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

Fleur L. Bouwer*, Carola M. Werner, Myrthe Knetemann, Henkjan Honing

Institute for Logic, Language and Computation, Amsterdam Brain and Cognition (ABC), University of Amsterdam, P.O. Box 94242, 1090 GE Amsterdam, The Netherlands

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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.

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.,

* Corresponding author.
E-mail address: bouwer@uva.nl (F.L. Bouwer).

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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, hihat and snare drum sounds that were used to induce a beat