The effect of stimulus type and tempo on sensorimotor synchronization during finger-tapping in cerebellar ataxia: Behavioral and neural evidence

Peer-reviewed author version

MOUMDJIAN, Lousin; FEYS, Peter; Moens, Bart; Manto, Mario; Cabaraux, Pierre; VAN WIJMEERSCH, Bart; Kotz, Sonja A.; Leman, Marc & Rosso, Mattia (2025) The effect of stimulus type and tempo on sensorimotor synchronization during finger-tapping in cerebellar ataxia: Behavioral and neural evidence. In: Cortex, 187 , p. 111 -123.

DOI: 10.1016/j.cortex.2025.04.005
Handle: http://hdl.handle.net/1942/46061

Abstract

Sensorimotor synchronization, coordination of movements with external rhythms, occurs daily. Finger-tapping tasks are often used to study biological mechanisms underlying sensorimotor synchronization. This study investigates how deviations in auditory stimulus tempo from spontaneous motor tempo affect sensorimotor synchronization in patients with cerebellar ataxia during active listening and finger-tapping. Specifically, the cerebellum's role in these tasks is investigated by quantifying behavioral and neural dynamics of auditory-motor coupling. Sixteen patients with cerebellar ataxia and 14 healthy controls listened and tapped to music and metronomes at seven tempi (-12%, -8%, -4%, 0%, +4%, +8%, +12% of spontaneous tapping tempo) in randomized order. Sixty-four channel EEG, stimulus beat- and finger-tapping onsets were recorded during each trial. Behavioral synchronization was quantified by synchronization precision and accuracy, whereas neural entrainment was quantified with the stability index. Cerebellar patients displayed higher, more variable spontaneous tapping tempi than controls. Although precision was lower in patients than controls, they achieved high precision values. Differences in synchronizing between metronomes and music were observed for both precision and accuracy, favoring metronomes in both groups. Accuracy was impacted, with lowest asynchrony observed in patients with music, and across groups at the slowest tempi (-12%) and highest tempi (4, 8 and 10%). EEG results revealed greater stability for music during tapping. Although patients with cerebellar ataxia showed synchronization deficits, they could sufficiently synchronize with isochronous metronomes and music containing higher complexity, likely through sensory accumulation as a compensation strategy. These findings support the use of sensorimotor synchronization strategies in rehabilitation for cerebellar disorders.

Keywords

Synchronization; cerebellum; finger-tapping; EEG; rhythm

1. Introduction

Coordinating body movements with external rhythms, also known as sensorimotor synchronization, occurs daily and across the lifespan (Drewing, 2006). A typical task to investigate sensorimotor synchronization is finger tapping to paced auditory sequences or rhythms (Repp & Su, 2013). This phenomenon has been studied in healthy adults and the elderly (Drewing, 2006; Repp & Su, 2013) as well as in persons with neurological diagnoses (L. Moumdjian, Rosso, M., Moens, B., De Weerdt, N., Leman, M., Feys, P., 2022; Schwartze, Keller, & Kotz, 2016; von Schnehen, Hobeika, Huvent-Grelle, & Samson, 2022). The latter evidence can inform biological models of sensorimotor synchronization as impairment allows to infer mechanistic underpinnings of the neurofunctional networks involved in sensorimotor synchronization (Dalla Bella, 2018; Grahn, 2012; Merchant, Grahn, Trainor, Rohrmeier, & Fitch, 2015; Molinari, Leggio, & Thaut, 2007; Morillon & Baillet, 2017; Nobre & van Ede, 2018; Nozaradan, Schwartze, Obermeier, & Kotz, 2017; Zalta, Petkoski, & Morillon, 2020).

Within this paradigm, coupling of a movement cycle (e.g., finger-taps) to an auditory stimulus (e.g., musical beats or metronome ticks) occurs. This involves a cascade of action-perception loops including auditory perception, the formation of internal models of temporal structure, and the engagement of the motor system to interface with the induced temporal structures. This action-perception cascade thus relies on sensorimotor integration for motor behavior (in this example, the finger-taps) to match the induced temporal structures of an auditory stimulus. A resolution is reached when the intrinsic timer (i.e., endogenous timing) and the induced auditory temporal structure entrain. Different theoretical accounts have been put forward to explain the mechanisms of dynamics underlying entrainment. Such accounts are the dynamical attending theory (Jones & Boltz, 1989; Jones, Moynihan, MacKenzie, & Puente, 2002), predictive coding (K. Friston, 2018; K. Friston, FitzGerald, T., Rigoli, F., Schwartenbeck, P., Pezzulo, G. , 2017; Koelsch, Vuust, & Friston, 2019; Vuust, Heggli, Friston, & Kringelbach, 2022) and the neural resonance theory (Large, Herrera, & Velasco, 2015; Large & Snyder, 2009). The result of coupling is entrainment of the motor and auditory oscillations over time, involving a process of phase and/or period alignment to reach a state of synchronization (Leman, 2016; Repp & Keller, 2004; Repp & Su, 2013). Studies also highlighted that our capacity to predict temporal events does not only rely on periodic structure (e.g., duration or interval-based) but can also extend to non-periodic ones (e.g., beat-based).

Neural encoding of rhythms can be traced with electroencephalographic recordings (EEG) and involve frequency tagging that relates the amplitude of the steady state evoked potential (SS-EP) with frequencies of interest during auditory stimulation (Nozaradan, Peretz, Missal, & Mouraux, 2011; Nozaradan, Zerouali, Peretz, & Mouraux, 2015). In prior studies, the authors employed a listening paradigm in healthy participants with two auditory rhythms: unsyncopated and syncopated at fast and slow tempi. Unsyncopated rhythms are those where accents fall on the strong beat (thus predictable and steady), while syncopated rhythms are those where the accents fall on the weak or off-beat (thus inducing unpredictability) (Reed, 2007). The authors showed prominent peaks of the SS-EP only at the beat frequencies as compared to the non-beat frequencies, indicating perception and encoding of sound periodicities (Nozaradan, Peretz, & Keller, 2016). In addition, they showed that this encoding differed for rhythm complexities and across different frequencies. That is, the greater SS-EP amplitude was found for the unsyncopated rhythm, and more so during the slow than the fast tempi, while this modulation was not found across tempi in the syncopated rhythm condition (Nozaradan et al., 2016). A synchronization tapping task followed the initial listening task, to compute the behavioral outcome of tap-to-beat synchronization in terms of the degree of precision (synchronization consistency) and accuracy (asynchrony). The authors correlated these outcomes with the amplitude of the SS-EPs at the beat frequencies recorded during the listening task and showed that greater synchronization accuracy was associated with a higher SS-EP amplitude. However, the SS-EP amplitude did not correlate with precision (Nozaradan et al., 2016).

In the current study, we extended these previous findings by investigating how deviations in stimulus tempo from the spontaneous motor tempo affected sensorimotor synchronization. We examined this effect during finger-tapping to various stimuli in patients with cerebellar ataxia. We quantified these effects both behaviorally and neurally (EEG) and compared them with those of healthy controls. Stimuli included isochronous metronomes and music, as music allows for an ideal comparison to isochronous metronomes to introduce hierarchical rhythmic levels (i.e., basic beats, subdivisions, larger groupings) while keeping the same beat periodicity between stimuli. This allowed us to investigate beat-based perception, as isochronous rhythms alone are not sufficient as prediction of the latter can rely on absolute intervals as well (Bouwer, Burgoyne, Odijk, Honing, & Grahn, 2018; Bouwer, Honing, & Slagter, 2020; Bouwer, Werner, Knetemann, & Honing, 2016). Secondly, the investigation focused on patients with cerebellar ataxia. Although previous studies have demonstrated that sensorimotor synchronization during finger-tapping to metronomes was disrupted and more variable in both pediatric (Provasi et al., 2014) and adults (Schwartze et al., 2016) with cerebellar pathology, there is also evidence pointing to spared abilities in this population. Examples are rhythm discrimination (Provasi et al., 2014), ability to encode beat frequencies to both syncopated and non-syncopated rhythms during an active listening task (Nozaradan et al., 2017), and behavioral (finger-tapping) (Schwartze et al., 2016) and neural tracking of period and phase perturbations at fast and slow tempi to auditory metronomes (Baliviera, under review). Lastly, we intended to capture the phase of a time-varying measure of the neural oscillations. Given that this aspect could not be captured with the frequency tagging approach (Rajendran & Schnupp, 2019), we used the 'stability index' that quantifies frequency fluctuations over time in an entrained oscillatory component (Rosso, Leman, & Moumdjian, 2021).

This study aimed to further establish the cerebellum's role in sensorimotor synchronization by examining the dynamics of auditory-motor coupling in individuals with cerebellar ataxia. To this end, we quantified both behavioral (precision and accuracy (L. Moumdjian, Buhmann, Willems, Feys, & Leman, 2018; Repp & Su, 2013)) and neural (stability index (Rosso et al., 2021)) dynamics during active listening and synchronized tapping tasks in music and metronomes at various tempi. We hypothesized that patients with cerebellar ataxia would synchronize with less precision and accuracy than healthy controls, and that their responses would similarly show in neural dynamics. We expected that behavioral performance and neural dynamics would be higher in the metronome compared to music conditions in both groups. Finally, we hypothesized that patients with cerebellar ataxia would achieve higher precision and accuracy when synchronizing to tempi closer to their spontaneous tempi as compared to the healthy controls, and that this response would also be reflected in their neural dynamics.

2. Methods

2.1 Participants

This case-control study was approved by the Medical Ethical Committee of Hasselt University and the local ethical committee of C.H.U. Charleroi and Erasme Hospital (B1152021000003), The National MS Center Melsbroek and Rehabilitation and MS center Noorderhart (B1152020000011. The study was registered in the European clinical trial registry (NCT04887753, NCT04639401).

Participants recruited were patients with cerebellar ataxia and age- and sex-matched healthy controls. The following inclusion criteria were established prior to data analysis and used for the cerebellar group: presence of cerebellar ataxia diagnosed by neurologist evidenced through MRI imaging (presence of a lesion and/or degeneration), or a minimum score of 1 on the Scale of Assessment and Rating of Ataxia. Participants were excluded if they had one of the following: cognitive impairment impeding understating of instructions, uncorrected hearing impairment, beat amusia, pregnancy. Eligible patients were asked to sign an informed consent and were invited to participate in two sessions: a descriptive testing session and the experimental session.

2.2 Descriptive tests

First, general demographic and disease information were collected. Then subscales of rhythm of the Montreal Battery for Amusia were used to evaluate amusia (Peretz, Champod, & Hyde, 2003), the S*cale for Assessment and Rating of Ataxia* (SARA), to evaluate the presence of ataxia with simple motor commands (stance, sitting, gait and others (Schmitz-Hubsch et al., 2006), the *9 Hole Peg Test* (9HPT) to evaluate manual dexterity of both hands, defined as the ability to manipulate small objects using fine motor (hand) movement (Oxford Grice et al., 2003), and the Edinburgh Handedness Inventory to determine hand dominance (Oldfield, 1971).

2.3 Experimental set-up

Participants sat on a comfortable chair in front of a table. A circular pad was placed in front of the participant on the table to record finger-tapping onsets. The auditory stimuli were presented via DefenderShield® airtube earbuds, and the volume was individually set by the participants before starting the experimental tasks. The stimulus sequences were played by a software designed specifically for the experiment, developed in Max MSP 8 (Cycling ’74, USA), and run on a research computer (Dell Latitude laptop, Core i5-1145, Windows 10 Pro, ASIO low-latency soundcard). An existing music database was used as in previous studies(L. Moumdjian, Moens, Maes, Van Geel, et al., 2019; L. Moumdjian, Moens, Maes, Van Nieuwenhoven, et al., 2019; L. Moumdjian, Moens, Vanzeir, et al., 2019) (for details of the music database development, see (Buhmann, 2016)). The EEG signal was recorded with an ANT-Neuro eego™ mylab system (ANT Neuro b.v., Netherlands) at a sampling rate of 1 kHz. Each participant wore an EEG headset with 64 electrodes (64-channel waveguard™ original with Ag/AgCl electrodes, 10-10 layout). A referential montage was used, with ‘Cpz’ set as reference for all the electrodes.

2.4 The experimental paradigm

Participants were asked to tap with their right index finger on a tapping-pad at their own comfortable tempo for one minute to register their spontaneous baseline tempo. They were then familiarized with the experimental task. Then, they underwent the experiment with two auditory conditions: music and metronomes, in randomized blocks. In each block, participants were asked to listen and tap to the stimuli at the following seven tempi: 0%, which equal their spontaneous tapping tempo, and -12%, -8%, -4%, +4% +8% +12% relative to their spontaneous tapping tempo. In the listening conditions, participants were asked to listen carefully to the auditory stimulus and mentally track the beats in the rhythm, while keeping their gaze on the tapping pad. In the tapping conditions, participants were instructed to synchronize their finger-taps to the beats in the auditory stimuli. The listening and tapping conditions were randomized within each block, and each trial lasted one minute.

2.5 Data processing

Finger-tapping onsets and beat onsets were registered with a Teensy 3.2 microcontroller, operating as serial/MIDI hub in the setting. More specifically, each time a finger-tap – captured by the piezo sensors of the pad – pushing the signal above a resting threshold, the microcontroller printed a timestamp on the serial port of the stimulation computer. The threshold was reported to be conservative enough to prevent false positives due to signal bouncing. For each beat onset of the presented stimuli, a MIDI message was sent to the microcontroller to log its timestamp on the serial port. All timestamps were rounded to 1 ms resolution, which corresponds to 1 kHz sampling rate. Since participants might push the pad for too long or accidentally lay their hand on it, finger-tapping onsets following the previous one by less than 350 ms were removed to prevent eventual false positives. To produce phase timeseries of beats and finger-taps (separately), the intervals between timestamps were linearly interpolated at 1 kHz sampling rate, producing a ramp wave bounded between 0 and 1. The ramp wave was then scaled to 2π, providing a phase estimate of the beats and the finger-taps with a temporal resolution of 1 ms. Finally, a relative phase timeseries was computed as the difference between the beats and the finger-taps phase timeseries.

The behavioral outcome measures were computed based on the timestamps (i.e., finger-tapping and beat onsets) and the relative phase timeseries. Data processing and analysis were carried out in Matlab ®.

EEG data were pre-processed using a set of functions from the *Fieldtrip* toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) for Matlab. Bad channels were visually inspected and manually removed for each participant. A sixth-order Butterworth high-pass filter with 1 Hz cut-off was applied to remove slow drifts; a low-pass sixth-order Butterworth filter with 40 Hz cut-off to remove high-frequency muscular activity; a fourth-order notch filtered at 50 Hz to remove power-line noise up to the third harmonic (Rosso, Moens, Leman, & Moumdjian, 2023). Excessively noisy channels were identified based on the visual inspection of raw time series and variance distribution across channels. The recordings were re-referenced to the average activity of all electrodes after channel rejection. The re-referencing was carried out after rejecting bad channels to avoid noise leakage into the common average. Subsequently, independent component analysis (ICA) was conducted as implemented in the "runica" *Fieldtrip* algorithm. Stereotyped artifacts such as eye blinks, lateral eye movements, and heartbeat were visually identified and removed based on visual inspection of their scalp topographies and activation timeseries.

2.6 Outcome measures

2.6.1 Behavioral measures

Resultant Vector Length (RVL). This measure expresses the stability of the relative phase angles over time. A unimodal distribution implies a high resultant vector length, whereas uniform and bipolar distributions result in a low resultant vector length. The measure was processed with the CircStats toolbox(Berens, 2009), using the relative phase time series as input. The measure ranges from 0 to 1, where 1 indicates high ***precision*** (consistent synchronization) during the trial.

Mean Asynchrony (mA). This consists of the mean difference between the participant's tap onsets and the respective closest metronome's beat onset, and thus quantifies error in ***accuracy***, and is expressed in milliseconds.

Inter-tap-intervals. This measure quantifies timing within tap onsets, expressed as inter-tap-intervals (ITI). The median (ITI_m) and the coefficient of variation (ITI_{cv}) are computed.

For details on the calculations of these metrics, please see Moumdjian and colleagues (2018)(L. Moumdjian et al., 2018).

2.6.2 Neural measures

Stability Index (SI). Source separation was performed on the pre-processed 64 channel EEG recordings via generalized eigendecomposition (GED) (M. X. Cohen, 2022) to extract from the multivariate signal an entrained component attuned to the stimulation frequency. GED allows to design a spatial filter to separate sources of oscillatory processes and reduce data dimensionality, based on the criterion to maximize the signal-to-noise ratio between narrowband and broadband neural activity. The target narrowband activity was defined by designing a different Gaussian filter for each participant and each experimental block, such that the center frequency would correspond to the stimulation chosen for the seven different tempi. The width of the filter at half of the maximum was kept constant at 0.3 Hz. With the exception of the filter definition, the entire GED procedure replicates the one described in detail in Rosso et al., 2021a (Rosso et al., 2021) and Rosso et al., 2023a (Rosso et al., 2023), resulting in the extraction of one single signal component.

The signal was then calculated by performing the Hilbert transform on the GED component, enabling the estimation of the signal's phase. Instantaneous frequency timeseries were computed as the first derivative of the unwrapped phase time series, and rescaled to Hz over time as indicated in Cohen (2014) (M.X. Cohen, 2014). The instantaneous frequency of an oscillatory system can be defined as the change in the phase per unit time (Boashash, 1992). A sliding moving median with a window width of 400 samples was used to smooth the instantaneous frequency time series, to remove occasional extreme bursts due to artifactual activity distorting the phase. Finally, we calculated the standard deviation of instantaneous frequency over the whole task was calculated as a global measure of frequency stability over time. This outcome is the stability index, where an index closer to 0 indicates a perfectly stable component, with the instantaneous frequency being a flat line intercepting the constant value of the stimulus frequency. For through details of the processing and computation, please see Rosso et al., 2021a (Rosso et al., 2021) and Rosso et al., 2023a (Rosso et al., 2023).

2.7 Statistical analysis

Descriptive measures were compared between groups using an independent t-test when the data exhibited a normal distribution determined by the Shapiro-Wilk test. For non-normally distributed data, a Wilcoxon-signed rank test was employed. Categorical descriptive measures were compared between groups using a Fisher test.

The behavioral outcome measures (mA, RVL, ITI_m, ITI_{cv}) were analyzed by using a mixed model analysis of variance, with random effects of the participants, fixed effects of group (patients with cerebellar ataxia, healthy controls), stimuli (music, metronome) and tempi (12%, -8%, -4%, 0% +4% +8% +12%) along with their interactions. Tukey's HSD test of multiple comparisons was performed to analyze significant interactions. Residuals of the models were checked for heterogeneity, and if violated, data were transformed. This was the case for the outcome measures RVL and $ITI_{cv.}$ Normal distribution was obtained by applying ranking to the RVL and applying log transformation to the ITI_{cv}. In addition, a Spearman's correlation analysis was conducted for each group between the primary outcome measures (mean asynchrony and RVL) and the Nine Hole Peg Test (9HPT) of the right upper extremity.

For the neural outcome measures (stability index), first, the quality of the GED application was assessed by inspecting and computing the modulated peak of the first component of the eigenspectrum across stimuli and tempi. The inspection revealed the presence of non-attuned (i.e., non-entrainment) components. Thus, the 0% music and metronome listening conditions were used to compute the median GED signal-to-noise ratio (this value equated to 1.6). Thus, GED components with a peak value ≤1.5 (i.e. non-entrained components) were removed from analysis. The SI was then computed and correlated with the behavioral outcome measure RVL, in order to replicate a correlation previously reported in previous work (Rosso et al., 2021). The SI was then fitted in a mixed model analysis of variance with backward modelling, with random effects of the subjects, fixed effects of Group (patients with cerebellar ataxia, healthy controls), Stimuli (music, metronome) and Tempi (12%, -8%, -4%, 0% +4% +8% +12%) along with their interactions. For the neural outcome measure, the factor of Task (listening, tapping) was added to the model. The pre-processing, GED computations and stability index computations were conducted in Matlab® (MathWorks Inc. version: 2023a).

Due to technical errors during recordings, 4.5% of metronome trials, and 1.6% music trials were removed. All statistical analyses were performed using JMP Pro 17.0.0, with the level of significance set at α=0.05.

Previous sensorimotor synchronization studies in cerebellar patients have typically included around 10 participants (Nozaradan et al., 2017; Schwartze et al., 2016). Therefore, in determining sample size, we sought to exceed this number despite the recruitment challenges associated with this patient population'.

3. Results

Sixteen (N = 16) patients with cerebellar ataxia and fourteen (N = 14) healthy controls were included in the study. All participants expect one person with cerebellar ataxia were right-handed. Figure 1 illustrates the experimental flow-chart of behavioral and neural data collected and analyzed.

Insert Figure 1

Table 1A and B present clinical information and descriptive characteristics of all participants. Participants did not significantly differ across groups in age, sex, or the rhythm subscale test for assessing Amusia. The two groups significantly differed at baseline in terms of ataxia

(SARA total score z= -4.41, p<.0001), and on the 9HPT of the right (and domain) hand z= -2.44, p=0.01).

Insert Table 1A and B. Descriptive characteristics of study participants

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The spontaneous tapping significantly differed at the 0% tempo between groups (p=0.04), resulting in a lower number of spontaneous taps per minute in the healthy control group. Table 2 presents the mean and standard deviation of the beats per minute used across tempi for both groups.

Insert Table 2

3.1 Behavioral outcome measures

Resultant Vector length (RVL)

Two significant main effects were found: Group ($F(1, 28.0) = 4.67$, $p=0.04$), indicating a lower precision in the cerebellar than the healthy control group; and Stimuli ($F(1, 358.2) = 58.81$, $p<.0001$), indicating a lower precision when tapping to music than to metronomes. Significant interactions effects were not found. Visualization of the results of RVL is seen in Figure 2.

Insert Figure 2

Mean Asynchrony

A main effect of Stimuli was found ($F(1, 336.7) = 99.61$, $p<0.001$), indicating that asynchrony was smaller when tapping to music than to metronomes. A significant interaction of Group*Stimuli was found ($F(1, 336.7) = 5.41$, p=0.02). The post-hoc test indicated that asynchrony was smaller in the cerebellar group when tapping to music compared to the control group when tapping to metronomes (t=4.18, p=0.0002). A main effect of Tempi ($F(1, 330.7) = 2.81$, p=0.01), and an interaction effect of Stimuli*Tempi was found ($F(6, 330.7) = 2.13$, p=0.05). The post-hoc test indicated smaller asynchrony in the music condition compared to the metronome conditions for the following tempi: -12% (t=-5.06, p<.0001), 4% (t=-4.92, p<.0001), 8% (t=-4.12, p=0.004), 12% (t=-5.56, p<.0001). Visualization of the results of Mean Asynchrony is seen in Figure 3.

Insert Figure 3

Median inter-tap-interval (ITI_m)

Three significant main effects were found. Main effect of Tempi $F(6, 342.0) = 86.27$, p<.0001*)*, indicating that participants changed their tapping duration to increase or decrease their tapping tempo across the different tempo conditions. A main effect of Group $F(1, 28.0) = 5.16$, p=0.03*)*, indicating that the cerebellar group was tapping faster than HCs. A main effect of Stimuli ($F(1, 342.6) = 4.18$, p=0.04), indicating faster tapping to metronomes than to music. One significant interaction effect of Group*Stimuli was found ($F(1, 342.6) = 7.93$, p=0.005*)*. The post-hoc test indicated that that the cerebellar group tapped slower to music than to metronomes (t=-3.42, p=0.004).

CV of inter-tap-interval (ITI_{cv})

A significant main effect of Stimuli $F(1, 362.7) = 26.89$, p<.0001*)* was found, indicating that tapping in the music condition displayed more variability in tapping tempo (i.e., duration of the ITI's) compared to when tapping to the metronome condition. Visualization of the results of ITI is found in Figure 4.

Correlation analysis

A weak and non-significant correlation was found for the 9HPT of the right (tapping) hand and synchronization consistency (RVL) for the cerebellar group (r=-0.1620, p=0.05), and control group (r=0.11, p=0.33).

A moderate significant correlation was found for the 9HPT of the right (tapping) hand and mean asynchrony for both the cerebellar group (r=0.33, p=0.0004), and control group (r=0.22, p<.0001).

Insert Figure 4

3.2 Neural outcome measure: Stability Index

a) Listening conditions

Trials in which the GED could not extract an entrained component constituted 15% of the data from healthy controls and 18% of data from cerebellar patients. The mixed model analysis revealed no significant main or interaction effects.

b) Tapping conditions

Trials in which the GED could not extract an entrained component constituted 24% of the data from healthy controls and 21% of data from patients with cerebellar ataxia. A non-significant correlation was found between the stability index and RVL for the cerebellar group (r=0.0254, p=0.89) and control group (r=-0.19, p=0.48). Only a significant main effect of Stimuli $F(1, 166.6) = 4.71$, p=0.03) was found, indicating that neural entrainment was more stable with music than with metronomes (t=2.17, p=0.03). Visualization of the stability index across tempi in both the listening and tapping conditions is found in Figure 5.

Insert Figure 5

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4. Discussion

The aim of the present study was to investigate behavioral and neural dynamics of auditory motor coupling in persons with cerebellar ataxia as compared to healthy controls, during listening and tapping tasks at tempi deviating from their spontaneous motor tempo.

While both groups received the same instructions across conditions, cerebellar patients presented higher spontaneous tapping tempi. Previously, cerebellar patient and controls differed in their degree of tapping variability but not in terms of absolute mean differences (Franz, Ivry, & Helmuth, 1996; Schwartze et al., 2016). We found similar results for variability, but also in absolute spontaneous tapping tempo. These results showed higher spontaneous tapping tempi in the patient group (on average 97 beats per minute; 617ms inter-beat intervals) than in the healthy control group (82.3 beats per minute; 729ms inter-beat intervals). These differences across studies could be explained by different instructions for completing the task. That is, while in the previous study participants were told to tap as regularly as possible (Schwartze et al., 2016), we instructed them to tap at a pace that felt comfortable which would allow them to keep tapping for an extended time period.

Regardless of the group differences in spontaneous tapping tempo, we found group differences regarding tapping precision, despite the median RVL being quite high (0.90 for the patient group and 0.95 for the healthy control group) across tempi. Of note is that precision (RVL) did not correlate with the right-hand function as measured by the 9HPT, although the cerebellar group had mild upper extremity dysfunction at a group level (see Table 1). Yet, precision did not significantly differ across tempi in both groups. This result contrasts conflicting prior evidence, stating that sensorimotor synchronization is less stable and accurate when the tempi are slower than spontaneous motor tempo (Drewing, 2006; Repp & Su, 2013). In line with this, other studies found that finger-tapping to auditory stimuli showed a higher precision for slower tempi than faster ones (Nozaradan et al., 2016). An explanation for the current results could be that the selected tempi did not contain extreme ranges of fast and slow (between -12 and +12% in increments of 4%) and was also individualized based on the preferred spontaneous motor tempo. Another aspect that may have played a role here is the duration of the trials, being one minute of finger-tapping to the auditory stimuli compared to previous experiments where trials lasted 33 seconds (Nozaradan et al., 2016). The longer duration of the current task might have allowed more time for performing the task and thus improving precision.

When comparing stimuli, higher synchronization precision was found for the metronome condition than the music condition in both groups. The higher precision to metronomes was previously reported in studies adopting other motor tasks such as walking in neurological patients and healthy controls (L. Moumdjian, Moens, Maes, Van Nieuwenhoven, et al., 2019). The extraction of temporal information from metronomes is easier given their isochronous and discrete structure, thus facilitating precision, compared to the more complex rhythmic structure in music, which can contain accents determining a metric structure and be more weakly periodic (Bouwer et al., 2018). Moreover, the prediction and forming of a temporal structure and thus, underlying mechanisms to do this, may differ. To elaborate, when entraining to the temporal structure of music, participants may be relying on beat-based expectations, which are dependent on beat interval duration, while when entraining to the metronomes, participants may rely on beat-based but also memory-based expectations(Bouwer et al., 2018). The latter implies learning the relationship between each beat and a particular temporal interval duration due to the isochronous temporal structure (Bouwer et al., 2020; Nobre & van Ede, 2018). The cerebellar group did not differ from the control group in terms of precision across stimuli, an observation also reflected in the deviation from the target inter-tap-intervals (Supplementary Figure 1). These results are in favor of the notion that the beat-based and memory-based expectations are subserved by shared mechanisms for temporal predictive processing (Rimmele, Morillon, Poeppel, & Arnal, 2018) and likely not limited to the cerebellum.

In the finger-tapping literature, the tendency of taps anticipating the beat is described by the negative mean asynchrony (Repp & Su, 2013). Previous evidence from cerebellar patients demonstrated larger asynchrony (i.e., synchronization accuracy) compared to healthy controls when synchronizing with pacing sequences, thus indicating a cerebellar involvement in the process of sensorimotor synchronization (Johnson, Belyk, Schwartze, Pinheiro, & Kotz, 2019; Kotz, Stockert, & Schwartze, 2014; Nozaradan et al., 2017; Schwartze et al., 2016). Here, both groups anticipated the beat as illustrated by negative mean asynchrony values. This was differentiated with a Group and Stimuli interaction. While both groups tapped with smaller asynchrony to music than to metronomes, the group interaction indicated that the patient group showed smaller asynchrony when tapping to music compared to controls tapping to metronomes. The behavioral response of the patient group in terms of median inter-tap-intervals also showed that patients tapped slower to music than metronomes, which can be mirrored in the results of the mean asynchrony (i.e., synchronization accuracy). While the slowing down of the tapping might have compromised accuracy, patient's might have used this as a compensation strategy for maintaining precision.

Although tapping to music resulted in smaller asynchronies, it has been argued that any positive asynchrony shorter than the shortest possible reaction time is still evidence of prediction, not directly to the beat proceeding the tap, but to the two beats proceeding the tap, thus a response to correct prediction errors as a result of sensory accumulation (Aschersleben, 2002; Repp & Su, 2013). Sensory accumulation as a strategy to correct errors can explain the patient group's lower accuracy when entrained to music compared to metronomes, either due to the beat-based expectation process of extracting temporal structures, or due to impaired motor coordination and fine control to correct the errors through the finger taps. Sensory accumulation can also explain the smaller mean asynchrony found for the more complex music stimuli across the slowest (-12%) and fastest tempi (4, 8 and 12%), as compared to all other tempi. At these tempi, the sensory accumulation load may have again impacted accuracy. The mean asynchrony was higher and similar at 0%, -4%, and 8% of the music tempi compared to all metronome tempi. This could be because temporal processing, sensorimotor integration, and error correction were not significantly challenged, as the tempi were close to the participants' internal timing and did not require excessive effort to entrain to.

To disentangle perceptual and sensorimotor neural components, we included in the experimental design a listening paradigm along with the finger-tapping. In these conditions, we recorded 64-channel EEG recordings to compute the stability index as an outcome measure quantifying the stability of the entrained neural components (Rosso et al., 2021). Based on the assessment of the explained variance of the extracted components, GED performed well on only 33% of the data collected during listening condition and 45% of the trials collected during the tapping conditions. The analysis conducted on the remaining valid data revealed no significant group, tempo, or stimulus effects in the listening conditions. The analysis conducted on the remaining valid data of the sensorimotor tapping conditions revealed a main effect of stimuli, indicating more stability of the neural entrained component for the music condition as compared to the metronome condition. However, results must be interpreted with caution, as behaviorally, we observed higher precision when tapping to the metronome condition than the music condition. Yet, the results of the stability index may be similar to previous studies which investigated the encoding of the beat frequency. These have also found that syncopated rhythms showed higher SS-EP amplitudes in an active listening task (Nozaradan et al., 2016). Thus, our results of stability index difference between stimuli may be a reflection of the neural activity related to dynamical attention required to track complex rhythms in the music conditions at beat frequencies.

The lack of significant EEG results may either be due to the presence of null results, or methodological limitations. The absence of group differences could be explained by the underlying timing mechanisms involved in beat-based timing. These mechanisms are primarily associated with the basal ganglia and SMA (Grahn, 2009; Grahn & Rowe, 2009), within the striato-thalamo-cortical network (Teki, Grube, & Griffiths, 2011) rather than the cerebellum(Grube, Cooper, Chinnery, & Griffiths, 2010). Whereas, duration and relative-beat based timing are associated with the olivocerebellar network (Teki et al., 2011). Thus, the lack of group differences observed in this study are consistent with the literature on beat-based timing mechanisms.

Methodologically, factors such as small sample size, multiple conditions and the short timeframe (1 minute) may not be optimal for the GED to extract oscillatory activity. This in turn, could have resulted in the loss of trials. We acknowledge that the method to compute the stability index was previously developed and validated with longer trial (7 minutes) (Rosso et al., 2021). Thus, future studies using the stability index should use longer trials while decreasing the number of conditions. Furthermore, a consideration for future research is the potential influence of lesion location on synchronization performance, which could not be assessed here as the sample was small and the lesion locations quite varied. Future studies with larger sample size and subgroups with defined lesion location would be warranted to investigate the effect of specific lesion sites on sensorimotor synchronization. Additionally, expanding the study design to include performance comparisons across both hands could further provide insight into how lateralized lesions impact sensorimotor synchronization.

These findings have clinical implications for rehabilitation strategies in cerebellar patients. The ability of patients to synchronize with auditory stimuli, despite reduced precision, suggest that incorporating such tasks could effectively target sensorimotor deficits in cerebellar ataxia (Bunn, Marsden, Voyce, Giunti, & Day, 2015; Panouilleres et al., 2018). Auditory-motor training paradigms can be gradually customized over time by adjusting stimulus tempo and rhythm complexity, making them well-suited for short or long-term personalized rehabilitation. This approach leverages training of the brain's capacity for error correction and prediction offering a promising avenue to train motor control and coordination in patients with cerebellar ataxia (Kakei et al., 2019; Manto et al., 2012; Mitoma, Manto, & Hampe, 2018; Shaikh, 2019).

5. Conclusion

The current findings show that although individuals with cerebellar ataxia show deficits in sensorimotor synchronization, they can successfully synchronize their finger taps with isochronous auditory metronomes at both faster and slower tempi, and to more complex musical rhythms. These results are supportive for the application of sensorimotor synchronization strategies in the context of rehabilitation in cerebellar clinical populations.

6. Acknowledgements

We thank Ivan Schepers (IPEM, UGent) for his technical support in the development of the tapping pad equipment, Nele Vanbilsen and Marie Poncelet's assistance and support with parts of data collection, and all study participants for their voluntary participation in the study.

7. CRediT statement

Lousin Moumdjian: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing – original draft, Writing – review & editing**. Peter Feys:** Conceptualization, Funding acquisition, resources, supervision, validation, writing – review & editing. **Bart Moens**: Methodology, Software, Validation, Writing – review & editing. **Mario Manto**: Data curation, Funding acquisition, Project administration, Validation, Writing – review & editing. **Pierre Cabaraux**: Data curation, Project administration, Writing – review & editing. **Bart Van Wijmeersch**: Data curation, Funding acquisition, Project administration, Validation, Writing – review & editing. **Sonja A. Kotz**: Conceptualization, Funding acquisition, Validation, Writing – review & editing. **Marc Leman**: Conceptualization, Funding acquisition, Resources, Supervision, Writing – review & editing. **Mattia Rosso**: Conceptualization, Data curation, Resources, Software, Validation, Writing – review & editing.

8. Data availability

All code used to process the data in this manuscript along with final dataset are available within the paper's supplementary materials.

9. Funding

Fonds Wetenschappelijk Onderzoek (FWO) project obtained by dr. Lousin Moumdjian, grant number 1295923N. Fonds Wetenschappelijk Onderzoek (FWO) project obtained by Prof. Peter Feys, grant number G082021N.

10. References

Aschersleben, G. (2002). Temporal control of movements in sensorimotor synchronization. *Brain Cogn, 48*(1), 66-79. doi:10.1006/brcg.2001.1304

Baliviera, E., Rosso, M., Moens, B., Poncelet, M., Manto, M., Cabaraux, P., Van Wijmeersch, B., Leman, M., Feys, P., Moumdjian, L. (under review). Spared behavioral yet distinct neural tracking of rhythmic auditory period & phase perturbations during finger-tapping in cerebellar ataxia

Berens, P. (2009). CircStat: A MATLAB Toolbox for Circular Statistics. *Journal of Statistical Software, 31*(10).

Boashash, B. (1992). Estimating and interpreting the instantaneous frequency of a signal. I. Fundamentals. *Proceedings of the IEEE, 80*(4), 520 - 538. doi:10.1109/5.135376

Bouwer, F. L., Burgoyne, J. A., Odijk, D., Honing, H., & Grahn, J. A. (2018). What makes a rhythm complex? The influence of musical training and accent type on beat perception. *PLoS One, 13*(1), e0190322. doi:10.1371/journal.pone.0190322

Bouwer, F. L., Honing, H., & Slagter, H. A. (2020). Beat-based and Memory-based Temporal Expectations in Rhythm: Similar Perceptual Effects, Different Underlying Mechanisms. *J Cogn Neurosci, 32*(7), 1221-1241. doi:10.1162/jocn_a_01529

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

Buhmann, J., Masson, J.-B., Cochen De Cock, V., Damm, L., Leman, M. . (2016). *Music selection: a user- and task specific protocol.* Paper presented at the Motor Behaviour and Emotion International Congress, Lille

Bunn, L. M., Marsden, J. F., Voyce, D. C., Giunti, P., & Day, B. L. (2015). Sensorimotor processing for balance in spinocerebellar ataxia type 6. *Mov Disord, 30*(9), 1259-1266. doi:10.1002/mds.26227

Cohen, M. X. (2014). Fluctuations in Oscillation Frequency Control Spike Timing and Coordinate Neural Networks. *Journal of Neuroscience, 34*(27), 8988-8998. doi:https://doi.org/10.1523/JNEUROSCI.0261-14.2014

Cohen, M. X. (2022). A tutorial on generalized eigendecomposition for denoising, contrast enhancement, and dimension reduction in multichannel electrophysiology. *Neuroimage, 247*, 118809. doi:10.1016/j.neuroimage.2021.118809

Dalla Bella, S. (2018). Music and movement: Towards a translational approach. *Neurophysiol Clin, 48*(6), 377-386. doi:10.1016/j.neucli.2018.10.067

Drewing, K., Aschersleben, G., Li, S.C. (2006). Sensorimotor synchronization across the life span. *International Journal of Behavioral Development, 30*(3). doi:10.1177/0165025406066764

Franz, E. A., Ivry, R. B., & Helmuth, L. L. (1996). Reduced Timing Variability in Patients with Unilateral Cerebellar Lesions during Bimanual Movements. *J Cogn Neurosci, 8*(2), 107-118. doi:10.1162/jocn.1996.8.2.107

Friston, K. (2018). Does predictive coding have a future? *Nat Neurosci, 21*(8), 1019-1021. doi:10.1038/s41593-018-0200-7

Friston, K., FitzGerald, T., Rigoli, F., Schwartenbeck, P., Pezzulo, G. . (2017). Active Inference: A process theory. *Neural Computation, 29*, 1-49.

Grahn, J. A. (2009). The role of the basal ganglia in beat perception: neuroimaging and neuropsychological investigations. *Ann N Y Acad Sci, 1169*, 35-45. doi:10.1111/j.1749-6632.2009.04553.x

Grahn, J. A. (2012). Neural mechanisms of rhythm perception: current findings and future perspectives. *Top Cogn Sci, 4*(4), 585-606. doi:10.1111/j.1756-8765.2012.01213.x

Grahn, J. A., & Rowe, J. B. (2009). Feeling the beat: premotor and striatal interactions in musicians and nonmusicians during beat perception. *J Neurosci, 29*(23), 7540-7548. doi:10.1523/JNEUROSCI.2018-08.2009

Grube, M., Cooper, F. E., Chinnery, P. F., & Griffiths, T. D. (2010). Dissociation of duration-based and beat-based auditory timing in cerebellar degeneration. *Proc Natl Acad Sci U S A, 107*(25), 11597-11601. doi:10.1073/pnas.0910473107

Johnson, J. F., Belyk, M., Schwartze, M., Pinheiro, A. P., & Kotz, S. A. (2019). The role of the cerebellum in adaptation: ALE meta-analyses on sensory feedback error. *Hum Brain Mapp, 40*(13), 3966-3981. doi:10.1002/hbm.24681

Jones, M. R., & Boltz, M. (1989). Dynamic attending and responses to time. *Psychol Rev, 96*(3), 459-491. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/2756068

Jones, M. R., Moynihan, H., MacKenzie, N., & Puente, J. (2002). Temporal aspects of stimulus-driven attending in dynamic arrays. *Psychol Sci, 13*(4), 313-319. doi:10.1111/1467-9280.00458

Kakei, S., Lee, J., Mitoma, H., Tanaka, H., Manto, M., & Hampe, C. S. (2019). Contribution of the Cerebellum to Predictive Motor Control and Its Evaluation in Ataxic Patients. *Front Hum Neurosci, 13*, 216. doi:10.3389/fnhum.2019.00216

Koelsch, S., Vuust, P., & Friston, K. (2019). Predictive Processes and the Peculiar Case of Music. *Trends Cogn Sci, 23*(1), 63-77. doi:10.1016/j.tics.2018.10.006

Kotz, S. A., Stockert, A., & Schwartze, M. (2014). Cerebellum, temporal predictability and the updating of a mental model. *Philos Trans R Soc Lond B Biol Sci, 369*(1658), 20130403. doi:10.1098/rstb.2013.0403

Large, E. W., Herrera, J. A., & Velasco, M. J. (2015). Neural Networks for Beat Perception in Musical Rhythm. *Front Syst Neurosci, 9*, 159. doi:10.3389/fnsys.2015.00159

Large, E. W., & Snyder, J. S. (2009). Pulse and meter as neural resonance. *Ann N Y Acad Sci, 1169*, 46-57. doi:10.1111/j.1749-6632.2009.04550.x

Leman, M. (2016). *The Expressive Moment: How Interaction (with Music) Shapes Human Empowerment*: MIT press.

Manto, M., Bower, J. M., Conforto, A. B., Delgado-Garcia, J. M., da Guarda, S. N., Gerwig, M., . . . Timmann, D. (2012). Consensus paper: roles of the cerebellum in motor control--the diversity of ideas on cerebellar involvement in movement. *Cerebellum, 11*(2), 457-487. doi:10.1007/s12311-011-0331-9

Merchant, H., Grahn, J., Trainor, L., Rohrmeier, M., & Fitch, W. T. (2015). Finding the beat: a neural perspective across humans and non-human primates. *Philos Trans R Soc Lond B Biol Sci, 370*(1664), 20140093. doi:10.1098/rstb.2014.0093

Mitoma, H., Manto, M., & Hampe, C. S. (2018). Time Is Cerebellum. *Cerebellum, 17*(4), 387-391. doi:10.1007/s12311-018-0925-6

Molinari, M., Leggio, M. G., & Thaut, M. H. (2007). The cerebellum and neural networks for rhythmic sensorimotor synchronization in the human brain. *Cerebellum, 6*(1), 18-23. doi:10.1080/14734220601142886

Morillon, B., & Baillet, S. (2017). Motor origin of temporal predictions in auditory attention. *Proc Natl Acad Sci U S A, 114*(42), E8913-E8921. doi:10.1073/pnas.1705373114
Moumdjian, L., Buhmann, J., Willems, I., Feys, P., & Leman, M. (2018). Entrainment and Synchronization to Auditory Stimuli During Walking in Healthy and Neurological Populations: A Methodological Systematic Review. *Front Hum Neurosci, 12*, 263. doi:10.3389/fnhum.2018.00263
Moumdjian, L., Moens, B., Maes, P. J., Van Geel, F., Ilsbroukx, S., Borgers, S., . . . Feys, P. (2019). Continuous 12 min walking to music, metronomes and in silence: Auditory-motor coupling and its effects on perceived fatigue, motivation and gait in persons with multiple sclerosis. *Mult Scler Relat Disord, 35*, 92-99. doi:10.1016/j.msard.2019.07.014
Moumdjian, L., Moens, B., Maes, P. J., Van Nieuwenhoven, J., Van Wijmeersch, B., Leman, M., & Feys, P. (2019). Walking to Music and Metronome at Various Tempi in Persons With Multiple Sclerosis: A Basis for Rehabilitation. *Neurorehabil Neural Repair, 33*(6), 464-475. doi:10.1177/1545968319847962
Moumdjian, L., Moens, B., Vanzeir, E., De Klerck, B., Feys, P., & Leman, M. (2019). A model of different cognitive processes during spontaneous and intentional coupling to music in multiple sclerosis. *Ann N Y Acad Sci, 1445*(1), 27-38. doi:10.1111/nyas.14023
Moumdjian, L., Rosso, M., Moens, B., De Weerdt, N., Leman, M., Feys, P. (2022). A case-study of a person with multiple sclerosis and cerebellar ataxia synchronizing finger-taps and foot-steps to music and metronomes. *Neuroimmunology Reports, 2*. doi:https://doi.org/10.1016/j.nerep.2022.100101
Nobre, A. C., & van Ede, F. (2018). Anticipated moments: temporal structure in attention. *Nat Rev Neurosci, 19*(1), 34-48. doi:10.1038/nrn.2017.141
Nozaradan, S., Peretz, I., & Keller, P. E. (2016). Individual Differences in Rhythmic Cortical Entrainment Correlate with Predictive Behavior in Sensorimotor Synchronization. *Sci Rep, 6*, 20612. doi:10.1038/srep20612
Nozaradan, S., Peretz, I., Missal, M., & Mouraux, A. (2011). Tagging the neuronal entrainment to beat and meter. *J Neurosci, 31*(28), 10234-10240. doi:10.1523/JNEUROSCI.0411-11.2011
Nozaradan, S., Schwartze, M., Obermeier, C., & Kotz, S. A. (2017). Specific contributions of basal ganglia and cerebellum to the neural tracking of rhythm. *Cortex, 95*, 156-168. doi:10.1016/j.cortex.2017.08.015
Nozaradan, S., Zerouali, Y., Peretz, I., & Mouraux, A. (2015). Capturing with EEG the neural entrainment and coupling underlying sensorimotor synchronization to the beat. *Cereb Cortex, 25*(3), 736-747. doi:10.1093/cercor/bht261
Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9*(1), 97-113. doi:10.1016/0028-3932(71)90067-4
Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput Intell Neurosci, 2011*, 156869. doi:10.1155/2011/156869
Oxford Grice, K., Vogel, K. A., Le, V., Mitchell, A., Muniz, S., & Vollmer, M. A. (2003). Adult norms for a commercially available Nine Hole Peg Test for finger dexterity. *Am J Occup Ther, 57*(5), 570-573. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/14527120
Panouilleres, M. T. N., Joundi, R. A., Benitez-Rivero, S., Cheeran, B., Butler, C. R., Nemeth, A. H., . . . Jenkinson, N. (2018). Author Correction: Sensorimotor adaptation as a behavioural biomarker of early spinocerebellar ataxia type 6. *Sci Rep, 8*(1), 7010. doi:10.1038/s41598-018-25324-9
Peretz, I., Champod, A. S., & Hyde, K. (2003). Varieties of musical disorders. The Montreal Battery of Evaluation of Amusia. *Ann N Y Acad Sci, 999*, 58-75. doi:10.1196/annals.1284.006
Provasi, J., Doyere, V., Zelanti, P. S., Kieffer, V., Perdry, H., El Massioui, N., . . . Droit-Volet, S. (2014). Disrupted sensorimotor synchronization, but intact rhythm discrimination, in children treated for a cerebellar medulloblastoma. *Res Dev Disabil, 35*(9), 2053-2068. doi:10.1016/j.ridd.2014.04.024

Rajendran, V. G., & Schnupp, J. W. H. (2019). Frequency tagging cannot measure neural tracking of beat or meter. *Proc Natl Acad Sci U S A, 116*(8), 2779-2780. doi:10.1073/pnas.1820020116

Reed, T. (2007). *Progressive Steps to Syncopation for the Modern Drummer*: Alfred Music.

Repp, B. H., & Keller, P. E. (2004). Adaptation to tempo changes in sensorimotor synchronization: effects of intention, attention, and awareness. *Q J Exp Psychol A, 57*(3), 499-521. doi:10.1080/02724980343000369

Repp, B. H., & Su, Y. H. (2013). Sensorimotor synchronization: a review of recent research (2006-2012). *Psychon Bull Rev, 20*(3), 403-452. doi:10.3758/s13423-012-0371-2

Rimmele, J. M., Morillon, B., Poeppel, D., & Arnal, L. H. (2018). Proactive Sensing of Periodic and Aperiodic Auditory Patterns. *Trends Cogn Sci, 22*(10), 870-882. doi:10.1016/j.tics.2018.08.003

Rosso, M., Leman, M., & Moumdjian, L. (2021). Neural Entrainment Meets Behavior: The Stability Index as a Neural Outcome Measure of Auditory-Motor Coupling. *Front Hum Neurosci, 15*, 668918. doi:10.3389/fnhum.2021.668918

Rosso, M., Moens, B., Leman, M., & Moumdjian, L. (2023). Neural entrainment underpins sensorimotor synchronization to dynamic rhythmic stimuli. *Neuroimage, 277*, 120226. doi:10.1016/j.neuroimage.2023.120226

Schmitz-Hubsch, T., du Montcel, S. T., Baliko, L., Berciano, J., Boesch, S., Depondt, C., . . . Fancellu, R. (2006). Scale for the assessment and rating of ataxia: development of a new clinical scale. *Neurology, 66*(11), 1717-1720. doi:10.1212/01.wnl.0000219042.60538.92

Schwartze, M., Keller, P. E., & Kotz, S. A. (2016). Spontaneous, synchronized, and corrective timing behavior in cerebellar lesion patients. *Behav Brain Res, 312*, 285-293. doi:10.1016/j.bbr.2016.06.040

Shaikh, A. G., Manto, M. (2019). Cerebellum: The Ultimate learning machine for flawless movements and master in machine learning to predict the future. *Frontiers in Cellular Neuroscience*. doi:doi: 10.3389/fncel.2019.00549

Teki, S., Grube, M., & Griffiths, T. D. (2011). A unified model of time perception accounts for duration-based and beat-based timing mechanisms. *Front Integr Neurosci, 5*, 90. doi:10.3389/fnint.2011.00090

von Schnehen, A., Hobeika, L., Huvent-Grelle, D., & Samson, S. (2022). Sensorimotor Synchronization in Healthy Aging and Neurocognitive Disorders. *Front Psychol, 13*, 838511. doi:10.3389/fpsyg.2022.838511

Vuust, P., Heggli, O. A., Friston, K. J., & Kringelbach, M. L. (2022). Music in the brain. *Nat Rev Neurosci, 23*(5), 287-305. doi:10.1038/s41583-022-00578-5

Zalta, A., Petkoski, S., & Morillon, B. (2020). Natural rhythms of periodic temporal attention. *Nat Commun, 11*(1), 1051. doi:10.1038/s41467-020-14888-8

Table 1 A. Diagnosis and clinical information of study participants.

Diagnosis	Year of diagnosis	MRI finding
Unknown etiology, suspicion of ischemic, inflammatory or neuropathic cause	2020	Left middle cerebellar peduncle lesion
Cerebellar stroke	2018	Left posterior cerebellar stroke (superior cerebellar artery)
Spinocerebellar ataxia type 6	2017	Global cerebellar atrophy predominantly cerebellar vermis
Cerebellar stroke	2019	Right posterior paravermis stroke (posterior inferior cerebellar artery)
Cerebellar stroke	2021	Right posterior paravermis stroke (posterior inferior cerebellar artery)
Cerebellar stroke	2021	Multiple lesions of bilateral cerebellar hemispheres
Anterior-venous stenosis malformation	2009	Bilateral posterior cerebellar hemispheric lesions and mild cerebellar atrophy
Cerebellar stroke	2019	Left hemispheric cerebellar stroke
Cerebellar stroke	2019	Bilateral posterior inferior cerebellar artery stroke
Cerebellar stroke	2019	Ischemia in left posterior cerebellar hemisphere (anterior superior cerebellar artery)
Relapsing Remitting multiple sclerosis	2022	Lesion at the left cerebellar peduncle and in the right cerebellar hemisphere body
Relapsing Remitting multiple sclerosis	2015	Lesion at the left border of 4th ventricle and cerebellar peduncle
Multiple Sclerosis	2004	No lesions or atrophy observed on imaging
Spinocerebellar ataxia type 6	2019	Global cerebellar atrophy
Cerebellar stroke	2023	Right hemisphere middle and anterior vermis stroke (Right antero-superior cerebellar artery)
Cerebellar stroke	2018	Left posterior parasagittal hemisphere stroke (Left posterior inferior cerebellar artery)

Table 1 B. Descriptive and clinical characteristics of study participants.

		Persons with Cerebellar Ataxia (n=16)	Healthy controls (n=14)	Statistical group difference (p-value)
Age (years)		59 ± 13.51	58 ± 12.72	Non-significant
Sex (Female : Male)		8:8	9:5	Non-significant
Montreal test Battery of Evaluation of Amusia; Rhythm subscale		12.73 ± 1.83	12 ± 2.49	Non-significant
Nine Hole Peg Test (average of two trials)	Right upper extremity (seconds)	26.48 ± 7.42	20.98: ± 2.44	p=0.01
	Left upper extremity (seconds)	30.75 ± 14.29	23.15: ± 2.54	Non-significant
Scale for Assessment and Rating of Ataxia (Total Score)	Gait	1.67 ±1.80	0	p<0.0001
	Stance	1.13 ± 1.55	0	p=0.0008
	Left Finger chase	0.53 ± 0.64	0	p=0.005
	Right Finger chase	0.33 ± 0.62	0	p=0.05
	Left Nose-finger test	0.60 ± 0.63	0	p=0.002
	Right Nose-finger test	0.40 ± 0.63	0	p=0.02
	Left Fast-alternating movements	0.36 ± 0.50	0	p=0.02
	Right Fast-alternating movements	0.21 ± 0.43	0	Non-significant
	Left Heel-shin slide	0.50 ± 1.09	0	p=0.04
	Right Heel-shin slide	0.50 ± 1.16	0	Non-significant
	Total score	4.63 ± 6.11	0	p<0.0001

Table 2. Mean and standard deviation of the beats per minute used across tempi for both groups.

Tempo	**Persons with Cerebellar Ataxia**		**Healthy controls**	
	Mean	Standard deviation	Mean	Standard deviation
-12%	85.5	16.4	73.4	11.6
-8%	89.6	17.2	76.8	12.1
-4%	93.3	18.0	79.6	13.1
0%	97.2	19.1	82.3	13.3
4%	101.2	19.5	85.9	14.7
8%	105.1	20.2	90.3	14.0
12%	109.0	21.1	93.6	14.6