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DOI
10.1016/j.neuropsychologia.2016.02.018

Publication date
2016

Document Version
Final published version

Published in
Neuropsychologia

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Link to publication

Citation for published version (APA):
Bouwer, F. L., Werner, C. M., Knetemann, M., & Honing, H. (2016). Disentangling beat perception from sequential learning and examining the influence of attention and musical abilities on ERP responses to rhythm. *Neuropsychologia*, *85*, 80-90. https://doi.org/10.1016/j.neuropsychologia.2016.02.018

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Download date:26 Jul 2022

Neuropsychologia 85 (2016) 80–90

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Disentangling beat perception from sequential learning and examining the influence of attention and musical abilities on ERP responses to rhythm

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ARTICLE INFO

Article history:
Received 16 October 2015
Received in revised form
22 February 2016
Accepted 23 February 2016
Available online 10 March 2016

Keywords:
Musical rhythm
Attention
Beat perception
ERP
Sequential learning

ABSTRACT

Beat perception is the ability to perceive temporal regularity in musical rhythm. When a beat is perceived, predictions about upcoming events can be generated. These predictions can influence processing of subsequent rhythmic events. However, statistical learning of the order of sounds in a sequence can also affect processing of rhythmic events and must be differentiated from beat perception. In the current study, using EEG, we examined the effects of attention and musical abilities on beat perception. To ensure we measured beat perception and not absolute perception of temporal intervals, we used alternating loud and soft tones to create a rhythm with two hierarchical metrical levels. To control for sequential learning of the order of the different sounds, we used temporally regular (isochronous) and jittered rhythmic sequences. The order of sounds was identical in both conditions, but only the regular condition allowed for the perception of a beat. Unexpected intensity decrements were introduced on the beat and offbeat. In the regular condition, both beat perception and sequential learning were expected to enhance detection of these deviants on the beat. In the jittered condition, only sequential learning was expected to affect processing of the deviants. ERP responses to deviants were larger on the beat than offbeat in both conditions. Importantly, this difference was larger in the regular condition than in the jittered condition, suggesting that beat perception influenced responses to rhythmic events in addition to sequential learning. The influence of beat perception was present both with and without attention directed at the rhythm. Moreover, beat perception as measured with ERPs correlated with musical abilities, but only when attention was directed at the stimuli. Our study shows that beat perception is possible when attention is not directed at a rhythm. In addition, our results suggest that attention may mediate the influence of musical abilities on beat perception.

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1. Introduction

The perception of a regular beat in music allows us to predict the timing of musical events and thus to synchronize and dance to music together, activities that may be crucial in understanding the origins of musicality (Honing et al., 2015). A musical beat can be defined as a regularly recurring salient moment in time (Cooper and Meyer, 1960) and is the regularity in music that we clap and dance to. The hierarchical structure of more and less salient moments in time is referred to as the metrical structure. Often, metrical salience in the form of a beat coincides with musical salience in the form of an accented event (Honing et al., 2014). However, once a beat is perceived, its perception can remain stable even if accents locally do not conform to the metrical structure. Thus, a perceived beat is a psychological construct and not necessarily physically present in a stimulus (Merchant et al., 2015).

Beat perception has been explained by Dynamic Attending Theory (DAT) as regular fluctuations in attentional resources, peaking at metrically salient positions (Large and Jones, 1999). Computationally and at a neural level, DAT has been linked to oscillator models (Henry and Herrmann, 2014; Large, 2008), with multiple oscillators present for multiple levels of regularity in a metrical hierarchy. When listening to music, internal oscillators entrain to the external regularity in a rhythm (Drake et al., 2000), and this allows a listener to generate precise temporal predictions about the occurrence of rhythmic events (Large, 2000; Phillips-Silver et al., 2011). Beat perception has been shown to be mediated by motor networks in the brain, and specifically the basal ganglia (Grahn and Brett, 2007). These motor areas are active during beat perception even when no movement is involved (Merchant et al.,

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http://dx.doi.org/10.1016/j.neuropsychologia.2016.02.018
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2015). This suggests that the mere perception of a beat relies on interactions between auditory and motor areas in the brain (Zatorre et al., 2007). One of the hypothesized roles of the motor areas in beat perception is the generation of temporal predictions (Grahn and Rowe, 2013; Merchant et al., 2015).

The predictions generated by a perceived beat not only allow for synchronization of movement to a beat, but can also affect processing of rhythmic events within a metrical structure. When predictions are generated about upcoming events, processing of auditory events that violate these predictions is enhanced, as is evidenced by three ERP components that have been specifically linked to processing of unexpected auditory events: the mismatch negativity (MMN), the N2b and the P3a. The larger the violation of expectations, the larger is the amplitude of these components (Näätänen et al., 2007; Polich, 2007). As such, these components provide a very useful way to examine beat perception. The perception of a beat leads to the prediction of events on the beat, while no events or softer events are predicted offbeat (Bouwer and Honing, 2015; Large, 2000). A perceived metrical structure can be probed by violating these predictions and measuring the ERP responses to prediction violations (Honing et al., 2014).

Earlier, using the strategy described above, we examined beat perception by comparing the ERP responses to silences on the beat, where they are unexpected, and offbeat, where they are more expected, and we showed that beat perception is independent of attention or explicit musical training (Bouwer et al., 2014). However, in studies using a similar approach it has been argued that attention is necessary to perceive temporal regularity in an auditory sequence (Geiser et al., 2009; Schwartze et al., 2011) and that musical training enhances the perception of a beat (Geiser et al., 2010). These conflicting findings may be due to the differences in materials used in these studies, ranging from stimuli resembling real music (Bouwer et al., 2014), to rhythms with a varying temporal pattern but with identical sounds (Geiser et al., 2010, 2009), to monotonous isochronous sequences (Schwartze et al., 2011). Many tasks aimed at measuring beat perception can in fact be accomplished by recruiting mechanisms that are not related to beat perception per se (Tranchant and Vuvan, 2015). In natural music, there is an abundance of cues indicating the metrical structure. This may additionally lead to recruitment of mechanisms related to beat perception that are not used when listening to an isochronous sequence. To understand how attention and musical training influence the perception of a beat, disentangling beat perception from other mechanisms (i.e., those that may contribute to or interact with beat perception) may be crucial.

First, it is important to note that beat perception relies on the perception of the relative proportions of the time intervals that make up a rhythm (Honing, 2013; Leow and Grahn, 2014). Relative or beat-based perception of rhythm is considered distinct from the perception of absolute time intervals in rhythm (Merchant and Honing, 2014; Teki et al., 2011). To separate beat-based perception from absolute interval perception, several studies have compared the responses to temporally regular, isochronous sequences with the responses to temporally irregular, jittered sequences (Fujioka et al., 2012; Schwartze et al., 2011; Teki et al., 2011). The prediction of events in jittered sequences has been suggested to rely on absolute interval perception, while the prediction of events in isochronous sequences has been suggested to recruit beat-based perception (Fujioka et al., 2012; Schwartze et al., 2011). However, humans can predict a sequence of temporal intervals relying solely on absolute interval perception, as is apparent from the possibility for humans to reproduce rhythms that do not contain a beat at all (Cameron and Grahn, 2014). A similar phenomenon is observed in nonhuman primates. While macaques have little or no ability to perceive a beat (Honing et al., 2012; Merchant and Honing, 2014), they respond more accurately to temporally regular than jittered sequences, suggesting a capacity for making temporal predictions (Zarco et al., 2009), which most likely depends on absolute interval perception (Merchant and Honing, 2014). Thus, it cannot be ruled out that humans, like macaques, can predict temporal intervals in an isochronous sequence based on absolute interval perception. Differences between responses to regular and jittered sequences (as reported by Fujioka et al. (2012) and Schwartze et al. (2011)) may be caused by enhanced predictions generated through absolute interval perception when temporal variability of a sequence is low. Therefore, the use of isochronous sequences may not be optimal for examining beat perception, as it is unclear whether the prediction of events in an isochronous sequence depends on beat-based perception, absolute interval perception, or both. To ensure that beat perception is measured, and not absolute interval perception, it is necessary to introduce some level of hierarchy in a rhythm to create a metrical structure. The perceived metrical structure can then be probed by comparing responses to events in different metrical positions, which differ in metrical salience, but have the same temporal properties.

One often-used way of introducing metrical hierarchy in a rhythm is by varying the temporal structure of the rhythm, while keeping all sounds identical. The temporal grouping of events in a rhythm can induce perceptual accents, which, if regularly spaced in time, can induce a beat (Povel and Essens, 1985). In two studies using such a non-isochronous rhythm with temporal accents, Geiser et al. (2009, 2010) found that ERP responses to unexpected intensity increases were larger offbeat than on the beat. Interestingly, in one of the studies (2009), this effect was only present when attention was directed towards the stimuli, while in the other (2010), the effect was also present when attention was directed away. Moreover, in the first study (2009), no effect of musical training was found, while in the second study (2010), musical training enhanced the difference between responses to events on the beat and offbeat. Thus, it is unclear how attention and musical abilities affect responses to non-isochronous rhythms with temporal accents. In an fMRI study using both rhythms with temporal accents and rhythms with acoustic cues indicating the metrical structure, Grahn and Rowe (2009) found that musicians showed more connectivity between premotor areas and auditory cortex than non-musicians, but only for the rhythms with temporal accents. This suggests that musical training may enhance the perception of a beat in rhythms when information about the metrical structure is only present in the temporal grouping of events. Acoustic cues to the beat as in real music may help especially musical novices to extract a beat and may thus be important to use when testing beat perception in musical novices.

In studying beat perception with more natural stimuli, such acoustic cues can be used to indicate the salience of events and thus to induce a hierarchical metrical structure (Ellis and Jones, 2009; Honing et al., 2014), ensuring that predictions cannot be solely made by relying on absolute interval perception. However, apart from being regularly spaced in time, metrical accents may also exhibit statistical regularity in the order of different events, which can influence the expectations of auditory events. To ensure that beat perception is measured when examining responses to rhythm, beat perception should thus be differentiated from statistical learning of the order of events in a rhythmic sequence (hereafter: *sequential learning*). For example, in the highly beat inducing sequences used by Bouwer et al. (2014), a comparison was made between ERP responses to unexpected omissions of events on the beat and offbeat. Beat perception was hypothesized to lead to strong expectations for the occurrence of events on the beat, making omissions on the beat less expected than omissions offbeat. In line with this, larger responses to omissions on the beat than offbeat were found. However, the patterns of bass drum, hi-hat and snare drum sounds that were used to induce a beat

exhibited statistical regularity in the order and the transitional probabilities of the different sounds. While the probability of an omission in general was relatively small, the probability of a hi-hat sound being followed by an omission was smaller (0.029) than the probability of a bass drum sound being followed by an omission (0.089). As an omission on the beat always followed a hi-hat sound and an omission offbeat always followed a bass drum sound, it could be that the omissions on the beat were less expected than the omissions offbeat not only because of metrical expectations, but also because of differences in transitional probabilities. Humans possess the ability to learn such transitional probabilities in both linguistic (Saffran et al., 1996) and non-linguistic sequences (Saffran et al., 1999; Tillmann and McAdams, 2004). In addition, learning of the statistical properties of sequences is possible, in principle, without attention (Schröger et al., 2007; Van Zuijen et al., 2006). Thus, one can argue that sequential learning rather than beat perception may have influenced responses to rhythms in previous studies (e.g., Bouwer et al., 2014; Ladinig et al., 2009; Vuust et al., 2005, 2009; Winkler et al., 2009).

In the current study we aimed to confirm previous findings showing that beat perception is independent of attention and musical training. We used rhythms with multiple acoustic cues indicating the metrical structure to facilitate beat perception for musical novices. We explicitly sought to disentangle beat perception from sequential learning, which may have biased results in previous studies (Bouwer et al., 2014; Winkler et al., 2009). Moreover, we used stimuli with a hierarchical structure to ensure that we measured beat perception and not absolute interval perception. We used a binary rhythmic pattern with alternating loud bass drum and softer hi-hat sounds indicating accented beats and unaccented offbeats. The bass drum and hi-hat sounds differed not only in intensity, but also in length and timbre, providing many cues for the listener to differentiate accented beats from unaccented offbeats. The alternating accented and unaccented sounds created a pattern with two metrical levels, the beat and subdivisions of the beat. We measured ERP responses to unexpected deviant tones in the form of intensity decrements on the beat and offbeat, both while participants were actively attending to the rhythm and while they directed their attention to a silent movie. Specifically, we were interested in the N2b response, which is recorded when people attend to a stimulus, and the MMN and P3a responses, which are recorded both under attended and unattended conditions. Intensity decrements are less expected on the beat than offbeat. Thus, when a beat is perceived, these ERP components, that are known to index the magnitude of a regularity violation (Näätänen et al., 2007; Polich, 2007) are expected to be larger in response to intensity decrements on the beat than offbeat (Bouwer and Honing, 2015; Potter et al., 2009).

ERPs are highly sensitive to the preceding acoustic context (Bouwer et al., 2014; Honing et al., 2014; Woldorff and Hillyard, 1991). Also, if a loud bass drum sound were always followed by a softer hi-hat sound and vice versa, a soft sound may be statistically more expected after a bass drum sound than after a hi-hat sound, making the comparison of responses to intensity decrements on the beat and offbeat biased. To avoid both acoustic and statistical effects of contextual differences, we frequently introduced bass drum sounds offbeat. This allowed deviants on the beat to not only be identical in sound to deviants offbeat, but also, like the deviants offbeat, to be preceded and followed by bass drum sounds.

While the bass drum sounds offbeat ensured that the transitional probabilities of consecutive sounds were the same for both deviants, louder sounds were statistically still more probable in odd positions (on the beat) and softer sounds in even positions (offbeat). Learning of this statistical regularity in the order of sounds may lead to larger ERP responses to intensity decrements in odd than in even positions regardless of beat perception. To disentangle beat perception from such an effect of sequential learning, we contrasted the responses to deviants in regular sequences, in which all inter-onset intervals were the same, with responses to deviants in jittered sequences, in which the inter-onset intervals were irregular. The statistical regularity in terms of the order of the different sounds was identical in the regular and jittered conditions. However, beat perception was only possible in the regular condition, but not in the jittered condition. We expected sequential learning of the pattern of alternating loud bass drum and softer hi-hat sounds to lead to larger ERP responses to deviants in odd than in even positions regardless of the temporal regularity of the sequence. If beat perception were present, we would expect this difference to be more pronounced in the regular than in the jittered condition, as beat perception would make the expectation for a loud event on the beat (in an odd position) even stronger. Thus, both in attended and unattended conditions, if a beat were perceived we would expect an interaction between the regularity of the sequence and the position of the deviant.

People vary widely in their ability to perceive a beat (Grahn and Schuit, 2012) and while this ability is highly correlated with musical training, it is possible for non-musicians to be extremely apt at hearing a beat in music. Previously, only the effect of musical training on beat perception was examined (Bouwer et al., 2014). However, there might be differences in beat perception abilities independent of musical training, with both musicians and non-musicians varying in how sensitive they are to a beat. Recently, a test battery has become available to get an estimate of musical abilities in the general population (Goldsmiths Musical Sophistication Index, or Gold-MSI; Müllensiefen et al., 2014). To separate the effects of formal instruction from those caused by a predisposition for beat perception, here we correlated beat perception as measured with ERPs in attended and unattended conditions with scores on both musical training and beat perception ability as measured with the Gold-MSI.

2. Methods

2.1. Participants

Thirty-four participants (23 women) took part in the experiment. They were on average 25.6 years old (SD 5.2 years, range 19–45 years). Their musical training ranged from no formal lessons at all to training as a professional musician. On average, they had 9.7 years of instrumental lessons (SD 9.6 years, range 0–34 years). None of the participants reported a history of neurological or hearing disorders. All participants provided written informed consent prior to the study. The study was approved by the Ethics Committee of the Faculty of Humanities at the University of Amsterdam.

2.2. Materials

2.2.1. Goldsmiths Musical Sophistication Index

To assess the overall musical training received by our participants, we used the Gold-MSI questionnaire (Müllensiefen et al., 2014). This questionnaire is designed to index musical sophistication in the general population and contains several subscales, including a subscale for musical training. In addition to instrumental lessons, this subscale also takes into account theory lessons, amount of practice, and number of instruments played. While highly correlated with the absolute years of music lessons received, the Gold-MSI provides us with a more nuanced measure of musical training. Both the original questionnaire and a Dutch translation were used, to accommodate both Dutch participants and those who did not speak Dutch. For each participant we

obtained a score for the musical training subscale. For details concerning the questionnaire and data norms, we refer to Müllensiefen et al. (2014).

2.2.2. Beat Alignment Test

To assess beat perception abilities, we used the beat alignment perception test (BAT) as implemented by Müllensiefen et al. (2014) and conceived by Iversen and Patel (2008). In this test, participants are required to listen to clips of music with overlaid metronome beeps. The metronome is either on the beat, has a slightly different tempo, or is shifted in phase. Participants are asked to judge whether the metronome is on the beat or not. The test contains 17 items and 3 practice items, with varying musical genres. For each participant, an accuracy score was calculated. Accuracy scores of 0.5 or lower show performance at chance level and were replaced by a value of 0.5, as performance below chance is not informative. For details of the music used in the test, see Müllensiefen et al. (2014).

2.2.3. Stimuli

Rhythmic sequences were created using two standard sounds. The first was a combination of simultaneously sounding bass drum and hi-hat sounds (for simplicity we will refer to these as bass drum sounds), and the second consisted of only a hi-hat sound. Both sounds were created using QuickTime's drum timbres (Apple Inc.). Bass drum sounds were longer (110 vs. 70 ms) and louder (16.6 dB difference in volume) than hi-hat sounds and as such were expected to be perceived as more salient than hi-hat sounds. Additional bass drum sounds attenuated with 25 dB (using Praat software; www.praat.org) were used as deviants. Four different two-tone configurations were constructed from these three sounds (see Fig. 1). The majority of the patterns (60%) consisted of a bass drum sound followed by a hi-hat sound (standard pattern S1; see Fig. 1A). A second pattern was constructed from two consecutive bass drum sounds (standard pattern S2, 30% of all patterns, see Fig. 1A). Two deviant patterns were used; one consisting of a deviant sound followed by a bass drum sound (deviant pattern D1; 5% of all patterns), and one with a bass drum sound followed by a deviant sound (deviant pattern D2; 5% of all patterns, see Fig. 1A).

The four patterns were concatenated to create continuous sequences for both the regular and jittered conditions (Fig. 1B). In the regular condition, all single tones were presented with an inter-onset interval of 225 ms. In this condition, the alternating salient bass drum sounds and less salient hi-hat sounds as occurring in pattern S1 were expected to induce a beat with an inter-beat interval of 450 ms, within the optimal range for beat perception in humans (Drake et al., 2000; London, 2012). In the regular condition, all sounds in the first position of a pattern, including deviant $D1_r$, can be considered on the beat, while all sounds in the second position, including deviant $D2_r$, are offbeat. In the jittered condition, the inter-onset intervals in the standard patterns were randomly distributed between 150 and 300 ms (flat distribution), which made beat perception impossible. The inter-

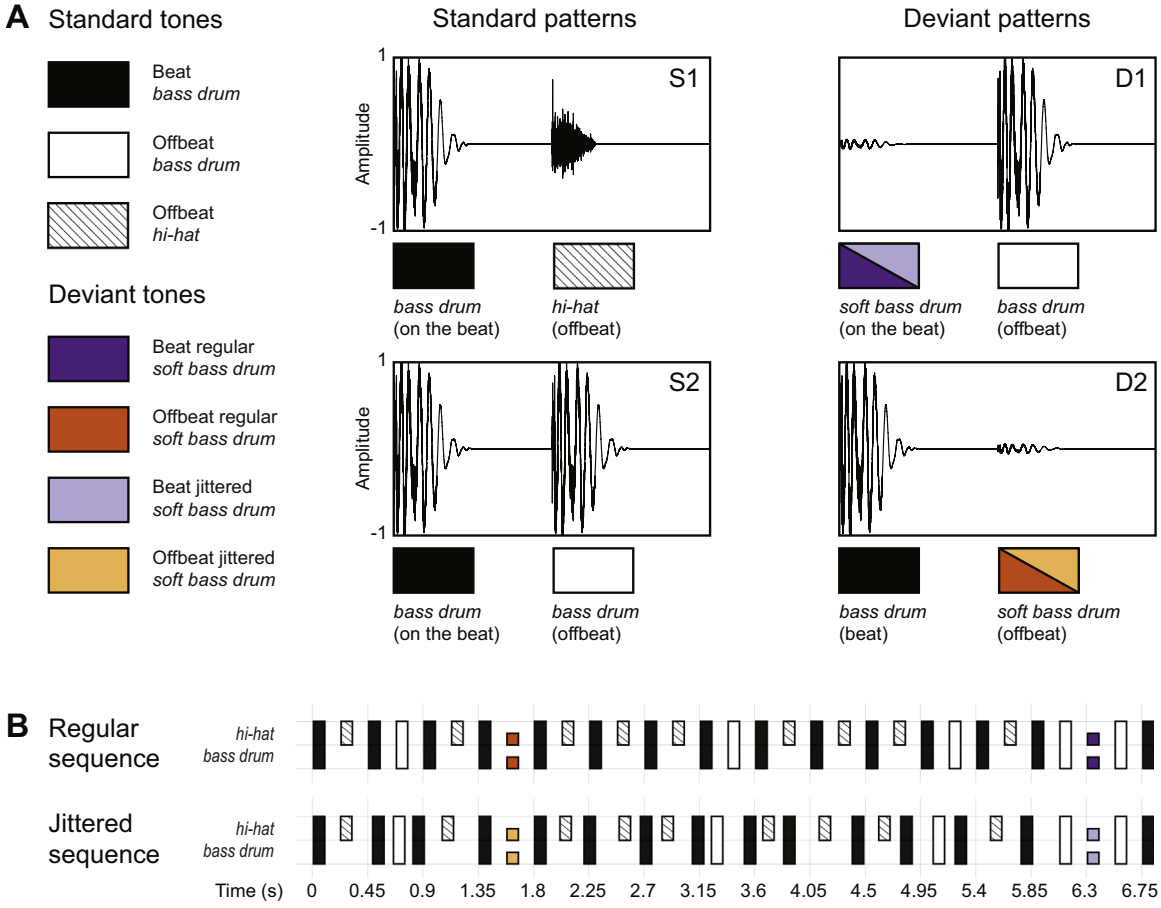

Fig. 1. Schematic overview of the stimuli. (A) Three different sounds were used to create two standard and two deviant patterns. The bass drum sound could occur in two different positions, both on the beat and offbeat. The hi-hat sound only occurred offbeat. An attenuated bass drum sound was used as deviant sound in two different positions, both on the beat and offbeat, and in two conditions, regular and jittered. (B) Patterns were concatenated into sequences. In the regular sequence, all inter-onset intervals were equal at 225 ms. In the jittered sequence, inter-onset intervals ranged from 150 to 300 ms. The inter-onset intervals before and after the deviant sounds were always fixed at 225 ms and deviants were always preceded and followed by a bass drum sound. Thus, acoustically, all four deviants and their contexts were identical.

onset interval before and following a deviant tone was kept constant at 225 ms. Note that we will refer to the deviants in the jittered context as on the beat ($D1_j$) and offbeat ($D2_j$), even though no beat can be heard in this condition, to clarify their relationship with the deviants in the regular context ($D1_r$ and $D2_r$).

In both the regular and the jittered condition, the concatenation of patterns was semi-randomized with four constraints on the randomization. First, to optimize beat perception in the regular condition, pattern S2, which contained a bass drum on the offbeat and did not contribute to the perception of the metrical hierarchy, was never presented more than once consecutively. Second, a maximum of four consecutive S1 patterns was allowed. Third, a deviant on the beat (D1) always followed a bass drum sound offbeat (S2). Finally, there were always at least five standard patterns between two deviant patterns. Note that for all four conditions of interest (two types of regularity and two metrical positions) the deviants ($D1_r$, $D1_j$, $D2_r$, $D2_j$) were preceded and followed by a bass drum sound with inter-onset intervals of 225 ms, creating identical acoustic contexts. For schematic examples of both the regular and jittered sequences, see Fig. 1B and Supplementary Sound 1 (regular) and 2 (jittered).

2.3. Procedure

Stimuli were presented in five-minute blocks consisting of five sequences of 54 s (120 patterns per sequence; 600 patterns per block). Regular and jittered blocks were presented in semi-random order, with a maximum of two blocks from the same condition following each other. In the unattended condition, twelve blocks were presented, for a total of 7200 patterns, of which 720 were deviant patterns (180 for each condition). In the attended condition, ten blocks were presented, for a total of 6000 patterns, with 600 deviant patterns (150 for each condition). To ensure attention to the rhythms, participants were asked to detect target tones that were presented unexpectedly early. By using temporal perturbations as targets we aimed to draw attention to the temporal structure of the rhythm, while avoiding noise from manual responses to the deviants. In the regular sequences, the inter-onset interval before a target tone was shortened with 40 ms. In the jittered sequences, the inter-onset interval before a target tone was set to 110 ms. In both conditions, the inter-onset interval after a target tone was lengthened with 40 ms. Each sequence in the attended condition could contain up to 2 target tones. Target tones and five patterns following target tones have been excluded from further analysis.

Participants were tested individually in a soundproof, electrically shielded booth at the University of Amsterdam. After providing consent, participants first completed the unattended EEG experiment and subsequently the attended EEG experiment. In the unattended condition, participants were instructed to ignore the rhythms and focus on a self-selected, muted and subtitled movie. In the attended condition, they were asked to focus on the rhythm and press a response button whenever a tone was unexpectedly early. Before the start of the attended condition, participants were presented with a practice block to get familiarized with the task. Participants could take breaks between blocks as needed. Rhythms were presented through two custom-made speakers at 60 dB SPL using Presentation® software (Version 17.4, www.neurobs.com). After the EEG experiment, participants performed the BAT perception task and filled out the questionnaire from the Gold-MSI to assess their beat perception skills and general musical sophistication (Müllensiefen et al., 2014). The entire session lasted on average 3.5 h.

2.4. EEG recording

EEG was recorded at a sampling rate of 8 kHz, using a 64 channel Biosemi Active-Two reference-free EEG system (Biosemi, Amsterdam, The Netherlands). Electrodes were positioned according to the 10/20 system and additional electrodes were placed at left and right mastoids, on the nose, above and below the right eye, and to the left and right of the eyes.

2.5. EEG analysis

Matlab (Mathworks, Inc.) and EEGLAB (Delorme and Makeig, 2004) were used for data preprocessing. EEG data was offline re-referenced to linked mastoids, down-sampled to 512 Hz, and filtered using 0.5 Hz high-pass and 20 Hz low-pass linear finite impulse response filters. For 4 participants, one or two bad channels were removed and replaced by values interpolated from the surrounding channels. Independent component analysis was used to remove eye-blinks. Epochs of 650 ms, starting 150 ms before and aligned to the onset of the deviant sound were extracted for the four deviant patterns ($D1_r$, $D1_j$, $D2_r$, $D2_j$). In addition, epochs of the same length were extracted for bass drum sounds from the standards in the regular condition, both on the beat (from S1, but only if preceded by S2) and offbeat (from S2). The acoustic context preceding all tones used for analysis, deviants and standards, was identical (a bass drum sound 225 ms before the onset of the epoch). Epochs with an amplitude change of more than 150 μV in a sliding 500 ms window were rejected from further analysis. Epochs were baseline corrected using the average voltage of the 150 ms prior to the onset of the tone and averaged to obtain ERPs for each condition and participant. We obtained difference waves by subtracting the ERP responses to the bass drum sounds from the standard patterns from the ERP responses to the deviant tones at the same position (beat or offbeat). Finally, we averaged over participants to obtain grand average ERPs and difference waves.

Both in the attended and the unattended condition, a negative deflection peaking between 100 and 200 ms after the onset of the deviants was visible in the grand average difference waves (Fig. 2 and Fig. 3), consistent with the latency of an N2b and an MMN respectively. Scalp distributions ranged from fronto-central for regular deviants on the beat ($D1_r$) to more posterior for jittered deviants offbeat ($D2_j$). To assess possible differences in scalp distribution, we performed the analysis for the two early components on electrodes FCz, Cz, and CPz. We defined the amplitude of the MMN and N2b as the average amplitude from a 60 ms window centered around the average peak latency across conditions on Cz. The MMN peaked on average at 130 ms and the N2b peaked on average at 155 ms. Amplitudes were thus defined as the average amplitude of the difference waves in a 100–160 ms time window for MMN and a 125–185 ms time window for N2b.

Both in attended and unattended conditions, a positive deflection followed the negative component in response to the deviants. In all conditions, this response was maximal over FCz, consistent with the scalp distribution of a P3a elicited by the novelty of a stimulus (Polich, 2007). The deviants were not used as targets in the attended condition and therefore not task-relevant, which explains why a P3a was observed and not a P3b. While for regular deviants on the beat ($D1_r$) a clear peak could be observed for the P3a both in the attended (at 241 ms) and in the unattended condition (at 225 ms), for the other deviants the peak was less pronounced. This was caused by overlap with the P1 response elicited by the next sound, which was presented at 225 ms after the onset of each deviant. This overlap prevented us from reliably estimating the peak latency of the P3a. To avoid contamination of the subsequent sound as much as possible in the analysis of the amplitudes, we defined the amplitudes for the P3a as the average

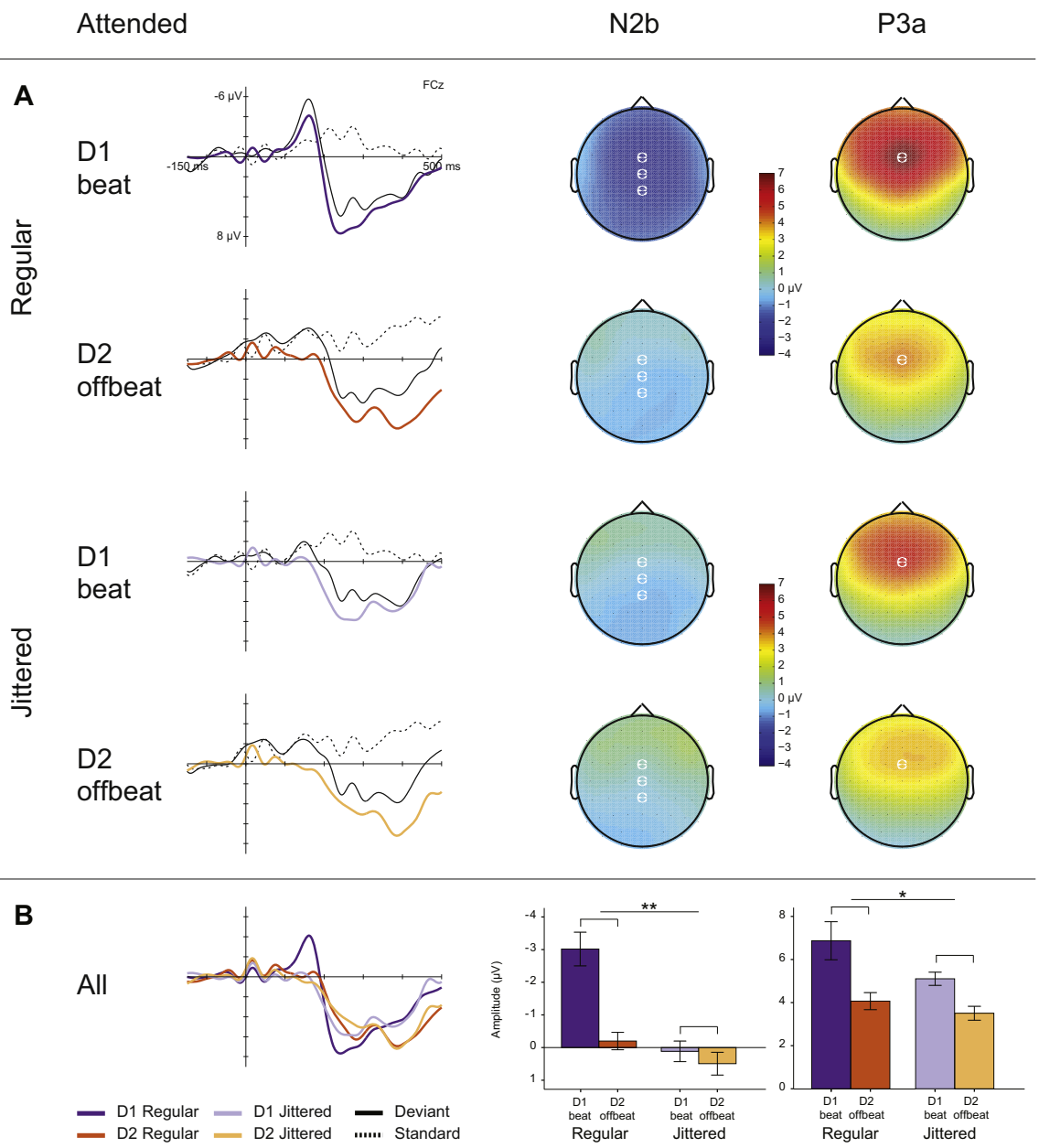

Fig. 2. ERP responses in the attended condition. (A) ERP responses on electrode FCz to standard and deviant tones in all four conditions, their derived difference waves and scalp distributions for the N2b and P3a components, averaged over the windows used for the analysis (125–185 and 205–265 ms respectively). The electrodes used for the analysis are indicated in white. (B) Differences waves for all four conditions and the average amplitudes in the time windows used for analysis for both N2b and P3a. **Significant interaction at $p < 0.0005$.*Significant interaction at $p = 0.046$. Note that significance of simple effects is not displayed. Error bars represent one standard error of the mean.

amplitude from the difference waves in a 60 ms window encompassing mostly the earlier portion of the P3a. To avoid overlap with the MMN and N2b components, we chose windows for the P3a starting 20 ms after the end of the windows used for the previous components in both the unattended (180–240 ms) and attended (205–265 ms) conditions. As the P3a was maximal over FCz for all conditions, we only included this fronto-central electrode in the analysis.

2.6. Statistical analysis

For both attended and unattended conditions, the amplitudes extracted from the difference waves were entered into repeated measures ANOVAs with within subject factors position (on the beat or offbeat) and regularity (regular or jittered). For the MMN and N2b, electrode (FCz, Cz, or CPz) was used as an additional factor. To correlate beat perception as measured with ERPs with measures of musical ability, we quantified beat perception as the magnitude of the interaction between position and regularity. For each participant, this measure was obtained by subtracting the difference between the responses to $D1_j$ and $D2_j$, which reflected only sequential learning, from the difference between the responses to $D1_r$ and $D2_r$, which reflected both sequential learning and beat perception. For all ERP components of interest, partial correlations were used to examine the association between beat perception and scores on the musical ability tests. To account for the possible correlation between scores on the BAT and musical training scores (Müllensiefen et al., 2014), each musical ability measure was correlated with beat perception while controlling for the other measure. All statistical analyses were conducted in SPSS

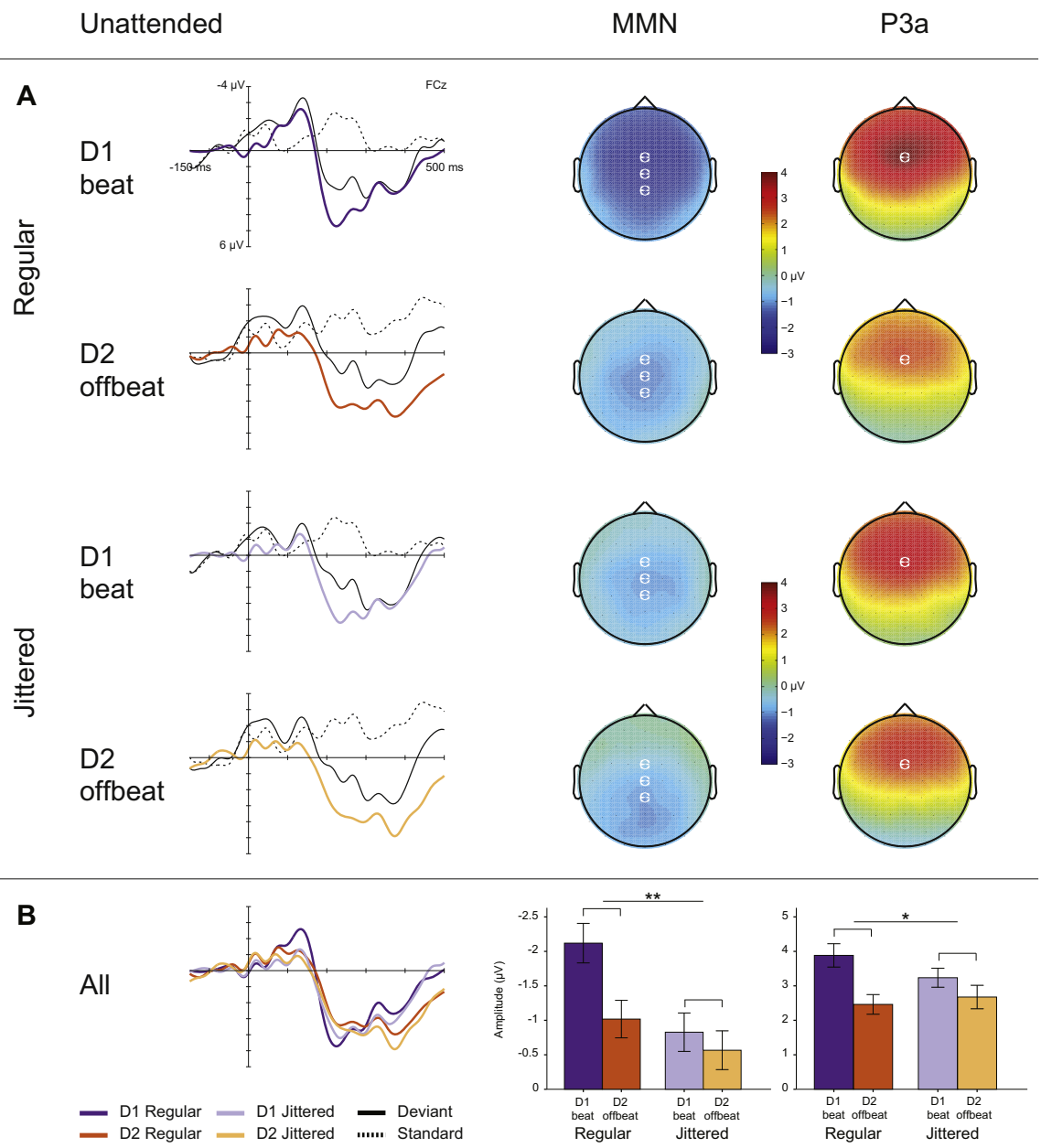

Fig. 3. ERP responses in the unattended condition. (A) ERP responses on electrode FCz to standard and deviant tones in all four conditions, their derived difference waves and scalp distributions for the MMN and P3a components, averaged over the windows used for the analysis (100–160 and 180–240 ms respectively). The electrodes used for the analysis are indicated in white. (B) Differences waves for all four conditions and the average amplitudes in the time windows used for analysis for both MMN and P3a. **Significant interaction at $p < 0.0005$.*Significant interaction at $p = 0.002$. Note that significance of simple effects is not displayed. Error bars represent one standard error of the mean.

(Version 22). Greenhouse-Geisser corrections were used when the assumption of sphericity was violated.

3. Results

3.1. Musical abilities

On average, participants scored 27.8 (SD 14.4) on the musical training subscale, which is slightly higher than the average score of 26.52 as reported in Müllensiefen et al. (2014). Also, the average accuracy on the BAT perception test was 0.79 (SD 0.17), while the average reported by Müllensiefen et al. (2014) was 0.70. The slightly higher scores in our sample as compared to the norm data is not surprising, as we specifically also included professional musicians in our sample to obtain a large spread in musical abilities. Scores on the musical training subscale correlated with the accuracy on the BAT ($r = 0.50$, $p = 0.003$), similar to Müllensiefen et al. (2014).

3.2. ERPs

Table 1 shows average amplitudes for all ERP components of interest. ERPs, difference waves and average amplitudes on electrode FCz for all deviants are depicted in Fig. 2 (attended) and Fig. 3 (unattended). In the N2b window (attended), there was a significant three-way interaction between electrode, position and regularity ($F_{2,66} = 15.3$, $p < 0.0005$, $\eta^2 = 0.32$). Resolving this interaction by electrode showed that the interaction between position and regularity was significant on FCz ($F_{1,33} = 29.7$, $p < 0.0005$,

Table 1
Mean average amplitudes (μV) for all components on FCz. Standard deviations in brackets.

	Attended		Unattended	
	N2b	P3a	MMN	P3a
Beat regular	−3.02 (3.02)	6.87 (5.15)	−2.12 (1.67)	3.88 (1.97)
Offbeat regular	−0.20 (1.56)	4.07 (2.32)	−1.02 (1.59)	2.46 (1.67)
Beat jittered	0.12 (1.84)	5.10 (1.78)	−0.83 (1.63)	3.24 (1.61)
Offbeat jittered	0.49 (2.03)	3.51 (1.89)	−0.57 (1.64)	2.68 (1.99)

$\eta^2=0.47$), Cz ($F_{1,33}=17.4$, $p<0.0005$, $\eta^2=0.35$), as well as CPz ($F_{1,33}=13.2$, $p=0.001$, $\eta^2=0.29$). The three-way interaction was due to the effect size for the two-way interaction being bigger on FCz than on Cz and bigger on Cz than on CPz. The interaction between position and regularity was also significant in the P3a window in the attended condition ($F_{1,33}=4.3$, $p=0.046$, $\eta^2=0.12$) and in the MMN and P3a windows in the unattended condition ($F_{1,33}=11.5$, $p=0.002$, $\eta^2=0.26$ and $F_{1,33}=9.1$, $p=0.005$, $\eta^2=0.22$). The three-way interaction between position, regularity and electrode did not reach significance for the MMN ($F_{2,66}=0.764$, $p=0.44$, $\eta^2=0.23$), showing that the interaction between position and regularity was equally large on all three electrodes. For all components, both in the attended and the unattended condition, the interaction was in the predicted direction (see Figs. 2 and 3), with a significantly larger difference between the responses to deviants on the beat and offbeat in the regular ($D1_r$ and $D2_r$) than in the jittered condition ($D1_r$ and $D2_r$). This suggests that a beat was perceived, both with and without attention directed at the rhythm.

An analysis of the simple effects of position showed that the difference between the responses to deviants on the beat and offbeat was not only significant in the regular condition ($p<0.0005$ for all ERP components), but also in the jittered condition. Responses to $D1_j$ were larger than to $D2_j$ in the attended condition in the N2b window on both Cz ($p=0.020$) and CPz.

($p=0.045$) and in the P3a window ($p<0.0005$). In the unattended condition, the responses to the jittered deviants differed significantly only in the P3a window ($p=0.015$) but not in the MMN window ($p=0.65$). These results suggest that participants could detect the statistical regularity in the order of the sounds in the jittered sequences, both when actively listening to the rhythms and when directing attention elsewhere. The simple effect of regularity was not only significant on the beat ($p<0.019$ for all components) but also offbeat. ERP responses to $D2_r$ were larger than responses to $D2_j$ in the N2b window (attended) on FCz ($p=0.012$) and Cz ($p=0.020$) and in the MMN window (unattended) on FCz ($p=0.044$). This suggests that the isochronicity of the regular sequence enhanced detection of the deviants, even in the offbeat position, in line with previous findings by Schwartze et al. (2011). Responses to $D2_r$ and $D2_j$ did not differ in the P3a windows (both in attended and unattended conditions $p>0.17$).

3.3. Correlations between ERPs and musical abilities

The interaction between position and regularity was maximal over FCz for all components. Thus, partial correlations between beat perception and musical abilities were calculated for this electrode (see Table 2). In the attended condition, beat perception as observed in the P3a correlated significantly with the scores on the BAT when controlling for musical training ($r=0.409$, $p=0.018$). In the N2b window, beat perception correlated with the scores on the musical training questionnaire when controlling for the scores on the BAT ($r=-0.420$, $p=0.015$). Interestingly, neither musical training, nor beat perception abilities correlated significantly with beat perception in the unattended condition (see Table 2).

Table 2
Partial correlations between beat perception as measured with ERPs on electrode FCz and musical training (while controlling for BAT scores) and BAT scores (while controlling for musical training).

	Attended		Unattended	
	N2b	P3a	MMN	P3a
Musical training	−**0.42****	−0.16	0.00	−0.27
BAT scores	0.21	**0.41****	−**0.18**	**0.17**

Note that correlations between a larger effect in ERPs and higher scores on the Gold-MSI tests are negative for N2b and MMN and positive for P3a, due to the polarity of the components. These correlations are indicated in bold. **Significant at $p<0.02$.

4. Discussion

In the current research we examined beat perception with and without attention, while disentangling beat perception from sequential learning. The effect of metrical position on the ERP responses elicited by deviants was much larger in the regular condition, in which both beat perception and sequential learning were possible, than in the jittered condition, in which only sequential learning was possible. This effect was present both when participants attended to the rhythm and when their attention was directed away from the rhythm, suggesting that participants perceived a beat in both conditions. Previously, beat perception was found to be possible without attention directed at the rhythm with ecologically valid stimuli or real music (Bolger et al., 2013; Bouwer et al., 2014). While these previous results may have been confounded with effects of sequential learning, here we show that even when controlling for transitional probabilities and pattern learning, beat perception is possible when attention is directed away from the rhythm.

The effect of metrical position in the jittered condition, while much smaller than in the regular condition, was significant for both N2b (attended) and P3a (attended and unattended) responses, with larger responses on the beat (in odd positions) than offbeat (in even positions). This effect can be explained by assuming that participants learned that the probability of a soft sound was smaller in odd (on the beat) than in even (offbeat) positions, as hi-hat sounds were softer than bass drum sounds and only occurred in even positions. This statistical regularity in the order of sounds would have made intensity decrements less expected in odd positions (on the beat) than in even positions (offbeat), as evidenced by larger ERP responses to deviants in odd than even positions. This shows that sequential learning can affect responses to rhythm, even when the rhythm is irregular and when attention is not directed at the rhythm. We thus replicate previous findings showing that humans have remarkable abilities to extract statistical regularities from auditory sequences, and that sequential learning can occur implicitly, not only when there is no intention to learn, but also when there is no intention to listen (Daltrozzo and Conway, 2014; Van Zuijen et al., 2006). This finding stresses the importance of controlling for statistical regularity in the order of sounds when testing beat perception using ERPs. It is not inconceivable, especially when listening to natural music, that a large part of predicting rhythmic events may be the result of learning patterns. For the perception of pitch and melody in music, models of statistical learning have had considerable success in explaining human behavior (Pearce et al., 2010). Extending existing models of beat perception with a statistical component may be

a promising avenue for future research to differentiate between various processes that contribute to rhythm perception, including beat perception and sequential learning.

The presence of statistical regularity in the order of sounds may aid beat perception by making accents more salient and more predictable. This may explain why real music is more effective in inducing a beat than abstract stimuli (Bolger et al., 2013). Similarly, it could be argued that temporal regularity may aid sequential learning. Indeed, it has been shown that sequential learning can benefit from regularity in grouping structure (Hoch et al., 2012) and metrical regularity (i.e., beat perception) in non-isochronous rhythms (Selchenkova et al., 2014b, 2014a). In the current study, sequential learning of the order of sounds may have benefitted from the lower temporal variability in the regular sequences than in the jittered sequences, and this may partly have caused the interaction between the regularity of the sequence and the metrical position of the deviant. To date, it remains unknown whether differences in temporal variability, as in the current study, affect sequential learning similarly to grouping structure (Hoch et al., 2012) and metrical structure (Selchenkova et al., 2014b, 2014a).

In addition to support for the presence of beat perception and sequential learning, we also found better deviant detection in the regular than in the jittered condition in offbeat positions, both in attended (N2b) and unattended (MMN) conditions. An advantage in the detection of deviants in regular as compared to in jittered sequences is in line with previous findings (Schwartze et al., 2011; Takegata and Morotomi, 1999). This advantage may be due to easier prediction of absolute time intervals in the regular than in the jittered sequences, as the former are less variable than the latter. Alternatively, it may be due to the recruitment of beat-based timing mechanisms during the perception of the regular but not the jittered sequences. On the basis of the current experiment, we cannot rule out either explanation.

The perception of a beat with multiple hierarchical levels may be a somewhat different process from the perception of regularity at one level (Fitch, 2013; Tierney and Kraus, 2014), even when both rely on beat-based timing. Thus, listening to isochronous sequences, as often used in beat perception research (Cirelli et al., 2014; Fujioka et al., 2012), may not only rely partly on absolute interval perception instead of beat-based perception, it may also tap into different beat-based processes than beat perception in real music, as isochronous sequences only contain one level of hierarchy. The view that perception of isochronous sequences differs from beat perception is supported by findings showing that a small portion of the population is unable to synchronize to music, while they can synchronize to a metronome (Sowiński and Dalla Bella, 2013). Understanding the relationship between absolute interval perception, beat-based perception, hierarchical perception of a metrical structure, and sequential learning will be an interesting challenge for future research.

While the influence of regularity on the detection of deviants in offbeat positions was visible in the MMN and N2b responses, it was absent in the P3a responses. This may have been due to a suboptimal estimate of the P3a responses caused by overlap with the responses elicited by subsequent sounds. An interesting alternative interpretation may be that the responses to the offbeat deviants in the regular condition were in fact actively suppressed. If beat perception in the current experiment indeed relied on entrainment of multiple oscillators (Large and Jones, 1999; Large, 2008), not only may the responses on the beat have benefitted from peaks in attentional resources, the responses offbeat may have suffered from troughs in attentional resources. Such suppression may provide an interesting way for future research to separate beat perception, which predicts suppression of responses offbeat, from predictions through absolute interval perception and enhanced sequential learning in regular compared to irregular sequences, neither of which would lead to such suppression.

Beat perception as indexed by the N2b response in the attended condition correlated with the responses on the musical training subscale of the Gold-MSI. Beat perception as indexed by the P3a response in the attended condition correlated with beat perception abilities as measured by the BAT perception task. Thus, confirming previous research (Grahn and Schuit, 2012), both beat perception abilities and musical training explained unique variance in the responses to metrical rhythm. However, in the current study, neither correlated significantly with beat perception in the unattended condition, which is in line with previous research showing no difference in beat perception without attention between musicians and non-musicians (Bouwer et al., 2014). Beat perception in unattended conditions may rely on a mechanism like neural entrainment, which has been suggested to be inherent in the structure of the brain (Large, 2008) and to be independent of attention (Escoffier et al., 2015). While we cannot directly compare the different ERP components measured in this study, the effect size for the interaction between position and regularity was much larger for the N2b, in the attended condition, than for the MMN, in the unattended condition. This could be interpreted as evidence showing that entrainment can be enhanced by attention. Alternatively, entrainment could be accompanied by additional mechanisms contributing to beat perception that do depend on attention and training. Previously, we have shown that beat perception consists of multiple mechanisms that together shape our perception of metrical rhythm (Bouwer and Honing, 2015). When not attending to the rhythm, participants may have relied only on entrainment, while when attending to the rhythm, they may have used additional mechanisms, which may be enhanced by musical abilities, to induce a beat.

5. Conclusion

In the current experiment, while controlling for sequential learning, we showed that beat perception is possible when attention is not directed at a rhythm. In addition, we showed that musical abilities, trained and untrained, are associated with beat perception, but only when attention is directed at the rhythm. Our results stress the importance of carefully defining beat perception, not only as a monolithic cognitive mechanism, but also in terms of the multiple underlying processes that together shape our perception of metrical rhythm. Which subcomponents of beat perception listeners recruit could well depend on the acoustical structure of the music, the resources a listener can devote to beat perception, and the musical abilities of the listener. Decomposing beat perception may be crucial in answering questions regarding the origins (Honing et al., 2015), mechanisms (Merchant et al., 2015), and possible applications (Nombela et al., 2013) of this unique human ability.

Acknowledgements

HH is supported by a Distinguished Lorentz fellowship granted by the Lorentz Center (2013/2014) for the Sciences and the Netherlands Institute for Advanced Study in the Humanities and Social Sciences (NIAS) and a Horizon grant (317-70-10) of the Netherlands Organization for Scientific Research (NWO).

We thank Dirk Vet for his technical assistance. We are grateful to Gábor Háden, István Winkler and two anonymous reviewers for their helpful comments on earlier versions of this manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2016.02.018.

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