Perceiving Temporal Regularity in Music: The Role of Auditory Event-Related Potentials (ERPs) in Probing Beat Perception

Henkjan Honing, Fleur L. Bouwer, and Gábor P. Háden

Abstract

The aim of this chapter is to give an overview of how the perception of a regular beat in music can be studied in humans adults, human newborns, and nonhuman primates using event-related brain potentials (ERPs). Next to a review of the recent literature on the perception of temporal regularity in music, we will discuss in how far ERPs, and especially the component called mismatch negativity (MMN), can be instrumental in probing beat perception. We conclude with a discussion on the pitfalls and prospects of using ERPs to probe the perception of a regular beat, in which we present possible constraints on stimulus design and discuss future perspectives.

Keywords

Auditory perception • Music cognition • Rhythm • Beat induction • Event-related potentials (ERP) • Mismatch-negativity (MMN) • Temporal expectation • Music

Introduction

In music, as in several other domains, events occur over time. The way events are ordered in time is commonly referred to as *rhythm*. In musical rhythm, unlike in other domains, we often perceive an underlying regularity in time, which is known as the pulse or the *beat*. The beat is a regularly recurring salient moment in time [1]. The beat often coincides with an event, but a beat can also coincide with plain silence ([2]; see Fig. 1). At a higher level, we can hear regularity in the form of regular stronger and weaker beats and at a lower level, we can perceive regular subdivisions of the beat. We thus can perceive multiple levels of regularity in a musical rhythm, which together create a hierarchical pattern of saliency known as *metrical structure* or simply, *meter*. In this chapter, we will mainly focus on the processes underlying the perception of the most salient level of regularity in this perceived metrical structure: the beat.

The sensory and cognitive mechanisms of beat perception have quite a history as a research topic [3–8]. These mechanisms have been examined in

H. Honing (✉) • F.L. Bouwer • G.P. Háden
Institute for Logic, Language and Computation (ILLC), Amsterdam Brain and Cognition (ABC), University of Amsterdam, Amsterdam, The Netherlands
e-mail: honing@uva.nl

Fig. 1 A rhythm notated in common music notation (labeled Score) and as *dashes* (sound) and *dots* (silence) on a *grid* (labeled Rhythm). The perceived beat is marked with *bullets*; one possible metrical interpretation is marked with a metrical tree, with the length of the branches representing the theoretical metric salience and bullets marking the regularities at each metrical level. The rest (labeled R) marks a 'loud rest' or *syncopation*: a missing event on an induced beat

many music perception studies, mostly from a theoretical and psychological point of view [4, 6, 9, 10]. More recently, beat perception has attracted the interest of developmental psychologists [11], cognitive biologists [12], evolutionary psychologists [13], and neuroscientists [14, 15]. In addition, in the last decades a change can be observed from studying beat perception from a psychophysical perspective (studying the relation between stimulus and sensation) using relatively simple stimulus materials [16], to studying beat perception with more ecologically valid materials that take the task and the effect of musical context into account [8, 17]. In its entirety this has resulted in a substantial body of work using a variety of methods. In this chapter we will focus on studying the perception of the beat using electrophysiological methods.

Beat Perception as a Fundamental Cognitive Mechanism

It seems a trivial skill: children that clap along with a song, musicians that tap their foot to the

music, or a stage full of line dancers that dance in synchrony. And in a way it is indeed trivial. Most people can easily pick up a regular pulse from the music or can judge whether the music speeds up or slows down. However, the realization that perceiving this regularity in music allows us to dance and make music together makes it a less trivial phenomenon. Beat perception might well be conditional to music [18], and as such it can be considered a fundamental human trait that, arguably, has played a decisive role in the origins of music [13]. Three properties of the ability to perceive a beat can be looked at when considering its role in the origins of music: whether it is an innate (or spontaneously developing) ability, whether it is specific to the domain of music and whether it is a species-specific ability.

Innateness, Domain- and Species-Specificity

Scientists are still divided whether beat perception develops spontaneously (emphasizing a biological basis) or whether it is learned (emphasizing a cultural basis). Some authors consider a sensitivity to the beat to be acquired during the first years of life, suggesting that the ways in which babies are rocked and bounced in time to music by their parents is the most important factor in developing a sense for metrical structure [19]. By contrast, more recent studies emphasize a biological basis, suggesting that beat perception is already functional in young infants [20] and possibly even in 2–3 day old newborns [21]. These recent empirical findings can be taken as support for a genetic predisposition for beat perception, rather than it primarily being a result of learning.

Furthermore, developmental studies suggest that infants are not only sensitive to a regular pulse, but also to regularity at a higher level (two or more levels of pulse; [22]). Thus it is possible that humans possess some processing predisposition to extract hierarchically structured regularities from music [23, 24]. To understand more about these capacities to hear regularity in music and to examine whether they are indeed

(partly) innate, research with newborns provides a suitable context [18, 21].

With regard to the domain-specificity of beat perception convincing evidence is still lacking, although it was recently argued that beat induction does not play a role (or is even avoided) in spoken language [25]. Furthermore, the perception of a beat occurs more easily with auditory than visual temporal stimuli [26], with audition priming vision [27], but not vice versa [28].

With regard to the species specificity of beat perception, it is still unclear which species have this ability. It was recently shown that rhythmic entrainment, long considered a human-specific mechanism, can be demonstrated in a select group of bird species [29–31], and not in more closely related species such as nonhuman primates [32, 33]. This is surprising when one assumes a close mapping between a genetic predisposition (specific genotypes) and specific cognitive traits. However, more and more studies show that genetically distantly related species can show similar cognitive skills; skills that more genetically closely related species fail to show [34]. The observations regarding beat perception in animals support the *vocal learning hypothesis* [35] that suggests that rhythmic entrainment is a by-product of the vocal learning mechanisms that are shared by several bird and mammal species, including humans, but that are only weakly developed, or missing entirely, in nonhuman primates [36]. Nevertheless it has to be noted that, since no evidence of rhythmic entrainment was found in many vocal learners (including dolphins and songbirds; [30]), vocal learning may be necessary, but clearly is not sufficient for beat perception and rhythmic entrainment. Furthermore, vocal learning itself may lie over a continuum rather than being a discrete ability, as for example sea lions (*Zalophus californianus*) seem capable of rhythmic entrainment [37] while there is little or no evidence of vocal learning [38]. Whereas research in human newborns can answer questions about the innateness of beat perception, research in various animals can answer questions about the species-specificity of beat perception.

Beat Induction

We use the term *beat induction* for the cognitive mechanism that supports the detection of a regular pulse from the varying surface structure of musical sound. This term stresses that the perception of a beat is not a passive process but an active one in which a listener induces a particular regular pattern from a rhythm. It emphasizes that a beat does not always need to be physically present in order to be perceived. This is, for example, the case when we hear a *syncopation* (or 'loud rest'; see Fig. 1), in which the beat does not coincide with an event in the musical surface, but with a silence [18].

As we have seen, beat perception and beat induction can be considered fundamental to music perception and production. Questions of innateness, domain-specificity and species-specificity need to be addressed to further reveal the relationship between beat perception and the origins of music. Before we turn to a possible method to answer these questions, first, the possible mechanisms that constitute beat perception and beat induction will be discussed.

Possible Mechanisms of Beat Induction

The Perception of a Beat

The perception of a beat is a bi-directional process: not only can a varying musical rhythm induce a regular beat, a regular beat can also influence the perception of the very same rhythm that induces it. Hence beat perception can be seen as an interaction between bottom-up and top down sensory and cognitive processes [10]. Initially, we induce a beat from various cues in the music. Once a context of regularity is established, we use the inferred beat to interpret the music within this context and to predict future events [7]. A perceived pulse is stable and resistant to change [39]. However, if the sensory input provides clear evidence for a different metrical structure, our perception of the

beat can change. The relation between the events in the music and the perceived temporal regularity thus is a flexible one, in which the perceived metrical structure is both inferred from the music and has an influence on how we perceive the music [40, 41].

Boundaries on Beat Perception

We can perceive regularity in music at different metrical levels and thus at different timescales. It should be noted that the perception of temporal regularity is restricted by several perceptual boundaries. We can perceive temporal regularity with a period roughly in the timescale of 200–2,000 ms [42]. Within this range, we have a clear preference for beats with a period around 600 ms or 100 beats/min. This rate is referred to as *preferred tempo* [3]. A beat at this tempo is usually very salient. Most empirical studies looking at beat perception use a rate of stimulus presentation that makes it possible to hear a beat at preferred tempo level.

Beat Induction Through Accent Structure

To infer a metrical structure from music we make use of accents. In a sequence of events, an accent is a more salient event because it differs from other, non-accented events along some auditory dimension [43]. When accents exhibit regularity in time, we can induce a regular beat from them. Accented tones are then usually perceived as on the beat or, on a higher level, as coinciding with a strong rather than a weak beat [44].

A sequence of events in time, such as a musical rhythm, also contains purely *temporal accents* that arise from the structure of event onsets rather than from acoustic changes in the sound. Events are perceived as more or less salient depending on their length and position in a rhythm. Povel and Essens [4] describe three ways in which a temporal accent can occur. First, when an onset is isolated relative to other onsets, it sounds like an accent. Second, when

two onsets are grouped together, the second onset sounds accented. Finally, for groups of three or more onsets, the first and/or last tone of the group will be perceived as an accent.

While it has been suggested that beat induction is mainly guided by these temporal accents [45], recently it has been shown that pitch accents also play a role in perceiving the beat [43, 46]. It is very likely that in natural music, many features of tones can contribute to an accent structure and our perception of the beat, including not only pitch, but also timbre and intensity. In line with this, Bolger et al. [27] and Tierney and Kraus [47] showed that the use of ecologically valid stimuli can actually enhance the perception of a beat. However, to date, melodic, timbre and intensity accents have been largely ignored in many studies examining beat perception.

Beyond Accents

While accents explain a large part of how we infer a beat and metrical structure from music, several other processes must be taken into account. First, it must be noted that we sometimes perceive temporal structure without any accents present. Rather, we actually imagine accents where they are not psychically present. This phenomenon has been termed *subjective rhythmization* and is very apparent when listening to a clock. Whereas every tick of a clock is equal, we often hear every other tick as an accent (e.g., 'tick-tock' instead of 'tick-tick'). Direct evidence for the presence of subjective rhythmization in isochronous sequences comes from studies comparing the brain response to tones in odd positions (which are subjectively accented) with the response to tones in even positions (which are not subjectively accented). It was found that slightly softer tones were perceived as more salient in odd than in even positions [48]. While this shows the presence of the effect, the mechanism underlying subjective rhythmization is still unclear [49].

A second influence on beat induction is our previous experience. Hannon and Trehub [50]

showed how cultural background and exposure to music can affect how well we can discern a metrical structure. In their study, participants listened to folk melodies with either a simple or a complex metrical structure. They were subsequently presented with two alterations of the melody, one in which the metrical structure was preserved, and one in which the metrical structure was violated. Participants then rated the similarity of the altered melodies to the original melody. Adults of Bulgarian and Macedonian origin, who are accustomed to complex metrical structures (i.e., compound meters like 5/8 or 7/8), differentiated between structure-preserving and structure-violating alterations in both complex and simple metrical structures. However, participants with a Western background did so only in the melodies with a simple meter. This was most likely due to the fact that Western listeners are not familiar with complex meters. Interestingly, 6 month-old infants responded differentially to structure-preserving and structure-violating alterations regardless of whether they occurred in a simple or complex metrical structure. This implies that the difference between the adults from Western and Balkan cultures is due to enculturation, which takes place sometime after the age of 6 months. It shows that the culture with which we are familiar influences how we perceive the metrical structure (for more evidence regarding the effect of culture on beat and meter perception, see [51]). In addition to the familiarity of different metrical structures, our culture can also provide us with template of certain patterns that specify a certain metrical structure. For example, snare drum accents in rock music often indicate the *offbeat* rather than the beat [7].

Finally, in addition to the influence of an accent structure, subjective rhythmization and our previous experience, the perception of a beat can also be guided by conscious effort. By consciously adjusting the phase or period of the regularity we perceive, we can influence which tones we hear on the beat. For example, when we listen to an isochronous series of tones, without any instruction, we will hear every other tone as accented [49]. However, by conscious effort, we

can project a beat on every third tone, thus adjusting the period of the beat to our will. This ability has been very useful in examining beat and meter perception, because it can allow us to hear a physically identical stimulus as on the beat or not, depending on the (instructions for examples, see [52, 53]). Any change in neural activity found can then reliably be attributed to beat perception, without having to control for physical differences between tones that are on or off the beat.

To summarize, beat induction is guided by the temporal and acoustic structure of events. It is constrained by our perceptual system and can be influenced by our earlier exposure to music, subjective rhythmization and conscious effort. When we listen to music, we induce a beat from the sensory input and then use that information to predict future events within a metrical framework. One way of understanding the mechanisms of beat perception is in the framework of the *predictive coding theory* (see Vuust et al., last chapter of this volume). Another prominent theory explaining the interaction between the varying sensory input and beat perception is the Dynamic Attending Theory [54].

Dynamic Attending Theory

Dynamic Attending Theory (DAT) explains the perception of metrical structure as regular fluctuations in attention. It proposes that internal fluctuations in attentional energy, termed *attending rhythms*, generate expectancies about when future events occur. When attentional energy is heightened an event is expected. Such a peak in attentional energy is perceived as a metrically strong position, i.e., on the beat. The internal fluctuations in attentional energy can entrain to the rhythm of external events, by adapting their phase and period, which corresponds to how we infer a metrical structure from events in the music. The attending rhythms are self-sustaining and can occur at multiple levels, tracking events with different periods simultaneously [6, 55]. These features correspond respectively to the stability of our metrical percept and the

perception of multiple hierarchical levels of regularity [39]. As such, DAT can explain many aspects of beat and meter perception. Behavioral support for DAT comes from studies showing a processing advantage in metrically strong positions for temporal intervals [6], pitch [56] and phonemes [57]. This is thought to be the result of the peaks in attentional energy associated with metrically salient positions.

At a neural level, beat and meter perception have been hypothesized to originate from neural oscillations that resonate to external events (*neural resonance*, see [39]). This view on the perception of metrical structure can be seen as an extension of DAT and makes largely the same predictions. Like the attending rhythms in DAT, neural oscillations are suggested to be self-sustaining and are suggested to adapt their phase and period to an external rhythm. In addition to these features, neural oscillations may arise at frequencies that are not in the stimulus, which may be an explanation for the phenomenon of subjective rhythmization [39].

Snyder and Large [58] provided some empirical evidence for the neural resonance theory, by showing that high frequency neural oscillations reflect rhythmic expectancy. They presented participants with a rhythm consisting of alternating loud and soft tones, while measuring their brain activity using electroencephalography (EEG). With this method it is possible to measure the electric activity of the brain with high temporal precision and thus, it is possible to show high frequency neuronal oscillations. The results showed that a peak in induced gamma oscillations (20–80 Hz) coincided with the sounds. When a loud sound was omitted, this peak was still present, which was interpreted as evidence that the induced activity represented the regular underlying beat, which continued even without physical input. Additional evidence in this line was provided by Zanto et al. [59], Iversen et al. [52] and Fujioka et al. [60]. In each of these studies, induced oscillatory activity was shown to relate to metrical expectations. The question remains, however, whether neural resonance is actively influencing rhythm perception or whether it is an emergent attribute of the EEG

response induced by the rhythmic structure of the stimulus itself [61]. Also, to date, support for neural resonance as an explanation for beat perception only comes from studies using isochronous stimuli. Whether neural resonance also explains phenomena such as subjective rhythmization and beat perception with more complex stimuli remains to be tested.

Metrical Structure Is Perceived in Motor Areas of the Brain

EEG provides excellent temporal resolution. However, to localize the networks involved in beat perception, the superior spatial resolution of functional magnetic resonance imaging (fMRI) is needed. The overall picture emerging from fMRI studies looking at beat perception is that of large involvement of the motor areas in the brain. Grahn and Brett [14] examined beat perception using different rhythmic sequences, containing temporal accents (i.e. accents that arise from the structure of event onsets; cf. [4]). In some rhythms these accents were spaced evenly, while in other rhythms they were irregular. Rhythms with regular accents were considered to be metrical rhythms and rhythms with irregular accents non-metrical. Only metrical rhythms induced a beat, as was confirmed by a behavioral test. Using fMRI it could be shown that during listening to metrical rhythms the basal ganglia and the supplementary motor area (SMA) were more active than during listening to non-metrical rhythms, implicating these areas in beat perception. The findings of Grahn and Brett [14] were confirmed by several subsequent studies showing activations not only in the basal ganglia and SMA, but also in the cerebellum and pre-motor areas [62–64]. Importantly, activity in a network of motor areas was consistently observed, even when participants were asked not to make overt movements. This shows that these areas are involved when people just listen to a metrical rhythm (for a review on the neural correlates of beat and meter perception, see [65, 66]).

Motor areas have been implicated in time perception in general. However, recently it was

shown that specific networks are dedicated to perceiving absolute and relative durations respectively. While a network comprising the cerebellum and the inferior olive is involved in absolute *duration-based* timing, a different network, including the basal ganglia and the SMA, is active for relative or *beat-based* timing [67]. The perception of a beat, which requires the perception of temporal regularity, thus appears to be a distinct process from the general perception of temporal intervals. We will refer to this as the auditory timing *dissociation hypothesis* (see also [68, 69]).

To summarize, regular fluctuations in attentional energy and neural resonance have been suggested to explain the perception of metrical structure. Also, a role for a network of motor areas in the brain, including the basal ganglia and the SMA, has been implicated. Finally, a dissociation between rhythm perception and beat perception has been suggested.

Beat Perception in Human Adults, Human Newborns, and Nonhuman Primates

As discussed in the Introduction, some of the main questions regarding beat perception are concerned with whether beat perception is innate (or spontaneously developing) and/or species-specific. These questions about beat perception can potentially be answered by testing human newborns and nonhuman animals. These questions ask for a method that is non-invasive and does not require an overt response from the participant. EEG is well suited for this task and has the temporal resolution to track the perception of a beat over time. One way of looking at beat perception with EEG is by measuring neural oscillations. While this provides a promising way of examining beat perception, this line of research is very recent and has mostly been tested in adult participants under attended conditions. It is not yet clear whether beat perception can be measured through neural resonance in special groups of participants, like children, newborns or animals, and in conditions

in which participants do not attend to the rhythm. Questions regarding the innateness and species-specificity of beat perception have been addressed using EEG with the more traditional and well-studied approach of looking at *event-related potentials* (ERPs). In the remainder of this chapter we will therefore focus on using auditory ERPs in probing beat perception.

Measuring Beat Induction with Event-Related Potentials (ERPs)

Using ERPs to Probe Beat Perception

ERPs are hypothesized to reflect the sensory and cognitive processing in the central nervous system associated with particular (auditory) events [70]. ERPs are isolated from the EEG signal by averaging the signal in response to many trials containing the event of interest. Through this averaging procedure, any activity that is not time-locked to the event is averaged out, leaving the response specific to the event of interest: the ERP. While ERPs do not provide a direct functional association with the underlying neural processes, there are several advantages to the technique, such as the ability to record temporally fine-grained and covert responses not observable in behavior. Also, several ERP components have been well studied and documented, not only in human adults, but also in newborns and animals. Some of these components, used in testing beat perception, are elicited with an *oddball paradigm*.

An auditory oddball paradigm consists of a regular sequence of stimuli (standards), in which infrequently a stimulus is changed (deviant) in some feature (e.g., pitch, intensity, etc.). The deviant stimulus thus violates a regularity that is established by the standard stimuli. Depending on the task of the subject a deviant stimulus elicits a series of ERP components reflecting different stages and mechanisms of processing. The *mismatch negativity* (MMN), which is a negative ERP component elicited between 100 and 200 ms after the deviant stimulus, reflects automatic deviance detection
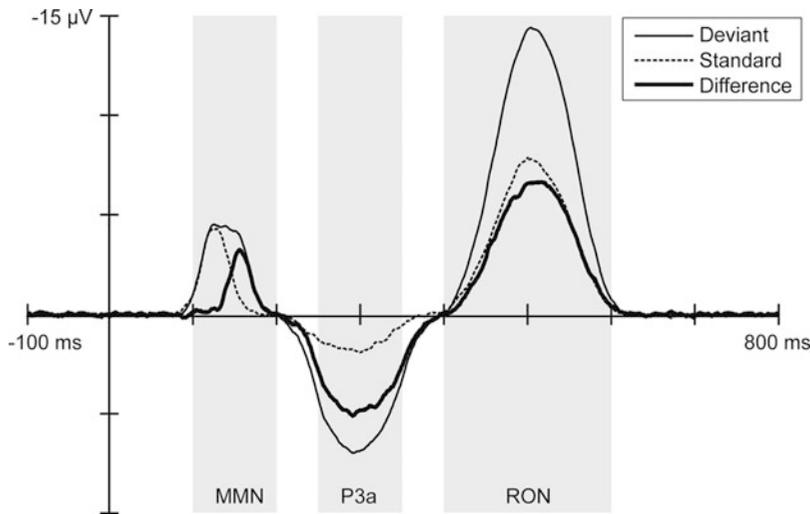
Fig. 2 Idealized event-related potential (ERP) responses to unattended stimuli in an oddball paradigm, showing the standard (*dotted line*), deviant (*solid line*) and deviant minus standard difference waveform (*bold line*). The mismatch negativity (MMN), P3a and reorientation negativity (RON) components are highlighted with *grey shading* indicating standard latency windows

through a memory-template matching process (see Fig. 2). The N2b is a component similar to the MMN in latency, polarity and function, but it is only elicited when the deviant is attended and relevant to the task. At around 300 ms after the deviant stimulus, a positive component can occur, known as the P3a, which reflects attention switching and orientation towards the deviant stimulus. For task relevant deviants, this component can overlap with the slightly later P3b, reflecting match/mismatch with a working memory representation [71, 72]. Finally, the reorientation negativity (RON; 400–600 ms) reflects switching back attention to the original task [73]. Several of these ERP components are known to index the magnitude of a regularity violation. A larger deviation from regularity yields a MMN, N2b, P3a and P3b with earlier latency and larger amplitude [74–77]. This property is exploited when probing beat perception with ERPs.

The general idea of using ERPs to probe beat perception is that an event on the beat is perceived differently from an event occurring not on the beat and thus that two physically identical events in different metrical positions should yield different brain responses. Moreover, because we perceive events on the beat as different from events not on the beat, we also perceive deviants on the beat as different from deviants not on the beat. An effect of metrical position on the ERP response to a deviant event is therefore interpreted as evidence for the presence of beat perception. In general, it is thought that deviant events on the beat are detected better than deviant events not on the beat and thus that the former elicit earlier and larger amplitude ERP responses than the latter [78].

An example of how deviant detection can show the presence of beat perception comes from studies examining subjective rhythmization [48, 49]. In these studies, participants were presented with an isochronous series of tones. They were hypothesized to perceive the tones in odd positions as stronger than tones in even positions. Infrequently, a softer tone was introduced, either in odd or in even positions. These deviants elicited an N2b and a P3b. The P3b to deviants in odd positions had a larger amplitude than the P3b to deviants in even positions, showing that the deviants were indeed detected better—or perceived as more violating—on the beat. Other studies have shown that the P3b component to deviants is

larger when the deviants occur in a regular sequence than when they occur in a sequence with random inter-onset intervals [78, 79].

While the elicitation of an N2b and a P3b requires attention and a conscious effort towards detecting deviant stimuli, the MMN is automatic and mostly independent of attention. As such, it has been possible to show MMN-like responses in newborn infants as well as in nonhuman species. This makes the MMN an ideal ERP component for interspecies comparisons and for testing the innateness of beat perception, provided that the MMN response is indeed sensitive to metrical structure and that beat perception can be shown to be *pre-attentive* in human adults. In the following sections, the MMN component and its relation to beat perception is discussed.

The Mismatch Negativity (MMN)

In general, the MMN is elicited when incoming sounds mismatch the neural representations of regularities extracted from the acoustic environment. Violations of the regularity in sound features such as pitch, duration or timbre can elicit an MMN [80, 81]. Also violations of abstract rules (i.e. one auditory feature predicting another; [82]) or stimulus omissions [83] can cause an MMN. The MMN is regarded as a predictive process [84] reflecting the detection of regularity-violations (for reviews see [85, 86]).

The processes underlying the MMN are thought to be automatic, however, the MMN can be modulated by attention [87] and even be completely eliminated when deviations in attended and unattended auditory streams vie for feature specific processing resources [88]. The fact that MMN can be elicited even in comatose patients [85], sleeping newborns [89] and anesthetized animals [90] illustrates the relative independence from attention. The latency and amplitude of the MMN are sensitive to the relative magnitude of the regularity violation [74, 76] and correspond to discrimination performance in behavioral tasks [91]. These properties can be exploited when, for example, beats on metrically strong and weak positions are compared or the relation between attention and beat perception is tested.

Using MMN to Probe Beat Perception in Human Adults

To date there has been only a handful of studies that used MMN to study beat perception. The different methods in these studies have two common design goals: First, all studies present subjects with stimuli that induce a metrical structure and the responses to regularity violations occurring on different metrical positions (e.g. on the beat and not on the beat) are compared. Second, all studies try to control attention to test whether the processes involved in differentiating between different metrical positions are automatic or dependent on attention, i.e. to study whether beat perception is pre-attentive [92]. The existing literature, however, contains inconsistent results (for a related review, see [65]).

Geiser et al. [93] presented subjects with rhythmic patterns containing temporal accents consistent with a regular 3/4 bar (e.g. the metrical structure of a waltz). In these metrically regular sequences infrequently a pitch deviant, a violation of the metrical structure or a violation of the temporal surface structure of the rhythm was introduced. The meter violations consisted of the addition or removal of an eight note to the regular 3/4 bar. To create the rhythm violations, one or two eight notes were substituted by two or four sixteenth notes, leaving the metrical structure intact. Subjects had to either ignore the changes in the temporal domain and detect the pitch changes (unattended condition) or ignore the pitch changes and detect the temporal changes (attended condition). Regardless of subjects' musical training, rhythm violations elicited an MMN-like component in both attended and unattended conditions. Meter violations however only elicited an MMN-like component in the attended condition, implying that attention is required to induce a beat. In an experiment with similar attentional control, Vuust et al. [94, 95] did find MMN responses to large temporal violations of the metrical

structure regardless of musical training and attention. Unfortunately the large changes violated not only the meter but also other parameters, like the underlying temporal grid. As this in itself would lead to a MMN response, it is not clear from these results whether the MMN system is indeed sensitive to metrical structure.

A converse result comes from the experiment of Geiser et al. [96] who used identical regular 3/4 bar sequences as in their earlier study [93]. However, in this study deviants in the form of intensity accents were introduced at meter-congruous and meter-incongruous positions. The attention control was achieved in this experiment by asking subjects to attend to a silenced movie, a common procedure in many MMN experiments [86]. Geiser et al. [96] found an enhanced MMN to accents in meter-incongruous positions for musicians and, to a lesser extent, for non-musicians, providing evidence in support of beat perception being pre-attentive. The conclusions drawn by this and the previous [93] study are radically different, while identical beat inducing stimuli were used. As such, these studies very clearly show how large the influence of different attentional controls and experimental design on the results can be.

Ladinig et al. [23, 24] took a somewhat different approach to meter perception in a study where they compared the responses of musically untrained subjects to omissions of tones with two different levels of metrical salience in a rock drum pattern (see Fig. 3). Two different levels of attention control were employed. In the *passive* condition subjects were attending to a silent movie, as in Geiser et al. [96]. In the *unattended* condition subjects were attending to intensity changes in a continuous stream of white noise. The latter condition was designed to be a strict control for attention as it required attention in the same modality, but for a different auditory stream. Results showed that the MMN responses elicited by infrequent omissions on the first beat (deviant D1; large violation of the metrical structure) and the second beat (deviant D2; smaller violation of the metrical structure) differed in latency but not in amplitude. The latency difference indicates faster processing for the larger

metric violation, suggesting that the metrical structure was picked up without attention.

Studying pre-attentive beat perception using the MMN is not as straightforward as one might like. Most notably, the use of acoustically rich stimuli (with potential differences between sounds in different metrical positions) may interfere in unforeseen ways with the ERP results (cf. [92]). One possible future direction is to strive for even more minimalistic paradigms and to test whether the auditory system automatically imposes structure to incoming unattended stimuli that have no apparent structure (e.g., isochronous sequences of the same sounds; subjective rhythmization). Alternatively, priming paradigms could be used that test how long externally imposed structure persists when the input is no longer structured. As the MMN responds not only to temporal but also to pitch and timbre deviants, it does allow studying more complex accent structures, a topic mostly ignored so far.

In summary, while the automatic nature of beat perception is not yet fully understood, MMN seems to be a promising candidate for measuring beat perception. In the next sections, we will discuss how ERPs in general and the MMN in particular can be used to examine beat perception in human newborns and nonhuman primates and other animals.

Measuring ERPs in Human Newborns

MMN-like ERP responses in newborns were first measured by Alho et al. [89]. Since then several studies tried to identify the correlates of developing and adult-like auditory processing. Recordings from newborns are inherently noisier than recordings from adults therefore MMN-like responses in newborns are not very robust. On the one hand the brain is in extremely rapid development during the first years of life. On the other hand the length of experiments are necessarily short and do not allow for complex experimental designs or extensive data collection to improve signal to noise ratio. ERPs both negative and positive in polarity and within a wide variety of latency ranges from about 80 ms up to

Fig. 3 Stimuli as used in several studies on beat and meter perception e.g., [21, 23, 33]. S1–S4 are the standards and D1 and D2 the deviants used in an oddball paradigm. The different percussion sounds are marked as hi-hat, snare and bass (see for more information www.mcg.uva.nl/newborns/ and www.mcg.uva.nl/monkeys/)
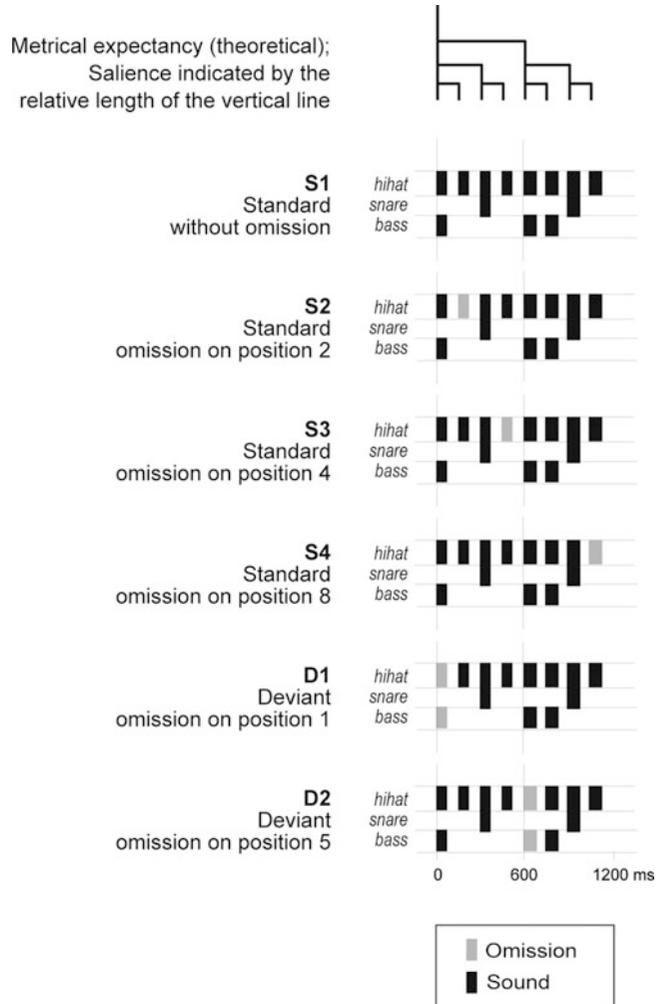
500 ms were found in response to oddball designs, also in absence of attention (the EEG recording in newborns is made during sleep). It is not yet clear whether the infants' responses are identical or only analogous to the adult MMN responses, but based on the different ERP responses to deviant and standard tones we can assume that the information on which the deviant-standard discrimination is based is available to the infant's brain. However, further processing steps are unclear. With these caveats in mind in the discussion below we will refer to these ERP responses found in newborns and young infants as MMN.

Several abilities that underlie music perception seem to be functioning already at birth.

Newborns are able to separate two sound streams based on sound frequency [97] and detect pattern repetitions which they incorporate into their model of the auditory scene [98]. Most important to beat perception is the ability to process temporal relations. Presenting a stimulus earlier or later than expected in an isochronous sequence elicits an MMN in 10-month old infants (Brannon et al. 2004), at least for large time intervals (500–1,500 ms). Newborns are also sensitive to shorter changes (60–100 ms) in stimulus length [99, 100] and 6-month old infants detect even shorter gaps (4–16 ms) inserted in tones [101, 102] showing the remarkable temporal resolution of the auditory system. Furthermore, Háden et al. [103] showed that newborns are sensitive to

changes in the presentation rate of the stimulation, can detect the beginning of sound trains, and react to the omission of expected stimuli. These results indicate that investigating phenomena reliant on temporal processing (e.g., beat perception) is viable.

Using MMN to Probe Beat Perception in Human Newborns

In the only experiment to date on beat perception in newborns Winkler et al. [21] used a variant of the paradigm used in Ladinig et al. ([23], see Fig. 3) to test whether newborns are able to extract a regular beat from a varying rhythmic stimulus. Sounds at the position of the strongest beat (the 'downbeat') in a 4/4 rock drum pattern were occasionally omitted (D1 in Fig. 3). The response to these omissions was compared to the response to omissions on weak metrical positions (e.g. not on the beat, S2–S4 in Fig. 3) and the response to omissions in a control sequence consisting of patterns in which the downbeat was always omitted. The ERP responses to the omissions on the downbeat differed significantly from responses to patterns without omission, omissions on weak positions and also omissions in the control sequence. The results were interpreted as proof to newborns ability to detect a beat.

Some reservations remain however. In the experimental design used there is no guarantee that the perceived phase of the control sequence was the same as the perceived phase of the other sequences (see also [23]). This is important because a different interpretation of the control sequence would mean that the position of the beat in the sequence might also be different. Another possible problem is that the acoustic context of weak and strong metrical positions is not identical. Finally, the omitted sounds on weak and strong positions are not physically identical. Therefore comparing them might be problematic (see also Discussion section).

The available evidence points to beat perception as an innate ability that is shaped by learning later on [11]. However, there is still some confirmation needed for newborn beat perception. New experiments should take into account the weaknesses of the Winkler et al. [21] design. In doing so, it would be beneficial to examine responses to temporal or spectral violations of regularity instead of omissions, as this would produce clearer electrical signals. In addition, this would allow for varying the tempo of the stimuli and loosen the constraint for relatively fast tempi (i.e., 150 inter-stimulus interval or shorter) that is needed for omission studies [83].

Measuring ERPs in Nonhuman Animals

There is quite some discussion on whether beat perception is species-specific [36]. The evidence that is in support of beat perception in certain species comes from experiments that test entrainment to a beat through overt behavior (e.g., [29]). However, if the production of synchronized movement to sound or music is not observed in certain species, this is no evidence for the absence of beat perception. It could well be that certain animals are simply not able to synchronize their movements to a varying rhythm, while they can perceive a beat. With behavioral methods that rely on overt motoric responses it is difficult to separate between the contribution of perception and action. Electrophysiological measures, such as ERP, that do not require an overt response, provide an attractive alternative to probe beat perception in animals.

Since the discovery of the MMN component researchers have tried to find analogous processes in animal models [104] and to integrate deviance detection and predictive processing into a general framework of auditory perception [105]. A wide range of electrophysiological methods from scalp electrodes to single-cell recordings have been used on animal models. These methods highlight different phenomena of varying spatial and temporal resolution. The most vital difference is that scalp and epidural recordings may yield components similar to the human MMN (i.e. electric responses generated by large brain areas), whereas local field potential, multiunit activity and single-cell recordings

work on a lower spatial scale and reflect *stimulus specific adaptation* (SSA; [106]). SSA has many common properties with MMN; both can be observed in similar paradigms and it is still debated whether SSA reflects the cellular level activity underlying MMN. However, this does not concern the main aim of this chapter and will not be discussed further (see Chap. 9 for more information on this topic).

Using epidural recording, MMN-like responses have been shown in different species including rats (for a review see [107]), cats [90, 108, 109] and macaque monkeys [110, 111]. In most of these studies, frequency and amplitude violations were used. In rats, deviance detection was shown for both a temporal feature, sound duration [107], as well as to an abstract feature, namely melodic contour [112]. Recordings from scalp electrodes showed MMN responses in mice [113] and in a single chimpanzee [114]. While not all attempts at recording MMN-like responses from animals were successful, it seems that MMN can be reliably elicited in animal models and thus can be used to study auditory processing in nonhuman animals.

Using MMN to Probe Beat Perception in Nonhuman Primates

Honing et al. [33] recorded ERPs from the scalp of macaque monkeys. This study demonstrates that an MMN-like ERP component can be measured in rhesus monkeys *(Macaca mulatta)*, both for pitch deviants and unexpected omissions. Together these results provide support for the idea that the MMN can be used as an index of the detection of regularity-violations in an auditory signal in monkeys.

In addition, the study showed that rhesus monkeys, using stimuli and an experimental paradigm identical to Winkler et al. [21], are not able to detect the regularity—the beat—induced by a varying rhythm, while being sensitive to the rhythmic grouping structure. These findings are in support of the hypothesis that beat perception is species-specific, and it is likely restricted to vocal learners such as a selected group of bird species, while absent in nonhuman primates such as rhesus monkeys.

The result is also in support of the dissociation hypothesis that posits different neural networks being active for interval-based and beat-based timing, of which only the former is shared between non-vocal learning species [33, 69].

Testing beat perception in animals has only started recently and there is still much work to be done [36]. The MMN component seems like a good index of beat perception as it can be elicited in several different species. Unfortunately most of the vocal learning species, such as cetaceans and pinnipeds, are not typical targets for ERP studies. Interestingly, a recent study suggests at least some level of vocal learning in mice [115]. This might prove to be an alternative starting point for testing beat perception in nonhuman animals.

Discussion and Conclusion

In this chapter we have seen that the perception of metrical structure seems specific to the domain of music and is shared with only a limited number of non-human animals. Nonetheless, this ability seems very basic to humans. People readily synchronize to a beat in a wide variety of settings, like concerts, demonstrations, when marching and when singing a song together. This apparent contradiction between the ease with which we are capable of hearing a beat and the uniqueness of this skill raises several questions about how fundamental the perception of metrical structure really is.

We have shown how ERPs can be used to answer fundamental questions about beat perception. Measuring ERPs is relatively straightforward, it can be realized in populations that are difficult to study behaviorally (like infants and monkeys), and it is a well-researched method. However, several issues remain.

One of the challenges in examining beat perception is to balance the need for highly controlled stimuli with the aim to use stimuli that are ecologically valid. On the one hand, future research must address the role of

different acoustic features in beat perception. Most research in this area has focused on temporal accents and has used either very simple or even isochronous sequences. While this is useful in controlling acoustic factors, it is not a very natural way of testing beat induction. In natural music, different types of accents often work together in shaping our metrical expectancies. The role of intensity accents, melodic accents and our previous experience has only been looked at very sparsely. However, using more natural stimuli can create problems in interpreting the results.

In natural music, a beat is induced by creating accents on the beat. Because accented sounds by definition need to stand out from non-accented sounds, this often means that tones on the beat have a different sound than tones that are not on the beat. When comparing the response to events on the beat and events that are not on the beat, these sound differences need to be taken into account. An example of this problem can be found in the work of Winkler et al. [21], who showed that newborn infants respond to the omission of a beat, but not to the omission of a sound that was not on the beat. While these results showed that the newborns differentiated between sounds in different metrical positions, it cannot be completely ruled out that they did so on the basis of differences in sound rather than position. The sounds that were on the beat were composed of a bass drum and a hi-hat sound, while the sounds that were not on the beat were composed of a single hi-hat sound. This means it is possible that the newborns responded differently to the omission of different sounds. To exclude alternative explanations like these, stimuli must be designed in which physical differences between the sounds in different metrical positions cannot influence the results [92]. Thus, balancing the design of ecologically valid stimuli with the experimental control needed to draw firm conclusions continues to be a challenge.

Another issue to be addressed in future research is the apparent gap between the sometimes contradicting, results obtained with the different methods used in probing beat perception. Some consensus is emerging on which brain networks are involved in the perception of beat and meter and how brain dynamics might be accountable for our metrical expectations. However, the connection between these findings remains unclear. Also, studies to date have all used slightly different stimuli and tasks, which in some cases results in radically different or even contradicting conclusions [23, 66, 93]. Once the different methods are used with similar paradigms, tasks and stimuli, it will be possible to directly compare the results and this will hopefully allow us to get a more coherent picture of the perception of beat and meter, and address its apparent innateness, domain- and species-specificity. All in all, this research will contribute to a better understanding of the fundamental role that beat and meter perception play in music.

References

1. Cooper G, Meyer LB. The rhythmic structure of music. Chicago: University of Chicago Press; 1960.
2. Longuet-Higgins HC, Lee CS. The rhythmic interpretation of monophonic music. Music Percept. 1984;1(4):424–41.
3. Fraisse P. Rhythm and tempo. In: Deutsch D, editor. Psychol music. New York: Academic; 1982. p. 149–80.
4. Povel D-J, Essens P. Perception of temporal patterns. Music Percept. 1985;2(4):411–40.
5. Clarke EF. Rhythm and timing in music. In: Deutsch D, editor. Psychol music. 2nd ed. New York: Academic; 1999. p. 473–500.
6. Large EW, Jones MR. The dynamics of attending: how people track time-varying events. Psychol Rev. 1999;106(1):119–59.
7. London J. Hearing in time: psychological aspects of musical meter. 2nd ed. Oxford: Oxford University Press; 2012.

8. Honing H. Structure and interpretation of rhythm in music. In: Deutsch D, editor. Psychol music. 3rd ed. London: Academic; 2013. p. 369–404.

9. Parncutt R. A perceptual model of pulse salience and metrical accent in musical rhythms. Music Percept. 1994;11(4):409–64.

10. Desain P, Honing H. Computational models of beat induction: the rule-based approach. J New Music Res. 1999;28(1):29–42.

11. Hannon EE, Trehub SE. Metrical categories in infancy and adulthood. Psychol Sci. 2005;16 (1):48–55. http://www.ncbi.nlm.nih.gov/pubmed/ 15660851.

12. Fitch WT. The biology and evolution of music: a comparative perspective. Cognition. 2006;100 (1):173–215. http://www.ncbi.nlm.nih.gov/pubmed/ 16412411.

13. Honing H, Ploeger A. Cognition and the evolution of music: pitfalls and prospects. Top Cogn Sci. 2012;4 (2012):513–24. http://www.ncbi.nlm.nih.gov/ pubmed/22760967.

14. Grahn JA, Brett M. Rhythm and beat perception in motor areas of the brain. J Cogn Neurosci. 2007;19 (5):893–906. http://www.ncbi.nlm.nih.gov/pubmed/ 17488212.

15. Grube M, Cooper FE, Chinnery PF, Griffiths TD. Dissociation of duration-based and beat-based auditory timing in cerebellar degeneration. Proc Natl Acad Sci U S A. 2010;107(25):11597–601. http:// www.ncbi.nlm.nih.gov/pubmed/20534501.

16. Handel S. Listening: an introduction to the perception of auditory events. Cambridge: MIT Press; 1989.

17. Clarke EF, Cook N. Empirical musicology: aims, methods, prospects. Oxford: Oxford University Press; 2004.

18. Honing H. Without it no music: beat induction as a fundamental musical trait. Ann N Y Acad Sci. 2012;1252(1):85–91. http://www.ncbi.nlm.nih.gov/ pubmed/22524344.

19. Phillips-Silver J, Trainor LJ. Feeling the beat: movement influences infant rhythm perception. Science. 2005;308(5727):1430. http://www.ncbi.nlm.nih. gov/pubmed/15933193.

20. Zentner M, Eerola T. Rhythmic engagement with music in infancy. Proc Natl Acad Sci U S A. 2010;107(13):5768–73. http://www.ncbi.nlm.nih. gov/pubmed/20231438.

21. Winkler I, Háden GP, Ladinig O, Sziller I, Honing H. Newborn infants detect the beat in music. Proc Natl Acad Sci U S A. 2009;106(7):2468–71. http:// www.pubmedcentral.nih.gov/articlerender.fcgi? artid=2631079&tool=pmcentrez& rendertype=abstract.

22. Hannon EE, Johnson SP. Infants use meter to categorize rhythms and melodies: implications for musical structure learning. Cogn Psychol. 2005;50 (4):354–77. http://www.ncbi.nlm.nih.gov/pubmed/ 15893524.

23. Ladinig O, Honing H, Háden GP, Winkler I. Probing attentive and preattentive emergent meter in adult listeners without extensive music training. Music Percept. 2009;26(4):377–86.

24. Ladinig O, Honing H, Háden GP, Winkler I. Erratum to probing attentive and pre-attentive emergent meter in adult listeners with no extensive music training. Music Percept. 2011;26:444.

25. Patel AD. Music, language and the brain. Oxford: Oxford University Press; 2008.

26. Repp BH, Penel A. Auditory dominance in temporal processing: new evidence from synchronization with simultaneous visual and auditory sequences. J Exp Psychol Hum Percept Perform. 2002;28 (5):1085–99.

27. Bolger D, Trost W, Schön D. Rhythm implicitly affects temporal orienting of attention across modalities. Acta Psychol (Amst). 2013;142 (2):238–44. http://www.ncbi.nlm.nih.gov/pubmed/ 23357092.

28. Grahn JA, Henry MJ, McAuley JD. FMRI investigation of cross-modal interactions in beat perception: audition primes vision, but not vice versa. Neuroimage. 2011;54(2):1231–43. http://www. pubmedcentral.nih.gov/articlerender.fcgi? artid=3002396&tool=pmcentrez& rendertype=abstract.

29. Patel AD, Iversen JR, Bregman MR, Schulz I. Experimental evidence for synchronization to a musical beat in a nonhuman animal. Curr Biol. 2009;19(10):827–30. http://www.ncbi.nlm.nih.gov/ pubmed/19409790.

30. Schachner A, Brady TF, Pepperberg IM, Hauser MD. Spontaneous motor entrainment to music in multiple vocal mimicking species. Curr Biol. 2009;19(10):831–6. http://www.ncbi.nlm.nih.gov/ pubmed/19409786.

31. Hasegawa A, Okanoya K, Hasegawa T, Seki Y. Rhythmic synchronization tapping to an audio–visual metronome in budgerigars. Sci Rep. 2011;1:1–8. http://www.nature.com/doifinder/10. 1038/srep00120.

32. Zarco W, Merchant H, Prado L, Mendez JC. Subsecond timing in primates: comparison of interval production between human subjects and rhesus monkeys. J Neurophysiol. 2009;102(6):3191–202. http://www.ncbi.nlm.nih.gov/pubmed/19812296.

33. Honing H, Merchant H, Háden GP, Prado L, Bartolo R. Rhesus monkeys (*Macaca mulatta*) detect rhythmic groups in music, but not the beat. PLoS One. 2012;7(12):e51369.

34. de Waal F, Ferrari PF. Towards a bottom-up perspective on animal and human cognition. Trends Cogn Sci. 2010;14(5):201–7. http://www.ncbi.nlm. nih.gov/pubmed/20363178.

35. Patel AD. Musical rhythm, linguistic rhythm, and human evolution. Music Percept. 2006;24(1):99–104. http://caliber.ucpress.net/doi/abs/10.1525/mp.2006.24. 1.99.

36. Fitch WT. Biology of music: another one bites the dust. Curr Biol. 2009;19(10):403–4. http://www.ncbi.nlm.nih.gov/pubmed/19467205.

37. Cook P, Rouse A, Wilson M, Reichmuth C. A California sea lion (*Zalophus californianus*) can keep the beat: motor entrainment to rhythmic auditory stimuli in a non vocal mimic. J Comp Psychol. 2013;127(2):412. http://doi.apa.org/getdoi.cfm?doi=10.1037/a0032345.

38. Arnason U, Gullberg A, Janke A, Kullberg M, Lehman N, Petrov EA, et al. Pinniped phylogeny and a new hypothesis for their origin and dispersal. Mol Phylogenet Evol. 2006;41(2):345–54. http://www.sciencedirect.com/science/article/pii/S1055790306001977.

39. Large EW. Resonating to musical rhythm: theory and experiment. In: Grondin S, editor. Psychol time. Bingley: Emerald Group; 2008. p. 189–231.

40. Grube M, Griffiths TD. Metricality-enhanced temporal encoding and the subjective perception of rhythmic sequences. Cortex. 2009;45(1):72–9. http://www.ncbi.nlm.nih.gov/pubmed/19058797.

41. Desain P, Honing H. The formation of rhythmic categories and metric priming. Perception. 2003;32(3):341–65. http://www.ncbi.nlm.nih.gov/pubmed/12729384.

42. London J. Cognitive constraints on metric systems: some observations and hypotheses. Music Percept. 2002;19(4):529–50.

43. Ellis RJ, Jones MR. The role of accent salience and joint accent structure in meter perception. J Exp Psychol Hum Percept Perform. 2009;35(1):264–80. http://www.ncbi.nlm.nih.gov/pubmed/19170487.

44. Lerdahl F, Jackendoff R. An overview of hierarchical structure in music. Music Percept. 1983;1(2):229–52.

45. Snyder JS, Krumhansl CL. Tapping to ragtime: cues to pulse finding. Music Percept. 2001;18(4):455–89. http://apps.isiknowledge.com/CitedFullRecord.do?product=UA&db_id=WOS&SID=N1keaj3j11cakI5aIIi&search_mode=CitedFullRecord&isickref=120772261.

46. Hannon EE, Snyder JS, Eerola T, Krumhansl CL. The role of melodic and temporal cues in perceiving musical meter. J Exp Psychol Hum Percept Perform. 2004;30(5):956–74. http://www.ncbi.nlm.nih.gov/pubmed/15462633.

47. Tierney A, Kraus N. Neural responses to sounds presented on and off the beat of ecologically valid music. Front Syst Neurosci. 2013;7:1–7. http://www.frontiersin.org/Systems_Neuroscience/10.3389/fnsys.2013.00014/abstract.

48. Brochard R, Abecasis D, Potter D, Ragot R, Drake C. The "ticktock" of our internal clock: direct brain evidence of subjective accents in isochronous sequences. Psychol Sci. 2003;14(4):362–6. http://www.ncbi.nlm.nih.gov/pubmed/12807411.

49. Potter DD, Fenwick M, Abecasis D, Brochard R. Perceiving rhythm where none exists: event-related potential (ERP) correlates of subjective accenting. Cortex. 2009;45(1):103–9. http://www.ncbi.nlm.nih.gov/pubmed/19027894.

50. Hannon EE, Trehub SE. Tuning in to musical rhythms: infants learn more readily than adults. Proc Natl Acad Sci U S A. 2005;102(35):12639–43. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1194930&tool=pmcentrez&rendertype=abstract.

51. Gerry DW, Faux AL, Trainor LJ. Effects of Kindermusik training on infants' rhythmic enculturation. Dev Sci. 2010;13(3):545–51. http://www.ncbi.nlm.nih.gov/pubmed/20443974.

52. Iversen JR, Repp BH, Patel AD. Top-down control of rhythm perception modulates early auditory responses. Ann N Y Acad Sci. 2009;1169:58–73. http://www.ncbi.nlm.nih.gov/pubmed/19673755.

53. Nozaradan S, Peretz I, Missal M, Mouraux A. Tagging the neuronal entrainment to beat and meter. J Neurosci. 2011;31(28):10234–40. http://www.ncbi.nlm.nih.gov/pubmed/21753000.

54. Jones MR. Musical time. In: Hallam S, Cross I, Thaut M, editors. Oxford handbook of music psychol. Oxford: Oxford University Press; 2009. p. 81–92.

55. Drake C, Jones MR, Baruch C. The development of rhythmic attending in auditory sequences: attunement, referent period, focal attending. Cognition. 2000;77(3):251–88. http://www.ncbi.nlm.nih.gov/pubmed/11018511.

56. Jones MR, Moynihan H, MacKenzie N, Puente J. Temporal aspects of stimulus-driven attending in dynamic arrays. Psychol Sci. 2002;13(4):313–9. http://pss.sagepub.com/lookup/doi/10.1111/1467-9280.00458.

57. Quené H, Port RF. Effects of timing regularity and metrical expectancy on spoken-word perception. Phonetica. 2005;62(1):1–13. http://www.ncbi.nlm.nih.gov/pubmed/16116301.

58. Snyder JS, Large EW. Gamma-band activity reflects the metric structure of rhythmic tone sequences. Cogn Brain Res. 2005;24(1):117–26. http://www.ncbi.nlm.nih.gov/pubmed/15922164.

59. Zanto TP, Large EW, Fuchs A, Kelso JAS. Gamma-band responses to perturbed auditory sequences: evidence for synchronization of perceptual processes. Music Percept. 2005;22(3):531–47.

60. Fujioka T, Trainor LJ, Large EW, Ross B. Internalized timing of isochronous sounds is represented in neuromagnetic Beta oscillations. J Neurosci. 2012;32(5):1791–802. http://www.ncbi.nlm.nih.gov/pubmed/22302818.

61. Smith LM, Honing H. Time–frequency representation of musical rhythm by continuous wavelets. J Math Music. 2008;2(2):81–97. http://www.tandfonline.com/doi/abs/10.1080/17459730802305336.

62. Grahn JA, Rowe JB. Feeling the beat: premotor and striatal interactions in musicians and nonmusicians

during beat perception. J Neurosci. 2009;29 (23):7540–8. http://www.pubmedcentral.nih.gov/ articlerender.fcgi?artid=2702750& tool=pmcentrez&rendertype=abstract.

63. Chen JL, Penhune VB, Zatorre RJ. Listening to musical rhythms recruits motor regions of the brain. Cereb Cortex. 2008;18(12):2844–54. http:// www.ncbi.nlm.nih.gov/pubmed/18388350.

64. Bengtsson SL, Ullén F, Ehrsson HH, Hashimoto T, Kito T, Naito E, et al. Listening to rhythms activates motor and premotor cortices. Cortex. 2009;45 (1):62–71. http://www.ncbi.nlm.nih.gov/pubmed/ 19041965.

65. Grahn JA. Neuroscientific investigations of musical rhythm: recent advances and future challenges. Contemp Music Rev. 2009;28(3):251–77. http:// www.informaworld.com/openurl?genre=article& doi=10.1080/07494460903404360& magic=crossref‖ D404A21C5BB053405B1A640AFFD44AE3.

66. Grahn JA. Neural mechanisms of rhythm perception: current findings and future perspectives. Top Cogn Sci. 2012;4(4):585–606. http://www.ncbi.nlm.nih. gov/pubmed/22811317.

67. Teki S, Grube M, Kumar S, Griffiths TD. Distinct neural substrates of duration-based and beat-based auditory timing. J Neurosci. 2011;31(10):3805–12. http://www.pubmedcentral.nih.gov/articlerender. fcgi?artid=3074096&tool=pmcentrez& rendertype=abstract.

68. Honing H, Ladinig O, Háden GP, Winkler I. Is beat induction innate or learned? probing emergent meter perception in adults and newborns using event-related brain potentials. Ann N Y Acad Sci. 2009;1169:93–6. http://www.ncbi.nlm.nih.gov/ pubmed/19673760.

69. Merchant H, Honing H. Are non-human primates capable of rhythmic entrainment? evidence for the gradual audiomotor evolution hypothesis. Front Neurosci. 2013;7:274.

70. Luck S. An introduction to the event-related potential technique. 2005. http://mitpress.mit.edu/catalog/ item/default.asp?tid=10677&ttype=2.

71. Polich J. Updating P300: an integrative theory of P3a and P3b. Clin Neurophysiol. 2007;118(10):2128–48. http://www.pubmedcentral.nih.gov/articlerender. fcgi?artid=2715154&tool=pmcentrez& rendertype=abstract.

72. Patel SH, Azzam PN. Characterization of N200 and P300: selected studies of the event-related potential. Int J Med Sci. 2005;2(4):147–54. http://www. pubmedcentral.nih.gov/articlerender.fcgi? artid=1252727&tool=pmcentrez& rendertype=abstract.

73. Horváth J, Winkler I, Bendixen A. Do N1/MMN, P3a, and RON form a strongly coupled chain reflecting the three stages of auditory distraction? Biol Psychol. 2008;79(2):139–47. http://www.ncbi. nlm.nih.gov/pubmed/18468765.

74. Rinne T, Särkkä A, Degerman A, Schröger E, Alho K. Two separate mechanisms underlie auditory change detection and involuntary control of attention. Brain Res. 2006;1077(1):135–43. http://www. ncbi.nlm.nih.gov/pubmed/16487946.

75. Comerchero MD, Polich J. P3a and P3b from typical auditory and visual stimuli. Clin Neurophysiol. 1999;110(1):24–30. http://www.ncbi.nlm.nih.gov/ pubmed/10348317.

76. Schröger E, Winkler I. Presentation rate and magnitude of stimulus deviance effects on human pre-attentive change detection. Neurosci Lett. 1995;193:185–8.

77. Fitzgerald P, Picton T. Event-related potentials recorded during the discrimination of improbable stimuli. Biol Psychol. 1983;17(4):241–76. http:// www.sciencedirect.com/science/article/pii/ 0301051183900030.

78. Schwartze M, Rothermich K, Schmidt-Kassow M, Kotz SA. Temporal regularity effects on pre-attentive and attentive processing of deviance. Biol Psychol. 2011;87(1):146–51. http://www.ncbi.nlm. nih.gov/pubmed/21382437.

79. Schmidt-Kassow M, Kotz SA. Attention and perceptual regularity in speech. Neuroreport. 2009;20:1643–7.

80. Winkler I. Interpreting the mismatch negativity. J Psychophysiol. 2007;21(3):147–63. http://psycontent. metapress.com/openurl.asp?genre=article& id=doi:10.1027/0269-8803.21.34.147.

81. Winkler I, Czigler I. Evidence from auditory and visual event-related potential (ERP) studies of deviance detection (MMN and vMMN) linking predictive coding theories and perceptual object representations. Int J Psychophysiol. 2012;83 (2):132–43. http://www.ncbi.nlm.nih.gov/pubmed/ 22047947.

82. Paavilainen P, Arajärvi P, Takegata R. Preattentive detection of nonsalient contingencies between auditory features. Neuroreport. 2007;18(2):159–63. http://www.ncbi.nlm.nih.gov/pubmed/17301682.

83. Yabe H, Tervaniemi M, Reinikainen K, Näätänen R. Temporal window of integration revealed by MMN to sound omission. Neuroreport. 1997;8(8):1971–4. http://www.ncbi.nlm.nih.gov/pubmed/9223087.

84. Bendixen A, SanMiguel I, Schröger E. Early electrophysiological indicators for predictive processing in audition: a review. Int J Psychophysiol. 2012;83 (2):120–31. http://www.sciencedirect.com/science/ article/pii/S0167876011002376.

85. Näätänen R, Paavilainen P, Rinne T, Alho K. The mismatch negativity (MMN) in basic research of central auditory processing: a review. Clin Neurophysiol. 2007;118(12):2544–90. http://www. ncbi.nlm.nih.gov/pubmed/17931964.

86. Kujala T, Tervaniemi M, Schröger E. The mismatch negativity in cognitive and clinical neuroscience: theoretical and clinical considerations. Biol Psychol. 2007;74(1):1–19. http://www.ncbi.nlm.nih. gov/pubmed/16844278.

87. Haroush K, Hochstein S, Deouell LY. Momentary fluctuations in allocation of attention: cross-modal effects of visual task load on auditory discrimination. J Cogn Neurosci. 2010;22(7):1440–51. http://www.ncbi.nlm.nih.gov/pubmed/19580389.

88. Sussman ES. A new view on the MMN and attention debate. J Psychophysiol. 2007;21(3):164–75. http://psycontent.metapress.com/openurl.asp?genre=article&id=doi:10.1027/0269-8803.21.34.164.

89. Alho K, Woods DL, Algazi A, Näätänen R. Inter-modal selective attention. II. effects of attentional load on processing of auditory and visual stimuli in central space. Electroencephalogr Clin Neurophysiol. 1992;82:356–68. http://www.ncbi.nlm.nih.gov/pubmed/1374704.

90. Csépe V, Karmos G, Molnár M. Evoked potential correlates of stimulus deviance during wakefulness and sleep in cat -animal model of mismatch negativity. Electroencephalogr Clin Neurophysiol. 1987;66(6):571–8. http://www.ncbi.nlm.nih.gov/pubmed/2438122.

91. Novitski N, Tervaniemi M, Huotilainen M, Näätänen R. Frequency discrimination at different frequency levels as indexed by electrophysiological and behavioral measures. Cogn Brain Res. 2004;20(1):26–36. http://www.ncbi.nlm.nih.gov/pubmed/15130586.

92. Bouwer F, van Zuijen TL, Honing H (in prep).

93. Geiser E, Ziegler E, Jancke L, Meyer M. Early electrophysiological correlates of meter and rhythm processing in music perception. Cortex. 2009;45(1):93–102. http://www.ncbi.nlm.nih.gov/pubmed/19100973.

94. Vuust P, Pallesen KJ, Bailey C, van Zuijen TL, Gjedde A, Roepstorff A, et al. To musicians, the message is in the meter pre-attentive neuronal responses to incongruent rhythm are left-lateralized in musicians. Neuroimage. 2005;24(2):560–4. http://www.ncbi.nlm.nih.gov/pubmed/15627598.

95. Vuust P, Ostergaard L, Pallesen KJ, Bailey C, Roepstorff A. Predictive coding of music–brain responses to rhythmic incongruity. Cortex. 2009;45(1):80–92. http://www.ncbi.nlm.nih.gov/pubmed/19054506.

96. Geiser E, Sandmann P, Jäncke L, Meyer M. Refinement of metre perception – training increases hierarchical metre processing. Eur J Neurosci. 2010;32(11):1979–85. http://www.ncbi.nlm.nih.gov/pubmed/21050278.

97. Winkler I, Kushnerenko E, Horváth J, Ceponiene R, Fellman V, Huotilainen M, et al. Newborn infants can organize the auditory world. Proc Natl Acad Sci U S A. 2003;100(20):11812–5. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=208846&tool=pmcentrez&rendertype=abstract.

98. Stefanics G, Háden GP, Huotilainen M, Balázs L, Sziller I, Beke A, et al. Auditory temporal grouping in newborn infants. Psychophysiology. 2007;44(5):697–702. http://www.ncbi.nlm.nih.gov/pubmed/17532802.

99. Čéponiené R, Kushnerenko E, Fellman V, Renlund M, Suominen K, Näätänen R. Event-related potential features indexing central auditory discrimination by newborns. Cogn Brain. 2002;13:101–13. http://www.sciencedirect.com/science/article/pii/S0926641001000933.

100. Cheour M, Čéponiené R, Leppänen P, Alho K, Kujala T, Renlund M, et al. The auditory sensory memory trace decays rapidly in newborns. Scand J Psychol. 2002;43:33–9. http://onlinelibrary.wiley.com/doi/10.1111/1467-9450.00266/abstract.

101. Trainor LJ, Samuel SS, Desjardins RN, Sonnadara R. Measuring temporal resolution in infants using mismatch negativity. Neuroreport. 2001;12(11):2443–8. http://www.ncbi.nlm.nih.gov/pubmed/11496126.

102. Trainor LJ, McFadden M, Hodgson L, Darragh L, Barlow J, Matsos L, et al. Changes in auditory cortex and the development of mismatch negativity between 2 and 6 months of age. Int J Psychophysiol. 2003;51:5–15. http://www.sciencedirect.com/science/article/pii/S016787600300148X.

103. Háden GP, Honing H, Winkler I. Newborn infants are sensitive to sound timing. 12th Intl. Conf Music Percept Cogn. 2012. p. 378–9.

104. Woodman GF. Homologues of human ERP components in nonhuman primates. In: Luck SJ, Kappenman ES, editors. Oxford handbook of event-related potential components. New York: Oxford University Press; 2011.

105. Näätänen R, Kujala T, Winkler I. Auditory processing that leads to conscious perception: a unique window to central auditory processing opened by the mismatch negativity and related responses. Psychophysiology. 2010;48:4–22. http://www.ncbi.nlm.nih.gov/pubmed/20880261.

106. Nelken I, Ulanovsky N. Mismatch negativity and stimulus-specific adaptation in animal models. J Psychophysiol. 2007;21(3):214–23. http://psycontent.metapress.com/openurl.asp?genre=article&id=doi:10.1027/0269-8803.21.34.214.

107. Nakamura T, Michie PT, Fulham WR, Todd J, Budd TW, Schall U, et al. Epidural auditory event-related potentials in the rat to frequency and duration deviants: evidence of mismatch negativity? Front Psychol. 2011;2:1–17. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3238418&tool=pmcentrez&rendertype=abstract.

108. Pincze Z, Lakatos P, Rajkai C, Ulbert I, Karmos G. Separation of mismatch negativity and the N1 wave in the auditory cortex of the cat: a topographic study. Clin Neurophysiol. 2001;112(5):778–84. http://www.ncbi.nlm.nih.gov/pubmed/11336892.

109. Pincze Z, Lakatos P, Rajkai C, Ulbert I, Karmos G. Effect of deviant probability and interstimulus/interdeviant interval on the auditory N1 and mismatch negativity in the cat auditory cortex. Cogn Brain Res. 2002;13(2):249–53. http://www.ncbi.nlm.nih.gov/pubmed/11958968.

110. Javitt DC, Schroeder CE, Steinschneider M, Arezzo JC, Vaughan HG. Demonstration of mismatch negativity in the monkey. Electroencephalogr Clin Neurophysiol.

1992;83(1):87–90. http://www.sciencedirect.com/science/article/pii/0013469492901377.

111. Javitt DC, Steinschneider M, Schroeder CE, Vaughan Jr HG, Arezzo JC. Detection of stimulus deviance within primate primary auditory cortex: intracortical mechanisms of mismatch negativity (MMN) generation. Brain Res. 1994;667 (2):192–200. http://www.sciencedirect.com/science/article/pii/0006899394914966.

112. Ruusuvirta T, Koivisto K, Wikgren J, Astikainen P. Processing of melodic contours in urethane-anaesthetized rats. Eur J Neurosci. 2007;26(3):701–3. http://www.ncbi.nlm.nih.gov/pubmed/17634069.

113. Umbricht D, Vyssotki D, Latanov A, Nitsch R, Lipp H-P. Deviance-related electrophysiological activity in mice: is there mismatch negativity in mice? Clin Neurophysiol. 2005;116(2):353–63. http://www.ncbi.nlm.nih.gov/pubmed/15661113.

114. Ueno A, Hirata S, Fuwa K, Sugama K, Kusunoki K, Matsuda G, et al. Auditory ERPs to stimulus deviance in an awake chimpanzee (*Pan troglodytes*): towards hominid cognitive neurosciences. In: Rustichini A, editor. PLoS One. Public Library of Science; 2008;3(1):5. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2174528&tool=pmcentrez&rendertype=abstract.

115. Arriaga G, Zhou EP, Jarvis ED. Of mice, birds, and men: the mouse ultrasonic song system has some features similar to humans and song-learning birds. In: Larson CR, editor. PLoS One. 2012;7(10):1–15. http://dx.plos.org/10.1371/journal.pone.0046610FigureLegends.