**Chapter 6.4: Neural underpinnings of music: The polyrhythmic brain**

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# Abstract

Musical rhythm, consisting of apparently abstract intervals of accented temporal events, has the remarkable ability to move our minds and bodies. Why do certain rhythms make us want to tap our feet, bop our heads or even get up and dance? And how does the brain process rhythmically complex rhythms during our experiences of music? In this chapter, we describe some common forms of rhythmic complexity in music and propose that the theory of predictive coding can explain how rhythm and rhythmic complexity are processed in the brain. We also consider how this theory may reveal why we feel so compelled by rhythmic tension in music. First, musical-theoretical and neuroscientific frameworks of rhythm are presented, in which rhythm perception is conceptualized as an interaction between what is heard (‘rhythm’) and the brain’s anticipatory structuring of music (‘the meter’). Second, three different examples of tension between rhythm and meter in music are described: syncopation, polyrhythm and groove. Third, we present the theory of predictive coding of music, which posits a hierarchical organization of brain responses reflecting fundamental, survival-related mechanisms associated with predicting future events. According to this theory, perception and learning is manifested through the brain’s Bayesian minimization of the error between the input to the brain and the brain’s prior expectations. Fourth, empirical studies of neural and behavioral effects of syncopation, polyrhythm and groove will be reported, and we propose how these studies can be seen as special cases of the predictive coding theory. Finally, we argue that musical rhythm exploits the brain’s general principles of anticipation and propose that pleasure from musical rhythm may be a result of such anticipatory mechanisms.

# Introduction

Music has a remarkable ability to move our bodies and brains. The ways in which apparently abstract rhythmic intervals of accented temporal events relate to each other can make us want to tap our feet, bop our heads and get up and dance. With the advent of musical styles of the 20th century, developed in the aftermath of the meeting between music brought to America from Africa and Western music, rhythm has become an increasingly important aspect of the listening experience. Why is rhythm so compelling, and how does the brain facilitate the rich and complex experiences we have with rhythm in music? In this chapter, we describe some of the most common forms of rhythmic complexity in music, review some theories of how rhythm and rhythmic complexity is processed in the brain, with particular focus on the theory of predictive coding, and propose why we may be attracted to rhythmic tension in music. First, we will present the music-theoretical and neuroscientific framework for understanding rhythm perception as an interaction between what is heard (‘rhythm’) and the brain’s anticipatory structuring of music (‘the meter’). Accordingly, the rhythmic experience is seen as the result of tension or discrepancy between rhythm and meter. Second, we will discuss the experience of three different musical examples of tension between rhythm and meter: syncopation, polyrhythm and groove. Third, we will present the theory of predictive coding of music, which posits a hierarchical organization of brain responses, reflecting fundamental, survival-related mechanisms associated with predicting future events. It argues that perception and learning occurs in a recursive Bayesian process by which the brain tries to minimize the error between the input and the brain’s expectation. Fourth, we describe a number of empirical studies in which the neural and behavioral effects of syncopation, polyrhythm and groove were investigated, and propose how these studies can be seen as special cases of the predictive coding theory. Here, we will touch upon the effect of individual background in rhythm processing, as exemplified by differences between groups of individuals with varying musical competence. Finally, we shall propose that neural processing of rhythm may be music’s way of exploiting general principles of anticipatory brain processing and that our extraordinary capacity for anticipating the future may be one of the reasons why we find so much pleasure in music.

# Rhythm and meter

Most theories of rhythm perception involve the notion of meter. *Rhythm,* broadly, is a pattern of discrete durations, and is largely thought to depend on the underlying perceptual mechanism of grouping. ([1](#_ENREF_1), [2](#_ENREF_2)) *Meter*, again broadly, is the temporal framework according to which rhythm is perceived. When we listen to a certain piece of music, we often automatically start tapping our feet in relation to the rhythm with isochronously spaced beats (a process also known as beat perception, or -production), and we may even accentuate some beats more than others. This process of differentially accentuating isochronously spaced beats is an expression of meter. Meter is often described as the temporal framework of rhythmic expectations. ([3](#_ENREF_3)) In other words, the meter provides the listener with a hierarchical expectancy structure underlying the perception of music, according to which each musical time-point encompasses a conjoint prediction of timing and salience. ([4](#_ENREF_4))

Despite growing interest in music research for the cognitive underpinnings of music perception, the definitions of meter, and particularly its relationship with rhythm is still under significant debate. This is despite music psychology researchers having attempted to define meter since the 1970’s, using a number of different theoretical and empirical approaches. (e.g. [1](#_ENREF_1), [5](#_ENREF_5), [6-10](#_ENREF_6))

In formal terms, meter generally refers to the alternation of strong and weak temporal accents, which provide a metric framework for a rhythmic pattern. According to music theory, this is expressed in the time signature of a given piece of music, such as 4/4, 3/4 or 6/8 . This formal expression of meter, however, can be quite different from how the meter is actually perceived or how it is expressed in sensorimotor synchronization, such as foot-tapping, since it is possible, in principle, to notate any given piece of music in more than one time signature. Furthermore, while the formal definition is relatively easy to handle, there is more disagreement about the perceptual definition of meter. At the most basic level, meter perception is understood as a subjective sense of pulse. Listeners often recognize the main pulse in rhythm, which is the pattern of isochronously spaced beats that commonly elicits spontaneous foot-tapping or synchronized body-movement. ([11](#_ENREF_11)) However, the hierarchical differentiation of pulse sequences beyond the main pulse (i.e. faster or slower pulses), the exact structure of this hierarchy and whether they determine the differences in metric salience of pulse events within a sequence, still remain unclear. An example of a highly hierarchical view of meter is proposed in Lerdahl and Jackendoff’s Generative Theory of Tonal Music. ([6](#_ENREF_6)) They claim that rhythm perception is underpinned by a framework of meter organized in a tree-like structure (Figure 6.4- 1.), implemented on the basis of a set of cognitive rules. Within this tree-structure, every node on a given hierarchical level is recursively subdivided into equally spaced nodes at the level below. The level of a given node, as well as the number of connections to other nodes at lower levels, determines the metric salience of notes occurring at that position in the framework. The higher up in the hierarchy, and the more connections, the stronger the metric accent. Although their emphasis on cognitive rules is often criticized for giving too much attention to top-down processes of music cognition and not enough focus on the role of the body, many researchers have since also adopted metric tree models in studying rhythm and meter. ([12-16](#_ENREF_12))

[INSERT FIGURE 6.4- 1. HERE]

Other models, in particular the dynamic attending theory (DAT), direct considerably more attention to the body. DAT was originally proposed by Jones and colleagues ([10](#_ENREF_10), [17-19](#_ENREF_17)) in order to conceptualize the cognitive mechanisms for time perception more broadly, but has since been widely appropriated to music, specifically. ([20-24](#_ENREF_20)) Here, the claim is that rhythm induces metric frameworks by way of entrainment: the listeners’ attention is captured and driven by the periodicities (or oscillations) in the rhythmic pattern, and the experience of metric salience corresponds to the relative strength of attention directed towards each rhythmic event. The hierarchical nature of meter in DAT is considerably more flexible and adaptive compared to Lerdahl and Jackendoff’s model. ([6](#_ENREF_6)) It was originally proposed as a *conceptual* model, using oscillation and resonance as metaphors for the functions of rhythm and meter in music. However, recent evidence suggests that the electrophysiological firing patterns of neurons in the brain are characterized by entrainment, and models of neural resonance are believed by some to explain rhythm and meter perception directly. ([9](#_ENREF_9), [25](#_ENREF_25))

Another relatively new way of modelling rhythm and meter perception is by way of computational models. ([26-30](#_ENREF_26)). One particularly influential theory is proposed by Temperley, ([13-15](#_ENREF_13)) who argues that probabilistic models of rhythm are the most appropriate ways of capturing the generative principles behind compositional processes. In one of his studies, ([15](#_ENREF_15)) he tests the performance of six probabilistic models based on the *Bayeseian rule of probability* on two corpuses of music, the Essens Folk Song Collection ([7](#_ENREF_7)) and a collection of string quartets by Haydn and Mozart. The Bayeseian model is one that allows the drawing of conclusions about how well an expression of data (e.g. a rhythmic pattern) fits with other expressions of the same type of data more generally (a model of rhythm, or meter). As will be discussed below, this type of model comparison, relying on Bayesian inference, is also integrative to the predictive coding theory.

# When metric expectancy is broken

# Syncopation

A key factor in our experience of rhythm is the extent to which a rhythmic pattern challenges our perception of meter. The most common example of such tension between rhythm and meter is *syncopation*. Most researchers and theorists generally define syncopation as an instance of rhythm that violates listeners’ metric expectations. Generally, it is assumed that listeners expect the majority of onsets in a rhythm to occur at metrically salient positions in a metric framework, while rests are expected to occur at metrically less salient positions (Figure 6.4- 2.A., Audio Example 6.4- 1.). A syncopation occurs when these expectations are violated (Figure 6.4- 2.B., Audio Example 6.4- 2.) and the rhythmic event coincides with the metrically less salient position, while the rest coincides with the metrically salient position. Building on the assumption of a hierarchical model of meter, Longuet-Higgins and Lee ([12](#_ENREF_12)) proposed a particularly influential theory of syncopation, formalizing an index of syncopation that can be used to calculate the perceptual effect of syncopation based on its contextualization within a model of metric salience.

[INSERT FIGURE 6.4- 2. HERE]

Since it was proposed, a number of researchers have tried to test Longuet-Higgins and Lee’s index. ([12](#_ENREF_12)) Ladinig, Honing and colleagues have primarily been interested in determining how the model reflects the actual perceptual properties of rhythm and meter, using syncopation as a tool. ([31-33](#_ENREF_31)) Ladinig et al. ([32](#_ENREF_32)) tested the perceptual effects of syncopations on listeners’ metric expectations and found that the degree of unexpectedness or perceived stability depended on the metric location at which the syncopation occurred. Their findings broadly support the idea that syncopation relies on the differentiation of metric salience in rhythm. Furthermore, their participants were all non-musicians, suggesting that not only listeners with extensive musical training exhibit hierarchical processing of meter and rhythm, as has previously been suggested. ([34](#_ENREF_34)) However, the metric frameworks indicated by these studies were not found to be as strictly hierarchical as the tree-model suggests. Generally, it seems we can be relatively confident that the downbeat has the strongest accent, but beyond that, the model remains unclear.

Other researchers have been more concerned with how syncopation affects sensorimotor synchronization: using syncopations as a way of increasing complexity in rhythmic patterns, they have investigated the extent to which such complexity affects the experience of a stable meter and the ability to synchronize body movements. ([16](#_ENREF_16), [35-37](#_ENREF_35)) Fitch and Rosenfeld ([16](#_ENREF_16)) adopted Longuet-Higgins and Lee’s index ([12](#_ENREF_12)) and showed that participants’ number and magnitude of tapping errors correlated linearly with the degree of syncopation. Furthermore, as the degree of syncopation increased, participants were more likely to “reinterpret” the rhythmic patterns as unsyncopated by resetting the phase of the perceived main pulse. In other words, the more syncopated a rhythmic pattern, the less likely listeners are to accurately perceive the meter and successfully synchronize body movements to it.

Importantly, syncopation is a way to musically conceptualize rhythmic complexity since it challenges the presumed perceptual model of the meter. In fact, in a correlational comparison of different measures of rhythmic complexity in music, Thul and Toussaint ([38](#_ENREF_38)) found that measures of syncopation outperformed other measures of rhythmic complexity, such as entropy, in explaining the behavioral data from four separate studies.

## Polyrhythm

In some styles of music, the meter may at times be only weakly (or not at all) acoustically actualized in the music itself, creating extreme instances of perceptual rhythmic complexity. An example is Cuban Son Montuno (e.g. Guillermo Portabales “Mi son Cubano” 1976). In this musical style, it is common for the bass to continuously avoid playing on the downbeat, i.e. the most salient position in the metric framework. As a listener unfamiliar with Cuban music, it is likely that the meter is ‘misinterpreted’ and the phase of the downbeat is shifted to comply with less complexly manifested rhythmic-metric relationships. An even more radically complex rhythmic practice is the pervasive use of polyrhythm, or even polymeter,[[1]](#footnote-1) throughout musical compositions, especially in (but not restricted to) jazz music. ([39](#_ENREF_39)) During polyrhythms, the formal meter may be completely absent in the actual acoustic signal and musicians rely on listeners’ ability to predict the formal metric framework. One example of polyrhythm is ‘cross-rhythm’, in which different overlaid rhythmic patterns can be perceived as suggesting different meters. A typical example is the so-called 3-against-4 pattern, which may be experienced by playing, for example on the drums, at the same time three equally spaced beats in one hand and four equally spaced beats in the other hand, so that the periods of both patterns add up at the end. In this case, it is possible to perceive the meter as a triple waltz meter (formal meter 3/4) and the four-beat pattern as a counter-metric pattern (Figure 6.4- 3.A., Audio Example 6.4- 3.) or as a duple meter (formal meter 4/4) with the three-beat pattern as the counter-metric pattern (Figure 6.4- 3.B., Audio Example 6.4- 4.). The rhythmic organization of these two patterns is exactly the same, that is, the cross-rhythmic relationships between the two streams within each pattern are identical. The lower pitch expresses the meter and the higher pitch the counter-rhythm in both patterns, but in the first pattern, the meter is triple, while in the second pattern, the meter is duple. These two experiences of the same polyrhythm (albeit with inverted instrumentation, i.e. whether the four- or three-beat pattern has the lower pitch) are phenomenologically different, and is thus analogous to ambiguous images such as the Rubin’s vase, which can be seen either as a vase on black background or faces on white background (Figure 6.4- 3.C.). In the case of the cross-rhythms, the meter is the background and the counter-metric rhythm is the foreground. Experiencing cross-rhythm in music can sometimes force the inexperienced listener to either shift the meter to comply with the counter-meter or to reinforce the sense of the original meter, for example through sensorimotor synchronization, such as foot-tapping. Polyrhythms thus provide the listener with a bistable percept ([40](#_ENREF_40)) that affords rhythmic tension and embodied engagement in music.

[INSERT FIGURE 6.4- 3. HERE]

Another example of polyrhythm is metric displacement, a structural strategy in which a rhythmic motif is first presented in relation to a specific metric framework (Figure 6.4- 4.A., Audio Example 6.4- 1.), and later shifted to start at a new metrical location, causing different layers to interlock in novel ways and form new rhythmically complex relationships (Figure 6.4- 4.B., Audio Example 6.4- 5.). The beginning of a metric displacement will therefore always be heard as metric incongruity and the tension caused by the displacement is prolonged, compared to other more momentary instances of rhythmic tension (e.g. syncopation).

In some jazz music, such as the music of the Miles Davis Quintet, polyrhythmic structures were used extensively during improvisation as an important means of communication. ([41](#_ENREF_41)) In fact, when applying established linguistic communicational models, such as Roman Jacobson’s model, ([42](#_ENREF_42)) the interactive exchange of polyrhythms in music displays functions comparable to the functions of spoken language. In jazz, the metric displacements and the accompanying rhythmic incongruities are often used for attracting attention and establishing communicational paths between musicians, whereas cross-rhythms are more typically used for building and playing with tension once a connection between musicians is established. In both cases, the effect of the polyrhythm relies on the listeners’ or musicians’ ability to predict the original meter.

[INSERT FIGURE 6.4- 4. HERE]

Albeit rarely, polyrhythms have been used in empirical investigations of rhythm and meter perception. ([34](#_ENREF_34), [43-49](#_ENREF_43)) The idea is that the ways in which complex rhythmic structures are processed can reveal the mechanisms underpinning rhythm and meter perception more generally. As will be described below, polyrhythms also provide unique insights into the ways in which the brain processes temporally incongruous information.

## Groove

Within musicology research, groove usually refers to music that is characterized by some degree of rhythmic complexity and expectancy violation, such as syncopation, metric displacement, cross-rhythms or microtiming.[[2]](#footnote-2) A groove can be just a drum-kit playing and repeating a two-bar pattern (Figure 6.4- 5.) or it may be the sonic interplay of a whole rhythm section of a band (e.g. drums, guitar, bass and vocals, Figure 6.4- 6.) Examples of groove-based genres are funk, soul, hip-hop, jazz and electronic dance music. In the context of groove, the rhythmically complex musical-structural strategies engender a somewhat different behavioral effect than when they are experienced in isolation. Importantly, in groove, the rhythmic complexity is continuously repeated, and the experiential result is a desire to move the body in synchrony with the meter ([53-56](#_ENREF_53)). Witek ([57, p4](#_ENREF_57)) provides the following definition of groove: Grooves are continuous multi-layered patterns of repeating units, commonly 2–4 bars in length, with varying degrees and expressions of rhythmic complexity, associated with a pleasurable desire to move.

[INSERT FIGURE 6.4- 5. HERE]

[INSERT FIGURE 6.4- 6. HERE]

Groove has until recently mainly been addressed theoretically, particularly in the context of embodied cognition ([50](#_ENREF_50), [58](#_ENREF_58)) and prediction. ([39](#_ENREF_39)) Furthermore, the first empirical studies on the subject have tended to focus on the behavioral effects exclusively, and only broadly drawn parallels between the musical structure and the psychological effects. In these studies, the positive drive towards body-movement has been the main focus. ([53-55](#_ENREF_53)) For example, Madison et al. ([55](#_ENREF_55)) found that the salience of the beat (i.e. the main pulse) and event density (i.e. sub-beat variability) correlated positively with ratings of groove (i.e. wanting to move). Janata et al. ([53](#_ENREF_53)) showed that groove was consistently defined by listeners in terms of movement-inducing properties, but also positive affective feelings. Through phenomenological considerations, behavioral investigations and computational correlations, their research demonstrated that the ‘quality’ of groove experience depends on the degree of sensorimotor synchronization coupling in ways that interacted with positive affect. Thus, it seems that in the context of continuous repetition, rhythmic structures that violate expectations, such as syncopation, metric displacement, cross-rhythm and microtiming, acquire subjectively manifested pleasurable effects.

# Music anticipation and predictive coding

The idea that our experience of rhythm is dependent on the mental anticipatory framework of meter and that this can be modeled as a Bayesian process ([13-15](#_ENREF_13), [59](#_ENREF_59)) resonates well with a novel theory about fundamental brain function, namely the *predictive coding theory* proposed by Karl Friston. As a general theory of brain function, it explains how brain areas exchange information. ([60](#_ENREF_60)) It was first applied to sensory perception, describing how the brain determines the sources of sensory input based on Bayesian inference. According to this argument, the brain predicts the causes of sensations based on the actual sensory input as compared with previous ‘knowledge’. ([60](#_ENREF_60), [61](#_ENREF_61)) This comparison is essential to the system, since a variety of environmental causes can result in similar sensory input. The predictive coding theory overcomes this perceptual challenge by using internal generative predictive models, which have been formed based on previous experience. These models continuously predict the causal relationship between sensory input and environmental events. In changing environments, the models are gradually updated to maximize the correspondence between the sensory input and the predictions and minimize prediction errors. In this way, the causes of our sensory input are not solely backtracked from the sensory input, but also inferred and anticipated based on contextual cues and previous sensory inputs. Thus, perception is a process that is mutually manifested between the perceiver and the environment.

Hence, the predictive coding theory offers a novel perspective on how specialized brain networks can identify and categorize causes of its sensory inputs, integrate information with other networks, and adapt to new stimuli by learning predictive patterns. It posits that perception and learning occurs in a recursive Bayesian process by which the brain tries to minimize the error between the input and the brain’s expectation (Figure 6.4- 7.). In other words, predictive coding is the mechanism by which the brain extracts the salient parts of the incoming signals and avoids processing redundant information. ([62](#_ENREF_62))

[INSERT FIGURE 6.4- 7. HERE]

# Perception and learning according to the predictive coding theory

In addition to the idea of minimizing prediction error, predictive coding theory is characterized by the hierarchical organization of neural networks in the brain. Each hierarchical level in the recursive process provides a predictive model (or models, since competing models at the same hierarchical level are present as soon as the situation becomes ambiguous or uncertain) of what the input to the specific level is expected to be. The hierarchical levels ‘communicate’ through forward and backward connections. ([60](#_ENREF_60), [63](#_ENREF_63)) The internal predictive models are communicated from high-level structures to specialized low-level structures through backward connections. These backwards connections have a strong modulatory effect on the functionally specialized brain areas, and can thus exert contextual constraints on the models of lower levels. Sensory information is processed through forward connections from lower to higher cortical levels, and works as driving signals. At each level, the sensory information is matched to the internal predictive model. If there is a mismatch between the model and the sensory input at any level of the hierarchy, a prediction error occurs and a neuronal error-message is fed forward to higher, more integrative levels. Here the prediction error is evaluated and depending on the degree to which it violates the internal prediction, the brain can either change its internal model or it can change the way it samples information from the environment. Consequently, prediction errors are fundamental for adaptive learning. When predictions change, the connectivity between neurons is believed to change accordingly. In this way, neuron A predicts neuron B’s response to a stimuli in a given context. ([60](#_ENREF_60), [63](#_ENREF_63)) The brain is constantly trying to optimize its internal model to correspond to the world, and thereby minimize prediction errors. ([63-65](#_ENREF_63)) Thus, the minimization of prediction errors is imperative for brain function, because neuronal prediction error signals are fundamental to learning and improvement of the internal model.

Importantly, the predictive coding theory states that the brain relies on prior experience to model expectations for the future. This prior experience gives a prior probability, describing the degree of probability of the internal hypothesis (or model). Prior probabilities are context-sensitive and hierarchical, hence we have a range of possibilities available to us, some more likely to be correct than others, and they change according to context. Thus, the hypotheses generated by the brain in a specific situation are constrained by hypotheses at the same or higher levels and guide the processing at lower levels. ([63](#_ENREF_63), [66](#_ENREF_66)) Therefore, when we have access to accurate information about the context, more specific hypotheses will be generated, due to the many contextual constraints, and hence the predictions of the sensory input will improve. Consequently, these predictions are a product of the interplay between the subject’s prior experience and the available sensory information, which forms the internal hypothesis. In this way, our predictions are built on prior experience and learning, but are still dynamic and context-sensitive.

## Predictive coding in music

The principles of predictive coding align very closely with the statistical learning approach proposed by Pearce and Wiggins, accounting for melodic perception in music ([67](#_ENREF_67), [68](#_ENREF_68)); the theory’s notion of initial neuronal error message followed by synchronized activity in various brain areas in response to low-probability sequences corresponds to a local prediction error at a low hierarchical level in predictive coding, while the following synchronization across various brain areas is analogous to the integration of new information into the models at higher hierarchical layers.

Recently, Vuust and colleagues ([47](#_ENREF_47), [69](#_ENREF_69), [70](#_ENREF_70)) have suggested that the predictive coding theory can provide a useful framework for understanding music perception in general and rhythm perception in particular. If meter is seen as the mental model and rhythm is the input, the relationship between the two complies with the predictive coding framework in a number of ways:

**Influences on meter perception:** First, the model can describe how the brain infers a hierarchical prediction model (the meter) from a given piece. Brochard and colleagues, ([71](#_ENREF_71)) as mentioned elsewhere in this book, (Chapter 5.2) provided strong evidence for the automaticity of this process in the simplest possible experimental setting. Specifically, they showed that listening to an undifferentiated metronome pattern causes the brain to register some beats as automatically more salient than others, in a duple meter. In predictive coding terms, the brain is interpreting the input, in this case metronomic beats, according to its own anticipatory framework. These anticipatory brain mechanisms are dependent on long-term learning, familiarity with a particular piece of music, deliberate listening strategies and short-term memory for the immediate musical past during listening. ([72](#_ENREF_72)) Brain structures underlying musical expectation are thus shaped by culture, personal listening history, musical training and biology (Figure 6.4- 7).

**Brain processing of syncopation:** Second, rhythmic violations of the brain’s metrical model, such as syncopations or metric displacement, should give rise to prediction error. Since the meter may be supported by the actual musical sounds to a varying extent, different expressions of syncopation and different types of rhythmic patterns could hence give rise to smaller or greater prediction error. These would first occur at certain lower level brain areas, which would subsequently be evaluated in a larger network including brain areas at higher hierarchical levels, leading to subjective evaluation and learning. This is an automatic process, and the size of the prediction error is affected by cultural and biological factors. In particular, the size of the error term is influenced by rhythmic or musical expertise. Expertise in predictive coding terms means that the metrical model is strengthened. Hence, musicians should show stronger brain signatures of prediction error than non-musicians, according to the predictive coding theory.

**Brain processing of polyrhythm:** Third, extreme instances of prediction error, such as in the case of continuous tension caused by polyrhythms suggesting counter-meter, should either cause the model to break down or lead to a continuous effort to sustain the main metrical model. Compared to instances of model shift and prediction error, the continuous effort in turn leads to sustained activity in the relevant brain areas and networks, including areas at a higher level than those primarily generating the prediction error. In contrast to the prediction error at the lower level, this brain activity at higher levels should reflect an inverse relationship between expertise and brain activity, since experts need less effort in order to maintain the main meter.

**Brain processing of groove**: Fourth, when the rhythmic violations are continuously repeated, such as in the context of groove, the string of hierarchically related prediction errors at different parts of the neural network should facilitate the characteristic experiential effect of groove, namely the positive drive towards body-movement. Because the tension between rhythm and meter repeats throughout the groove, the prediction errors at the lower levels of the coding hierarchy, caused by for example syncopation, metric displacement or instances of cross-rhythm, become predicted at the higher levels.[[3]](#footnote-3) Thus, the original metric model is maintained, while the metrically deviating rhythmic structures facilitate embodied and affective responses.

## Predictive coding error messages indexed by the MMN

As mentioned, the predictive coding mechanism can account for the extracting of the salient parts of an incoming signal and the avoidance of processing redundant information. Accordingly, neuronal networks extract the statistical regularities in the incoming stimulus and reduce redundancy by removing the predictable components, leaving only what is not predictable (the residual errors in prediction). This mechanism has received significant attention from researchers interested in visual perception, as it is consistent with both the spatial and temporal receptive fields found in the retina. ([62](#_ENREF_62))

The predictive coding theory provides an equally feasible explanation for pre-attentive auditory prediction and this has been studied extensively through the ‘mismatch negativity’ (MMN) paradigm. The MMN is a component of the auditory event-related potential (ERP) in the brain that can be recorded using electroencephalography (EEG) and relates to change in different sound features, such as pitch, timbre, location of sound source, intensity, rhythm or other more abstract auditory changes, such as streams of ascending intervals. ([74](#_ENREF_74), [75](#_ENREF_75)) The trajectory of the response peaks around 100-200 ms after deviation onset and the amplitude and latency of the MMN depends on deviation magnitude and related perceptual discriminability, such that larger deviations yield larger and faster MMNs. ([76](#_ENREF_76)) The MMN, primarily originating in the auditory cortices bilaterally, is often accompanied by a later component, the P3a, also in the auditory cortices, which is usually associated with the evaluation of the salient change for subsequent behavioral action. It is believed to indicate activity in a network which contains frontal, temporal and parietal sources. ([77](#_ENREF_77))

The MMN signal appears to have properties analogous to the error signal in a predictive coding framework. It is dependent on the establishment of a pattern or model and responds only when the predictive pattern is broken. MMNs have been found in response to pattern deviations determined by physical parameters, such as frequency, ([78](#_ENREF_78)) intensity, ([76](#_ENREF_76)) spatial localization, ([79](#_ENREF_79)) and duration, ([79](#_ENREF_79)) but also to patterns with more abstract properties. ([80](#_ENREF_80), [81](#_ENREF_81)) Importantly the size of the mismatch negativity adjusts as the pattern adapts, ([82](#_ENREF_82)) hence the size of the error message is dependent on the brain’s model of the incoming input as well as on the input itself.

The MMN is also strongly dependent on the expertise of the participants. Musicians who adjust the tuning of their instrument during performance, such as violinists, display a greater sensitivity to small differences in pitch compared to non-musicians and other musicians playing other instruments ([83](#_ENREF_83)); singers respond with a stronger MMN than instrumentalists to small pitch changes ([84](#_ENREF_84)); and conductors process spatial sound information more accurately than professional pianists and non-musicians. ([85](#_ENREF_85)) Recently, it was shown that the characteristics of the style/genre of music played by musicians influence their perceptual skills and the brain processing of sound features embedded in a musical context as indexed by larger MMN. ([86](#_ENREF_86), [87](#_ENREF_87))

## The influences of musical expertise on brain processing of syncopation

Vuust and colleagues investigated whether differential violations of the hierarchical prediction model provided by musical meter would produce error messages indexed by the MMN and whether musical expertise influenced the ERPs. ([88](#_ENREF_88)) They compared rhythmically unskilled non-musicians with expert jazz musicians on two different types of metric violations: syncopations in the bass drum of a drum kit pattern (a musically common violation), and a more drastic disruption of the meter (a musically less common violation). Jazz musicians perform highly complex rhythmic music and are therefore ideal candidates for identifying putative competence-dependent differences in the processing of metric violations. The researchers found event-related responses to strong rhythmic incongruence (metric disruption) in all subjects, the magnetic equivalence of the MMN (MMNm) peaking at 110-130 ms and the P3am around 80 ms after the MMNm in expert jazz musicians. Some of the rhythmically unskilled subjects also exhibited the P3am. Furthermore, responses to more subtle rhythmic incongruence (syncopation) were found in most of the expert musicians. The MMNms were localized to the auditory cortices, whereas the P3am showed greater variance in localization between individual subjects. MMNms of expert musicians were stronger in the left hemisphere than in the right hemisphere in contrast to P3ams showing a slight non-significant right-lateralization.

The MMNm and P3am were interpreted as reflecting an error term generated in the auditory cortex and its subsequent evaluation in a broader network including generators in the auditory cortex as well as higher level neuronal sources. The researchers also found evidence of model adjustment in two of the jazz musicians. These findings are thus in keeping with expectations based on the predictive coding theory and suggests that there is a congruous relationship between perceptual experience of rhythmic incongruities and the way that these are processed by the brain. However, it should be noted that other researchers have suggested that the predictive coding processes possibly underlying the MMN generation could in principle happen within the different layers of the auditory cortex. ([89](#_ENREF_89)) More research is needed to determine the localization of the computational networks supporting the predictive models leading to the MMN.

The study by Vuust et al. ([88](#_ENREF_88)) described above, showed quantitative and qualitative differences in brain processing between the participant groups indicating that the prediction error generated by meter violation correlates positively with musical competence, A predictive coding interpretation of this would posit that the metrical model of musicians is stronger than that of non-musicians, leading to greater prediction error. However, greater competence does not necessarily lead to more efficient brain processing in a linear fashion. “More” is not necessarily “more”.

## Predictive coding of polyrhythmic music

As described above, polyrhythm is an extreme example of how rhythmic complexity is established as interplay between the brain’s anticipatory framework and the incoming stimulus during music listening and performance. For example, when listening to the soprano sax solo on Sting’s “The Lazarus Heart”, the rhythm suddenly changes to a different meter for the duration of six bars, with no trace of the original meter in the actual sound. It is still possible to keep the original meter overall, since the subdivisions and metric frameworks of the two different meters eventually coincide after the six bars. However, what makes it almost impossible for a listener to avoid adjusting to the new beat during the six bars, for example by shifting the phase of foot-tapping or head-nodding, is that the saxophone’s melodic solo completely switches to the new meter by emphasizing its complete hierarchical structure of subdivisions. For a listener with jazz music training, it would be imperative to try to keep the original meter, primarily since the rhythmic tension between the old and new meter is important to the experience of this piece, but also because it is necessary for all musicians to mentally maintain the original metric framework in order for collective improvisation to work. Hence, there is a big difference in experienced complexity between an expert listener who stays in the original meter, and the inexperienced listener who switches back and forth between the two meters, avoiding much of the tension.

In two studies of polyrhythm, Vuust and colleagues used this Sting example to investigate neural correlates of polyrhythmic tension by way of functional Magnetic Resonance Imaging (fMRI). ([46](#_ENREF_46), [49](#_ENREF_49)) fMRI is a brain scanning technique which enables the measurement of the blood oxygenated level dependent (BOLD) signal in the brain, by contrasting this signal during different perceptual or task-related epochs. As the source of the signal can be localized with great spatial resolution in the brain, this technique provides, indirectly, indications of the activity in areas of the brain that are associated with different tasks. The extent of the spatial resolution is greater in fMRI than in MEG/EEG, but when studying auditory stimuli such as music, there are important drawbacks of using fMRI. Importantly, the temporal resolution of this technique is of the order of seconds or more and can thus not capture sub-second musical temporal events, such as microtiming.

However, since the experience of polyrhythm typically evolves over seconds, fMRI was found suitable for a study in which the neural correlates of epochs of polyrhythm (counter-meter and main meter) were contrasted with epochs containing only the main meter. ([46](#_ENREF_46)) 17 subjects, all ‘rhythm-section’ players, specifically drummers, bassists, pianists and guitarists, were recruited for the study. During the first experiment, they were required to tap along to the main meter while being asked to focus first on the main meter, and second on a strong counter-meter. In the second experiment, the participants listened to the main meter throughout the study but were asked to tap the main meter followed by the counter-meter. In both experiments, the BOLD analyses showed activity in a part of the inferior frontal gyrus, specifically Brodman’s area 47 (BA 47), most strongly in its right-hemispheric homologue (Figure 6.4- 8). This area is typically associated with language, in particular semantic processing. (For reviews, see [90](#_ENREF_90), [91](#_ENREF_91)) Hence, this area may serve more general purposes, such as sequencing or hierarchical ordering of perceptual information than formerly believed. Interestingly, BA 47 was active both in relation to the experience of polyrhythmic tension (experiment 1, in which the motor task was identical throughout) and the production of polyrhythmic tension (experiment 2, in which the auditory input was constant). It thus seems that this area, bilaterally, reflects processing of the prediction error in the polyrhythm per se. Importantly, the activity in BA 47 was inversely related to the rhythmic expertise of the subjects as measured by the standard deviation of tapping accuracy. Hence the effort to maintain the metrical model shows a negative correlation between expertise and brain activity, presumably since experts need less effort to maintain the main meter. It was also found that BA 40, an area previously related to language prosody and bistable percepts (e.g. Rubin’s vase, Figure 6.4- 3.C.), was active during tapping to polyrhythms (Figure 6.4- 8). Thus, the results showed that this area might be involved in the encoding of stimuli that allow for more than one interpretation, across as language, vision and audition. However, the fMRI data does not allow us to conclude whether the activity in the inferior frontal lobe could be preceded by a prediction error at a lower hierarchical level in the brain directly related to the polyrhythms, since the temporal resolution of fMRI is limited. Broca’s area has recently also been suggested to have a more general role related to hierarchical organization of information. ([92](#_ENREF_92))

[INSERT FIGURE 6.4- 8. HERE]

## Predictive coding in groove

In recent experiments, Witek and colleagues ([93](#_ENREF_93)) investigated the relationship between syncopation in groove and the desire to move and feelings of pleasure. Their stimuli consisted of 50 groove-based (funk) drum-breaks, in which 2-bar rhythmic phrases were repeated 4 times, with varying degrees of syncopation. Using a web-based survey, participants were asked to listen to the drum-breaks and rate to what extent the rhythms made them want to move and how much pleasure they experienced with the rhythms. The results showed an inverted U-shaped relationship between degree of syncopation and ratings, indicating that a positive increase in syncopation in groove increases embodied and affective responses, until an optimal point, after which a continued increase in syncopation causes the desire to move and pleasure to decrease. The inverted U is a familiar shape in aesthetics psychology, and has been found in the relationship between a number of forms of perceptual complexity in art and arousal (e.g. physical, physiological and evaluative). Berlyne ([94](#_ENREF_94)) famously proposed that appreciators of art prefer medium degrees of perceptual complexity, and this has been supported in a number of studies involving music. ([61](#_ENREF_61), [95](#_ENREF_95), [96](#_ENREF_96)) Accordingly, Witek et al.’s study showed that systematic increase in a form of rhythmic complexity, namely syncopation, increased the positive drive towards body-movement, but that beyond medium degrees of rhythmic complexity in groove, embodied and affective engagements with the music was prevented. Interestingly, rather than being affected by the participants’ formal musical training, it was found that those who enjoyed dancing and often danced to music rated the drum-breaks as eliciting more desire to move and more pleasure, overall. Thus, it seems that more broadly embodied previous engagements with music may affect the subjective experience of rhythmically complex music, such as groove, rather than institutionalized formal training, such as the ability to play an instrument.

The inverted U-shape found between degree of syncopation in groove and wanting to move and feelings of pleasure can again be seen as complying with the predictive coding theory. At low degrees of syncopation, there is little incongruence between the rhythm of the groove (the input to the model) and the meter (the predicted model), and thus the experiential effect, facilitated most explicitly at the higher levels of the hierarchical neural network, is weak. At high levels of syncopation, the degree of complexity is so high and the rhythm deviates too much from the metric framework causing the model to break down, and preventing pleasure and desire for movement. However, at intermediate degrees of syncopation in groove, the balance between the rhythm and the meter is such that the tension is sufficient to elicit positive affective and embodied responses, yet not so complex as to cause the meter to break down. In terms of predictive coding, the input and the model are incongruent, but not incompatible, and the prediction error affords the string of hierarchical encoding and evaluation from lower to higher levels in the brain. It is important to remember that the effect of syncopation in groove relies on the repetition of the syncopated patterns, and that it is the continuous effect of the tension caused by the relationship between rhythm (input) and meter (model) that causes the subjectively experienced tendencies towards body-movement and pleasure. In this way, the experience of groove is different from the experience of polyrhythm, as it is used in e.g. jazz, since polyrhythmic epochs usually have a relatively short duration and thus constitutes a momentary shift between weak and strong rhythmic tension.

## Perspectives

In this chapter, we have considered interval timing in music as integrated in a general view of brain processing, characterized by a dynamic interplay between an internal model, represented by the meter, and the incoming input, provided by rhythms in music. We have shown how such an understanding of the relationship between rhythm and meter supports theories of predictive coding mechanisms by which the brain tries to minimize the error between the rhythm and the meter. This mechanism can be exemplified by processing of different forms of rhythmic complexity in music, such as syncopation, polyrhythms and groove, and can also account for the experience of these phenomena as well as interpersonal differences in preference and competence. Importantly, the pleasure that many people experience with rhythms that do not conform entirely to the prescribed meter may be part of a predictive coding balance between meter and rhythm. Such notions fit nicely with theories of reward processing taking place during pleasure cycles mediated by the brain’s constant search for a balance of dopamine levels. ([97](#_ENREF_97), [98](#_ENREF_98)) However, a discussion of such links between prediction in music and reward are beyond the scope of the present chapter. ([cf. 69](#_ENREF_69)) As an important footnote, it should be mentioned that dopamine mediates both pleasure and motor processing in the brain, ([99](#_ENREF_99)) which points to a possible link between predictive coding theories and embodied approached to music cognition. ([100](#_ENREF_100)) While predictive coding is still a novel theory, which needs to be further empirically investigated in order to be more confidently applied as a general theory of brain function, the examples shown in the present chapter demonstrate how it has the potential to encompass different aspects of musical experience, particularly with regard to rhythm and meter. On the one hand, brain science thus offers a window into the underlying mechanisms of people’s rich and complex, affective and embodied engagements with music. On the other hand, the study of musical rhythm may provide us with novel insights into the predictive brain.

# Current state of the field

As the three chapters of this section have demonstrated, the study of the neurobiology of music and rhythm offers greater understanding of not just how we perceive music, but how the brain operates more generally. Chapter 5.1 has described how the functions associated with music are distributed in the brain, in ways that both overlap and are dissociable from language and speech processing. Using state-of-the-art neuroimaging techniques, as reported in Chapter 5.2, there is now increasing evidence that beat perception is both a fundamental and innate cognitive mechanism, the functions of which go beyond purely musical listening. And in the present chapter, we show how complex musical rhythms, such as syncopation, polyrhythm and groove, are processed, allowing us to make inferences about the role of temporal prediction as a fundamental organizing principle of the brain. However, a number of crucial aspects of the neurobiology of rhythm remain to be determined. The study of non-human animal perception of rhythm is still in its infancy, and a continued interest in such issues has great prospects for revealing the biological origin of music. Questions regarding the exact nature of metric hierarchies are still unanswered, and developing computational models that offer empirical tools for applying the hierarchical model of predictive coding might prove fruitful in answering such questions. Finally, although great progress has been made in the acknowledgement of action and body-movement in rhythm perception, more can be done to integrate such embodied theories of rhythm with affective models. With new neuroscientific tools developing rapidly, we might soon be able to tell you more about why abstract patterns of interval timing, such as rhythm, give us so much pleasure.

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# Figure 6.4- captions

**Figure 6.4- 1.** Metric tree-model. Each metric level (or value) is recursively subdivided into equally spaced parts (or values) at the level below, determining the metric salience of positions within the metric framework. The higher the value in the hierarchy, the more salient the position in the meter. Numbers designate serial positions within the meter, at 16th note resolution.

**Figure 6.4- 2.** A: Pattern with no syncopation (Audio Example 6.4- 1.). B: Pattern with syncopation, in red circle (Audio Example 6.4- 2.). Blue dots designate the main pulse (the background click in Audio Example 6.4-s 1. and 2.), and metric salience indicated above (strong and weak).

**Figure 6.4- 3.** A: Three-beat triple meter with four-beat pattern as counter-rhythm (Audio Example 6.4- 3.). B: Four-beat duple meter with three-beat counter-rhythm (Audio Example 6.4- 4.). Blue dots designate the main pulse . C: The bistable percept of Rubin’s vase.

**Figure 6.4- 4.** A: Metrically congruous pattern (Audio Example 6.4- 1.). B: Pattern metrically displaced by one eight-note, resulting in a metrically incongruous pattern (Audio Example 6.4- 5). Blue dots designate the main pulse (the background click in Audio Example 6.4-s 1. and 5.) and metric salience indicated above (strong and weak).

**Figure 6.4- 5.** Drum-break of “Ode to Billy Joe” by Lou Donaldson (1976).

**Figure 6.4- 6.** Groove of “Sex Machine” by James Brown (1970).

Figure 6.4- 7: The experience and learning of music takes place in a dynamic interplay between anticipatory structures in music, such as the build-up and relief of tension in rhythm, melody, harmony, form and other intra-musical features on one side, and the predictive brain on the other. The real time brain model is dependent on cultural background, personal listening history, musical competence, context (e.g. social environment), brain state (including attentional state and mood), and innate biological factors. The brain is constantly trying to minimize the discrepancy between its interpretation model and the musical input by iteratively updating the real time brain model (or prior) by weighting this model with the likelihood (musical input) through Bayes’ theorem. This leads to a constantly changing musical experience and long-term learning.

**Figure 6.4- 8.** Areas of activity in the brain during tapping to polyrhythms. Modified from Vuust et al. ([46](#_ENREF_46))

1. Although often used interchangeably, the difference between polyrhythm and polymeter is important to maintain. In the former, more than one rhythmic pattern is played simultaneously, underpinned by the same meter, while in the latter, more than one rhythm based on different meters is played simultaneously. [↑](#footnote-ref-1)
2. Microtiming, otherwise known as expressive timing or ‘swing’, refers to patterns of rhythmic events that do not occur exactly ‘on’ the pulse, but slightly ‘late’ or ‘early’ in relation to it. ([50-52](#_ENREF_50)) [↑](#footnote-ref-2)
3. According to this understanding, the meter can be seen as conveying what has elsewhere been termed schematic expectations, whereas the perceptually syncopated rhythmic patterns are perceived according to veridical expectations. ([73](#_ENREF_73)) [↑](#footnote-ref-3)