain is theorized to construct top-down predictions about future sensory experiences that are then used to update those predictions[52,53].

Pickups are especially intriguing because they might be thought to reinforce the pulse and meter rather than challenge it, and thus compensate for the subversive effect of syncopations which lack the subsequent event on the strong beat[33,54]. In predictive coding terms, both pickups and syncopations may produce local prediction errors since they fall on weak beats (i.e., they violate isochrony), but they propagate different information to higher-order predictions about the metric structure. Because pickups are paired with strong beat events that confirm predictions of the global rhythmic structure, the local prediction errors from the pickups are more precise than those arising from the more unexpected syncopations that lack immediate clarification and consequently call the global rhythmic structure into question. That is, rather than being perceived as unexpected events, pickups' close proximity to a strong beat event immediately resolves the challenge to isochrony and strengthens the global model whereas this challenge goes unchecked for syncopations. Neurophysiologically, the brain may release norepinephrine to increase the gain of the picked up strong beat and strengthen the metric model, whereas the omission of this strong beat in syncopations needs to be suppressed with movement because it calls the metric model into question. Thus, while syncopations generate the metrical uncertainty that may demand resolution through movement, pickups strengthen the internal model that could be used to guide movements. These movements are then used to reinforce the metric model itself in a feedback loop.

Limitations and future directions. While we believe our results are consistent with predictive coding, the inverted U-shaped relationship found in the groove ratings and pupil drift rate could potentially be a result of familiarity since most music composed in the Western musical traditions contains moderate amounts of rhythmic complexity (e.g., a mixture of both pickups and syncopations). Predictive coding elegantly posits that music

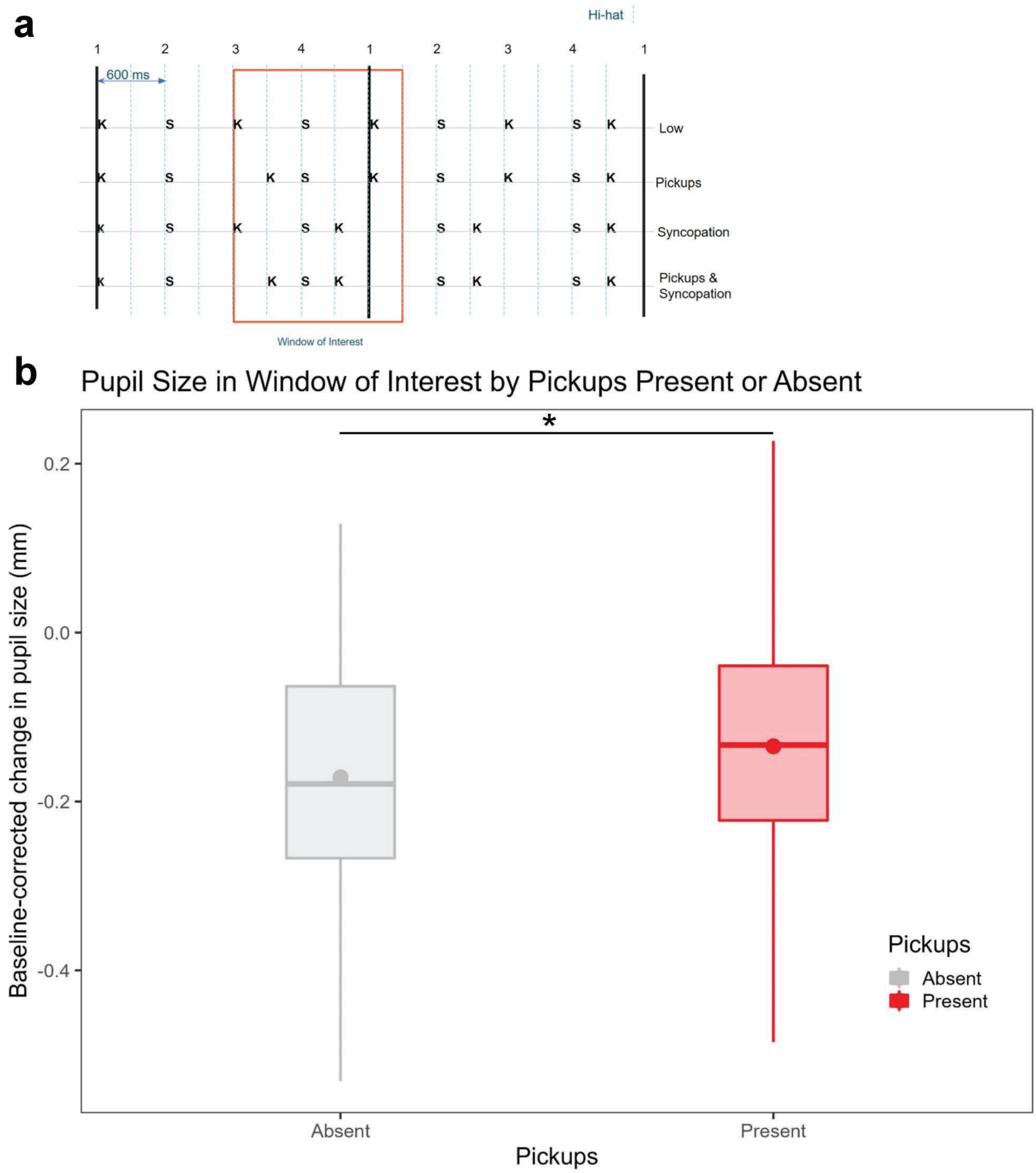

Figure 7. Pupil Size analysis by pickups (Present or Absent) and syncopations (Present or Absent) in the window of interest where the pickup manipulation occurred. (**A**) Window of interest for further analysis. Dashed lines represent hihat hits while Ks represent kick drum hits and Ss represent snare drum hits. Low = Pickups absent, Syncopations Absent, Pickups = Pickups Present, Syncopations Absent, Syncopation = Pickups Absent, Syncopations Present, Pickups and Syncopation = Pickups Present, Syncopations Present. (**B**) Boxplots showing pupil size in the window of interest by Pickups and Syncopation. Large dots and triangles represent group averages.

was composed this way because of predictive processes, but it is entirely possible that this occurred for other reasons that then became encultured and familiar. This hypothesis would be consistent with recent evidence presented by Sioros et al.[6], where algorithmically-generated random syncopation patterns were less effective in evoking groove than the original syncopating patterns of the music excerpts that had a similar degree of syncopation but were created by musicians. We did not assess familiarity in this study because we composed our own stimuli (thus, the participants should not have explicitly recognized any of our drumbeats), but cross-cultural work should be done to disentangle the effects of enculturation and rhythmic complexity.

An alternative explanation for why pickups elicited greater pupil dilations is that the pickups created phenomenal accents on the subsequent strong beat[55]. That is to say, the pickup primed the following beat so that it sounded illusorily louder than other notes, which then evoked a dilation in the pupil. Indeed, past psychoacoustics research has reported small enhancements in perceived loudness of secondary tones with paired sound sequences around the same time interval as our stimuli (300 ms)[56,57]. Since physical loudness differences have been shown to result in greater pupil dilations[58,59], this account seems plausible and indeed we cannot rule out this possibility with the data presented here. However, because accents direct attention, we take this interpretation to be complementary to our own that pickups cue attention to strong beats to emphasize the metric model in a sort of attentional priming[60].

Another reason why pickups resulted in greater pupil dilations is potentially because of the number of events. Although we controlled for this as best as we could by ensuring that there were equal kick, snare, and hihat hits in each condition, it is possible that the pupillary response to syncopations occurs at a longer timescale than for pickups. Because syncopations can only be appraised as such after the omitted strong beat has passed, the response for syncopations may have extended beyond our window of interest while the more immediate dilation for pickups was captured. While this confound may have been mitigated by the additional 300 ms after the downbeat in our window of interest (600 ms after the kick in the syncopated conditions), we nevertheless contend that any potential dilation delay is captured by the drift rate analyses.

On a related note, a shortcoming of pupillometry is that the temporal resolution is limited and we cannot directly probe the evoked responses to individual pickups and syncopations. Many researchers have cleverly found ways to remedy this with deconvolution[61–64]. However, as Fink et al.[65] note, estimating the delay between stimuli and the pupil responses is not always so straightforward and has been shown to differ depending on whether motor responses are required[63]. Temporal alignment may prove even more difficult when using musical stimuli where anticipation changes response latency over time. Moreover, this temporal alignment may also vary with different types of musical anticipation (e.g., for syncopations vs. pickups). Fink and colleagues' forward modeling method avoids this issue, but the interpretation shifts from evoked pupil responses to fitting predictive models. In order to more directly measure both rhythmic entrainment and quick, evoked responses without introducing theoretical assumptions, we plan to record EEG in further investigations of groove for its greater temporal resolution. In addition to entrainment, event-related potentials to on- and off-beat notes in different rhythmic contexts could elucidate finer differences between pickups and syncopations.

We further plan to extend our behavioral findings regarding the effect of repetition at high levels of rhythmic complexity by beat perception ability to lower levels of complexity. Does repeating a rhythm continue to result in higher groove ratings for only those with strong beat perception abilities or does it generalize to everyone when the beat is easier to perceive? In this way, we can directly modulate global predictions through repetition at every level of metric complexity to disentangle pure predictive processes from musicological ones.

Conclusions

To our knowledge, this is the first rigorously controlled study of pupil size changes over a broad range of rhythmic complexity that encompasses both pickups and syncopations in order to investigate the neurophysiological correlates of groove. Previous studies either did not fully explore the upper end of complexity or did not clearly distinguish the role of pickups. Here we replicate the canonical inverted U-shaped relationship between rhythmic complexity and groove ratings, including that this effect is enhanced by musical ability using a psychoacoustic test rather than participant demographics. These results seem consistent with the pupil drift rate, suggesting that groovier rhythms hold attention longer than ones rated less groovy. Moreover, we found divergent but complementary effects of syncopations and pickups on groove ratings and pupil size, respectively, extending previous findings by discovering a distinct predictive role for pickups. Specifically, while syncopations may demand our movement to enforce the metric model, pickups evoke greater pupil dilations and cue our attention to strong metric positions without our own movement. This thus lends correlative support to the predictive coding account where groove is envisioned as an embodied resolution of precision-weighted prediction error[8,9]

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References

1. Câmara, G. S. & Danielsen, A. Groove. in The Oxford Handbook of Critical Concepts in Music theory (eds. Rehding, A. & Rings, S.) (Oxford University Press, 2018).
2. Janata, P., Tomic, S. T. & Haberman, J. M. Sensorimotor coupling in music and the psychology of the groove. *J. Exp. Psychol. Gen.* **141**, 54 (2012).
3. Madison, G. Experiencing groove induced by music: consistency and phenomenology. *Music Percept.* **24**, 201–208 (2006).
4. Madison, G. & Sioros, G. What musicians do to induce the sensation of groove in simple and complex melodies, and how listeners perceive it. *Front. Psychol.* **5**, 894 (2014).
5. Sioros, G., Miron, M., Davies, M., Gouyon, F. & Madison, G. Syncopation creates the sensation of groove in synthesized music examples. *Front. Psychol.* **5**, 1036 (2014).
6. Sioros, G., Madison, G., Cocharro, D., Danielsen, A. & Gouyon, F. Syncopation and groove in polyphonic music: Patterns matter. *Music Percept. Interdiscip. J.* **39**, 503–531 (2022).
7. Witek, M. A., Clarke, E. F., Wallentin, M., Kringelbach, M. L. & Vuust, P. Syncopation, body-movement and pleasure in groove music. *PLoS One* **9**, 94446 (2014).

8. Koelsch, S., Vuust, P. & Friston, K. Predictive processes and the peculiar case of music. *Trends Cogn. Sci.* **23**, 63–77 (2019).
9. Vuust, P. & Witek, M. A. Rhythmic complexity and predictive coding: A novel approach to modeling rhythm and meter perception in music. *Front. Psychol.* **5**, 1111 (2014).
10. Vuust, P., Dietz, M. J., Witek, M. & Kringelbach, M. L. Now you hear it: A predictive coding model for understanding rhythmic incongruity. In *Annals of the New York Academy of Sciences* (2018).
11. Witek, M. A. Filling in: Syncopation, pleasure and distributed embodiment in groove. *Music Anal.* **36**, 138–160 (2017).
12. Repp, B. H. & Su, Y. H. Sensorimotor synchronization: A review of recent research (2006–2012). *Psychon. Bull. Rev.* **20**, 403–452 (2013).
13. Large, E. W. & Jones, M. R. The dynamics of attending: How people track time-varying events. *Psychol. Rev.* **106**, 119 (1999).
14. Morillon, B., Schroeder, C. E. & Wyart, V. Motor contributions to the temporal precision of auditory attention. *Nat. Commun.* **5**, 1–9 (2014).
15. Schroeder, C. E., Wilson, D. A., Radman, T., Scharfman, H. & Lakatos, P. Dynamics of active sensing and perceptual selection. *Curr. Opin. Neurobiol.* **20**, 172–176 (2010).
16. Yon, D. & Frith, C. D. Precision and the Bayesian brain. *Curr. Biol.* **31**, 1026–1032 (2021).
17. Alnæs, D. *et al.* Pupil size signals mental effort deployed during multiple object tracking and predicts brain activity in the dorsal attention network and the locus coeruleus. *J. Vis.* **14**, 1–1 (2014).
18. Joshi, S., Li, Y., Kalwani, R. M. & Gold, J. I. Relationships between pupil diameter and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron* **89**, 221–234 (2016).
19. Wilhelm, B., Wilhelm, H. & Lüdtke, H. Pupillography: Principles and applications in basic and clinical research. In *Pupillography: Principles, Methods and Applications* 1–11 (1999).
20. Kahneman, D. & Beatty, J. Pupil diameter and load on memory. *Science* **154**, 1583–1585 (1966).
21. Laeng, B., Sirois, S. & Gredebäck, G. Pupillometry: A window to the preconscious?. *Perspect. Psychol. Sci.* **7**, 18–27 (2012).
22. Laeng, B. & Alnaes, D. Pupillometry. In *Eye Movement Research* 449–502 (Springer, 2019).
23. Dahl, M. J., Mather, M., Sander, M. C. & Werkle-Bergner, M. Noradrenergic responsiveness supports selective attention across the adult lifespan. *J. Neurosci.* **40**, 4372–4390 (2020).
24. Grueschow, M., Kleim, B. & Ruff, C. C. Role of the locus coeruleus arousal system in cognitive control. *J. Neuroendocrinol.* **32**, 12890 (2020).
25. Kahneman, D. *Attention and Effort*. vol. 1063 (Prentice-Hall, 1973).
26. Mather, M., Clewett, D., Sakaki, M. & Harley, C. W. Norepinephrine ignites local hotspots of neuronal excitation: How arousal amplifies selectivity in perception and memory. *Behav. Brain Sci.* **39**, e200 (2016).
27. Oliva, M. Pupil size and search performance in low and high perceptual load. *Cogn. Affect. Behav. Neurosci.* **19**, 366–376 (2019).
28. Kanai, R., Komura, Y., Shipp, S. & Friston, K. Cerebral hierarchies: Predictive processing, precision and the pulvinar. *Philos. Trans. R. Soc. B Biol. Sci.* **370**, 20140169 (2015).
29. Bowling, D. L., Graf Ancochea, P., Hove, M. J. & Fitch, W. Pupillometry of groove: Evidence for noradrenergic arousal in the link between music and movement. *Front. Neurosci.* **12**, 1039 (2019).
30. Skaansar, J. F., Laeng, B. & Danielsen, A. Microtiming and mental effort: Onset asynchronies in musical rhythm modulate pupil size. *Music Percept.* **37**, 111–133 (2019).
31. Kennedy, M. & Kennedy, J. *The Oxford Dictionary of Music*. (Oxford University Press, 2013).
32. Sioros, G., Davies, M. E. & Guedes, C. A generative model for the characterization of musical rhythms. *J. New Music Res.* **47**, 114–128 (2018).
33. Huron, D. *Sweet Anticipation: Music and the Psychology of Expectation*. (The MIT Press, 2006).
34. Senn, O., Kilchenmann, L., Bechtold, T. & Hoesl, F. Groove in drum patterns as a function of both rhythmic properties and listeners' attitudes. *PLoS One* **13**, 0199604 (2018).
35. Witek, M. A. *et al.* Syncopation affects free body-movement in musical groove. *Exp. Brain Res.* **235**, 995–1005 (2017).
36. Madison, G., Gouyon, F., Ullén, F. & Hörnström, K. Modeling the tendency for music to induce movement in humans: First correlations with low-level audio descriptors across music genres. *J. Exp. Psychol. Hum. Percept. Perform.* **37**, 1578 (2011).
37. Harrison, P. M. C. & Müllensiefen, D. (2018) https://doi.org/10.5281/zenodo.1415353.
38. Harrison, P. M. C. & Müllensiefen, D. Development and validation of the Computerised Adaptive Beat Alignment Test (CA-BAT). *Sci. Rep.* **8**, 1–19 (2018).
39. Matthews, T. E., Witek, M. A., Heggli, O. A., Penhune, V. B. & Vuust, P. The sensation of groove is affected by the interaction of rhythmic and harmonic complexity. *PLoS One* **14**, 0204539 (2019).
40. Leow, L. A., Parrott, T. & Grahn, J. A. Individual differences in beat perception affect gait responses to low-and high-groove music. *Front. Hum. Neurosci.* **8**, 811 (2014).
41. Association, W. M. World Medical Association Declaration of Helsinki. Ethical principles for medical research involving human subjects. *Bull. World Health Organ.* **79**, 373–374 (2001).
42. Team, A. Audacity(R): Free Audio Editor and Recorder [Computer application]. *Version* **2** (2019).
43. Kleiner, M., Brainard, D. & Pelli, D. What's new in Psychtoolbox-3? (2007).
44. Hove, M. J., Martinez, S. A. & Stupacher, J. Feel the bass: Music presented to tactile and auditory modalities increases aesthetic appreciation and body movement. *J. Exp. Psychol. Gen.* **149**, 1137 (2019).
45. Lenc, T., Keller, P. E., Varlet, M. & Nozaradan, S. Neural tracking of the musical beat is enhanced by low-frequency sounds. *Proc. Natl. Acad. Sci.* **115**, 8221–8226 (2018).
46. Stupacher, J., Hove, M. J. & Janata, P. Audio features underlying perceived groove and sensorimotor synchronization in music. *Music Percept. Interdiscip. J.* **33**, 571–589 (2016).
47. Dyck, E. *et al.* The impact of the bass drum on human dance movement. *Music Percept. Interdiscip. J.* **30**, 349–359 (2013).
48. Vrieze, S. I. Model selection and psychological theory: A discussion of the differences between the Akaike information criterion (AIC) and the Bayesian information criterion (BIC. *Psychol. Methods* **17**, 228 (2012).
49. Team, R. C. R: A Language and Environment for Statistical Computing. In *R Foundation for Statistical Computing* (2013).
50. Tsukahara, J. S. pupillometry: An R Package to Preprocess Pupil Data. (2020).
51. Mathôt, S., Fabius, J., Heusden, E. & Stigchel, S. Safe and sensible preprocessing and baseline correction of pupil-size data. *Behav. Res. Methods* **50**, 94–106 (2018).
52. Clark, A. *Surfing Uncertainty: Prediction, Action, and the Embodied Mind*. (Oxford University Press, 2015).
53. Hohwy, J. *The Predictive Mind*. (Oxford University Press, 2013).
54. London, J. *Hearing in Time: Psychological Aspects of Musical Meter*. (Oxford University Press, 2012).
55. Lerdahl, F. & Jackendoff, R. S. *A Generative Theory of Tonal Music, Reissue, with a New Preface*. (MIT Press, 1996).
56. Irwin, R. J. & Zwislocki, J. J. Loudness effects in pairs of tone bursts. *Percept. Psychophys.* **10**, 189–192 (1971).
57. Scharf, B. Loudness. *Handb. Percept.* **4**, 187–242 (1978).
58. Liao, H. I., Kidani, S., Yoneya, M., Kashino, M. & Furukawa, S. Correspondences among pupillary dilation response, subjective salience of sounds, and loudness. *Psychon. Bull. Rev.* **23**, 412–425 (2016).
59. Boswijk, V., Loerts, H. & Hilton, N. H. Salience is in the eye of the beholder: Increased pupil size reflects acoustically salient variables. *Ampersand* **7**, 100061 (2020).

60. Netser, S., Ohayon, S. & Gutfreund, Y. Multiple manifestations of microstimulation in the optic tectum: Eye movements, pupil dilations, and sensory priming. *J. Neurophysiol.* **104**, 108–118 (2010).
61. Hoeks, B. & Levelt, W. J. Pupillary dilation as a measure of attention: A quantitative system analysis. *Behav. Res. Methods Instrum. Comput.* **25**, 16–26 (1993).
62. Kang, O. & Wheatley, T. Pupil dilation patterns reflect the contents of consciousness. *Conscious. Cogn.* **35**, 128–135 (2015).
63. McCloy, D. R., Larson, E. D., Lau, B. & Lee, A. K. Temporal alignment of pupillary response with stimulus events via deconvolution. *J. Acoust. Soc. Am.* **139**, 57–62 (2016).
64. Wierda, S. M., Rijn, H., Taatgen, N. A. & Martens, S. Pupil dilation deconvolution reveals the dynamics of attention at high temporal resolution. *Proc. Natl. Acad. Sci.* **109**, 8456–8460 (2012).
65. Fink, L. K., Hurley, B. K., Geng, J. J. & Janata, P. A linear oscillator model predicts dynamic temporal attention and pupillary entrainment to rhythmic patterns. *J. Eye Mov. Res.* **11**, 12 (2018).

Author contributions
All authors were involved with the conception and design of the experiment. Stimuli were designed, created, and edited by A.D., G.S., and C.S. All data were collected and analyzed by C.S., with G.S. and A.D. contributing processing and analysis for the drift rate and pickups by syncopation analyses, respectively. All authors collaborated on the interpretation of the data and C.S. wrote the first draft of the work. All authors revised the manuscript and approved the final submission.

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Competing interests
The authors declare no competing interests.

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Practice Makes Perfect: Beat Perception is Enhanced by Musical Training Not Active Music Playing

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1. Abstract

The ability to perceive the beat in music is crucial for both music listeners and players with expert musicians being notably skilled at noticing fine deviations in the beat. However, it is unclear whether this beat perception ability remains stable once trained or whether it diminishes with disuse. Thus, we investigated this by comparing active musicians', inactive musicians', and nonmusicians' beat perception ability scores on the Computerised Adaptive Beat Alignment Test (CA-BAT). 97 adults with diverse musical experience participated in the study, reporting their years of musical training, number of instruments played, hours of weekly music playing, and hours of weekly music listening, in addition to their demographic information. The analysis showed that there was no significant difference between active musicians', inactive musicians', and nonmusicians' CA-BAT scores once differences in musical training had been accounted for. Regression analysis confirmed that years of musical training was the only significant predictor of beat perception ability. These results suggest that expertly perceiving fine differences in the beat is not a use-dependent ability that degrades without regular maintenance through practice or musical engagement. Instead, beat perception appears to be a stable ability once sufficiently trained.

Keywords: {beat perception, active musicians, inactive musicians, nonmusicians, machine learning, musical training}

2. Introduction

2.1 Background

Practice makes perfect, but do you remain perfect after all that practice or do you lose it if you don't use it? Humans' ability to master a variety of skills has fascinated psychologists and neuroscientists for decades, culminating in a vast domain in and of itself (Chi et al., 2014; Ericsson & Charness, 1994; Feltovich et al., 2006; Sternberg & Grigorenko, 2003), spanning everything from sports (Shea & Paull, 2014) to chess (Charness, 1991). These impressive abilities are often described as the result of extensive practice and effort (Lehmann et al., 2018; Sloboda et al., 1996). Of particular interest to this work is how these factors impact musical expertise (Lehmann et al., 2018; Sloboda, 1991) and more importantly, whether they have a lasting effect once the practice comes to an end.

Musicians refine a number of different perceptual, motor, and cognitive skills to play their instrument(s) with fluency (Lehmann et al., 2007; Sloboda, 1991). Psychologically, this manifests in musicians outperforming nonmusicians in discriminating different pitches (Kishon-Rabin et al., 2001; Micheyl et al., 2006; Tervaniemi et al., 2005), tapping to rhythms (Chen et al., 2008; Franěk et al., 1991; Repp & Doggett, 2007; Skaansar et al., 2019), and remembering auditory stimuli (Cohen et al., 2011; Pallesen et al., 2010; Talamini et al., 2018). With the advent of neuroimaging tools, many studies have now shown that these differences manifest in a host of functional and anatomical changes to the brain as well (Amunts et al., 1997; Brattico et al., 2001; Criscuolo et al., 2022; Dawson, 2014; Imfeld et al., 2009; Jäncke, 2009). While there are clearly many investigations in the literature comparing musicians and nonmusicians, fewer break the dichotomy down into different types of musicianship and when they do, the results are often mixed. For instance, some studies have compared professional to amateur musicians and nonmusicians (Appelgren et al., 2019; Gaser & Schlaug, 2003; Hove et al., 2010; Kauffman & Carlsen, 1989; Krause et al., 2010; Mikutta et al., 2014; Repp, 2010), early- vs. late-trained musicians (Bailey et al., 2014; Bailey & Penhune, 2010, 2013; Shenker et al., 2022; Steele et al., 2013; Watanabe et al., 2007), and active vs. inactive musicians (Bonde et al., 2018; Hanna-Pladdy & Gajewski, 2012; Romeiser et al., 2021). This last classification of active vs. inactive musicians is especially important for investigating how ingrained these musical abilities truly are – do they dull without regular maintenance or are they set in stone once perfected?

One foundational musical ability is beat perception, the ability to detect temporal periodicities in musical rhythms (Nguyen et al., 2018; Schulze, 1978). The behavioral literature comparing beat perception in musicians and nonmusicians is somewhat mixed (Grahn & Rowe, 2009; Madsen, 1979; Rammsayer & Altenmüller, 2006) with clear individual differences present (Grahn & McAuley, 2009; Grahn & Schuit, 2012). Specifically, musicians have been shown to be more accurate in judging tempo (Madsen, 1979) and beat alignment (Grahn & Schuit, 2012) as well as displaying better rhythm perception (Rammsayer & Altenmüller, 2006) and greater subjective experience of the beat, but only when one was present (Grahn & Rowe, 2009). Conversely, other researchers found no difference between musicians and nonmusicians on rhythm discrimination (Grahn & Brett, 2007), temporal generalization (Rammsayer & Altenmüller, 2006), or (after an outlier was removed) beat strength tasks (Grahn & McAuley, 2009). This could be due to the multidimensionality of rhythmic abilities in general, with many different perceptual, cognitive, and genetic factors contributing (Fiveash et al., 2022; Niarchou et al., 2022). One factor that could potentially distinguish differences in beat perception between musicians that has remained largely unexplored is whether active maintenance of rhythmic abilities change through continued music playing or devolve when discontinued.

2.2 The Present Study

Therefore, the present study was conducted to investigate possible differences in beat perception between active and inactive musicians and nonmusicians. We hypothesized that trained musicians who continue to play music regularly would be able to discriminate finer deviations from the beat than nonmusicians and, to a lesser degree, inactive musicians who no longer play their instruments. A working hypothesis based on the 'use it or lose it' principle of brain plasticity (e.g., Shors et al., 2012) further suggests that inactive musicians may simply revert to a previous stage of the ability, though it is unclear whether this stage is comparable to or more advanced than nonmusicians. Alternatively, sufficient musical training may cement heightened abilities regardless of regular rehearsal or other metrics of musical engagement.

3. Methods

3.1 Participants

To this end, we analyzed beat perception ability scores obtained with the Computerised Adaptive Beat Alignment Test (CA-BAT) (Harrison & Müllensiefen, 2018b, 2018a) for previous studies by Spiech and colleagues (Spiech et al., 2022; Spiech et al., 2022; Spiech et al., 2022, in prep). Data from 97 unique participants recruited for three past studies on beat synchronization to challenging 'groovy' beats (Spiech et al., 2022; Spiech, et al., 2022, submitted; Spiech et al., 2022c, in prep) was used in this analysis. The participants included 46 women, of which 7 were left handed and 50 men. One individual did not report demographic information and we used the `mlim` R package (Haghish, 2022) to impute the missing observations. Participants were 27.2

years old on average (range: 18-56, SD: 6.1 years) and listened to music for an average of 17 hours per week (range: 1-84, SD: 15.1 hours).

First, we classified participants into Active Musicians, Inactive Musicians, and Nonmusicians using their self-reported instruments played, musical training, and weekly music playing. Active Musicians (N=48) were classified as any subjects who reported playing music weekly (M: 5.7, range: 1-27, SD: 5.9 hours). Active Musicians reported receiving 10.4 years of musical training on average (range: 0-34, SD: 7.6 years) and played a variety of instruments (29 stringed instrumentalists, seven percussionists, four brass instrumentalists, 18 pianists, 11 vocalists, and nine other instrumentalists including electronic music producers). Inactive Musicians (N=27) were classified as any subjects who reported *not* playing music weekly but had either received some musical training or reported being able to play an instrument. Inactive Musicians had an average of 5.4 years of musical training (range: 0-20, SD: 5.033 years) with nine playing stringed instruments, two playing percussion, five playing brass instruments, 12 playing piano, and one singing. The remaining participants (N=21) reported having no musical training nor having learned to play any instrument and were thus classified as Nonmusicians (N=21). These group characteristics are depicted in Table 1 below.

Musicianship Group	Number of Participants	Hours Played Weekly	Years of Musical Training	Number of Instruments Played
Active Musicians	48	5.7 (1-27)	10.4 (0-34)	1.7 (1-4)
Inactive Musicians	27	0	5.4 (0-20)	1.1 (0-2)
Nonmusicians	21	0	0	0

Table 1. Summary statistics of the different Musicianship groups. For hours played weekly, years of musical training, and number of instruments played, the first values represent the group average while the values in parentheses are the range.

3.2 Procedure

For the purposes of comparing uniform data, only the information from the custom-made musicianship questionnaire (results of which are summarized in the Participants section) and from the CA-BAT were used. The CA-BAT is a reliable and valid psychoacoustic test that measures participants' ability to discriminate fine differences in the timing of a musical beat (Grahn & Schuit, 2012; Harrison & Müllensiefen, 2018a, 2018b; Iversen & Patel, 2008; Leow et al., 2014; Ross et al., 2018; Spiech et al., 2022; Spiech, Connor et al., 2022; Tranchant et al., 2021). The CA-BAT achieves this by playing 25 short musical clips with overlaid beep tracks. Each clip is played twice, once with the beep track aligned to the beat and once where the beep track is misaligned (by a constant proportion) to some extent. Participants are then asked to select the clip where they thought the beep track was aligned to the beat. These beep tracks can be misaligned by Owing to item response theory and its adaptive design (i.e., correct responses result in smaller differences between beep tracks while incorrect responses result in greater differences), the test itself only takes around 10 minutes to estimate a participant's beat perception ability.

3.3 Statistical Analysis

First, a one-way analysis of variance (ANOVAs) with Beat Perception Ability as the dependent variable was used to assess Musicianship (Active vs. Inactive vs. Nonmusician) group differences. Follow-up two-tailed Welch's independent samples *t*-tests were then used to test for differences in Beat Perception Ability between groups because the variances between groups were expected to be unequal (Delacre et al., 2017). These tests were corrected for multiple comparisons using the false discovery rate (FDR, Benjamini & Hochberg, 1995). Second, to investigate the degree to which any of these differences could be related to disparities in musical training, we repeated the same tests with Years of Musical Training as the dependent variable. Data analyses were carried out in R version 4.1.3 (R Core Team, 2013) using the ‘ez’ and ‘effectsize’ packages (Ben-Shachar et al., 2020; Lawrence, 2011) and results were visualized using the ‘ggplot2’ package (Wickham, 2016).

Lastly, to fully explore the relationships between demographic and music-related variables with Beat Perception Ability, we performed a generalized linear regression with participants’ age, gender, handedness, years of musical training, number of musical instruments played, number of hours of weekly music playing, and number of hours of weekly music listening as independent variables to predict beat perception ability score. Because we expected the music-related variables to be highly correlated with one another, we employed a non-parametric and non-linear regressions with Gradient Boosting Machine (GBM, Friedman, 2001), Random Forest (RF, Breiman, 2001), and Extreme Gradient Boosting (XGBoost, Chen et al., 2015; Chen & Guestrin, 2016) algorithms. Tree-based algorithms such as GBM, RF, and XGBoost are not prone to collinearity and, unless the correlation between the predictors is very high, they can effectively rank the importance of the predictors based on reduction of residual deviance or gains in other loss functions, while taking interactions between the variables into account. In this way, we sought to identify the most important factors related to beat perception ability by extracting estimated variable importance from the model to further examine whether state-of-the-art non-parametric machine learning models also confirm the results of the linear regression analysis. The variable importance was estimated by the loss function gains in the process of constructing the trees and next, to simplify the interpretation, we scaled them to range from 0 to 1. We used the `h2o.ai` software to carry out the machine learning analysis (Click et al., 2017).

4. Results

The one-way ANOVA with Beat Perception Ability as a dependent variable revealed a significant effect of Musicianship (F(2,93)=4.123, *p*=0.019, η2G=0.081). FDR-corrected follow-up two-tailed Welch's independent samples *t*-tests revealed that Active Musicians exhibited moderately greater Beat Perception Ability than Inactive Musicians (*t*(39.442)=2.213, *p*=0.050, *d*=0.56) and even greater Beat Perception Ability than Nonmusicians (*t*(33.82)=2.337, *p*=0.050, *d*=0.63). Inactive Musicians' Beat Perception Ability, on the other hand, did not differ from that of Nonmusicians (*t*(46)=-0.087, *p*=0.931). These results are displayed in Figure 1 below. However, when this same analysis was conducted with three outliers removed (subjects with Beat Perception Ability scores more than ±2.5 standard deviations from the dataset's mean), this effect was extinguished so this result should be taken with caution.

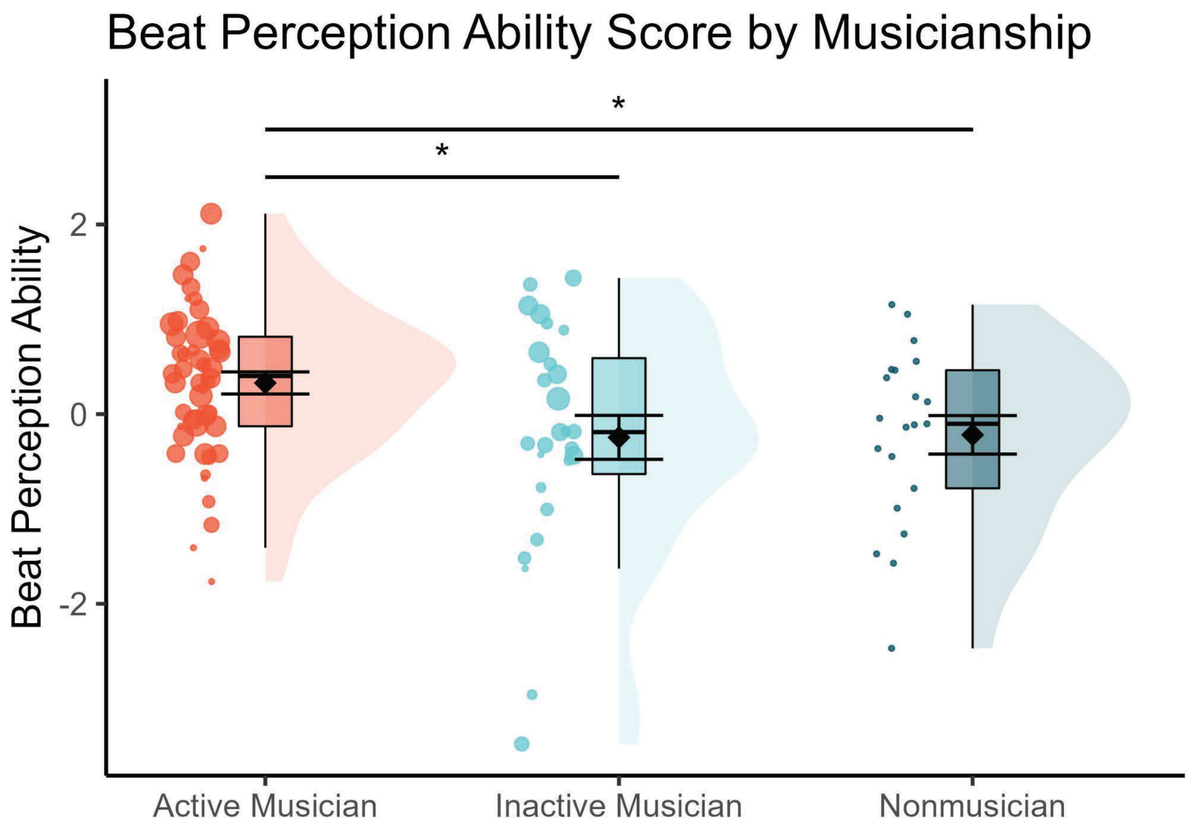

Figure 1. Raincloud plots displaying Beat Perception Ability scores by Musicianship. Dots are individual subject scores and are scaled in size relative to years of musical training while large diamonds are group averages. Error bars represent standard errors of the mean. Asterisks depict statistical significance at $p<0.05$.

Unsurprisingly, Years of Musical Training also differed between Musician groups as revealed by a one-way ANOVA ($F(2,93)=22.506$, $p<0.001$, $\eta 2G=0.326$). FDR-corrected follow-up two-tailed Welch's independent samples *t*-tests demonstrated that all groups differed from each other with the largest differences being both musician groups having substantially more musical training than Nonmusicians (Active Musicians: $t(47)=9.448$, $p<0.001$, $d=1.93$; Inactive Musicians: $t(26)=5.621$, $p<0.001$, $d=1.53$), indicating that our grouping factor accounted for a difference. However, Active Musicians also had more Years of Musical Training than Inactive Musicians ($t(70.997)=3.378$, $p=0.001$, $d=0.77$), potentially confounding our findings about music playing and necessitating the subsequent regression analyses.

The regression analysis had an R^2 of 0.147 and mean residual deviance of 0.820 and showed that only Years of Music Training was a significant positive predictor of Beat Perception Ability. Table 2 presents the coefficients, standard errors, *p*-values, and standardized coefficients of the GLM predictors.

Predictor	Coefficient	Standard Error	*p*-value	Standardized Coefficient
Age	0.006	0.019	0.322	0.036
Handedness	0.322	0.382	0.400	0.084
Gender	-0.207	0.219	0.348	-0.103
Years of Musical Training	0.046	0.020	0.024*	0.335
Hours Played Weekly	-0.002	0.020	0.938	-0.009
Hours Listened Weekly	0.006	0.007	0.406	0.087
Number of Instruments Played	0.022	0.134	0.871	0.021

Table 2. Output of the generalized linear model. Only Years of Musical Training was significant, indicating that with more years of musical training, beat perception increased and that once this was accounted for, no music-related or demographic variables had any impact.

Fine-tuning the GBM, RF, and XGBoost models provided similar evidence as the linear model, demonstrating that Years of Music Training was the most important predictor of Beat Perception Ability. The Mean Residual Deviance of the fine-tuned GBM, RF, and XGBoost models were 0.65, 1.00, and 0.70, respectively (lower values indicate lower prediction error).

Extracting and rescaling the variable importance measure from the model revealed that Years of Musical Training was the most important predictor of Beat Perception Ability, explaining more of the variance compared to Number of Instruments Played, Hours of weekly music listening, and particularly, Hours of Weekly Music Playing. Table XX shows the scaled variable importance of all the predictors.

Variable	GBM	RF	XGBoost
Years of Musical Training	1.00	1.00	1.00
Age	0.65	0.92	0.60
Hours Listened Weekly	0.61	0.83	0.88
Hours Played Weekly	0.33	0.53	0.60
Gender	0.14	0.24	0.07
Number of Instruments Played	0.12	0.31	0.45
Handedness	0.01	0.08	0.09

Table 3. Scaled variable importance of GBM, RF, and XGBoost models. The analysis also indicates that number of music instruments played has no relation with beat perception ability, once years of training and music playing are taken into account.

5. <u>Discussion</u>

In this study, we compared the beat perception abilities of active musicians to those of inactive musicians and nonmusicians. We found that active musicians possessed significantly greater beat perception abilities than both inactive musicians and nonmusicians who performed similarly on the CA-BAT. However, all groups differed in their years of musical training, indicating that this may have confounded the observed beat perception differences. Subsequent regression analyses using machine learning algorithms confirmed this was the case; years of musical training dwarfed all other music-related and demographic factors. These findings suggest that with adequate musical training, beat perception remains elevated even without regular maintenance.

This explanation falls in line with common notions of expertise where practice enhances ability (Ericsson & Lehmann, 1996; Sloboda et al., 1996). Active musicians received more years of musical training and likely accrued more hours of beat perception refinement through their continued engagement with their instruments, resulting in better performance on the CA-BAT than both their inactive counterparts and nonmusicians. However, these marginal effects of continued practice were superfluous for sharpening beat perception since the regression analyses demonstrated that years of musical training sufficiently explained differences in CA-BAT scores. Thus, it seems that with enough training, the neural circuits for beat perception become hardwired and continued musical engagement is not necessary to preserve the ability.

Alternatively, it also seems plausible that people with better beat perception ability are more motivated to stick with musical training for more years, further exercising their rhythmic skills. This is supported by Albert Bandura's self-efficacy theory where one's beliefs about one's competencies influences subsequent motivation and performance (Bandura, 1982, 1997). This has already been shown in the context of music performance (Hendricks, 2016; McPherson & McCormick, 2006) and so it could potentially apply to lower level musical abilities as well. It seems logical that better beat perception could result in more of Bandura's "mastery experiences" while training, which then motivates them to pursue more formal musical education and learn more rhythmically challenging pieces in a virtuous circle.

Another explanation could be that the CA-BAT may not be sensitive to finding beat perception differences that could arise from musical engagement factors like regular playing. The CA-BAT measures the ability to detect fine-grained phase offsets and this is often not necessary for many instruments in a variety of musical traditions. Indeed, the perceptual center (when a sound's onset is perceived) has been shown to vary considerably depending on a number of musical qualities (Danielsen et al., 2019), how it's measured (London et al., 2019), and genre expertise (Danielsen et al., 2022). It's possible that only highly trained musicians develop an enhanced beat perception ability that generalizes across sounds well enough to be observed with the CA-BAT. Said another way, the CA-BAT may not be ecologically valid for untrained listeners.

Additionally, the CA-BAT's two-alternative forced choice design introduces cognitive demands on working memory that may explain dissociations with beat tapping and production abilities (Bégel et al., 2017; Fiveash et al., 2022). These cognitive demands could be correlated with latent educational or genetic variables that could not be studied here; more years of musical training could be associated with more years of education in general or certain genetic predispositions. With genetics alone explaining roughly 13-16% of beat synchronization abilities (Niarchou et al., 2022), for example, this may explain why the predictors in our generalized linear model only explained about 15% of the CA-BAT scores' variance.

A substantial limitation of this study is that our dataset did not contain potentially important details about participants' musicianship because it was not the focus of the original studies where the data was collected. One such detail is the age that musical training began. A sensitive period for musical ability has been proposed (Bailey & Penhune, 2013; Penhune, 2011); early-trained musicians have been found to exhibit greater sensorimotor synchronization performance (Bailey et al., 2014; Bailey & Penhune, 2010; Watanabe et al., 2007) and executive functioning (J. Chen et al., 2022) alongside neuroanatomical differences (Amunts et al., 1997; Bailey et al., 2014; Imfeld et al., 2009; Shenker et al., 2022; Steele et al., 2013). It could be possible that only early-trained musicians (who could then accrue more years of musical training overall) develop an enduring beat perception while those who began their training outside of the sensitive period may either fail to cultivate better beat perception than nonmusicians or lose any gains they may have made after they stopped playing music. In our study, it is unclear to what extent our results are driven by early training so further experiments are needed to rule this out.

Given that musical training was the single most important predictor of beat perception, it would be interesting to explore the quality of this training in future studies. For instance, it's conceivable that more intense training (i.e., more hours spent practicing) could induce more enduring beat perception abilities later in life. Furthermore, some types of musical training (e.g., private lessons, training in large or small ensembles, rigorous self-teaching) may be better or worse at enhancing beat perception. Finally, certain musical styles and traditions require more precise beat timing than others (e.g., math rock requires better timing abilities than ambient soundscapes) so musicians trained in these genres could plausibly develop enhanced beat perception to meet their needs. Longitudinal and intervention-based studies manipulating and controlling for these various factors should thus be carried out to conclusively rule out the influence of these variables.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

Author CS conceived the study and carried out the statistical analyses and data visualizations with author EFH. Author CS wrote the first draft of the manuscript. Authors TE, BL, AD, and EFH all provided feedback and revised the manuscript.

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6. References

Amunts, K., Schlaug, G., Jäncke, L., Steinmetz, H., Schleicher, A., Dabringhaus, A., & Zilles, K. (1997). Motor cortex and hand motor skills: Structural compliance in the human brain. *Human Brain Mapping*, *5*(3), 206–215. https://doi.org/10.1002/(SICI)1097-0193(1997)5:3<206::AID-HBM5>3.0.CO;2-7

Appelgren, A., Osika, W., Theorell, T., Madison, G., & Bojner Horwitz, E. (2019). Tuning in on motivation: Differences between non-musicians, amateurs, and professional musicians. *Psychology of Music*, *47*(6), 864–873. https://doi.org/10.1177/0305735619861435

Bailey, J. A., & Penhune, V. B. (2010). Rhythm synchronization performance and auditory working memory in early- and late-trained musicians. *Experimental Brain Research*, *204*(1), 91–101. https://doi.org/10.1007/s00221-010-2299-y

Bailey, J. A., & Penhune, V. B. (2013). The relationship between the age of onset of musical training and rhythm synchronization performance: Validation of sensitive period effects. *Frontiers in Neuroscience*, *7*. https://doi.org/10.3389/fnins.2013.00227

Bailey, J. A., Zatorre, R. J., & Penhune, V. B. (2014). Early Musical Training Is Linked to Gray Matter Structure in the Ventral Premotor Cortex and Auditory–Motor Rhythm Synchronization Performance. *Journal of Cognitive Neuroscience*, *26*(4), 755–767. https://doi.org/10.1162/jocn_a_00527

Bandura, A. (1982). Self-efficacy mechanism in human agency. *American Psychologist*, *37*(2), 122–147. https://doi.org/10.1037/0003-066X.37.2.122

Bandura, A. (1997). *Self-efficacy: The exercise of control*. W.H. Freeman.

Bégel, V., Benoit, C.-E., Correa, A., Cutanda, D., Kotz, S. A., & Dalla Bella, S. (2017). “Lost in time” but still moving to the beat. *Neuropsychologia*, *94*, 129–138.

https://doi.org/10.1016/j.neuropsychologia.2016.11.022

Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society Series B (Methodological)*, *57*(1), 289–300. http://dx.doi.org/10.2307/2346101

Ben-Shachar, M., Lüdecke, D., & Makowski, D. (2020). effectsize: Estimation of Effect Size Indices and Standardized Parameters. *Journal of Open Source Software*, *5*(56), 2815. https://doi.org/10.21105/joss.02815

Bonde, L. O., Juel, K., & Ekholm, O. (2018). Associations between music and health-related outcomes in adult non-musicians, amateur musicians and professional musicians—Results from a nationwide Danish study. *Nordic Journal of Music Therapy*, *27*(4), 262–282. https://doi.org/10.1080/08098131.2018.1439086

Brattico, E., Näätänen, R., & Tervaniemi, M. (2001). Context Effects on Pitch Perception in Musicians and Nonmusicians: Evidence from Event-Related-Potential Recordings. *Music Perception*, *19*(2), 199–222. https://doi.org/10.1525/mp.2001.19.2.199

Breiman, L. (2001). Random forests. *Machine Learning*, *45*(1), 5–32.

Charness, N. (1991). *Expertise in chess: The balance between knowledge and search.*

Chen, J. L., Penhune, V. B., & Zatorre, R. J. (2008). Moving on Time: Brain Network for Auditory-Motor Synchronization is Modulated by Rhythm Complexity and Musical Training. *Journal of Cognitive Neuroscience*, *20*(2), 226–239. https://doi.org/10.1162/jocn.2008.20018

Chen, J., Scheller, M., Wu, C., Hu, B., Peng, R., Liu, C., Liu, S., Zhu, L., & Chen, J. (2022). The relationship between early musical training and executive functions: Validation of effects of the sensitive period. *Psychology of Music*, *50*(1), 86–99.

https://doi.org/10.1177/0305735620978690

Chen, T., & Guestrin, C. (2016). Xgboost: A scalable tree boosting system. *Proceedings of the 22nd Acm Sigkdd International Conference on Knowledge Discovery and Data Mining*, 785–794.

Chen, T., He, T., Benesty, M., Khotilovich, V., Tang, Y., Cho, H., Chen, K., & others. (2015). Xgboost: Extreme gradient boosting. *R Package Version 0.4-2*, *1*(4), 1–4.

Chi, M. T. H., Glaser, R., & Farr, M. J. (Eds.). (2014). *The Nature of Expertise* (0 ed.). Psychology Press. https://doi.org/10.4324/9781315799681

Click, C., Malohlava, M., Candel, A., Roark, H., & Parmar, V. (2017). Gradient boosting machine with h2o. *H2O. Ai*.

Cohen, M. A., Evans, K. K., Horowitz, T. S., & Wolfe, J. M. (2011). Auditory and visual memory in musicians and nonmusicians. *Psychonomic Bulletin & Review*, *18*(3), 586–591. https://doi.org/10.3758/s13423-011-0074-0

Criscuolo, A., Pando-Naude, V., Bonetti, L., Vuust, P., & Brattico, E. (2022). An ALE meta-analytic review of musical expertise. *Scientific Reports*, *12*(1), 11726. https://doi.org/10.1038/s41598-022-14959-4

Danielsen, A., Nymoen, K., Anderson, E., Câmara, G. S., Langerød, M. T., Thompson, M. R., & London, J. (2019). Where is the beat in that note? Effects of attack, duration, and frequency on the perceived timing of musical and quasi-musical sounds. *Journal of Experimental Psychology: Human Perception and Performance*, *45*(3), 402–418. https://doi.org/10.1037/xhp0000611

Danielsen, A., Nymoen, K., Langerød, M. T., Jacobsen, E., Johansson, M., & London, J. (2022). Sounds familiar (?): Expertise with specific musical genres modulates timing perception and micro-level synchronization to auditory stimuli. *Attention, Perception, & Psychophysics*, *84*(2), 599–615.

Dawson, W. J. (2014). Benefits of Music Training Are Widespread and Lifelong: A Bibliographic Review of Their Non-Musical Effects. *Medical Problems of Performing Artists*, *29*(2), 57–63. https://doi.org/10.21091/mppa.2014.2014

Delacre, M., Lakens, D., & Leys, C. (2017). Why Psychologists Should by Default Use Welch's *t*-test Instead of Student's *t*-test. *International Review of Social Psychology*, *30*(1), 92. https://doi.org/10.5334/irsp.82

Ericsson, K. A., & Charness, N. (1994). Expert performance: Its structure and acquisition. *American Psychologist*, *49*(8), 725–747. https://doi.org/10.1037/0003-066X.49.8.725

Ericsson, K. A., & Lehmann, A. C. (1996). Expert and exceptional performance: Evidence of maximal adaptation to task constraints. *Annual Review of Psychology*, *47*(1), 273–305.

Feltovich, P. J., Prietula, M. J., & Ericsson, K. A. (2006). *Studies of expertise from psychological perspectives.*

Fiveash, A., Bella, S. D., Bigand, E., Gordon, R. L., & Tillmann, B. (2022). You got rhythm, or more: The multidimensionality of rhythmic abilities. *Attention, Perception, & Psychophysics*, *84*(4), 1370–1392. https://doi.org/10.3758/s13414-022-02487-2

Franěk, M., Mates, J., Radil, T., Beck, K., & Pöppel, E. (1991). Finger tapping in musicians and nonmusicians. *International Journal of Psychophysiology*, *11*(3), 277–279. https://doi.org/10.1016/0167-8760(91)90022-P

Friedman, J. H. (2001). Greedy function approximation: A gradient boosting machine. *Annals of Statistics*, 1189–1232.

Gaser, C., & Schlaug, G. (2003). Gray Matter Differences between Musicians and

Nonmusicians. *Annals of the New York Academy of Sciences*, *999*(1), 514–517. https://doi.org/10.1196/annals.1284.062

Grahn, J. A., & Brett, M. (2007). Rhythm and beat perception in motor areas of the brain. *Journal of Cognitive Neuroscience*, *19*(5), 893–906.

Grahn, J. A., & McAuley, J. D. (2009). Neural bases of individual differences in beat perception. *NeuroImage*, *47*(4), 1894–1903. https://doi.org/10.1016/j.neuroimage.2009.04.039

Grahn, J. A., & Rowe, J. B. (2009). Feeling the Beat: Premotor and Striatal Interactions in Musicians and Nonmusicians during Beat Perception. *Journal of Neuroscience*, *29*(23), 7540–7548. https://doi.org/10.1523/JNEUROSCI.2018-08.2009

Grahn, J. A., & Schuit, D. (2012). Individual differences in rhythmic ability: Behavioral and neuroimaging investigations. *Psychomusicology: Music, Mind, and Brain*, *22*(2), 105–121. https://doi.org/10.1037/a0031188

Haghish, E. F. (2022). *mlim: Multiple Imputation with Automated Machine Learning*. https://CRAN.R-project.org/package=mlim

Hanna-Pladdy, B., & Gajewski, B. (2012). Recent and Past Musical Activity Predicts Cognitive Aging Variability: Direct Comparison with General Lifestyle Activities. *Frontiers in Human Neuroscience*, *6*. https://doi.org/10.3389/fnhum.2012.00198

Harrison, P. M. C., & Müllensiefen, D. (2018a). Development and validation of the Computerised Adaptive Beat Alignment Test (CA-BAT. *Scientific Reports*, *8*(12395), 1–19. https://doi.org/10.1038/s41598-018-30318-8

Harrison, P. M. C., & Müllensiefen, D. (2018b). https://doi.org/10.5281/zenodo.1415353

Hendricks, K. S. (2016). The Sources of Self-Efficacy: Educational Research and Implications for Music. *Update: Applications of Research in Music Education*, *35*(1), 32–38.

https://doi.org/10.1177/8755123315576535

Hove, M. J., Spivey, M. J., & Krumhansl, C. L. (2010). Compatibility of motion facilitates visuomotor synchronization. *Journal of Experimental Psychology: Human Perception and Performance*, *36*(6), 1525–1534. https://doi.org/10.1037/a0019059

Imfeld, A., Oechslin, M. S., Meyer, M., Loenneker, T., & Jancke, L. (2009). White matter plasticity in the corticospinal tract of musicians: A diffusion tensor imaging study. *NeuroImage*, *46*(3), 600–607. https://doi.org/10.1016/j.neuroimage.2009.02.025

Iversen, J. R., & Patel, A. D. (2008). *The Beat Alignment Test (BAT): Surveying beat processing abilities in the general population*.

Jäncke, L. (2009). The plastic human brain. *Restorative Neurology and Neuroscience*, *27*(5), 521–538. https://doi.org/10.3233/RNN-2009-0519

Kauffman, W. H., & Carlsen, J. C. (1989). Memory for intact music works: The importance of music expertise and retention interval. *Psychomusicology: A Journal of Research in Music Cognition*, *8*(1), 3–20. https://doi.org/10.1037/h0094235

Kishon-Rabin, L., Amir, O., Vexler, Y., & Zaltz, Y. (2001). Pitch Discrimination: Are Professional Musicians Better than Non-Musicians? *Journal of Basic and Clinical Physiology and Pharmacology*, *12*(2). https://doi.org/10.1515/JBCPP.2001.12.2.125

Krause, V., Pollok, B., & Schnitzler, A. (2010). Perception in action: The impact of sensory information on sensorimotor synchronization in musicians and non-musicians. *Acta Psychologica*, *133*(1), 28–37. https://doi.org/10.1016/j.actpsy.2009.08.003

Lawrence, M. A. (2011). *package ez: Easy analysis and visualization of factorial experiments*. http://CRAN.R-project.org/package=ez

Lehmann, A. C., Gruber, H., & Kopiez, R. (2018). Expertise in Music. In K. A. Ericsson, R. R.

Hoffman, A. Kozbelt, & A. M. Williams (Eds.), *The Cambridge Handbook of Expertise and Expert Performance* (2nd ed., pp. 535–549). Cambridge University Press. https://doi.org/10.1017/9781316480748.028

Lehmann, A. C., Sloboda, J. A., & Woody, R. H. (2007). *Psychology for Musicians*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195146103.001.0001

Leow, L. A., Parrott, T., & Grahn, J. A. (2014). Individual differences in beat perception affect gait responses to low-and high-groove music. *Frontiers in Human Neuroscience*, *8*, 811.

London, J., Nymoen, K., Langerød, M. T., Thompson, M. R., Code, D. L., & Danielsen, A. (2019). A comparison of methods for investigating the perceptual center of musical sounds. *Attention, Perception, & Psychophysics*, *81*(6), 2088–2101.

Madsen, C. K. (1979). Modulated Beat Discrimination Among Musicians and Nonmusicians. *Journal of Research in Music Education*, *27*(2), 57–67. https://doi.org/10.2307/3344892

McPherson, G. E., & McCormick, J. (2006). Self-efficacy and music performance. *Psychology of Music*, *34*(3), 322–336. https://doi.org/10.1177/0305735606064841

Micheyl, C., Delhommeau, K., Perrot, X., & Oxenham, A. J. (2006). Influence of musical and psychoacoustical training on pitch discrimination. *Hearing Research*, *219*(1–2), 36–47. https://doi.org/10.1016/j.heares.2006.05.004

Mikutta, C. A., Maissen, G., Altorfer, A., Strik, W., & Koenig, T. (2014). Professional musicians listen differently to music. *Neuroscience*, *268*, 102–111. https://doi.org/10.1016/j.neuroscience.2014.03.007

Nguyen, T., Gibbings, A., & Grahn, J. (2018). Rhythm and Beat Perception. In R. Bader (Ed.), *Springer Handbook of Systematic Musicology* (pp. 507–521). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-55004-5_27

Niarchou, M., Gustavson, D. E., Sathirapongsasuti, J. F., Anglada-Tort, M., Eising, E., Bell, E., McArthur, E., Straub, P., McAuley, J. D., Capra, J. A., & others. (2022). Genome-wide association study of musical beat synchronization demonstrates high polygenicity. *Nature Human Behaviour*, 1–18.

Pallesen, K. J., Brattico, E., Bailey, C. J., Korvenoja, A., Koivisto, J., Gjedde, A., & Carlson, S. (2010). Cognitive Control in Auditory Working Memory Is Enhanced in Musicians. *PLoS ONE*, *5*(6), e11120. https://doi.org/10.1371/journal.pone.0011120

Penhune, V. B. (2011). Sensitive periods in human development: Evidence from musical training. *Cortex*, *47*(9), 1126–1137. https://doi.org/10.1016/j.cortex.2011.05.010

Rammsayer, T., & Altenmüller, E. (2006). Temporal Information Processing in Musicians and Nonmusicians. *Music Perception*, *24*(1), 37–48. https://doi.org/10.1525/mp.2006.24.1.37

Repp, B. H. (2010). Sensorimotor synchronization and perception of timing: Effects of music training and task experience. *Human Movement Science*, *29*(2), 200–213. https://doi.org/10.1016/j.humov.2009.08.002

Repp, B. H., & Doggett, R. (2007). Tapping to a Very Slow Beat: A Comparison of Musicians and Nonmusicians. *Music Perception*, *24*(4), 367–376. https://doi.org/10.1525/mp.2007.24.4.367

Romeiser, J. L., Smith, D. M., & Clouston, S. A. P. (2021). Musical instrument engagement across the life course and episodic memory in late life: An analysis of 60 years of longitudinal data from the Wisconsin Longitudinal Study. *PLOS ONE*, *16*(6), e0253053. https://doi.org/10.1371/journal.pone.0253053

Ross, J. M., Iversen, J. R., & Balasubramaniam, R. (2018). The Role of Posterior Parietal Cortex in Beat-based Timing Perception: A Continuous Theta Burst Stimulation Study. *Journal* *of Cognitive Neuroscience*, *30*(5), 634–643. https://doi.org/10.1162/jocn_a_01237

Schulze, H.-H. (1978). The detectability of local and global displacements in regular rhythmic patterns. *Psychological Research*, *40*(2), 173–181. https://doi.org/10.1007/BF00308412

Shea, J. B., & Paull, G. (2014). Capturing expertise in sports. In *The road to excellence* (pp. 321–335). Psychology Press.

Shenker, J. J., Steele, C. J., Chakravarty, M. M., Zatorre, R. J., & Penhune, V. B. (2022). Early musical training shapes cortico-cerebellar structural covariation. *Brain Structure and Function*, *227*(1), 407–419. https://doi.org/10.1007/s00429-021-02409-2

Shors, T. J., Anderson, M. L., Curlik Ii, D., & Nokia, M. (2012). Use it or lose it: How neurogenesis keeps the brain fit for learning. *Behavioural Brain Research*, *227*(2), 450–458.

Skaansar, J. F., Laeng, B., & Danielsen, A. (2019). Microtiming and Mental Effort: Onset Asynchronies in Musical Rhythm Modulate Pupil Size. *Music Perception*, *37*(2), 111–133. https://doi.org/10.1525/mp.2019.37.2.111

Sloboda, J. A. (1991). Musical expertise. *Toward a General Theory of Expertise: Prospects and Limits*, 153–171.

Sloboda, J. A., Davidson, J. W., Howe, M. J. A., & Moore, D. G. (1996). The role of practice in the development of performing musicians. *British Journal of Psychology*, *87*(2), 287–309. https://doi.org/10.1111/j.2044-8295.1996.tb02591.x

Spiech, C., Sioros, G., Endestad, T., Danielsen, A., & Laeng, B. (2022). Pupil drift rate indexes groove ratings. *Scientific Reports*, *12*(1), 11620. https://doi.org/10.1038/s41598-022-15763-w

Spiech, Connor, Hope, Mikael, Schmidt Câmara, Guilherme, Sioros, George, Endestad, Tor, Laeng, Bruno, & Danielsen, Anne. (2022). *Sensorimotor Synchronization Increases Groove*. https://doi.org/10.5281/ZENODO.6908098

Steele, C. J., Bailey, J. A., Zatorre, R. J., & Penhune, V. B. (2013). Early Musical Training and White-Matter Plasticity in the Corpus Callosum: Evidence for a Sensitive Period. *Journal of Neuroscience*, *33*(3), 1282–1290. https://doi.org/10.1523/JNEUROSCI.3578-12.2013

Sternberg, R. J., & Grigorenko, E. L. (Eds.). (2003). *The psychology of abilities, competencies, and expertise*. Cambridge University Press.

Talamini, F., Altoè, G., Carretti, B., & Grassi, M. (2018). Correction: Musicians have better memory than nonmusicians: A meta-analysis. *PLOS ONE*, *13*(1), e0191776. https://doi.org/10.1371/journal.pone.0191776

Team, R. C. (2013). R: A language and environment for statistical computing. In *R Foundation for Statistical Computing*. http://www.R-project.org/.

Tervaniemi, M., Just, V., Koelsch, S., Widmann, A., & Schr�ger, E. (2005). Pitch discrimination accuracy in musicians vs nonmusicians: An event-related potential and behavioral study. *Experimental Brain Research*, *161*(1), 1–10. https://doi.org/10.1007/s00221-004-2044-5

Tranchant, P., Lagrois, M.-É., Bellemare, A., Schultz, B. G., & Peretz, I. (2021). Co-occurrence of Deficits in Beat Perception and Synchronization Supports Implication of Motor System in Beat Perception. *Music & Science*, *4*, 205920432199171. https://doi.org/10.1177/2059204321991713

Watanabe, D., Savion-Lemieux, T., & Penhune, V. B. (2007). The effect of early musical training on adult motor performance: Evidence for a sensitive period in motor learning. *Experimental Brain Research*, *176*(2), 332–340. https://doi.org/10.1007/s00221-006-0619-z

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis* (2nd ed. 2016). Springer International Publishing : Imprint: Springer. https://doi.org/10.1007/978-3-319-24277-4