Université de Montréal

Individual rhythmic abilities and temporal predictability: an electrophysiological approach

Par

Melissa Kadi

Département de Psychologie, Faculté des Arts et des Sciences

Mémoire présenté à la Faculté des études supérieures et postdoctorales en vue de l'obtention

du grade de Maitre ès Sciences (M.Sc.) en psychologie

Avril 2021

Université de Montréal

Faculté des études supérieures et postdoctorales

Ce mémoire intitulé :

Individual rhythmic abilities and temporal predictability: an electrophysiological approach

Présenté par

Melissa Kadi

A été évalué(e) par un jury composé des personnes suivantes

Isabelle Peretz
Président-rapporteur

Simone Dalla Bella
Directeur de recherche

Simon Rigoulot
Codirecteur

Floris Van Vugt
Membre du jury

Résumé

Les habiletés rythmiques varient considérablement d'un individu à l'autre. Cependant, notre compréhension du lien entre ces variations au niveau comportemental et les marqueurs électrophysiologiques qui les sous-tendent est incertaine. L'objectif du travail actuel était d'examiner la signature cérébrale (EEG) des différences individuelles des habiletés rythmiques impliquant la prédiction temporelle (i.e., perceptuelles, sensorimotrices). Les participants (n=43) ont effectué deux tâches provenant de la *Battery for the Assessment of Auditory Sensorimotor and Rhythmic abilities* (BAASTA, Dalla Bella et al., 2017). De plus, l'activité cérébrale de ces participants a été enregistrée lors d'une tâche de prédiction temporelle. Cette tâche utilisant le paradigme du stimulus discordant (i.e., *oddball paradigm*) consistait en la présentation de sons purs standards (i.e., non pertinents) et discordants (i.e., pertinents) sur des séquences isochrones ou non-isochrones (i.e., régulières ou non). Les résultats ont montré des différences individuelles dans les habiletés rhythmiques se reflétant au niveau des composantes ERP. Chez tous les participants, des meilleures habiletés sensorimotrices ont été associées à de plus petites amplitudes de la P50 lors de la présentation de sons standards, suggérant une inhibition accrue des stimuli non pertinents. Aussi, l'amplitude de la composante N100 pourrait servir de marqueur de la capacité de traitement de la discordance des stimuli. Effectivement, les individus ayant de bonnes habiletés de traitement du rythme, présente des amplitudes moins négatives de la N100 pour les sons discordants présentés régulièrement, suggérant une discrimination accrue des sons discordants. Ainsi, ces résultats ajoutent à notre compréhension des processus sous-jacents aux différences individuelles dans les habiletés rhythmiques.

Mots-clés *:* habiletés rythmiques, prédiction temporelle, perception, synchronisation sensorimotrice, potentiel évoqué, structure temporelle, structure formelle

Abstract

It is known that rhythmic abilities vary widely in the general population. However, our understanding of the link between these variations at the behavioral level and their underlying brain electrophysiological patterns is uncertain. The aim of the present work was to investigate the electrophysiological correlates of individual differences in rhythmic abilities (i.e., perceptual, sensorimotor). Participants (n=43) performed two tasks of rhythmic abilities (beat alignment test and paced tapping) from the Battery for the Assessment of Auditory Sensorimotor and Rhythmic abilities (BAASTA, Dalla Bella et al., 2017). Moreover, the brain activity (EEG) of these participants was recorded while they performed a temporal predictability task. This task consisted in an oddball paradigm where standard (i.e., irrelevant tones) and deviant (i.e., relevant tones) sinusoidal tones were presented in isochronous (i.e., regular) and temporally random (i.e., irregular) sequences. Results indicated that individual differences in rhythmic abilities are reflected in electrophysiological markers of temporal predictability. Across all participants, improved sensorimotor abilities were associated with smaller amplitudes of the P50 auditory evoked potential to standard tones, suggesting increased inhibition of irrelevant stimuli. Moreover, the amplitude of the N100 component serve as a potential marker of the ability to process stimuli deviance. Indeed, individuals with good rhythm abilities have less negative amplitudes of N100 for deviant tones presented in the isochronous sequence, suggesting enhanced discrimination of deviant tones. Altogether, these findings add to our understanding of the processes underlying individual differences in rhythmic abilities.

Keywords: rhythmic abilities, temporal predictability, beat perception, sensorimotor synchronization, evoked potential, temporal predictability, temporal structure, formal structure.

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List of abbreviations

BAASTA: Battery for the Assessment of Auditory Sensorimotor and Rhythmic abilities

BAT: Beat alignment test

BTI: Beat tracking index

EEG: Electroencephalography

ERP: Event-related potential

ISI: Inter-stimulus-interval

Theoretical Background

Introduction

The experience of time and its regularity is fundamental for humans. It is essential in numerous activities such as walking, talking, or dancing. For instance, dancing with music is based on the extraction of the pulse (i.e., the beat) from a rhythmic auditory stimulus and moving spontaneously or deliberately to it (Repp, 2010; Sowiński & Dalla Bella, 2013). Rhythm is a temporal pattern in a sequence of events that can be both produced and perceived. Rhythm and movement are strongly linked in humans, as shown when spontaneously moving to music (Schaefer, 2014). For example, tapping our foot or moving our head to the musical beat are commonly observed behaviors. Moreover, rhythm perception and synchronized movements both involve accurate timing processes (Dalla Bella et al., 2015, Dalla Bella et al., 2017). Even small deviations from the beat are promptly detected and the movement timing is adjusted accordingly when we move to music.

The capacity of following the beat (i.e., predicting the occurrence of the following events) is referred to as beat tracking (Drake & Gerard, 1989; Pancutt 1994). In a synchronization task, beat tracking relies on both perceptual and motor rhythmic abilities. In the context of this work, the term “beat tracking” will refer to the ability to find a regular beat in a rhythmic auditory stimulus and move with it. The capacity of tracking a beat varies greatly in healthy individuals (e.g., Grahn & Schuit, 2013; Repp, 2010; Sowiński & Dalla Bella, 2013). A better understanding of this variability would shed light on the mechanisms underlying fundamental human rhythmic abilities. Unfortunately, the literature lacks evidence about how individual variations of rhythmic abilities (perceptual and sensorimotor) are reflected in the electrophysiological brain networks of temporal predictability. Hence, the aim of this research was to investigate the relationship between individual differences of rhythmic abilities and their electrophysiological correlates by combining behavioral tasks assessing perceptual and sensorimotor tasks involving temporal predictability with electrophysiological activity during an auditory oddball paradigm. An additional objective of this work was to examine the influence of cognitive functions (e.g., inhibition, flexibility) on the individual differences in rhythmic abilities and their electrophysiological correlate

Rhythm Perception

Rhythm refers to the temporal organization of sound events that makes up an auditory sequence (London, 2012; McAuley, 2010; Patel, 2008). From the temporal regularities of a sequence of sounds, we can extract an underlying pulse, a beat. The beat corresponds to events in time that occur at regular intervals to which people usually move, tap, or dance (Lerdahl & Jackendoff, 1983; Large & Jones, 1999; London, 2012). The tempo, or “beat frequency”, is the speed at which these pulses unfold over time. The term “spontaneous tempo” refers to the period at which a person taps when asked to tap regularly in the absence of a regular stimulus to synchronize to (McAuley, 2010; McAuley et al., 2006). Interestingly, individual differences affect the spontaneous tempo. In fact, an individual’s preferred spontaneous tempo can influence the period at which they perceive a beat (Iversen et al., 2008; Martens, 2011). Moreover, musical rhythms are characterized by different periodicities (i.e., different beat levels) grouped hierarchically according to a metrical structure (i.e., meter) (Lerdahl & Jackendoff, 1983; Patel, 2008; Kasdan et al., 2020). Sequences of strong and weak beats convey the metrical structure. Changes in the intensity, pitch, or duration of sounds usually accentuate strong beats (Hannon et al., 2004; Lerdahl & Jackendoff, 1983; McKinney & Moelants, 2006; Patel, 2008; Palmer & Krumhansl, 1990).

Beat perception is a universal and fundamental trait for auditory and temporal organization (Honing, 2012; Iversen, 2016). Whether it is in music or the ticking of a clock, beat perception is a widespread ability in the general population and does not require musical training (Dalla Bella & Sowiński, 2015). Beat perception happens when listening to auditory sequences that have periodically regular events (Grahn, 2012). The properties of the auditory stimulus can influence the perception of a beat. For instance, several studies show that variations in pitch can influence beat perception. Indeed, inconsistency between the melodic and temporal accents in a rhythm and an atonal musical context can reduce the ability to follow the beat and to synchronize with it (Hannon et al., 2004; Lerdahl & Jackendoff, 1983; McKinney & Moelants, 2006). Beyond beat perception, the ability to synchronize to the beat is another rhythmic ability that will be discussed further.

Sensorimotor synchronization

Once listeners find the beat of a rhythmic auditory stimulus, they may clap their hands or tap their feet along with it. This combination of perception and action is a form of sensorimotor synchronization, i.e., the temporal coordination of an action with a predictable external event (Repp, 2005). Sensorimotor synchronization to an external rhythm appears to be widespread in the general population (e.g., Repp, 2010; Sowinski & Dalla Bella, 2013). Studies have shown that most people synchronize their movements precisely to the beat, such that the beat and the motor action are often only a few milliseconds apart (Repp, 2005; Repp & Su, 2013; Sowinski & Dalla Bella, 2013; Van Der Steen & Keller, 2013). Moreover, performance in a sensorimotor synchronization task (e.g., in a tapping task) is a good indicator of the precision of the temporal predictability made about the timing of upcoming events (Repp, 2005; Repp & Su, 2013; Van Der Steen & Keller, 2013). Furthermore, sensorimotor synchronization is often voluntary, but it can occur spontaneously with external auditory rhythms, such as a metronome or music (Bouvet et al., 2019).

Perceptual and motor rhythmic abilities (i.e., beat perception and sensorimotor synchronization) influence each other. For instance, beat perception enhances rhythm reproduction and discrimination by encoding the temporal intervals marked by the stimulus onset as subdivisions of the beat rather than unrelated intervals (Hebert & Cuddy, 2002; Patel et al., 2005). It is also easier to reproduce complex sequences when a beat is perceived compared to sequences where the rhythmic structure does not permit the perception of a beat (Chen et al., 2008b; Grahn & Brett, 2007, 2009). In fact, the most predictable form of rhythmic sequences is the isochrony, which displays a regularity as opposed to random rhythmic sequences. The isochrony reflects a regular pattern where all the intervals between the presented events are equal (Ravignani & Madison, 2017). A key concept for understanding the connection between movement and the perception of a beat is the process of neural entrainment, which will be discussed in the following section.

The Dynamic Attending Theory

The ability to predict the occurrence of a beat while listening to a rhythmic sequence has been explained by entrainment mechanisms, which allow prediction and synchronization of a response with the temporal regularities of an external rhythmic stimulus (Large et al., 2015; Large & Snyder, 2009). This entrainment mechanism allows the anticipation of a future event in a rhythmic and predictable context (e.g., a beat), thus enabling a listener to plan his/her motor action and synchronize it to that event (Patel, 2008; Patel & Iversen, 2014). Entrainment happens when an internal oscillator becomes synchronized to the temporal properties of an auditory stimulus, by allowing changes in its period and its phase in reaction to the external stimulus (Kotz et al., 2018; Large, 2008; Large & Kolen, 1994). The prevailing model of entrainment is the dynamic attending theory (DAT; Jones, 1976, 1987; Jones & Boltz, 1989; Large & Jones, 1999). According to this theory, the synchronization of internal oscillators with an external rhythm allows attentional processes to focus on recurring, predictable events in the rhythmic sequence, and hence facilitate the coordination of a response to events (Large & Jones, 1999). These oscillations are crucial in the synchronization of brain activity and enhancing the neural processes underlying memory, cognition, perception, and behavior (Neustadter et al., 2016).

In accordance with the DAT, the neural resonance theory suggests that the extraction of periodicities from auditory rhythmic sequences (i.e., beat perception) occurs when the internal oscillatory rhythms synchronize to the external rhythmic stimulus (Large & Snyder, 2009) and results in adjustments of temporal expectancies (Nozaradan et al., 2013). Along this line, several EEG studies supporting models of beat-based entrainment have shown greater energy of the brain’s electrical response at the frequency corresponding to the beat of a rhythmic sequence. For example, in a previous study by Nozaradan (2014), the EEG response of participants was recorded while listening to rhythmic patterns. Results indicated multiple peaks of energy at the frequencies corresponding exactly to the rhythmic patterns’ structure. Furthermore, a selective enhancement was found for the responses that were elicited at beat and meter frequencies, in contrast with frequencies that had no relevance to beat or meter. Interestingly, this selective enhancement was reduced for rhythmic patterns played too fast or too slow, when the tempo was far from the ecological musical tempo range. The researchers concluded that the results provided evidence of a selective enhancement of the neural response at beat and meter frequencies that are related to the perceived beat and meter elicited by complex rhythms. Further studies have provided additional evidence of rhythmic sequences eliciting peaks at frequencies associated with the beat and to different metrical levels of the stimulus, reflecting a selective enhancement of the responses to beat frequencies (Nozaradan et al., 2016; Nozaradan et al., 2011; Nozaradan et al., 2012; Stupacher et al., 2017; Tierney & Kraus, 2014b). The relevance of perceptual and sensorimotor rhythmic abilities becomes even clearer when these mechanisms are distorted by brain damage or neuronal degeneration. Moreover, it emphasizes the importance to comprehend changes in rhythmic abilities within a healthy population in order to discern the mechanisms accountable for the deficits in rhythmic abilities. Accordingly, the following section will address diverse profiles of individual differences in rhythmic abilities.

Individual differences

A complex neural network involving multiple brain regions underlies the ability to perceive a beat and move along with it. This network includes the premotor cortex and the supplementary motor area (Dalla Bella & Sowiński, 2015), as well as subcortical structures, such as the basal ganglia and the cerebellum (Coull et al., 2011; Grahn & Watson, 2013). Brain damage or neuronal degeneration (e.g., Parkinsons's disease) disrupt this network and result in poor temporal predictability (Fries & Swihart, 1990; Wilson et al., 2002).

A study by Puyjarinet and collaborators (2017) investigated individual differences in rhythmic abilities across participants with ADHD when tracking a beat using a combined perceptual and sensorimotor measure (i.e., the beat tracking index variable, BTI, calculated from the performances on BAT and paced tapping tasks). Participants who performed well on these tasks involving temporal predictability were designated as "*good beat trackers*", while those who performed poorly were considered as "*poor beat trackers*". The researchers concluded that poor tracking abilities may point to deficits in the way participants attend to events dynamically over time and may be an indicator of a deficit in the entrainment to an external stimulus, reflecting beat-based deficits. However, poor temporal predictability also manifests in healthy individuals without any brain damage. In fact, even though most healthy individuals can perceive an auditory rhythm and synchronize their movements to a beat, there are important exceptions. A condition, referred to as "beat deafness", consists in significant difficulties observed in some individuals to synchronize their movements to the beat of music and/or to perceive it (Sowiński & Dalla Bella, 2013; Phillips-Silver et al., 2011; Palmer et al., 2014). In 2011, the case of Mathieu was described (Phillips-Silver et al., 2011). Mathieu was a university student who could not synchronize to the beat of popular rhythmic songs despite having perfectly preserved motor, cognitive, hearing, and musical pitch processing abilities. Mathieu could synchronize only to simple isochronous sequences (e.g., a metronome) and his poor synchronization was associated with poor beat perception (Peretz et al., 2003). Mathieu also showed difficulties in a rhythm perception task, in which the subject had to dance in time with the auditory soundtrack of 5 video clips. Yet, his pitch perception was spared, thus showing that musical deficits can selectively impact the rhythm dimension.

Both rhythm perception and synchronization to the beat of music appear to be deficient in most cases of rhythm disorders (Sowiński & Dalla Bella, 2013; Dalla Bella & Peretz, 2003; Launay et al., 2014). Yet, a growing number of studies show that there is not one single type of rhythm disorders in the general populations, but rather different phenotypes, showing dissociations between perception and action (Sowiński & Dalla Bella, 2013; Bégel et al., 2017; Palmer et al., 2014). For example, poor synchronization can still occur even though rhythm perception is spared (Sowiński & Dalla Bella, 2013); the opposite dissociation, with spared synchronization coexisting with impaired perception can also be found (Bégel et al., 2017).

In addition to the evidence of diverse profiles of individual differences arising from rhythmic abilities in the general population, further evidence suggests that these discrepancies may be linked to alterations in cognitive domains, such as executive functions (EF) or working memory (WM). Tierney and Kraus (2013), observed that in a normally developing population, perceptual and synchronized tapping abilities relate to sustained attention, reading ability and a measure of temporal precision within the auditory system (i.e., backward masking). Additionally, this study showed that these relationships were not driven by general intelligence (i.e., two-scale WASI IQ). Parallel to this result, the study of Puyjarinet and collaborators (2017) previously discussed investigated whether the variability in rhythmic abilities was associated with cognitive impairment and found that the performance of *good beat trackers* was closely linked to better inhibition and flexibility, but not the I.Q nor short-term memory. In another study, authors discovered that executive functions (i.e., updating, switching and inhibition) influence rhythmic abilities (i.e., temporal generalisation, reproduction, and verbal estimation) (Ogden et al., 2014). These findings led authors to the conclusion that perceptual and sensorimotor abilities depend on several interrelated cognitive functions. It is possible, therefore, that individual differences of rhythmic abilities are affected by executive functions. Accordingly, these individual variations could be explained, at least in part, by executive functions.

Essentially, these important findings converge in indicating that, in the general population, there are important and interpretable individual differences in terms of rhythmic abilities, which require further investigation. To this aim, it is paramount to use appropriate tasks that provide sensitivity to individual differences.

Tests of rhythmic abilities

Rhythmic abilities can be evaluated with perceptual tasks (e.g., detecting a deviation from isochrony in a sequence of tones, Ehrlé & Samson, 2005) and sensorimotor tasks (e.g., paced tapping to the sounds of a metronome or to music, Repp, 2005; Repp & Su, 2013; Dalla Bella et al., 2017). Batteries of tests combining perceptual and sensorimotor tasks have recently been devised, offering a comprehensive assessment of these abilities in the general population (i.e., individuals without musical training) (e.g., M-BAT Tranchant et al., 2018; BAASTA, Dalla Bella et al., 2017; H-BAT, Fuji & Schlaug, 2013). These batteries are particularly important as they enable the characterization of rhythmic abilities within distinct populations as well as inter-individual differences (Bégel et al., 2017; Benoit et al., 2014; Cochen De Cock et al., 2018; Dalla Bella et al., 2017, 2018; Falk et al., 2015; Puyjarinet et al., 2017). Dalla Bella and collaborators (2017), developed a Battery for the Assessment of Auditory Sensorimotor and Rhythmic abilities

(BAASTA) that is well suited to measure and discover specific profiles of rhythmic abilities. In fact, this battery presents an advantage in its capacity to successfully identify variability in both perceptual and sensorimotor abilities in the general population. Two tasks that are notably sensitive to individual differences and involve temporal predictability are the beat alignment test (i.e., BAT) and the paced tapping task (Puyjarinet et al., 2017; Dalla Bella et al., 2017). These tasks will be used in the context of this work to investigate individual differences of rhythm abilities involving temporal predictability.

Even though the subject of individual differences in rhythm abilities has sparked a lot of interest, many questions remain unanswered. Namely, what is the influence of executive functions such as inhibition, memory, attention, and flexibility on rhythmic abilities, and importantly, what are the electrophysiological correlates underpinning these individual differences in rhythmic abilities? These questions will be answered by examining aspects of rhythmic abilities such as perception and sensorimotor synchronization using the Battery for the Assessment of Auditory Sensorimotor and Rhythmic abilities (BAASTA) as well as electrophysiological correlates proven to be markers of temporal predictability.

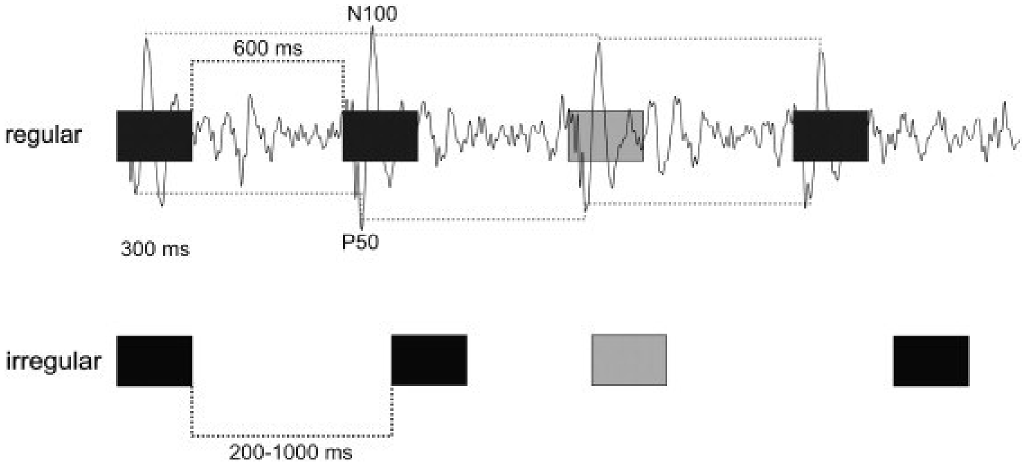
Electrophysiological correlates of temporal predictability

When listening to an auditory sequence of tones, establishing the type of event that is expected at a certain point in time is based on the formal structure of the stimulus (Fraisse, 1984), whereas determining when an event is most likely to occur is predicted by the temporal structure. The formal structure refers to the characteristics that define the identity of an event, i.e., what is expected (such as an increasing pitch). In contrast, the temporal structure shows the temporal relation between successive events, i.e., when the event is expected (Schwartze et al., 2012, Schwartze et al., 2013). Hence, correctly predicting what is expected and when it will happen relies on specific and accurate rhythmic abilities (Schwartze et al., 2013; Schwartze et al., 2011).

The temporal regularity present in auditory rhythmic patterns can be studied through the neuroimaging method of electroencephalography (EEG) (Nozaradan et al., 2016; Nozaradan et al., 2011; Nozaradan et al., 2013). EEG provides high temporal resolution leading it to be the most effective way of studying temporal predictability (Schwartze et al., 2013). Recent studies show a significant contribution of the study of steady-state evoked potentials (SS-EPs) as well as event-related potentials (ERPs) in the perception of a musical rhythm and a metronome (Nozaradan et al., 2013). SS-EPs occur when cortical activity is produced by neural populations at the frequency of the periodic event (Regan, 1989; Nozaradan et al., 2012) thereby reflecting neural entrainment responses to a beat. In contrast, ERPs assess changes in voltages in the brain accompanying or preceding the onset of a stimulus (Blackwood & Muir, 1990).

For the purpose of this work, we will focus on ERPs. A method used to measure temporal predictability is the oddball paradigm. First described by Ritter and Vaughn (1969) as a signal-detection paradigm, it was later used in the auditory modality by Squires and Hillyard (1975). This paradigm consists of the continuous presentation of a homogenous sequence of sounds known as standard stimuli (or regular, frequent, irrelevant stimuli) that are infrequently interrupted by physically deviant stimuli (also known as oddball, relevant, nonfrequent stimuli) (Näätänen, 1975; Näätänen et al., 1978; Donchin, 1981; Jääskeläinen, 2012; Schlüter & Bermeitinger, 2017). Studies widely use this paradigm in examining the underlying cognitive and electrophysiological components of change detection (Schlüter & Bermeitinger, 2017). The oddball paradigm requires subjects to respond to the deviant stimulus (i.e., relevant stimulus) and not to the standard stimulus (i.e., irrelevant stimulus). This paradigm asserts that deviant stimuli (i.e., oddball tones differing on their formal structure) attract more attention than standard stimuli (Birngruber et al., 2014; Pariyadath & Eagleman, 2007; Schindel et al., 2011; Tse et al., 2004).

Researchers used the oddball paradigm with success for studying temporal predictability in auditory stimuli by manipulating the formal structure (i.e., standard versus deviant) and temporal structure (i.e., isochronous versus random) of the stimulus sequence (Schwartze et al., 2011, Schwartze et al., 2013; Schwartze et Kotz, 2015). This paradigm comprised the presentation of two different sound sequences. The first was a sequence containing two tones differing in their formal structure (i.e., pitch), presented following a regular temporal structure (isochronous sequence), while the second sequence contained the same tones presented with a random temporal structure (see Figure 1). By focusing on formal and temporal predictability under attentive (i.e., required attention) and pre-attentive (i.e., unsolicited attention) conditions,



Schwartze and collaborators (2011, 2013) observed specific ERP components (P50, N100, and P300) related to temporal and formal predictability. However, the relation between these ERP measures of temporal and formal predictability, and behavioral measures of rhythmic abilities involving temporal predictability requires further investigation. The ERP components showing sensitivity to temporal and/or formal predictability are described below.

Figure 1. – Visualization of the oddball paradigm (Schwartze et al., 2013).

P50

The P50 ERP component is characterized by a positive peak approximately 50 ms (between 35 and 85 ms) after the onset of a sound (Freedman et al., 1994). This component is principally impacted by exogenous factors (i.e., physical features of a stimulus) as opposed to endogenous factors, namely the evaluation of the environment or expectations (Picton et al., 1974). P50 reflects mainly a process of sensory gating and early preattentional processing (Jerger et al., 1992). Sensory gating is the capacity of the brain to modulate its response to incoming sensory stimulus. This process allows individuals to focus their attention on selectively relevant stimuli and ignore irrelevant, frequent, or repetitive stimuli (Light & Braff, 2003). Hence, it reflects the ability to minimize the response to irrelevant stimuli and the ability to respond to the presentation of a novel stimulus (Boutros et al., 1999). The P50 was shown to be a marker of formal predictability. In fact, the P50 can be elicited in an oddball paradigm where sensory gating is operationally defined as the difference between amplitudes of responses to deviant stimuli and standard stimuli (i.e., formal structure). Higher differences can either represent lower amplitudes to standard stimuli (i.e., stronger inhibition of irrelevant stimuli) or greater amplitudes in response to deviant stimuli (i.e., stronger response to relevant, novel stimuli) (Boutros et al., 1995). Accordingly, evidence showed smaller amplitudes of the P50 component in response to irrelevant stimulation (i.e., standard tones) in contrast to relevant stimulation (i.e., deviant tones) (Marshall et al., 2004, Moura et al., 2010, Pratt et al., 2008), thus reflecting successful inhibition of irrelevant stimuli (Boutros et al., 1999).

Moreover, according to a study by Schwartze and collaborators (2013) this component is an automatic marker of predictability modulated by differences in formal (i.e., standard versus deviant) and temporal (i.e., isochronous versus random) structures. Interestingly, only amplitude responses and not latency indicated effects of temporal and formal structure. In fact, the authors found that predictable events (standard stimuli in an isochronous sequence, maximized prediction) elicit smaller P50 amplitudes, whereas higher P50 amplitudes occur in response to unpredictable stimuli (deviant stimuli in a random sequence, minimized prediction). An explanation would be that the decreased amplitude to predictable stimuli reflects the ability to minimize the response to repetitive stimuli, while the increase in amplitude of P50 to deviant stimuli indicates a pre-attentive recognition of new stimuli (Boutros et al., 1995).

In sum, findings report P50 component as an automatic index of sensory gating and an automatic marker of predictability modulated by both formal and temporal predictability.

N100

The N100 component is a negative peak occurring 100 ms after the auditory stimulus onset. This component reflects auditory processing, detection, and discrimination (Tomé et al., 2014) and is observed when an unexpected stimulus is presented (Sur & Sinha, 2009). The N100 is an exogenous component known to be sensitive to the physical properties of a stimulus (e.g., frequency, amplitude, pitch) (Butler, 1968; Picton et al., 1978; Näätänen, 1992). A study by Butler (1968), investigated the effect of frequency on the N100 component by presenting test tones of 1000 Hz (i.e., standard tones) every 5 sec in addition to 3 intervening tones (i.e., deviant tones) ranging from 250 Hz to 4000 Hz embedded in the presentation of the test tones. Results indicated smaller N100 amplitudes elicited by the test tone (i.e., standard tone) when its frequency was identical to the intervening tone (i.e., deviant tone) and higher amplitudes when the frequency difference increased. It was concluded that the decrease in N100 amplitudes reflected an activation of feature detectors analyzing the stimulus properties. This supports the notion that the N100 can serve as a measure of processing of neurophysiological difference between any two auditory stimuli (Butler, 1968, 1972; Näätänen, 1992). Moreover, the effects of selective attention on the N100 component were studied by using a dichotic presentation of auditory stimuli with a high presentation rate where the attention of the subjects was focused on one ear and ignored the other. The difference of amplitudes between the attended and non-attended source was defined as the effect of selective attention. Results showed a N100 response modulated by attention as shown by various studies postulating an increase of the N100 amplitudes when attention is present (Hillyard et al., 1973; Näätänen et al., 1978; Hillyard et al., 1995).

In an oddball paradigm, a larger amplitude in response to targets (i.e., deviant tones) may be a result of their deviance from the preceding sounds (i.e., frequency difference) or their status as a target (i.e., selective attention) (Butler, 1968). Moreover, the amplitude of the N100 decreases following stimulus repetition (Butler, 1968; Näätänen & Picton, 1987; Zhang et al., 2011). This effect has been attributed to the neural adaptation and refractoriness processes of neurons (Thompson & Spencer, 1966; Zhang et al., 2011). Adaptation reflects the decreased responses of neurons resulting from the repetition of the stimulus (Delgutte, 1997), whereas refractoriness reflects the process in which neurons recover before they are able to respond to the next signal (Barry et al., 1992; Budd et al., 1998). Hence, the decrease of the N100 amplitude reflects a reduction in neural responsiveness due to stimulus repetition and the resulting neural adaptation and refractory processes (Zhang et al., 2011).

Moreover, this component provides an indication of predictive processes (Schwartze et al., 2013). In a study by Schwartze and collaborators (2013), stimuli differing in their formal (i.e., standard versus deviant) and temporal structure (i.e., isochronous versus random) were presented to participants in an attentive session. The results confirmed the encoding of formal and temporal predictability and an inverse relationship of N100 amplitude and predictability (i.e., N100 responses smaller for regular sequences versus irregular sequences). More specifically, the analyses revealed an effect of temporal structure for deviant but not for standard stimuli, which was reflected in a greater N100 response to deviant tones presented in an irregular sequence as opposed to a regular sequence. These effects on the N100 response showed that temporal predictability influences the quality of deviance processing by modulating processes underlying the allocation of attention in time. Thus, the increase of N100 response for deviant events with low temporal predictability reflects an emerging influence of attention. However, regarding the latency of this component, no effects of formal and temporal predictability were found (Shwartze, et al., 2013).

In conclusion, various studies postulate that the N100 component increases with larger frequency differences between tones (frequency specificity) (Näätänen et al., 1988), with selective attention (Hillyard et al., 1973; Näätänen et al., 1978; Hillyard et al., 1995) and decreases with repetition (Butler, 1968; Näätänen & Picton, 1987). Moreover, this component increases in response to irregular sequences (i.e., low temporal predictability), particularly to deviant tones embedded in these sequences (Schwartze et al., 2013).

P300

The P300 wave is a positive peak latency of approximately 300 ms that occurs when a subject detects an informative task-relevant stimulus (Picton, 1992). The P300 is an endogenous component since it is produced when subjects are required to attend and discriminate stimuli that differ from one another on a particular dimension (Polich & Bondurant, 1996). Its response reflects cognitive processes such as the activation of immediate memory and attention allocation (Polich & Kok, 1995). Thus, the activity of this component depends greatly on the task to be performed, the processing of the stimulus context, and the levels of attention and arousal of the subject (Polich & Kok 1995; Hansenne, 2000). More specifically, a larger amplitude of this component appears to be linked to greater selective attention (Sur & Sinha, 2009) and the subject's arousal state (Hansenne, 2000). Moreover, evidence suggests that the P300 is strongly associated with temporal probability by indicating an inverse relation between the P300 amplitude and the temporal frequency of a targeted stimuli (i.e., probability of presentation) (Duncan-Johnson & Donchin, 1977; Picton & Stuss, 1980; Picton, 1981). Indeed, less frequent events elicit larger P300 amplitudes, while more frequent (i.e., high probability) events elicit a smaller P300 amplitude. This effect of enhancement of the P300 amplitudes to less frequently (i.e., low probability) presented stimuli is believed to reflect the number of attentional resources involved in the process of memory updating that occurs following the presentation the infrequent stimuli (Sutton et al., 1965; Tueting et al., 1971; Duncan-Johnson & Donchin, 1977). As for the P300 latency, it is usually interpreted as the result of a discrimination of the stimuli that is reflected by the speed of stimulus classification. In fact, shorter latencies, as opposed to longer latencies, suggest an enhanced mental performance (Hansenne, 2000).

P300 has commonly been investigated with the oddball paradigm since the subject's task is to detect an occasional targeted stimulus (i.e., deviant, relevant stimuli) embedded in a sequence of frequent irrelevant stimuli (i.e., standard, irrelevant stimuli) (Picton, 1992; Linden, 2005). Generally, results showed an increased amplitude when the target stimuli presented and an increased latency when they were harder to discriminate from the standard stimuli (Picton, 1992; Fabiani et al., 1987). These effects may be explained by the influence of cognitive functions. In fact, to select the relevant stimulus from the irrelevant stimulus, the features of the standard stimulus must be maintained to be compared to the deviant stimulus. Thus, both attention and working memory are required (Kok, 2001). To sum up, previous research suggested that P300 amplitude is modulated by temporal probability (i.e., increased amplitudes related to lower probability of presentation); while P300 latency is modulated by stimulus discrimination.

The P300 is frequently divided into two subcomponents, P3a and P3b. While the amplitude of the P3a component increases for standard tones (i.e., task-irrelevant stimuli), the P3b peaks after the presentation of a deviant tone (i.e., task relevant stimuli) (Linden, 2005; Luck & Kappenman, 2011; Polich & Criado, 2006). A study by Schwartze and collaborators (2011) investigated the impact of temporal predictability on the P3a and P3b components. This was tested in a protocol involving the processing of deviance in sound sequences in a pre-attentive and attentive session, respectively. Results showed no significant effect of regularity manipulation in the pre-attentive session on the P3a. However, a significant effect was observed for the P3b component which was larger for deviant events embedded in an isochronous context. The authors concluded that this effect might reflect the quality of stimulus-driven synchronization and a larger attention-dependent effect to regular temporal structures.

In sum, based on previous studies, three specific ERP components are linked with temporal and formal predictability as conveyed by a sequence of auditory stimuli. First, the P50 component, described as a marker of sensory gating, displays smaller amplitudes for standard events and predictable events as opposed to deviant events and unpredictable events, whereas its latency is not sensitive to temporal nor formal structure. Second, the N100 component increases with larger frequency differences between tones (frequency specificity) and with selective attention. Additionally, this component increases in response to irregular sequences, and especially to deviant tones embedded in such sequences. Moreover, results on its latency responses indicate no effects of formal and temporal predictability. Finally, the P300 component's amplitude is enhanced when the probability of presentation of targeted events (i.e., deviant tones) is low; moreover, increased latency of this component is linked to more difficult discrimination of deviant tones relative to standard. In addition to that, the P3b sub-component of the P300 component was shown to increase to the presentation of deviant events in an isochronous sequence. Notably, none of these studies examined the relation between these ERP electrophysiological correlates of temporal predictability and behavioral rhythmic abilities (tested with perceptual and sensorimotor tasks).

Goal & Hypotheses

The goal of this study is to shed light on the electrophysiological correlates underlying individual differences in rhythmic abilities (i.e., perceptual, and sensorimotor). We will achieve this goal by submitting participants to behavioral tasks that measure perceptual and sensorimotor abilities, and to an EEG oddball protocol in which we will record electrophysiological brain activity during a temporal predictability task.

Based on previous studies regarding temporal predictability, we expect the individual differences in rhythm abilities assessed with behavioral tasks to correlate with the electrophysiological responses. Specifically, compared to low beat trackers, good beat trackers will exhibit smaller P50 amplitude for standard tones within a predictable structure (isochronous sequence), and larger N100 and P300 amplitudes for deviant tones presented with low temporal predictability (random sequence).

A corollary aim of this work will be to investigate the impact of cognitive functions on the relation between individual differences in rhythmic abilities and their electrophysiological correlates (ERP responses).

Methods & Material

Participants and recruitment

Forty-three non-musician participants (with less than 2 years of formal musical training) were recruited for this study and a companion study on the effect of age on temporal predictability (Brinkmann, Kadi et al., under revision). The main group was divided into two age sub-groups: young adults (n = 22, 8 males, M_{age} = 23 years, age range: 19-29 years), and older adults (n = 21, 6 males, M_{age} = 68.5 years, age range: 59-80 years). However, for this study, age was not considered as an important variable because no significant differences were found between the two age groups for the behavioral variables of interest (i.e., beat alignment test (BAT, d'), paced tapping (logit-transformed vector length), and the beat tracking index (BTI, combination measure of the BAT and paced tapping)). All participants were right-handed, except one participant in the young group. Participants did not have a history of alcohol or drug abuse, did not take medication acting on the nervous system, did not have previous head trauma, neurodevelopmental disorders, psychopathology, and visual, hearing, or motor disabilities. Recruitment took place via advertisements, presentations in community centers, elderly homes, and word of mouth. The study was approved by the Comité d'Ethique de la Recherche en Education et en Psychologie (CEREP) at the University of Montréal and adhered to the Declaration of Helsinki. Participant signed an informed consent form upon arrival at the laboratory, and they were reimbursed with $10/h.

Procedure

The experiment comprised two sessions. The first session included audiometric measurements, neuropsychological tests, and behavioral tests, while the second one comprised an EEG task. Both testing sessions were performed in the same order two weeks apart on average (Figure 2).

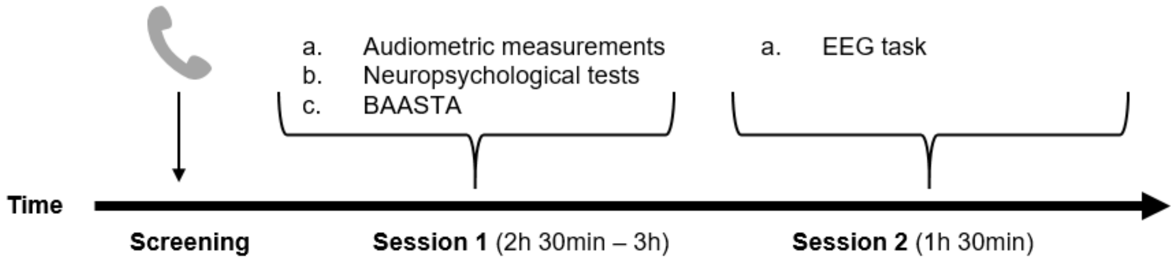


Figure 2. – Schematic overview of the experimental set-up. BAASTA = Battery for the Assessment of Auditory Sensorimotor and Rhythmic abilities (Brinkmann et al., under review).

First Session

Participants completed questionnaires on socio-demographic information and musical training. Following this, their normal hearing was assessed by audiometry (i.e., tests of hearing thresholds levels for 500, 1000, 2000, 3000, 40000, 6000 and 8000 Hz, for each ear: Inter-acoustics AC40 machine). Next, participants performed neuropsychological tests to evaluate crucial cognitive functions and subsequently completed the BAASTA (see below).

Neuropsychological tests

To estimate participants' intellectual functioning, the Vocabulary and Matrix subtests of the Wechsler Abbreviated Scale of Intelligence (WASI, Version II; Wechsler, 1999) were used to measure intellectual potential at the verbal level by having the participant define a list of words, and nonverbal level by requiring the subject to find the rationale behind a series of images and select the one corresponding to a missing one. To assess general cognitive functions (memory, attention, and executive functions), three subtests of the Test of Attentional Performance (TAP; Zimmermann & Fimm, 2002) were used: 1) a target detection task (numbers and letters/numbers alternating) during the simultaneous presentation of a laterally presented number and letter (flexibility); 2) a go/no-go task where the participant must detect a cross in the presentation of crosses and "+" signs by pressing a button on one condition and lifting it in the other (inhibition); 3) a 1-back task where sequences of numbers were presented during which the participant must press a button when the number that appears is identical to the one that appeared previously (working memory).

BAASTA

To assess rhythm and timing skills, we administered selected tasks from the Battery for the Assessment of Auditory Sensorimotor and Rhythmic abilities (BAASTA) (Dalla Bella et al., 2017). For the present study, participants performed one beat perception task, i.e., the Beat Alignment Test (BAT), in addition to finger tapping tasks. The BAT (Iversen and Patel, 2008; Dalla Bella et al., 2017) was used to assess beat-based rhythm perception. Participants had to indicate whether a metronome (woodblock sound) superimposed onto musical excerpts of Bach’s “Badinerie” and Rossini’s “Willian Tell Overture” was aligned or not to the musical beat. BAT includes 72 excerpts overall, with three inter-beat intervals (450, 600 and 750ms), and both period and phase misalignments of the metronome relative to the beat (for details, see Dalla Bella et al., 2017). Additionally, we used finger tapping tests to assess the participants’ spontaneous motor rhythm (unpaced tapping) and the motor synchronization to an auditory stimulus (paced tapping). In the unpaced tapping task, spontaneous motor tapping was tested by asking the participants to tap for 60 seconds at a comfortable and constant tapping rate. In the paced tapping task, the participant was asked to tap to the beat of either a metronome (presented at different inter-onset intervals: 600, 450 and 750ms), or of musical excerpts (from “Badinerie” and “William Tell Overture”).

Before each task, participants performed training trials. All BAASTA tasks were implemented on a tablet interface (Bégel et al., 2018) and administered in a counterbalanced order across participants. Stimuli were presented via Beyerdynamic DT 770 PRO headphones.

Second Session

For the second session, participants returned to the lab (the average time between the two sessions was 13.5 days) and performed an EEG experiment in which they listened to sequences of tones differing in their temporal structure (i.e., isochronous vs. random) and formal structure (i.e., standard versus deviant tones).

EEG

Task.

The EEG task consisted of an adaptation of the oddball paradigm employed in previous studies by Schwartze and colleagues (Schwartze et al., 2013; Schwartze & Kotz, 2015; Schwartze et al., 2011). The employed paradigm contained two oddball sequences that differed in their temporal structure i.e., the inter-stimulus interval (ISI) was either fixed (ISI = 1000ms; isochronous sequence) or random (between 600ms and 1400ms; average ISI = 1000ms; random sequence), while keeping the duration of each auditory stimulus constant (150ms, 10ms rise and fall). Each sequence contained 723 tones (deviant = 146, standard = 577). In total, 1446 tones were presented: 1154 standard (600 Hz), and 292 oddballs (660 Hz) sinusoidal tones (approximating the ratio of 4:1). The presentation of the tones was pseudorandomized to ensure that each sequence started with four standard tones and that a maximum of two deviant tones were presented in succession. The order of the oddball sequences was counterbalanced to avoid carry-over effects.

*I*nstructions.

Participants were instructed to fixate an asterisk on a computer screen and to count the number of deviant tones, which had to be reported to the experimenters at the end of each sequence. This ensured that the participants paid attention during the task. Stimuli were presented via inserts and using Presentation (NeuroBehavioral Systems, NBS).

Data Acquisition.

To record EEG data, a Biosemi ActiveTwo system was used. Reference free brain activity from 64 channels, arranged according to the international 10 -20 system (Sharbrough, 1991) and grounded to a two-electrode feedback loop, was recorded at a sampling rate of 1024 Hz. Six additional electrodes were bilaterally placed at mastoid and lateral ocular sites and unilaterally inferior to one eye and on the nose. Thereby, impedances were kept below 5 kOhms.

Preprocessing.

The EEG data were preprocessed using EEGlab (Delorme & Makeig, 2004) and the ERPLab toolbox (Lopez-Calderon & Luck, 2014), while following Makoto's preprocessing pipeline (Miyakoshi, 2018). First, signals were down-sampled to 256 Hz, then a high-pass filter (0.1 Hz) was applied. The plug-in clean_rawdata was used to remove bad channels, which were then interpolated from the original dataset (Mullen et al., 2015). EEG data was re-referenced to the average of the electrodes and the plug-in CleanLine was used to eliminate line noise (Mullen, 2012). To remove muscular and ocular artefacts, independent component analyses (ICA) were applied (Delorme & Makeig, 2004). After baseline correction, epochs starting -200 ms before stimulus onset and ending 600 ms post-stimulus were created for each bin (standard and deviant tones). In the following steps, three rounds of artifact rejection were performed. First, epochs exceeding ± 40 µV were excluded. Then a 100 µV threshold using a moving window peak to peak was used to check the absence of blinks. Finally, a 30 µV threshold for detecting step-like artifacts was used to remove trials containing remaining horizontal ocular movement artifacts. On average, 10% of trials were rejected (old adults = 13.9%, young adults = 6.1%).

Data Analyses

Behavioral Data

Performance on the BAASTA tests was analyzed using the same procedures implemented in previous studies from our lab (for details, Dalla Bella et al., 2017). For the BAT, the sensitivity index (*d'*) of detection of mis-aligned sounds was calculated from the rates of hits and false alarms, using the loglinear adjustment (Stanislaw & Todorov, 1999). For the unpaced tapping task, we calculated the average inter-tap-interval (ITI) and motor variability (coefficient of variation, CV, corresponding to the ratio of the SD of the ITIs over the mean ITI). For the paced tapping task, synchronization consistency was computed using circular statistics (Carr et al., 2014;

Sowiński & Dalla Bella, 2013; Puyjarinet et al., 2017). Synchronization consistency is a value between 0 to 1. When consistency is equal to 0, it indicates that participants tapped randomly. In contrast, a consistency equal to 1 shows that the interval between the beat and the taps is always the same. Consistency was submitted to a logit transformation, a common procedure for this measure (e.g., Falk et al., 2015), before proceeding to further analyses.

To obtain a general measure of rhythm abilities (i.e., beat tracking) capable of reflecting individual differences, we calculated the *Beat Tracking Index,* a composite score used in a previous study in our lab (BTI, Puyjarinet et al., 2017). This measure is obtained by first calculating z-scores for the overall sensitivity index (d') from the BAT, and for synchronization consistency in paced tapping, and then averaging the two z-scores. As in the previous study by Puyjarinet and collaborators (2017) the BTI served to divide participants into "*poor beat trackers*" (BTI < -2) and "*good beat trackers*" (BTI > -2). However, in contrast our participants were divided based a median split of the BTI measure into "*poor beat trackers*" (BTI < 0.10) and "*good beat trackers*" (BTI > 0.10).

Neuropsychological data analyses

Several measures were used for analyses of cognitive abilities from the WASI-II and the TAP. From the WASI-II, we took the composite I.Q. score of its two subtests as a measure of intellectual potential. The TAP measures were selected as follows: for cognitive flexibility, the Total Performance indices were calculated using the following equation: Total Performance Index = .707 * (TMdn + Terror – 100) for both tasks (Numbers and Letters /Numbers alternating) (for details, see Zimmermann & Fimm, 2002). A negative value on this index indicates a performance below average (i.e., high number of errors and slower reactions), whereas a positive value corresponds to performance above average (i.e., low number of errors and faster reactions). The mean reaction time of both the Go/NoGo and the working memory task was used to evaluate inhibition and working memory given that it is an indicator of general speed processing (Zimmermann & Fimm, 2002).

ERP data analyses

For further analysis, the regions of interest (ROIs) were selected by spatial principal component analyses (PCA, Spencer et al., 1999, 2001) and computed over 64 electrodes as dependent variables and time points (205), on both groups together (N = 43) and conditions (isochronous versus random sequences) as observations. A Varimax rotation was performed using SPSS (V.24 software). After inspection of the loadings on the spatial factors, electrodes exceeding the threshold of .707 were selected and grouped into separate ROIs. The loading threshold of .707 was applied because these electrodes explained more than 50% of the variance in the EEG data (Rigoulot et al., 2014). The PCA defined three ROIs. The first ROI was located in the parietal region of the scalp (T7, TP7, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, Poz, P4, P10, PO8, PO4, O2), the second one fronto-centrally (F1, F3, FC3, FC1, C1, C3, Afz, Fz, F2, FC4, FC2, FCz, Cz, C2) and the third one centro-parietally (CP3, CP1, CPz, CP2). Based on previous literature, subsequent analyses of the P50 and N100 were based on the fronto-central ROI, while for the P300 the centro-parietal ROI was analyzed (Korzyukov et al., 2007; Linden, 2005; Polich & Criado, 2006). After visual inspection of the grand averages and individual waveforms, the time windows for the three ERP components were selected: P50 (35-70 ms), N100 (75-130 ms), P300 (240-526ms) for mean amplitude and peak latency values, respectively.

Statistical Analyses

Data were analyzed using R (R Core Team, 2019). A preliminary analysis to determine whether any of the behavioral measures (BTI, BAT and paced tapping) differed between the young and old groups was conducted using independent-samples *t*-tests. Because no group differences were found (see Results), the groups were combined for all subsequent analyses.

To link individual differences in behavioral measures of rhythmic abilities to electrophysiological markers of temporal predictability, linear regressions were performed. In these analyses, the dependent variable was the difference in amplitude or latency between the isochronous and random sequences for standard and deviant tones. Regressions were run separately for each combination of P50, P300 and N100 component as dependent variables, and BTI, BAT (d’) and paced tapping (logit-transformed vector length) as independent variables.

To examine if specific individual differences in behavioral tasks of rhythmic abilities are associated with electrophysiological correlates, participants were split into two groups labeled "*good beat trackers*" and "*poor beat trackers*" based on a median split of the BTI score. Independent-samples t-tests were then conducted in order to assess the differences between the two groups on each variable of interest (i.e., differences in amplitude or latency between the isochronous and random sequences for standard and deviant tones for P50, N100 and P300).

In order to assess if the ERP responses (i.e., P50, N100, P300) to formal (i.e., standard versus deviant tones) and temporal predictability (isochronous versus random sequences) are predictors of beat tracking abilities, we developed a logistic regression model (Kleinbaum & Klein, 2010). First, each predictor considered to be likely contributing to the dependent variable were selected for further testing and were normalized by converting to z-scores: P50, N100, P300 differences of amplitudes and latency responses between the isochronous and random sequences to deviant and standard tones. Next, the BTI dichotomous variable (*good beat trackers* vs *poor beat trackers*) was entered as a dependent variable and the candidate ERP predictors were entered as independent variables. Predictors were dropped from the model if they did not improve the model fit. ERP component latencies were considered in a separate model selection process from ERP component amplitudes.

The logistic models constructed in the previous step were then extended to investigate whether additional measures of rhythmic perception and synchronization from the BAASTA could improve prediction of *good* and *poor beat tracker* classification. Starting with the base regression model previously calculated, we extracted the residuals of this model and calculated the correlations between these residuals and z-score values of each of the additional candidate variables from BAASTA: unpaced tapping (CV ITI, mean ITI), paced tapping to music (logit of tapping consistency by stimulus, and averaged across stimuli), and paced tapping to metronome (logit of tapping consistency by stimulus, and averaged across stimuli). Then the variable having the highest correlation with the base model's residuals was added to the base model. Improvement in the model fit was evaluated via the Akaike information criterion (AIC; Vrieze, 2012). If the variable improved the model fit, it was retained in the model and the next variable (by correlation with residuals) was evaluated, otherwise the model selection process was stopped. Finally, the logistic model optimization process continued with the three selected neuropsychological variables from the TAP battery (total performance index for the flexibility tasks, the mean RT for the Go/NoGo task and the mean RT for the working memory task) and the composite scores for the WASI-II to determine if either of them could improve the logistic regression model.

Results

The present study focuses on individual differences in rhythmic abilities and ERP response regardless of age, given that age was the focus of another study sharing the same data set (Brinkmann et al., under revision). However, preliminary analysis was conducted to test whether age could play a role in the behavioral variables of interest in this study. No significant differences were found between the two age groups in the beat alignment test (BAT) (*t (*39) = -.30, *p = .76*, paced tapping (*t* (37) = 1.21, *p = .23*, or for BTI (*t* (35) = .53, *p = .60*). Therefore, data from the two age groups were pooled in the following analyses. Results from the two age groups in the beat alignment test, the paced tapping, the unpaced tapping and neuropsychological tests are reported in Table 1.

(Table 1 about here)

Beat Tracking Abilities

The distribution of BTI scores, resulting from combining the performance in the BAT and paced tapping tasks, showed considerable variability across the participants indicating important individual differences (Figure 3). The distribution already makes it possible to observe that some participants have good rhythmic abilities while others can be distinguished by their poor abilities.[1]

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[1] We observed a positive correlation (*r* = .37, *p = .01*) between the two components of the BTI: beat perception (d' in the BAT) and tapping consistency (i.e., in the paced tapping test, metronome and music) across all participants. This indicates that an improved performance on one of these tasks, improves the performance on the other. However, 63% of the variance is not shared between these two measures of temporal predictability, suggesting that, while a good perception of a beat is followed by a good

(Figure 3 about here)

ERPs.

Overall, our findings show relations between rhythmic abilities and electrophysiological correlates of temporal predictability. These results confirm that participants indeed paid attention to the tonal sequences. Additionally, the presence of deviance effects in these components demonstrates that the oddball paradigm worked properly.

The linear regressions indicated a significant relation (F(1,41) = 5.78, p = 0.02, $R^2 = 0.12$) between tapping consistency and the difference of amplitudes between deviant tones and standard tones within the random sequence for the P50 component (see Figure 4 and 5).

(Figure 4 about here)

(Figure 5 about here)

Additionally, a relation was found between the BTI and the difference in N100 component amplitude for deviant tones between isochronous and random conditions (F(1,41) = 10.62, p = .01, R^2= 0.20, Figure 6 and 7), where enhanced beat tracking abilities were associated with increased amplitude differences for deviant tones in the isochronous and random conditions. This relation was reflected in both components of the BTI, i.e., the BAT (F(1,41) = 7.49, p = .01, R^2 = 0.15 Figure 8 A) and paced tapping (F(1,41) = 6.47, p = .01, R^2 = 0.12, Figure 8 B) scores when tested separately.

(Figure 6 about here)

(Figure 7 about here)

(Figure 8 about here)

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ability to synchronize with it, combining them into a *Beat Tracking Index* (BTI) would offer a more comprehensive measure of individual differences on temporal predictability.

No significant effects were observed with the beat tracking index, beat alignment test, and paced tapping for the P50 and P300 components amplitudes difference of deviant tones in the isochronous and random conditions (*p*s ≥ *.32*). Also, when testing the equivalent regressions for peak latencies for each ERP component, there were no significant relations (*p*s ≥ *.54*).

Individual differences

Electrophysiological signatures of beat tracking abilities (as assessed by the BTI)

Independent-samples t-tests on the two groups defined by BTI performance, i.e., *good* and *poor beat trackers,* showed that the P50, N100 and P300 amplitude difference between isochronous and random conditions was not significant across all components (ps ≤ 0.29).

However, another independent-sample t-test on the two groups defined by BTI performance, i.e., good and poor beat trackers, indicated that N100 amplitude difference of deviant tones in the isochronous and random conditions was different (t(32.84) = 2.53, p-value = .02, see Figure 9) between the *good beat trackers* (M = .19, SD = 0.21) and *poor beat trackers* (M = -0.03 SD = 0.34).

(Figure 9 about here)

These results suggest that individual differences of rhythmic abilities are linked to specific electrophysiological correlates. Examining the N100 amplitudes across the different stimulus conditions showed that the *good beat trackers*, i.e., those with heightened beat tracking abilities, had less negative N100 amplitudes for deviant tones in the isochronous sequence (M = -1.38) than for the random sequence (M = -1.57) (Figure 10 A). In the *poor beat trackers*, there was no close to no difference of N100 mean amplitude for deviant tones in the isochronous condition (M = -1.48) compared to the random condition (M = -1.45) (Figure 10 B).

(Figure 10 about here)

No effects of individual differences between *good* and *poorer beat trackers* were linked to the P50 and P300 ERP responses.

Marker of beat tracking abilities (as assessed by the BTI)

Based on the previous results, further analyses were conducted to assess if the ERP responses (i.e., P50, N100, P300) to formal (i.e., standard versus deviant tones) and temporal predictability (isochronous versus random sequences) could be markers of beat tracking abilities and be used to predict good and poor beat tracking abilities. To do so, the data were submitted to logistic regression analyses, which demonstrated that good vs poor beat tracking abilities were predicted by amplitudes differences for deviant tones in the isochronous and random conditions for the N100 component (p = .03), but not the P50 component (p = .78) or the P300 component (p = 1).

Controlling for other BAASTA variables and cognitive functions.

The previous logistic model was extended to evaluate whether the relation between BTI and the N100 response could be better modeled by including additional measures of rhythmic perception or synchronization (from BAASTA), or cognitive abilities (from TAP and WASI-II). None of the additional BAASTA measures: unpaced tapping (CV ITI, mean ITI), paced tapping to music (logit of tapping consistency by stimulus, and averaged across stimuli), and paced tapping to metronome (logit of tapping consistency by stimulus, and averaged across stimuli). or cognitive measures from the TAP battery (total performance index for the flexibility tasks, the mean RT for the Go/NoGo task and the mean RT for the working memory task) and the composite scores for the WASI-II yielded an improvement in the initial model fit.

Discussion

This study investigated individual differences in behavioral rhythmic abilities involving temporal predictability within the general population and their link to specific electrophysiological signatures of temporal predictability. Based on previous findings, we expected individual differences in rhythmic abilities (indexed by the BTI) to be reflected in measures of ERP components of temporal predictability. Importantly, we expected improved behavioral rhythmic abilities to accompany smaller P50 amplitudes for standard tones presented with a high predictability (i.e., isochronous sequence), increased N100 amplitude for deviant events with low temporal probability (i.e., random sequence), and an enhanced P300 amplitude for deviant tones presented with low predictability (i.e., random sequence). Our results are mostly in line with our expectations and revealed specific electrophysiological correlates underlying individual differences of rhythmic abilities. Analyses showed enhanced sensorimotor abilities associated with an increased difference of the P50 amplitude between deviant and standard tones in the random sequence. Moreover, enhanced rhythmic abilities (indexed by the BTI) were associated with a difference of N100 amplitude for deviant tones between the isochronous and random conditions. However, the P300 component did not show relations with any measures of rhythmic abilities. Finally, logistic regression modelling showed that the difference in terms of the N100 component's amplitude for deviant tones between the isochronous and random conditions was the only predictor of rhythmic abilities (as assessed by the BTI). This effect is robust, as it persisted when measures of cognitive functions (i.e., inhibition, flexibility, working memory) and additional rhythmic tasks were added as potential moderator variables in the model. These results will be discussed in more details hereafter.

Individual differences in behavioral rhythmic abilities reflected by ERP measures of temporal predictability

Association of behavioral rhythmic abilities and P50 electrophysiological responses

We anticipated modulation of P50 as a marker of sensory gating by formal structure to reflect the individual differences of rhythmic abilities. More specifically, based on previous studies, we hypothesized that *good beat trackers* would exhibit smaller P50 amplitude for standard events on a predictable structure (isochronous sequence). Findings on the manipulations of formal and temporal structure for this component showed a link between better tapping consistency and an increased difference between deviant and standard tones for the random sequence. This suggests that a greater performance in the production task (i.e., sensorimotor ability), but not rhythmic abilities as measured by the BTI, can be reflected in a larger amplitude of the P50 component elicited by deviant tones within an irregularly timed sequence. Along with this, our results provide evidence that better sensorimotor rhythmic abilities are associated with smaller amplitude responses to unpredictable standard tones (i.e., irrelevant tones presented randomly). In line with previous studies, this result might indicate enhanced inhibitory processing of irrelevant stimuli (i.e., standard tones) (Marshall et al., 2004; Moura et al., 2010; Pratt et al., 2008). Thus, individuals with greater sensorimotor abilities would display an enhanced inhibitory process, as indicated by a smaller P50 response to irrelevant stimuli (standard tones) presented with low predictability.

Moreover, the finding that greater sensorimotor abilities are connected to larger amplitudes in response to deviant tones might be explained by a stronger response to new stimulation (Boutros et al., 1995). This suggests the presence of an enhanced individual's ability to recognize new stimuli (i.e., deviant tones) and minimize the response to irrelevant stimuli. Previous results by Schwartze and collaborators (2013), showed an effect of the formal structure (i.e., standard versus deviant tone) and the temporal structure (i.e., isochronous versus random) on the P50 response. In contrast, our findings indicated that only the formal structure of the tones was associated with enhanced sensorimotor abilities. Interestingly, smaller amplitudes for standard in comparison to deviant tones were elicited only when presented with an unpredictable structure (i.e., the random sequence) and were linked to higher tapping consistency performance. As a marker of sensory gating, P50 is known to be sensitive to stimulus repetition and stimulus changes (e.g., Boutros et al., 1999). Thus, the greater amplitudes in response to deviant tones presented on the random sequence might be due to the unpredictable occurrence of the novel tones presented (i.e., standard tones in the random sequence).

In sum, the smaller amplitudes of the P50 component to frequent stimuli (i.e., standard tones) might reflect a stronger inhibition capacity of the individuals with enhanced sensorimotor abilities. Additionally, higher amplitudes to infrequent stimuli (i.e., deviant tones) could be explained by a stronger response to rare stimuli (Boutros et al., 1995). In contrast, the association between low sensorimotor abilities and larger amplitudes responses to standard tones (i.e., frequent stimuli) could result from diminished inhibitory processes and responses to stimulus changes, and this may in turn indicate the presence of a weakened sensory gating mechanism alongside poorer sensorimotor abilities.

Association of behavioral rhythmic abilities and N100 electrophysiological responses

Importantly, analyses showed that enhanced rhythmic abilities are associated with a difference of amplitudes for deviant tones between the isochronous and random conditions. More specifically, individuals with better rhythmic abilities (as measured by the beat tracking index) (i.e., g*ood beat trackers*) show a difference of electrophysiological responses between deviant tones presented regularly (i.e., isochronous sequence) and deviant tones presented irregularly (i.e., random sequence). *Good beat trackers* present smaller N100 amplitudes (i.e., less negative) when tones are predictable (i.e., isochronous sequence) and enhanced N100 amplitudes when the tones are unpredictable (i.e., random sequence). Accordingly, this difference in N100 following the manipulation of temporal and formal structure is present for *good beat trackers*, while that difference is not found in the *poorer beat trackers*. Thus, suggesting a better deviance processing in *good beat trackers* for deviant tones and a better sensitivity to predictable events. These results could potentially be explained by frequency specificity, selective attention, inter-stimulus interval (i.e., ISI) and the adaptive pattern of the N100.

These findings could be explained by the frequency difference between standard and deviant tones in our study. As previously indicated, a smaller N100 amplitude is elicited by the target tone (i.e., deviant tone) when its frequency is the same as the standard tone (Butler, 1968). In our study, the frequency of deviant tones was 660 Hz and 600 Hz for the standard tones. The frequency difference between our target tone and the standard tone could explain the increased amplitude of the N100 in response to deviant tones. As previous researchers concluded, this increased amplitude could be reflected by an enhanced activation of feature detectors distinctive of the N100 component, enabling the differentiation of any two auditory stimuli (Butler, 1968, 1972; Näätänen 1992). As seen in previous studies, a larger amplitude in response to deviant tones could be a result of a frequency difference from the preceding tones or its status as a target, thus involving selective attention (Butler, 1968; Hillyard et al., 1973). Accordingly, there is an agreement that the N100 is related specifically to triggering attention and to orienting attention towards a stimulus (Bomba & Pang, 2004; Boutros et al., 1999; Lijffijt et al., 2009). Moreover, it was previously indicated that temporal predictability modulates the processes underlying dynamic attending, and thus the deviance processing (Schwartze, et al., 2013). Since individuals in our study were required to count deviant tones, their attention was focused on these tones, and this could explain why the N100 response to deviant is increased.

Moreover, our results are in keeping with a previous study by Schwartze and collaborators (2013), in which findings showed that the N100 response differentiated between the temporal structure of the stimuli (i.e., isochronous versus random sequences). This suggested differential temporal predictability processes for N100 amplitudes in a sequence where the prediction is maximized (i.e., isochronous sequence) and when the prediction is minimized (i.e., random sequence). Our research provides additional evidence by linking this effect to enhanced behavioral rhythmic abilities (as measured by the beat tracking index). Indeed, this finding could indicate enhanced sensitivity in *good beat trackers* to temporally predictable sequences (i.e., isochronous sequence) in contrast to temporally unpredictable sequences (i.e., random sequence). This effect might be explained through neural adaptation. Indeed, findings in previous studies showed a decrease in N100 amplitude following stimulus repetition (Butler, 1968; Näätänen & Picton, 1987; Zhang et al., 2011) that has been largely attributed to neural adaptation (Thompson & Spencer, 1966). In fact, evidence of N100 amplitude decrement to repeated stimulation and the direct relation between repetition rates and the decrease of amplitude have supported the adaptive pattern of the N100 (Thompson & Spencer, 1966). Additionally, neural adaptation has been suggested to enhance the sensitivity to novel stimuli (Delgutte, 1997). Hence, neural adaptation might provide clarifications to the observed link between good rhythmic abilities and an enhanced N100 response to deviant tones embedded in an unpredictable sequence.

Furthermore, researchers suggested that the required period in which neurons recover before being able to respond to following signals (i.e., refractoriness period) is another mechanism underlying the adaptive pattern of N100 (Barry et al., 1992; Budd et al., 1998). This mechanism stipulates that a neuron can only respond to a stimulus after a sufficient period of recovery following a preceding stimulus (Shore, 1995; Fitzpatrick et al., 1999). This leads us to a crucial factor influencing both neural adaptation and refractoriness: the inter-stimulus interval (i.e., ISI) (Budd et al., 1998; Zhang et al., 2011). Findings on the influence of ISI on the N100 amplitude state that its amplitude increases with increasing ISI and reaches a plateau at approximately 8 to 10s (Davis et al., 1966). This implies that it takes about 8 to 10s between the presentation of the stimuli for the neurons to be able to fully respond again. In line with this interpretation, findings suggest that a short mean ISI, i.e., as short as 350 msec is needed to produce a clear effect of the N100 amplitude (Schwent et al., 1976). In fact, speeding the stimulus processing to avoid being caught by the next stimulus while still processing the previous one results in shorter N100 amplitude (Hillyard et al., 1973; Hartley, 1970). In contrast, the greater ISI (mean of 1000 ms) used in our study might explain the increased amplitudes of *the good beat trackers*. In fact, using a higher ISI gives the subjects time for unnecessary processing (Naatanen et al., 1987; Schwent et al., 1976). Thus, subjects with better rhythmic abilities had abundant time to process each stimulus presented and did not process the stimuli at their maximal speed, resulting in increased amplitude of the N100.

Altogether, the capacity of the brain to differentiate between deviant tones presented in a predictable sequence and an unpredictable sequence is related to rhythmic abilities (as indicated by the BTI). Interestingly, this difference in N100 following the manipulation of temporal and formal structure is present for *good beat trackers*, but not for the *poor beat trackers*. In fact, the N100 response to deviant tones in the regular presentation and irregular presentation does not differ for *poorer beat trackers.* A potential explanation could be that *poor beat trackers* have lower rhythm abilities and have difficulty predicting when deviant tones are presented in a regular or irregular rhythmic context (isochronous and random). In contrast, *good beat trackers* can capitalize on the temporal structure of the stimuli, which then reflects in a difference in N100 amplitude of regular and irregular deviant tones. Thus, lower beat tracking capacities could be reflected by a smaller recognition or prediction of deviant tones on a temporal structure. These findings may suggest different mechanisms of entrainment to an external stimulus for *good* and *poor beat trackers*, reflecting a lower ability to attend to events dynamically over time for *poor beat trackers*. However, to draw more concrete conclusions regarding neural entrainment, further studies should be conducted investigating SS-EPs and oscillatory activity (*e.g.,* Sauvé et al., 2019; Nozaradan et al., 2016; Henry et al. 2017).

Association of behavioral rhythmic abilities and P300 electrophysiological responses

No association between the P300 component and rhythmic abilities was found. This result could be in contrast with previous findings by Schwartze and collaborators (2011) of a P3b differentiation on temporal predictability. This inconsistency might be explained by the different inter-stimulus intervals (ISI) used in the two experiments and might reflect a limitation in the procedure used in our study. In the study by Schwartze and collaborators (2011), the ISI was 600 ms in the isochronous sequence and between 200 ms and 1000 ms for the random sequence. In contrast, the isochronous sequence of our study had an ISI of 1000 ms, whereas in the random sequence it was between 600 ms and 1400 ms. The fact that our values were 1000 ms or higher could account for the absence of effect in our study. In fact, the boundary of attention-dependent temporal predictability mechanisms is commonly associated with values close to 1000 ms. Since the values used in our study are very close and even higher than this boundary, it could explain the absence of effect of the P300 component. However, these findings should be interpreted with caution, because when analyzing the P300 component, the differentiation of the P3a and P3b sub-components was not examined. On the other hand, the purpose of our study was to investigate which electrophysiological components affected by the predictability of an auditory stimulus are enhanced by greater rhythmic abilities, whereas the study by Schwartze and collaborators (2011) did not measure rhythmic abilities. Following this line of thought, further analyses should be conducted to investigate the modulation of the two sub-components of the P300 by formal and temporal predictability, and especially their link with behavioral rhythmic abilities.

Effect of cognitive functions and additional measures of rhythmic abilities

The fact that the large variability observed in the performance of behavioral rhythmic tests may be linked to other factors was a possibility. To test this, logistic regression models were evaluated to identify the best predictors of a beat tracking ability profile, first considering ERP differences between isochronous and randomly timed deviants (amplitude and latency of P50, N100 and P300) and then potential contributions from specific rhythmic ability measures and cognitive abilities. The results showed that only the N100 amplitude difference was associated with *good* vs *poor beat trackers*, without additional moderation by cognitive functions (i.e., measures of flexibility, composite scores for the WASI-II, inhibition and working memory). Hence, executive functions do not explain the link previously observed between individual differences of rhythmic abilities and predictability. Furthermore, the analyses considered potential influences from additional rhythmic tasks measures on the prediction of beat tracking ability by N100 but did not indicate any improvement from these measures.

In sum, our results suggest that measures of flexibility, inhibition and working memory as well as other rhythmic tasks exert minor influences on cognitive ERP components and their relationship with rhythmic abilities, strengthening the interpretation of our results that N100 amplitudes reflect individual differences of rhythmic abilities involving temporal predictability (as assessed by the BTI).

Conclusion

In conclusion, the present work examined individual differences in behavioral rhythmic abilities and the electrophysiological correlates underlying them. The findings were mostly in line with our expectations. Interestingly, we found smaller P50 amplitudes for standard tones presented irregularly to reflect enhanced sensorimotor abilities, as measure by the paced tapping task. This result potentially suggests that individuals with better sensorimotor abilities have a better capacity to recognize new stimuli and enhanced inhibitory processes. Additionally, enhanced beat tracking abilities (as assessed by the beat tracking index) are reflected in a reflected by a smaller N100 amplitude elicited by deviant tones in the isochronous sequence and a larger response to deviant tones in the random sequence. Thus, possibly reflecting an enhanced processing of temporally predictable deviant tones. However, no relation was found between the P300 component and rhythmic abilities. Furthermore, the influence of cognitive functions and additional rhythmic tasks was minor, supporting the observed relation between rhythmic abilities (as determined by the beat tracking index BTI) and the N100 component's response.

The main goal of our study was reached by identifying the electrophysiological correlates underlying individual differences in rhythmic abilities. The findings of this work add to our understanding of behavioral and neural signatures of temporal predictability within a general population and could potentially help future research to investigate the roots of rhythm disorders.

Tableau 1. – Performance of the young and old groups for the BTI, BAASTA tasks and neuropsychological tests.

		Young adults (n =22)	Old adults (n= 21)		
Variables	Variable	Mean (SD)	Mean (SD)	t	p
Behavioral measures					
Beat Tracking index	Z-scores [BAT (d'); Paced tapping (logit tempi averaged)]	-0.63 (0.99)	0.07 (0.64)	-0.13	.597
Beat Alignment Test	d' (all tempi averaged)	2.80 (1.13)	2.70 (0.90)	0.30	.764
Paced Tapping	Metronome and Music (all logit tempi averaged)	2.31 (1.10)	2.66 (0.82)	0.25	.232
Unpaced Tapping	Inter-tap interval (ms)	677.14 (215.31)	604.61 (140.67)	1.31	.197
	Motor variability (CV iti)	0.07 (0.05)	0.06 (0.04)	0.97	.335
Neuropsychological Tests					
WASII-II	Composite score (CS)	118.18 (10.69)	122.19 (17.95)	0.88	.376
Flexibility tasks	Numbers (Total performance index)	6.76 (6.76)	0.71 (12.50)	1.96	.053
	Letters & numbers alternating (Total performance index)	2.80 (9.35)	9.63 (7.39)	2.66	.011*
GO/NoGo	Mean RT	542.35 (45.48)	30.9	4.75	<.001*
Working Memory	Mean RT	619.50 (153.42)	100	2.33	.022*

Note: p-values reported are two-tailed and uncorrected for multiple comparisons

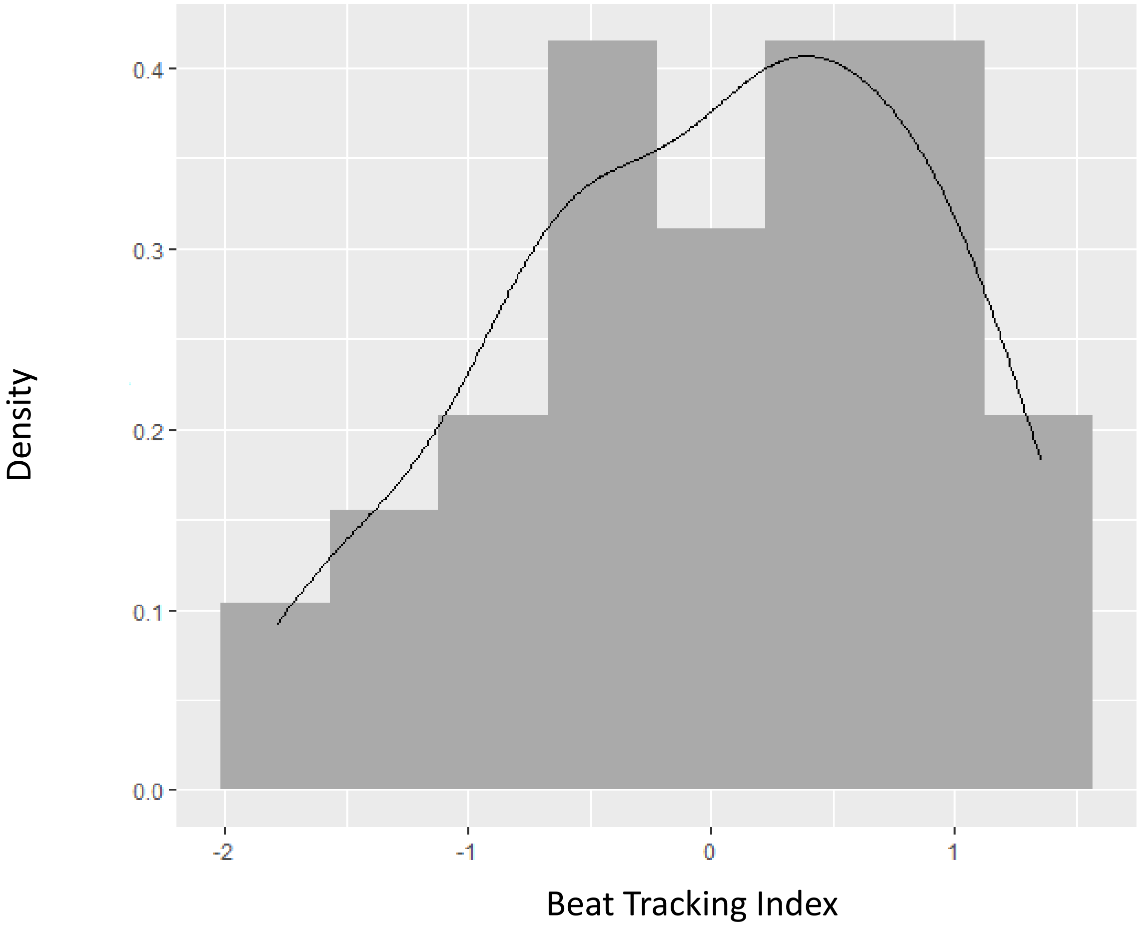

Figure 3. – Variability of rhythmic abilities (BTI) across all participants. Beat tracking performance (composite score computed by averaging z-scores of the beat alignment test (BAT, d’) and paced tapping (logit vector length) across all participants

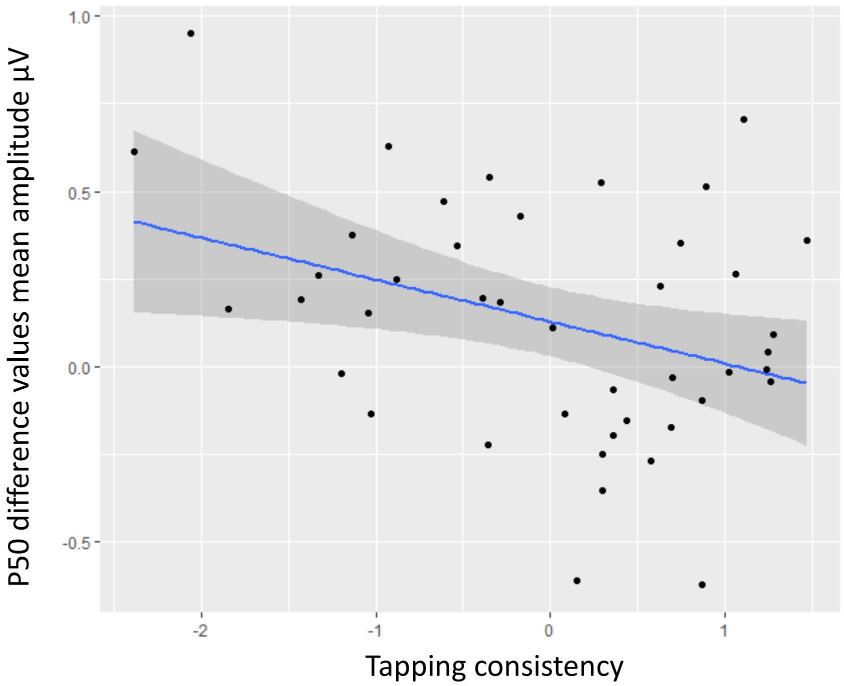

Figure 4. – Relation between sensorimotor abilities and the P50 ERP component. Scatterplot of the relations between tapping consistency (standardized average logit vector length) with the P50 mean amplitude difference between deviant and standard tones.

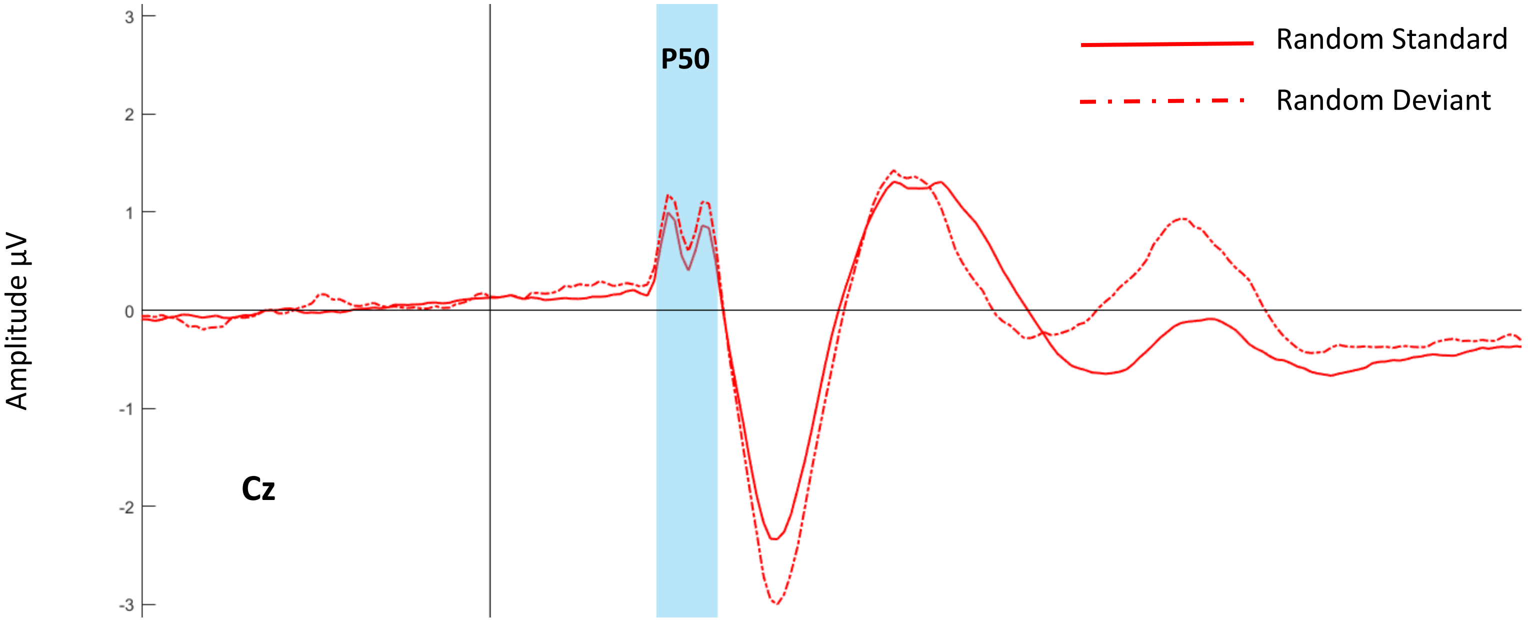

Figure 5. – ERP results for the P50 component. P50 component on mean amplitude differences for standard and deviant tones presented in the random condition across all participants.

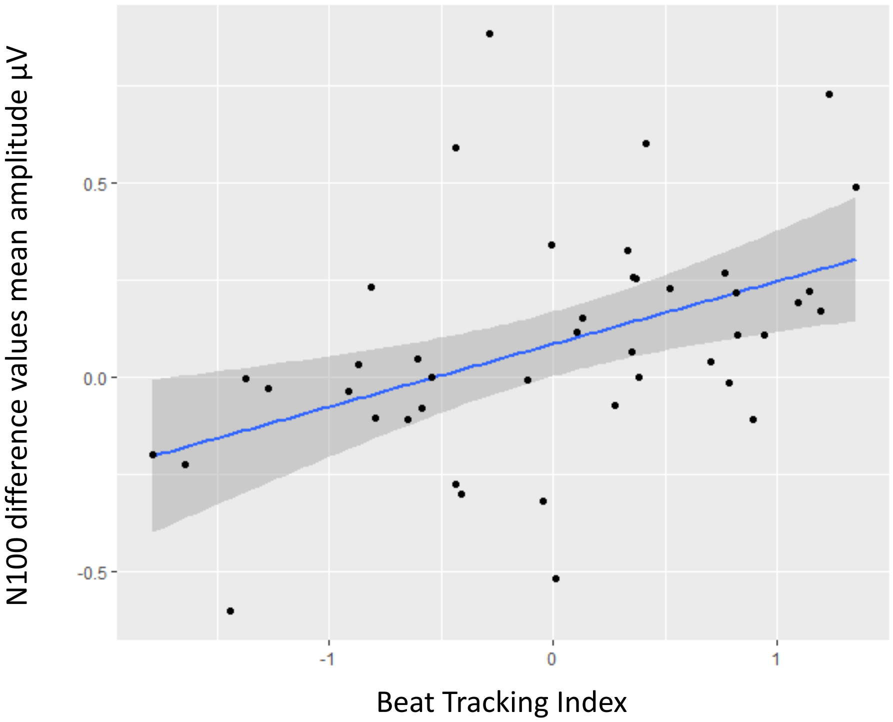

Figure 6. – Relation between rhythmic abilities (BTI) and the N100 ERP component. Scatterplot of the relation between the BTI and the N100 amplitudes difference for the deviant tones in the isochronous and random conditions across all participants.

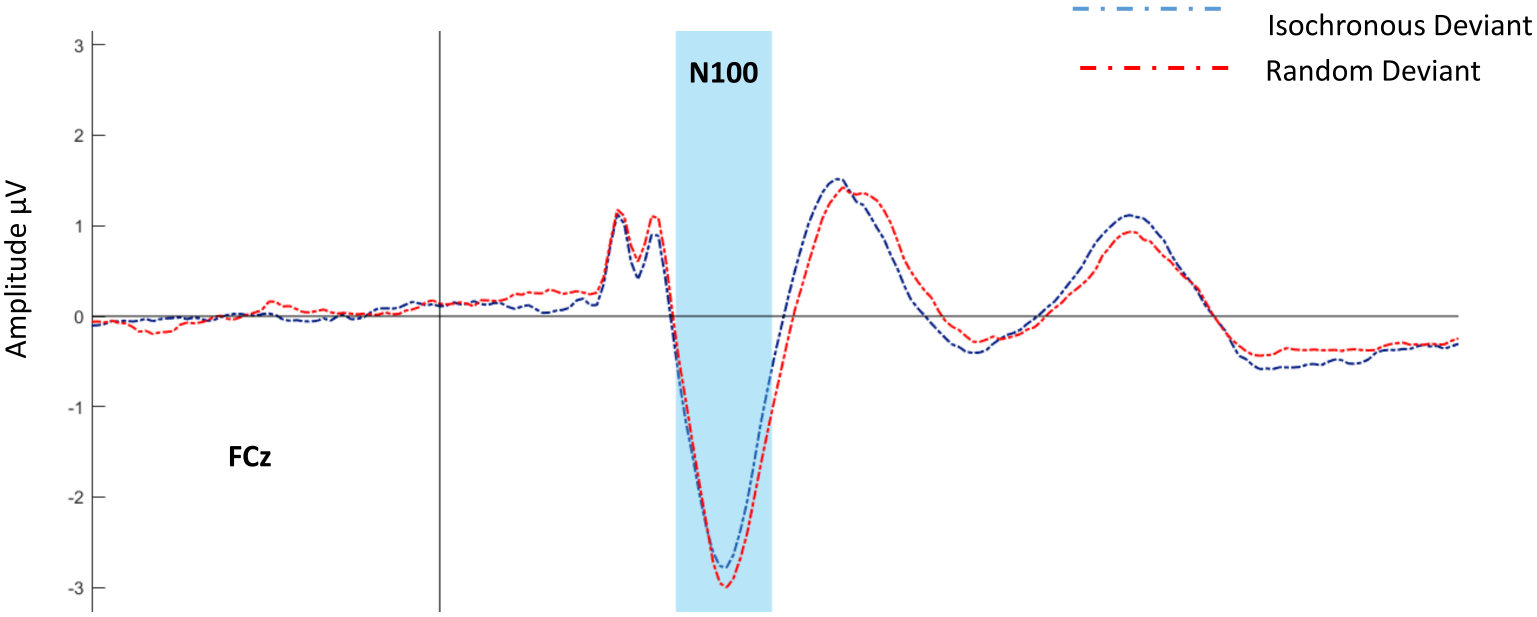

Figure 7. – ERP results for the N100 component. N100 component on mean amplitude differences of deviant tones presented in the isochronous and random conditions across all participant

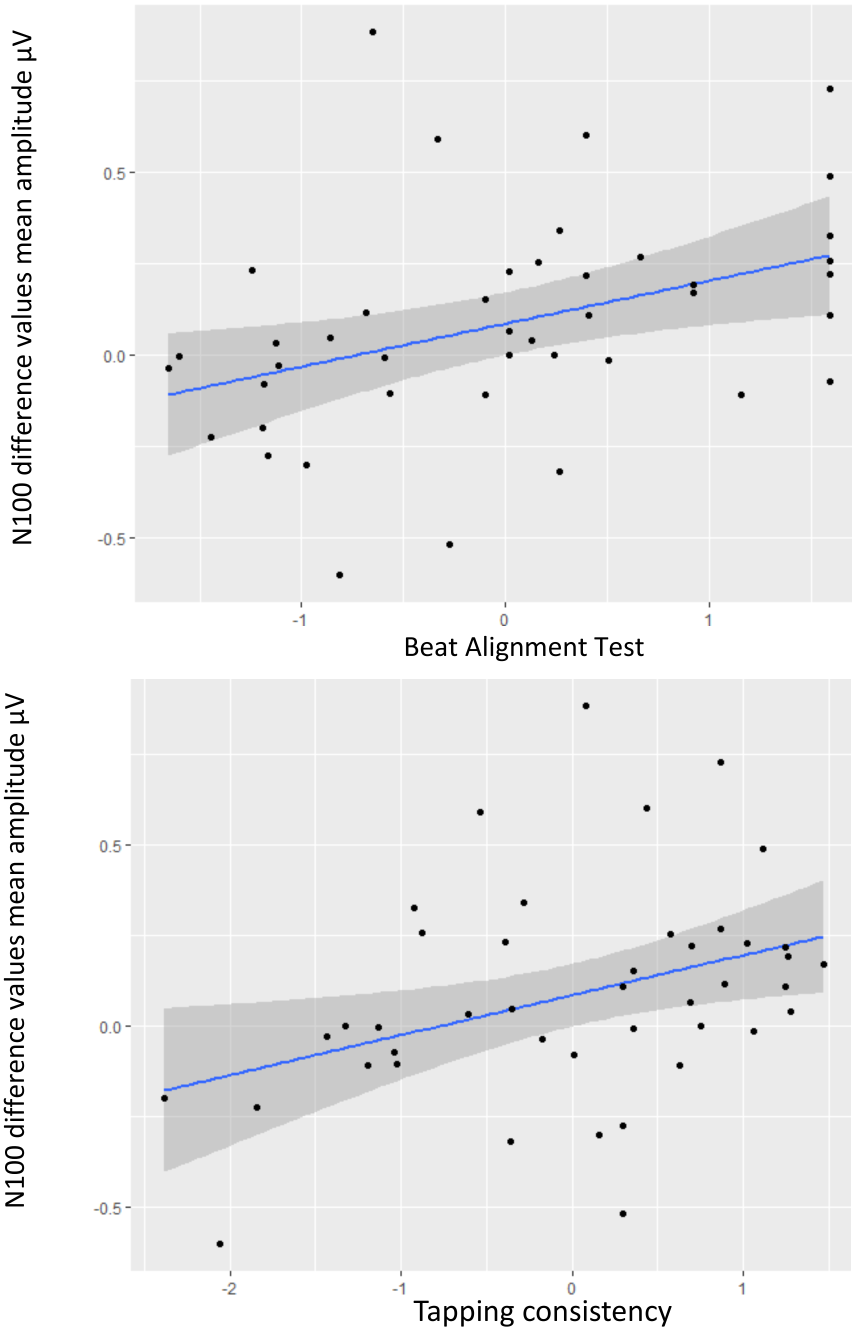

Figure 8. – Link between beat perception, tapping consistency and ERP results of the N100 component mean amplitude differences of deviant tones between the isochronous and random sequences. Scatterplots of the relations between A) beat perception (standardized average d` in the BAT) and the N100 amplitudes difference for the deviant tones in the isochronous and random conditions B) tapping consistency (paced tapping, standardized average logit vector length) and the N100 amplitudes difference for the deviant tones in the isochronous and random conditions.

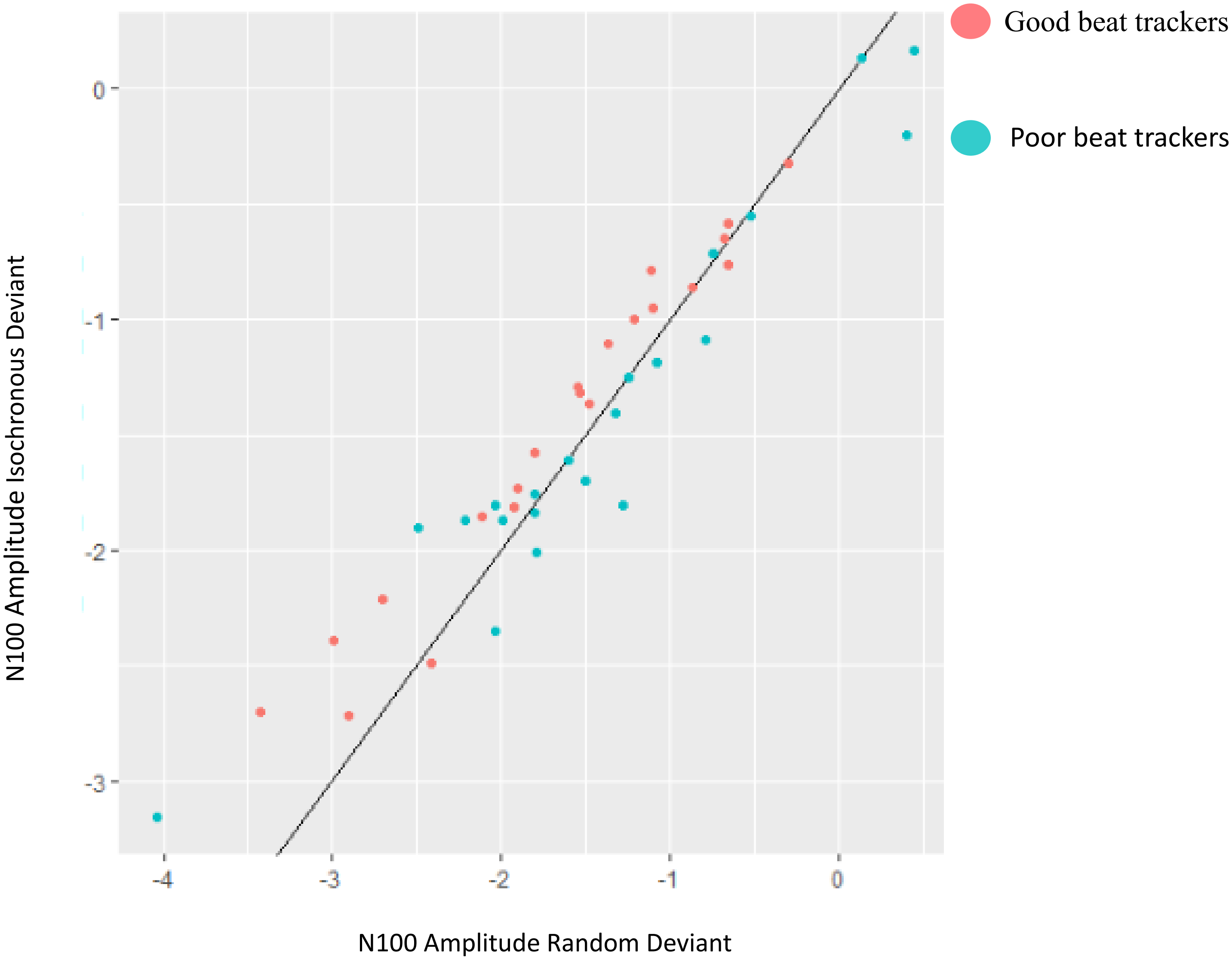

Figure 9. – Rhythmic abilities: difference between *Good beat trackers* and *Poorer beat trackers.* Scatterplot of the relation between *Good beat trackers* and *Poorer beat trackers* (BTI performance) and the N100 mean amplitude difference for deviant tones on the isochronous and random sequences.

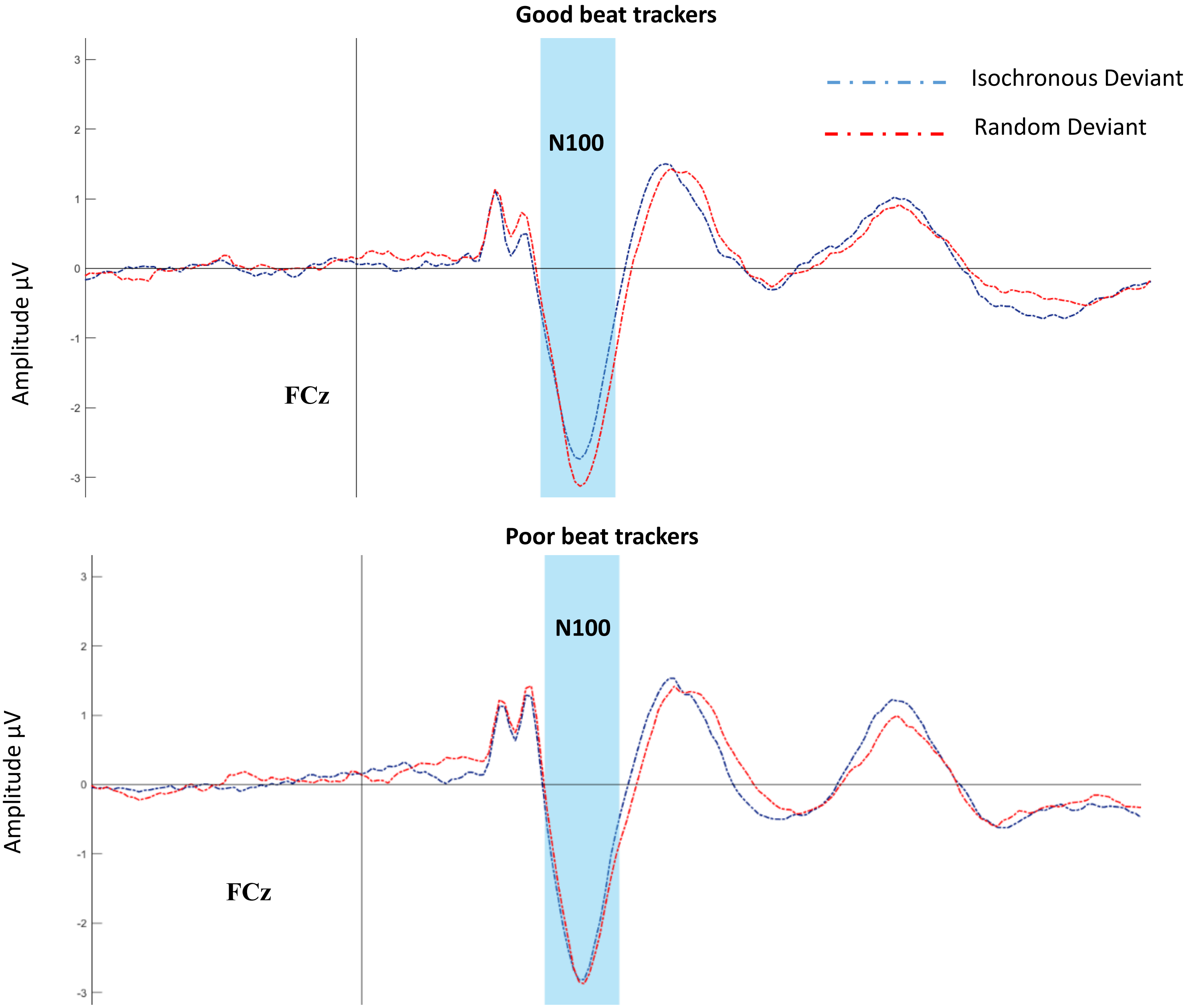

Figure 10. – Link of ERP results of N100 component and individual differences of rhythmic abilities. N100 mean amplitude differences for deviant tones in the isochronous and random conditions for good beat trackers and poorer beat trackers**. (A)** Good beat trackers: results show a more positive amplitude for deviant tones in the isochronous condition (M = -1.38) relative to the random condition (M = -1.57). **(B)** Poorer beat trackers: results show no difference of N100 amplitude for deviant tones in the isochronous condition and the random condition

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