Aging effects on neural processing of rhythm and meter

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15 **Abstract**

16 When listening to musical rhythm, humans can perceive and move to beat-like metrical pulses.
17 Recently, it has been hypothesized that meter perception is related to brain activity responding to the
18 acoustic fluctuation of the rhythmic input, with selective enhancement of the brain response elicited
19 at meter-related frequencies. In the current study, the electroencephalography (EEG) was recorded
20 while younger (<35) and older (>60) adults listened to rhythmic patterns presented at two different
21 tempi while intermittently performing a tapping task. Despite significant hearing loss compared to
22 younger adults, older adults showed preserved brain activity to the rhythms. However, age effects
23 were observed in the distribution of amplitude across frequencies. Specifically, in contrast with
24 younger adults, older adults showed relatively larger amplitude at the frequency corresponding to the
25 rate of individual events making up the rhythms as compared to lower meter-related frequencies. This
26 difference is compatible with larger N1-P2 potentials as generally observed in older adults in
27 response to acoustic onsets, irrespective of meter perception. These larger low-level responses to
28 sounds have been linked to processes by which age-related hearing loss would be compensated by
29 cortical sensory mechanisms. Importantly, this low-level effect would be associated here with
30 relatively reduced neural activity at lower frequencies corresponding to higher-level metrical
31 grouping of the acoustic events, as compared to younger adults.

32 **1 Introduction**

33 When listening to music, listeners entrain to regularities that are perceived as a musical beat, an
34 integral part of music perception (Huron, 2006). These regularities are usually organized into a meter.
35 A metrical structure consists of a pattern of nested pulse-like beats, which can be, but are not

necessarily, prominent in the acoustic signal itself (Large, 2008). Increasing evidence suggests that meter perception may be related to selective enhancement of neural activity at the meter periodicities and their harmonics. This selective enhancement can be observed in the EEG signal recorded while listeners are presented with a rhythmic pattern inducing perception of a metrical structure (Lenc et al., 2018, 2020, 2021; Nozaradan et al., 2011, 2012, 2016). This selective enhancement has been observed not only in response to regular rhythms with high acoustic energy at the meter frequencies but also in syncopated rhythms, with no prominent acoustic cues to the meter frequencies. These observations suggest that this enhanced neural activity at the meter-related frequencies is not simply stimulus-driven or driven by low-level subcortical processes of the auditory system (Nozaradan, Keller, Rossion & Mouraux, 2018; see also Lenc et al., 2018, 2020, 2021; Nozaradan et al., 2016).

Little is known about the neural processing of rhythmic inputs in older adults. What is known is focused on speech perception, where overall, the literature suggests that older adults respond more strongly but less precisely to temporally regular stimulation at low (speech-paced) frequencies, approximately 3-4 Hz (Anderson et al., 2012; Bidelman et al., 2014; Goossens et al., 2016; Henry et al., 2017; Herrmann et al., 2016; Presacco et al., 2016), a pattern ascribed to the inhibition theory of aging (Casparly et al., 2008; Salthouse & Mein, 1995). This theory ascribes an increase in overall brain activity to a decrease in GABA, an inhibitory neurotransmitter, in the aging brain (Casparly et al., 2008). This decrease in inhibitory activity can also explain the decrease in temporal encoding precision often observed in older compared to younger adults (Anderson et al., 2012; Presacco et al., 2016).

On the other hand, the few pieces of evidence about music perception in older adults suggests that it is generally preserved (Halpern et al., 1995, 1996, 1998, 2017). In some cases the performance of a musical task is preserved, but the underlying brain activity changes, suggesting that older adults may automatically compensate for declining cognitive or perceptual abilities in the musical domain (Halpern et al., 2017; Lagrois et al., 2018). This may be due to the development of compensatory mechanisms similar to those found for speech in noise perception, where older adults use contextual information to help overcome age-related changes in hearing and cognitive abilities (Birren & Fisher, 1995; Horn, 1982; Horn & Cattell, 1967; Madden, 1992; Pichora-Fuller et al., 1995). When rating the fit of a note in a melody, older adults rely more heavily on scale degree information, derived from knowledge of the tonal hierarchy, whereas younger adults rely more heavily on note-to-note information (Bharucha & Krumhansl, 1983; Halpern et al., 2017). In addition to increased use of contextual and crystallized knowledge, the neural compensation theory of aging stems from the observation of patterns of over- and under-activation, reduced asymmetry and reduced connectivity of brain activity in the brains of older adults as compared to younger adults when performing a similar task at a similar level (Cabeza, 2002; Cabeza et al., 2004; Davis et al., 2011; Grady et al., 2003; Reuter-Lorenz, 2002; Reuter-Lorenz et al., 2000; Reuter-Lorenz & Cappell, 2008). For example, a frontal shift in activity has been observed in older adults associated with compensation for declining perceptual abilities (Park & Reuter-Lorenz, 2009).

In terms of rhythm perception, Sauv et al. (2019) used frequency tagging to compare neural activity in older and younger adults while passively listening to a metronome. This study found that older adults, compared to younger adults, had reduced amplitude of neural activity at the frequency of the metronome and to a lesser extent also at the first three harmonics of the metronome frequency (Sauv et al., 2019), which could not be fully accounted for by age-related changes in hearing as measured by pure-tone thresholds. In other words, older adults demonstrated a reduced response to the metronome frequency compared to younger adults, a pattern in line with literature suggesting that temporal precision degrades in the aging brain (Anderson et al., 2012; Herrmann et al., 2019).

The goal of the current study was to explore differences in neural processing of rhythm between older adults and younger adults actively listening to two rhythms. One rhythm contained prominent acoustic energy at the meter-related frequencies compared to meter-unrelated frequencies (i.e. non-syncopated rhythm). In contrast, the second rhythm was characterized by a lack of prominent acoustic energy at meter-related frequencies compared to meter-unrelated frequencies (i.e., syncopated rhythm; see Lenc et al. 2018, 2020). In the syncopated rhythm, perception of the meter thus likely relies on endogenous processes, and selective enhancement of the neural activity at meter-related frequencies cannot be explained by acoustic confound or subcortical processing enhancing prominent acoustic features of the input (Lenc et al. 2020). To the best of our knowledge, the current study is thus the first to explore the impact of aging on neural processing of rhythm, especially when the meter is inferred but not conveyed by a strictly (i.e. metronomic) or strongly periodic (i.e. non-syncopated) stimulus.

Based on our previous findings (Sauvé et al., 2019), together with the fact that older adults have increased exposure to musical patterns due to their age, and that older adults rely on internalized musical structure as a way to compensate for an age-related hearing impairment as compared to younger adults (Halpern et al., 2017), it is expected that older adults will show similar neural activity to younger adults in response to both rhythms despite age-related hearing loss, thus with preserved selective enhancement at the meter-related frequencies irrespective of rhythm complexity. Moreover, given known topographic neural shifts associated with aging (e.g. Park & Reuter-Lorenz, 2009), we also examined possible differences in topographic maps between older and younger adults.

2 Materials and Methods

2.1 Participants

Twenty-nine participants (the same as in Sauvé et al., 2019) took part in this study and provided written informed consent in accordance with the Interdisciplinary Committee on Ethics in Human Research at Memorial University of Newfoundland. Participants were divided into two *age groups*: 15 older adults (>60 yrs; 10 female) and 14 younger adults (<25 yrs; 7 female). All participants self-reported being healthy, right-handed and free of any cognitive deficit. All participants were non-musicians although some had music training in childhood. Hearing abilities were assessed using standard clinical pure-tone (PT) audiometry, which revealed significant differences between the two age groups as detailed in Table 1. All participants received a small cash honorarium for their participation. Table 1 summarizes participant demographics.

Table 1. Participant Demographics

	Age	Formal Education (Years)*	Pure-tone Average (dB HL)**
Younger Adults	20.3 (1.84)	14.6 (2.23)	6.2 (5.07)
Older Adults	63.4 (3.68)	12.87 (3.46)	13.28 (9.03)

* $t(28) = 1.6$, $p = .12$; standard deviation in brackets

** Binaural average of pure-tone threshold at 500, 1000 & 2000; $t(28) = 40.55$, $p < .001$; standard deviation in brackets

2.2 Stimuli

The selected rhythmic patterns were similar to those of previous studies (Nozaradan et al., 2016, 2017; Nozaradan, Schönwiesner, et al., 2018; see also Lenc et al., 2018) and presented into four conditions: two rhythms (*non-syncopated* and *syncopated*) at two tempi (*slow*: 0.416 Hz cycle rate, i.e. rhythmic pattern of 2400 ms duration; and *fast*: 0.833 Hz cycle rate, i.e. 1200 ms pattern duration). One of the hallmarks of aging is that older adults tend to have more difficulty processing stimuli presented at a faster rate (Salthouse & Mein, 1995). It is therefore possible that differences between older and younger adults are more pronounced at a higher tempo. The structure of the rhythms was based on the alternation of 12 events, consisting of sounds and silent intervals. The individual sounds consisted of 1000Hz pure tones, presented at ~75 dB SPL, with 10ms rise and fall times, and were either 100 ms or 200 ms long for the fast or slow tempo, respectively. All stimuli were presented via insert earphones (Etymotic E3A). As described in Nozaradan et al. (2016) and Lenc et al. (2018), rhythms were designed to induce the perception of a meter based on a preference for grouping by 2 and 4 events per cycle (grouping by 4 events corresponding to the periodicity mostly tapped by participants when asked to tap on the rhythm; see Lenc et al., 2018). The first rhythm was non-syncopated, with regular structure congruent with the periodicities perceived as the meter, while the second rhythm was syncopated, with no prominent acoustic structure matching the perceived meter periodicities. Stimuli were generated in Reaper (V 5.16), and presented to participants using Eprime (V 3.0).

Figure 1. Audio signal representation of the non-syncopated and syncopated rhythms at slow tempo (with 200 ms individual sounds).

2.3 Procedure

After providing written informed consent, participants completed a short demographics questionnaire, and were given the possibility to practice tapping to the 4 rhythms that would be

presented during the study. Each participant was prepared for EEG recording and was seated in a double-walled, electrically shielded sound-attenuating booth (Eckel). Participants were given a response box (Chronos, EPrime), and could see a computer monitor. They were further instructed to tap their finger in time with the perceived beat on one of the response buttons whenever the green light came up on the response box, and the computer monitor said, “Tap”. When the response box buttons became red, and the computer monitor said “Stop Tapping”, participants were instructed to stop tapping, but to maintain the beat mentally. Each participant was told that they would be expected to start tapping as soon as the green light came back on. Alternating between a Tapping Phase and a Listening Phase was done to ensure that participants actively maintained the meter throughout the task. To avoid eye movement, participants were told to either fixate on the monitor or response box during the task, and to minimize switching between the two.

The two rhythms (non-syncopated, syncopated) were presented at the two tempi (slow, fast) in four separate blocks. The order of the blocks was identical for each participant (non-syncopated rhythm, slow and fast, and then syncopated rhythm, slow and fast). This fixed order was used to ensure that participants could easily tap the perceived meter during the tapping phase, and were thus likely to perceive the meter also when listening without tapping. Indeed, pilot testing suggested that participants had increased difficulty tapping to the fast vs. slow stimuli, and to the syncopated vs. the non-syncopated rhythm, even after a short practice session. In contrast, the participants seemed overall more comfortable tapping when they were first presented with the non-syncopated rhythms and the slow tempi. Each block started with a Tapping Phase that lasted 48 s. After this Tapping Phase, there were 10 repetitions of a 48 s Listening Phase and a 12 s Tapping Phase.

2.4 EEG data processing

Neuroelectric brain activity was digitized at a sampling rate of 1024 Hz from 134 electrodes using the radial layout system, with a highpass filter set at 0.1 Hz using a Biosemi ActiveTwo system (Biosemi Inc., Amsterdam, Netherlands). Six electrodes were placed bilaterally at mastoid, inferior ocular and lateral ocular sites.

Data was analysed using the Letswave 6¹ (Mouraux & Iannetti, 2008) signal processing toolbox for Matlab. Eye blinks and eye movements were identified for each participant using an independent component analysis (ICA). Components related to eye movements were removed from the EEG signal. Next the EEG data were referenced to the average of all scalp electrodes. Each condition was divided into ten 48 s epochs corresponding to the Listening Phases, and then averaged into a single 48 second epoch, yielding 4 epochs (*non-syncopated slow*, *syncopated slow*, *non-syncopated fast*, *syncopated fast*) per channel and participant. EEG data recording during the tapping phase was not used for further analysis, as the purpose of the current study was not to focus on the neural activity related to overt rhythmic movement production. However, this limited tapping data can provide a behavioral index about the perceived meter using inter-tap interval (ITI) information (see SI).

To measure the amplitude at the meter-related and meter-unrelated frequencies elicited in response to the rhythms, a fast Fourier transform (FFT) was applied to the four EEG epochs for each EEG channel and participant, with a resulting spectral resolution of approximately 0.02 Hz (i.e. 1/48 s). These spectra were then corrected using a noise subtraction with bin range (+/-) 3-13. This function, which subtracts from the amplitude at each frequency bin the amplitude averaged across the neighboring frequency bins from the 3rd to the 13th bin on each side (Mouraux et al., 2011;

¹ <https://www.letswave.org/>

Nozaradan et al., 2013; 2015), thus centers the amplitude spectrum around zero. Therefore, the amplitude measured at the target frequencies should tend toward zero if no significant neural activity is elicited at those specific frequencies. The amplitude of neural activity obtained from this analysis will be referred to as simply *amplitude* throughout this paper.

For each *condition* the amplitudes at targeted frequency bins were extracted from a montage of frontocentral electrodes in increasingly large concentric circles (see Figure 2). The *core circle montage* was selected based on signal distribution and consistent with previous work (Lenc et al., 2018; Nozaradan et al., 2012, 2016), while each subsequent *outer circle* includes one electrode in each direction from the core. This analysis was done to investigate any potential topographical differences between age groups. Previous work has suggested a compensation theory of aging (Reuter-Lorenz & Cappell, 2008), which predicts larger responses or more widespread activation in older adults. Given that the magnitude of the response and the extent of the spatial distribution are difficult to separate, it is important to test both possible effects by comparing both the magnitude of the responses, and their spatial spread. By testing topographic patterns as a function of age, the possibility of age-related differences during meter perception tasks can be explored.

Figure 2. 128+2 radial electrode layout illustrating core and outer circle electrode montages.

As in Lenc et al. (2018), the amplitude at 12 target frequencies was extracted, corresponding to the duration of the whole pattern/cycle rate (0.416 Hz or 0.833 Hz for the two different tempi, respectively) and its harmonics up to the period of single acoustic events (5 Hz; 10 Hz). These 12 frequencies were then tagged as meter-related frequencies and meter-unrelated frequencies (Lenc et al., 2018). The meter-related frequencies were based on the periodicities of the meter assumed to be perceived for these rhythms and their harmonics, as informed by behavioral data collected in a large number of participants in previous studies and corroborated by the tapping data collected during the Tapping Phases. These meter periodicities consisted in the smallest inter-sound intervals, and grouping of these intervals by two, four, and twelve intervals (see Lenc et al., 2018 for example), thus yielding five meter-related frequencies (i.e. the first, third, sixth, ninth and twelfth frequencies

from the 12 target frequencies, further labeled F1, F3, F6, F9 and F12). The remaining frequencies were considered meter-unrelated. Amplitudes were obtained for each frequency of interest from the closest spectral bin from each frequency.

2.5 Statistical analysis

Statistical analyses were conducted using mixed effects multiple linear regression modelling implemented in the R (3.3.2) *lme4* (Bates, Mächler, Bolker, & Walker, 2015) package. All analysis models were maximally fitted to reflect the experimental design, as per Barr et al. (2013), where models included random intercepts on participants and random slopes on participants by stimulus condition. All categorical variables were factors, where each level was compared to a base level. These base levels are *slow* for *tempo*, *non-syncopated* for *rhythm*, *younger* for *age group*, *meter-related* for *frequency type*, *F1* for *frequency* and *core* for *electrode montage*. Models were evaluated using Pearson's correlation between the model's predictions and the data along with the correlation's 95% CIs. Statistical significance of each individual factor level for a given predictor was evaluated using 95% CIs, where an interval not including zero indicates a significant predictor. In each analysis, follow-up independent sample two-tailed t-tests with Bonferroni correction were conducted to investigate simple effects of age.

2.5.1 Frequency analysis

For each participant and condition, we first averaged the amplitudes for meter-related frequencies and meter-unrelated frequencies, separately. Then, we compared the amplitude of the response at meter-related and meter-unrelated frequencies to measure selective enhancement of brain activity at meter-related frequencies across stimuli, regardless of the physical structure of the stimulus, which in the case of the syncopated rhythm, does not include prominent meter-related frequencies. To do so, a model predicting spectral amplitude of neural activity included *frequency type* (*meter-related*, *meter-unrelated*), *tempo* (*slow*, *fast*), *rhythm* (*non-syncopated*, *syncopated*) and *age group* (*younger*, *older*) as fixed effects including interactions and *PTAv* (pure tone threshold average) score as a fixed main effect. *PTAv* was calculated by taking the binaural average of pure-tone threshold at 500, 1000 and 2000 Hz and was used to check for low-level effects of poorer hearing in older adults while channel accounts for variance between electrodes. As expected, the *PTAv* was larger in older adults compared to younger adults, demonstrating normative age-related changes in hearing thresholds (see Table 1).

Next, to investigate age effects on meter-related entrainment, a model predicting spectral amplitude of neural activity in response to meter-related frequencies included *tempo* (*slow*, *fast*), *rhythm* (*non-syncopated*, *syncopated*), *frequencies* (*F1*, *F3*, *F6*, *F9*, *F12*), *age group* (*younger*, *older*), and *PTAv* score as fixed effects. In all models, interactions with *PTAv* were not modelled. Finally, the neural compensation hypothesis predicts more widespread activation in older adults than in younger adults (Reuter-Lorenz & Cappell, 2008). To test this, *montage* (*core*, *outer 1*, *outer 2*, *outer 3*) was added to the meter-related entrainment model as a fixed effect, including interactions (except with *PTAv*).

2.5.2 Tapping analysis

The tapping task was included to ensure the participant was focusing on the metrical structure while further listening without moving. The tapping data were also used as a behavioral index confirming the assumed perceived metrical structure. As expected, participants were mostly tapping at intervals aligning with grouping by two, four or eight intervals. Because only a small number of taps were recorded between each rest period and because a proper analysis of the precision of tapping for example requires significantly higher number of taps (i.e. >100 in Zendel, Ross & Fujioka, 2011), the

tapping data were not used for further exploration of the tapping performance, and are thus presented as supplementary materials (see Supplementary Materials 2).

3 Results

3.1 Meter-related vs. Meter-unrelated frequencies

First, we tested for selective enhancement of brain activity elicited at frequencies corresponding to the meter by comparing amplitudes at meter-related frequencies vs. meter-unrelated frequencies using a linear mixed effects model. Figures 3 and 4 present the brain responses along with topographic maps for each meter-related frequency for the *slow* and *fast* tempi respectively. For brevity, only significant predictors with R^2 above .01 are included in Table 2; full tables can be found in Supplementary Materials 1. Main effects of *tempo* (*slow* > *fast*), *rhythm* (*non-syncopated* > *syncopated*) and *frequency type* (*meter-related* > *meter-unrelated*) were significant while *age group* and *PTAv* were not. Significant interactions include two-way interactions between *rhythm* and *frequency type*, *tempo* and *rhythm*, *age* and *rhythm* and *age* and *tempo*, three-way interactions between *age*, *rhythm* and *frequency type* and *age*, *tempo*, and *rhythm* and a four-way interaction between all variables. These interactions were driven by the size of the effect of frequency type and age. In the case of frequency type, the effect was smallest in the *fast syncopated* condition ($d = 0.39$), moderate for the *slow non-syncopated* and *slow syncopated* conditions ($d = 0.52$ and $d = 0.43$ respectively), and largest for the *fast non-syncopated* condition ($d = 0.86$). In the case of age, Figure 5 illustrates the size of the effects. There was no main effect of age, but there were some interactions involving age, showing that selective enhancement of meter frequencies was larger in younger adults in some conditions but not all. Figure 5 illustrates the mean amplitude of neural activity for all meter-related and meter-unrelated frequencies and all four conditions for older and younger participants.

Figure 3. EEG spectra, slow tempo. Amplitude of neural activity at electrode Cz ranging from 0.5Hz to 6Hz for *younger adults* (A, C) and *older adults* (B, D) adults for *non-syncopated* (A, B) and *syncopated* (C, D) rhythms for *slow tempo*, along with topographic maps corresponding to each meter-related frequency. Frequency and amplitude scales are identical across conditions and groups to allow direct comparison across spectra. The scales of the topographical maps are adjusted for each condition, group and frequency for optimal visualization of topographical distribution across the EEG channels.

Figure 4. EEG spectra, fast tempo. Amplitude of neural activity at electrode Cz ranging from 0.9Hz to 12Hz for *younger adults* (A, C) and *older adults* (B, D) for *non-syncopated* (A, B) and *syncopated* (C, D) rhythms for *fast tempo*, along with topographic maps corresponding to each meter frequency.

Table 2. Summary of significant predictors with $R^2 > .01$ from the maximally fitted multiple linear regression model predicting amplitude at meter-related vs. meter-unrelated frequencies including coefficient, Wald 95% confidence intervals and R^2 for each predictor (where there are multiple levels, R^2 is given for the predictor as a whole). Random effects account for < 0.00 variance and are therefore not reported.

Predictor	Coefficient	2.5%	98.5%	R^2
Intercept	0.07	0.06	0.08	.07
Frequency Type	-0.04	-0.05	-0.04	.07

Note: $r = .39$, 95% CIs [.38, .40], $p < .01$

Figure 5. Amplitude of neural activity at meter-related and meter-unrelated frequencies across the four conditions and groups. Boxes represent the first quartile, median and third quartile of data, with points representing outliers; data represents amplitude values for each peak, channel and participant. ** $p < .006$ for age group comparisons.

3.2 Amplitude across meter-related frequencies

Next, we analyzed the amplitudes across the meter-related frequencies to determine whether the pattern of distribution of the amplitudes was affected by age (Sauvé et al., 2019). Table 3 presents the linear mixed effects model for the amplitude of neural activity elicited at meter-related frequencies for all participants across conditions. For brevity, only significant predictors with R^2 above .01 were included in Table 3; full tables can be found in Supplementary Materials 1 along with corresponding summary statistics. Significant predictors included main effects of *rhythm* (*nonsyncopated* > *syncopated*), *age group* (*younger* > *older*), *tempo* (*fast* > *slow*) and *frequency* ($F1 < F3 > F6 = F9 < F12$) as well as multiple two-, three- and four-way interactions. To further understand the interactions of *age group* with *tempo*, *rhythm* and *frequency*, follow-up t-tests were conducted (see Supplementary Materials 1). Age effects were observed at F3 in all but one tempo and rhythm condition (fast non-syncopated), where younger adults had larger amplitudes than older adults (Figure 6). Younger adults also had significantly larger amplitudes than older adults at F6 and at F1 in all but one condition (slow syncopated), where for F6 neural activity amplitudes for both age groups are similar and for F1 older adults had larger amplitudes than younger adults. This opposite age effect, where older adults had larger amplitudes than younger adults, was observed at F12 in all conditions. In summary, younger adults had larger amplitudes than older adults at the F1, F3 and F6

while older adults had larger amplitudes than younger adults at F12. Figure 6 presents the mean amplitude for *younger* and *older* adults as a function of *rhythm*, *tempo* and *frequency*, where significant age effects are annotated with asterisks.

Finally, in order to further characterize the amplitude profiles, t-tests with Bonferroni correction were conducted between F3 and F1 and F3 and F12 amplitudes for each age group and condition (see Figure 5 and Supplementary Materials 1 for details). F3 had larger neural amplitude than F1 for both age groups in all conditions except for older adults in the *slow syncopated* condition, where amplitude at F1 was larger than at F3. The F3 was larger than the F12 in younger adults, while this difference was not significant in older adults, except during the *fast non-syncopated* condition.

Table 3. Summary of significant predictors with $R^2 > .01$ from the maximally fitted multiple linear regression model predicting neural activity amplitude at meter-related frequencies, including coefficient, Wald 95% confidence intervals and R^2 for each predictor (where there are multiple levels, R^2 is given for the predictor as a whole). Random effects account for < 0.00 variance and are therefore not reported.

Predictor	Coefficient	2.5%	98.5%	R ²
Intercept	0.21	0.19	0.23	.10
F1	-0.22	-0.23	-0.20	
F6	-0.15	-0.16	-0.13	
F9	-0.18	-0.19	-0.16	.22
F12	-0.13	-0.14	-0.11	
Age:F1	0.05	0.03	0.07	
Age:F6	0.05	0.03	0.08	
Age:F9	0.09	0.07	0.11	.01
Age:F12	0.12	0.10	0.14	
Rhythm:F1	0.16	0.14	0.19	
Rhythm:F6	0.06	0.04	0.08	
Rhythm:F9	0.09	0.07	0.12	.03
Rhythm:F12	0.09	0.07	0.12	

Note: $r = .64$, 95% CIs [.63, .66], $p < .01$

Figure 6. Amplitude of neural activity at the different meter-related frequencies across the four conditions. Boxes represent the first quartile, median and third quartile of data, with points representing outliers; data represents amplitude values for each peak, channel and participant. ** = $p < .003$, lines under the bars represent significant F1-F3 and F3-F12 frequency comparisons for each age group, $p < .006$.

317

318 3.3 Neural compensation

319 Finally, we investigated the distribution of the signal at meter-related frequencies to test the
 320 hypothesis that older adults demonstrated more widespread neural activation than younger adults.
 321 First, the main effect of *montage* was significant, where overall mean amplitude decreased with
 322 increasing distance from the *core montage*. This main effect was qualified by two-way interactions
 323 with *rhythm* and *frequency*, and three-way interactions with *age* and *frequency*, and *tempo* and
 324 *frequency*. The three-way interaction involving age is driven by the difference between F3 and F12,
 325 where younger adults have larger amplitudes than older adults at F3 and vice versa for F12. In the
 326 case of *rhythm*, mean amplitude was always higher for non-syncopated than for syncopated rhythms
 327 but the differentiation between the two decreased as distance from the core increased ($t(6393) =$
 328 $7.28, p < .01$, $t(6020) = 5.11, p < .01$, $t(4589) = 0.46, p = .063$ and $t(5925) = 0.32, p = .74$ for core
 329 montage to outer montage 3 respectively). Finally, in the case of frequency, the overall pattern was
 330 similar across electrode montages except for F1 where the amplitude of F1 diminished faster than the
 331 other target frequencies as distance from the core increased.

332 4 Discussion

In this study we examined differences between older and younger adults in neural activity to a syncopated and a non-syncopated rhythm presented at two different tempi. Overall, the amplitude of neural activity elicited at meter-related frequencies was larger compared to the activity elicited at frequencies unrelated to meter periodicities, even in the syncopated rhythm where the meter-related frequencies are not prominent acoustic features of the input. This finding is consistent with previous work (Lenc et al., 2018; 2020; Nozaradan et al., 2016, 2018). Most importantly for our experiment, this effect was similar across older and younger adults, thus suggesting that the processes by which the meter-related frequencies are selectively enhanced is preserved in aging, despite hearing loss. Moreover, the difference in pure tone audiometric thresholds between age groups did not have a significant impact on the amplitudes of neural activity. Therefore, differences in neural activity observed here between age groups are unlikely to be fully attributable to low-level hearing abilities.

Though both age groups show selective enhancement at the meter periodicities, the distribution of amplitudes across the different meter-related frequencies differs between age groups. In older adults we observe lower amplitude at F3 across stimulus conditions compared to younger adults, consistent with an overall decline in delta band frequency activity in normal aging (Polich, 1997). This age effect is in line with the findings of Sauvé et al. (2019), where the same participants were listening to an isochronous rhythm at 1.25 and 2.5 Hz, but do not directly fit with the speech neural entrainment literature which shows increased amplitude of neural activity at low (syllable-paced) frequencies of 3-4 Hz in older adults (Goossens et al., 2016; Herrmann et al., 2016, 2019). One case where younger adults showed higher neural amplitude in response to a 2.8Hz frequency-modulated stimulus than older adults involved attentional control: younger adults demonstrated more activity at 2.8Hz in an active task when compared to as passive task, where older adults had no difference and had activity similar to younger adults during the passive task (Henry et al., 2017). However, in Sauvé et al (2019), the task was passive so attentional control cannot explain younger adults' larger amplitudes as compared to younger adults. Furthermore, these studies only investigated neural responses at the fundamental frequency corresponding to the periodicity of the isochronous sequence, while Sauvé et al. (2019) also included harmonics of that frequency, observing a different pattern of distribution of amplitude across the fundamental frequency of stimulation and its harmonics in older adults compared to younger adults.

In the current study, younger adults demonstrate larger amplitude at F3 compared to F12 in the two rhythms and tempi, in contrast with older adults who do not show such distribution across meter-related frequencies. Sauvé et al. (2019) also observed an overall more equally distributed amplitude across the fundamental frequency and harmonics in older vs. younger adults in the EEG response to an isochronous sound at 1.25 and 2.5 Hz. Since the difference is not modulated by rhythmic complexity, it could be explained by an aspecific change in low-level response to auditory rhythmic inputs, irrespective of meter processing. This is compatible with previous observation of larger N1-P2 evoked potentials elicited in response to auditory stimuli in older adults than younger adults (Alain & Woods, 1999; Anderer et al., 1996; Ross et al., 2009; Zendel & Alain, 2014). This low-level sensory effect has been linked to reduced adaptation recovery times underlying temporal processing of tone sequences (Herrmann et al., 2016). In the context of this study, it is important to note that the frequencies corresponding to individual acoustic events used to make up the inputs (i.e. frequency F12, corresponding to 200 ms and 100 ms in slow and fast tempo respectively) are congruent with the temporal course of typical N1-P2 potentials. Therefore, based on the evidence that older adults generally demonstrate larger N1-P2 amplitudes, it would be expected to find proportionally larger amplitudes at F12 compared to the slower frequency F3 in older adults compared to younger adults, regardless of rhythm complexity and tempo. As expected, this effect was found in most conditions, thus suggesting that differences in the shape of the automatic response

to auditory stimuli between older and younger adults is likely to explain the differences observed here. This result could also be consistent with the compensation hypothesis of aging, where older adults increase activity to each single acoustic onset in order to compensate for hearing loss. The relative increase in amplitude at faster vs. slower frequencies observed here in older adults compared to younger adults is the opposite pattern to existing literature (e.g. Clinard et al., 2010; Goossens et al., 2016) and is surprising, given that perceiving and tracking beat subdivisions is more difficult than tracking a beat at fast tempi. Further research is necessary to confirm and investigate this age effect in more detail.

Our spatial analysis however does not support a compensation theory of aging. In previous literature (Halpern et al., 2017; Reuter-Lorenz & Cappell, 2008), older adults demonstrate activity over a larger surface area in the frontal regions of the brain than younger adults. This pattern is not observed here, suggesting that older adults do not recruit larger neural areas to perform the same task as younger adults overall. Finally, the hypothesized interaction between age and rhythm, where older adults' long-term exposure to Western music may help them compensate for the lack of prominent acoustic feature at meter-related frequencies in the syncopated rhythm was not borne out in our results, suggesting that such experience did not manifest itself in this particular study.

Importantly, the design with fixed order of conditions does not appear to have had a significant effect on our results. If fatigue had been an important factor, we would expect overall neural activity to decrease from one condition to the next. This is not the case as illustrated by Figures 3 and 4, which both present the data in the same order as participants completed blocks, from left to right. However, it is impossible to parse out any potential effects of fatigue. Though this is a disadvantage of a fixed order design, it does have an advantage. Due to the endogenous nature of meter perception, one way to capture indices of the perceived meter is to ask the participants to tap periodically while listening to the rhythm. The participants of this study could successfully perform this task as indicated by the obtained mean and standard deviation of the inter-tap intervals (see SI for details), though the tapping sequences were too short to further compare tapping performance across conditions. A fixed order ensures that each participant has received the same amount of "practice" before each condition and therefore has the same opportunity to learn to mentally establish the meter in each condition, which was identified as important in pilot participants. Conversely, while a counterbalanced order design would eliminate any order or fatigue effects, meter perception in each condition may have differed due to more or less experience with the stimuli over time, depending on where the condition occurred in the experiment and was expected to be especially difficult if the fast, syncopated condition was presented first. Future work should explore a counterbalanced design to (i) ensure that the effects reported here are not related to fatigue, and (ii) exploit this potential learning effect from the order of the blocks to directly test the link between enhanced neural activity at meter frequencies and the ability to tap the perceived meter.

To summarize, this study has demonstrated subtle differences between older and younger adults on neural activity to a rhythmic stimulus. In older adults, we observed preserved selective enhancement of neural activity at meter-related frequencies despite significant hearing loss, even in the syncopated rhythms in which the meter-related frequencies were not prominent acoustic features in the input. Moreover, younger adults showed lower amplitude at the frequency corresponding to single acoustic events making up the sequences relative to the other, slower meter-related frequencies which were proportionally larger. In contrast, this difference was reduced in older adults, who showed relatively larger responses at the frequency of single acoustic events compared to activity elicited at slower frequencies. These results are compatible with previous results showing increased amplitude of N1-P2 complexes in response to single acoustic events, and indicate that this effect of

aging can also affect responses to acoustic events presented in long rhythmic sequences. Future research is necessary to better understand the difference in response shape between younger and older adults.

5 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

6 Author Contributions

SAS: Formal analysis, Writing original draft, Writing – review & editing. **ELWB:** Investigation, Formal analysis. **SN:** Conceptualization, Methodology, Writing – review & editing. **BRZ:** Conceptualization, Funding acquisition, Supervision, Resources, Writing – review & editing. Funding

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567 9 Data Availability Statement

568 The datasets generated for this study are not publicly available as participants did not consent to
569 public sharing of their data. The data is available from the corresponding author upon request.

Supplementary Materials 1 - Summary statistics, model specification details and follow-up t-test results

Table 1. Summary statistics for meter-unrelated peaks

Age	Tempo	Rhythm	Frequency	Mean Amplitude	Standard Error
Younger	Slow	Non-syncopated	0.83	0.0780057	0.0084729
Younger	Slow	Non-syncopated	1.66	0.0142428	0.0030411
Younger	Slow	Non-syncopated	2.08	0.0203644	0.0032852
Younger	Slow	Non-syncopated	2.91	0.0375499	0.0039400
Younger	Slow	Non-syncopated	3.33	0.0347361	0.0026435
Younger	Slow	Non-syncopated	4.16	0.0082533	0.0019121
Younger	Slow	Non-syncopated	4.57	0.0000824	0.0015144
Younger	Slow	Syncopated	0.83	0.0684450	0.0054068
Younger	Slow	Syncopated	1.66	0.0651119	0.0036049
Younger	Slow	Syncopated	2.08	0.0422580	0.0032515
Younger	Slow	Syncopated	2.91	0.0286044	0.0021018
Younger	Slow	Syncopated	3.33	0.0088772	0.0015495
Younger	Slow	Syncopated	4.16	0.0223526	0.0026422
Younger	Slow	Syncopated	4.57	0.0026887	0.0014577
Younger	Fast	Non-syncopated	1.66	0.0192275	0.0029082
Younger	Fast	Non-syncopated	3.33	0.0231274	0.0022974
Younger	Fast	Non-syncopated	4.16	0.0385591	0.0024789
Younger	Fast	Non-syncopated	5.83	0.0149206	0.0023665
Younger	Fast	Non-syncopated	6.66	0.0202689	0.0019773
Younger	Fast	Non-syncopated	8.33	0.0101402	0.0013623
Younger	Fast	Non-syncopated	9.16	0.0004522	0.0010637
Younger	Fast	Syncopated	1.66	0.0372886	0.0064486
Younger	Fast	Syncopated	3.33	0.0857562	0.0042886
Younger	Fast	Syncopated	4.16	0.0579578	0.0039490
Younger	Fast	Syncopated	5.83	0.0258373	0.0033213
Younger	Fast	Syncopated	6.66	0.0099667	0.0022307
Younger	Fast	Syncopated	8.33	0.0052247	0.0019539
Younger	Fast	Syncopated	9.16	0.0143075	0.0013541
Older	Slow	Non-syncopated	0.83	0.0159153	0.0068904
Older	Slow	Non-syncopated	1.66	0.0231684	0.0033219
Older	Slow	Non-syncopated	2.08	0.0068296	0.0024809
Older	Slow	Non-syncopated	2.91	0.0058791	0.0021596

Older	Slow	Non-syncopated	3.33	0.0148497	0.0025553
Older	Slow	Non-syncopated	4.16	0.0011534	0.0018447
Older	Slow	Non-syncopated	4.57	0.0052663	0.0014733
Older	Slow	Syncopated	0.83	0.0526863	0.0049276
Older	Slow	Syncopated	1.66	0.0295822	0.0015906
Older	Slow	Syncopated	2.08	0.0279113	0.0017079
Older	Slow	Syncopated	2.91	0.0206890	0.0015823
Older	Slow	Syncopated	3.33	0.0157329	0.0012585
Older	Slow	Syncopated	4.16	0.0114314	0.0011923
Older	Slow	Syncopated	4.57	0.0082055	0.0006783
Older	Fast	Non-syncopated	1.66	0.0286830	0.0036746
Older	Fast	Non-syncopated	3.33	0.0266107	0.0022738
Older	Fast	Non-syncopated	4.16	0.0204777	0.0018767
Older	Fast	Non-syncopated	5.83	0.0086279	0.0016437
Older	Fast	Non-syncopated	6.66	0.0147253	0.0015365
Older	Fast	Non-syncopated	8.33	0.0070732	0.0010811
Older	Fast	Non-syncopated	9.16	0.0073590	0.0010355
Older	Fast	Syncopated	1.66	0.0500489	0.0082244
Older	Fast	Syncopated	3.33	0.0528557	0.0039821
Older	Fast	Syncopated	4.16	0.0538440	0.0033813
Older	Fast	Syncopated	5.83	0.0141220	0.0020992
Older	Fast	Syncopated	6.66	0.0096782	0.0012665
Older	Fast	Syncopated	8.33	0.0200754	0.0016987
Older	Fast	Syncopated	9.16	0.0096550	0.0016027

Table 2. Summary statistics for meter-related peaks

Age	Tempo	Rhythm	Frequency	Mean Amplitude	Standard Error
Younger	Slow	Non-syncopated	0.41	-0.0090419	0.0116278
Younger	Slow	Non-syncopated	1.25	0.2139752	0.0086961
Younger	Slow	Non-syncopated	2.50	0.0599340	0.0043373
Younger	Slow	Non-syncopated	3.75	0.0307553	0.0028445
Younger	Slow	Non-syncopated	5.00	0.0833212	0.0068019
Younger	Slow	Syncopated	0.41	0.0492761	0.0101707
Younger	Slow	Syncopated	1.25	0.1043801	0.0056635
Younger	Slow	Syncopated	2.50	0.0147049	0.0024240
Younger	Slow	Syncopated	3.75	0.0203156	0.0024042
Younger	Slow	Syncopated	5.00	0.0719328	0.0065555

Younger	Fast	Non-syncopated	0.83	0.0672375	0.0055117
Younger	Fast	Non-syncopated	2.50	0.1869922	0.0083230
Younger	Fast	Non-syncopated	5.00	0.0410084	0.0027795
Younger	Fast	Non-syncopated	7.50	0.0382612	0.0037386
Younger	Fast	Non-syncopated	10.00	0.0884871	0.0051882
Younger	Fast	Syncopated	0.83	0.0745292	0.0100574
Younger	Fast	Syncopated	2.50	0.1687050	0.0069872
Younger	Fast	Syncopated	5.00	0.0232339	0.0023889
Younger	Fast	Syncopated	7.50	0.0095987	0.0022955
Younger	Fast	Syncopated	10.00	0.0799961	0.0050560
Older	Slow	Non-syncopated	0.41	-0.0366809	0.0137984
Older	Slow	Non-syncopated	1.25	0.1300885	0.0066984
Older	Slow	Non-syncopated	2.50	0.0342812	0.0036252
Older	Slow	Non-syncopated	3.75	0.0431644	0.0035857
Older	Slow	Non-syncopated	5.00	0.1233665	0.0048650
Older	Slow	Syncopated	0.41	0.0886093	0.0074337
Older	Slow	Syncopated	1.25	0.0747768	0.0033805
Older	Slow	Syncopated	2.50	0.0145671	0.0015539
Older	Slow	Syncopated	3.75	0.0269940	0.0016075
Older	Slow	Syncopated	5.00	0.0754394	0.0035759
Older	Fast	Non-syncopated	0.83	0.0286081	0.0059339
Older	Fast	Non-syncopated	2.50	0.1709451	0.0117460
Older	Fast	Non-syncopated	5.00	0.0308389	0.0021506
Older	Fast	Non-syncopated	7.50	0.0417021	0.0025352
Older	Fast	Non-syncopated	10.00	0.1190852	0.0058380
Older	Fast	Syncopated	0.83	0.0185427	0.0067978
Older	Fast	Syncopated	2.50	0.1005168	0.0048617
Older	Fast	Syncopated	5.00	0.0041525	0.0011969
Older	Fast	Syncopated	7.50	0.0163796	0.0019675
Older	Fast	Syncopated	10.00	0.1102473	0.0049182

Table 3. Summary of the maximally fitted multiple linear regression model predicting spectral amplitude for meter-related and meter-unrelated peak frequencies including coefficient, Wald 95% confidence intervals and R^2 for each predictor (where there are multiple levels, R^2 is given for the predictor as a whole). Random effects account for < 0.00 variance and are therefore not reported.

Predictor	Coefficient	2.5%	98.5%	R^2
Intercept	0.078	0.067	0.089	0.067

Type	-0.048	-0.054	-0.042	0.075
Rhythm	-0.024	-0.033	-0.014	0.001
Tempo	0.009	0.001	0.016	0.000
Age	-0.014	-0.030	0.003	-0.000
PTA	-0.000	-0.001	0.000	0.000
Type:Rhythm	0.030	0.021	0.039	0.009
Type:Tempo	-0.018	-0.027	-0.009	0.001
Rhythm:Tempo	0.010	0.001	0.020	0.000
Type:Age	-0.000	-0.009	0.008	0.000
Rhythm:Age	0.021	0.007	0.034	0.000
Tempo:Age	0.011	0.000	0.021	0.000
Type:Rhythm:Tempo	-0.001	-0.013	0.011	0.000
Type:Rhythm:Age	-0.014	-0.026	-0.002	0.000
Type:Tempo:Age	0.005	-0.008	0.017	0.001
Rhythm:Tempo:Age	-0.036	-0.049	-0.023	0.001
Type:Rhythm:Tempo:Age	0.027	0.010	0.044	0.001

Table 4. Follow-up t-test results comparing age groups for meter-related and meter-unrelated frequencies in each condition including t-statistic, p-value and Cohen's d effect size.

Tempo	Rhythm	Type	t-statistic	p-value	Effect size
Slow	Non-syncopated	Related	2.917	0.004	0.140
Slow	Non-syncopated	Unrelated	7.979	0.000	0.322
Slow	Syncopated	Related	-1.088	0.277	-0.053
Slow	Syncopated	Unrelated	6.199	0.000	0.252
Fast	Non-syncopated	Related	1.321	0.187	0.063
Fast	Non-syncopated	Unrelated	1.578	0.115	0.064
Fast	Syncopated	Related	5.088	0.000	0.244
Fast	Syncopated	Unrelated	1.655	0.098	0.067

Table 5. Summary of maximally fitted multiple linear regression model predicting spectral amplitude at meter-related frequency peaks, including coefficient, Wald 95% confidence intervals and R^2 for each predictor (where there are multiple levels, R^2 is given for the predictor as a whole). Random effects account for < 0.00 variance and coefficients for all channel predictors are < 0.00, and are therefore not reported.

Predictor	Coefficient	2.5%	98.5%	R^2
(Intercept)	0.216	0.193	0.240	0.105
Age	-0.078	-0.110	-0.046	0.000
Tempo	-0.027	-0.044	-0.010	0.007
Rhythm	-0.110	-0.128	-0.091	-0.000
Peak0	-0.223	-0.239	-0.207	0.224
Peak2	-0.154	-0.170	-0.138	
Peak3	-0.183	-0.199	-0.167	
Peak4	-0.131	-0.147	-0.115	
PTA	-0.001	-0.002	0.001	0.000
Age:Tempo	0.068	0.045	0.091	0.000
Age:Rhythm	0.054	0.028	0.080	0.000
Tempo:Rhythm	0.091	0.069	0.114	0.000
Age:Peak0	0.056	0.034	0.078	0.017
Age:Peak2	0.058	0.036	0.080	
Age:Peak3	0.096	0.074	0.118	
Age:Peak4	0.124	0.102	0.146	
Tempo:Peak0	0.103	0.081	0.126	0.005
Tempo:Peak2	0.008	-0.014	0.031	
Tempo:Peak3	0.034	0.012	0.057	
Tempo:Peak4	0.032	0.010	0.055	
Rhythm:Peak0	0.168	0.145	0.190	0.033
Rhythm:Peak2	0.064	0.042	0.087	
Rhythm:Peak3	0.099	0.077	0.122	
Rhythm:Peak4	0.098	0.076	0.121	
Age:Tempo:Rhythm	-0.106	-0.138	-0.075	0.002
Age:Tempo:Peak0	-0.079	-0.110	-0.048	0.004
Age:Tempo:Peak2	-0.052	-0.084	-0.021	
Age:Tempo:Peak3	-0.077	-0.108	-0.045	
Age:Tempo:Peak4	-0.077	-0.109	-0.046	
Age:Rhythm:Peak0	0.013	-0.019	0.044	0.001
Age:Rhythm:Peak2	-0.029	-0.060	0.003	
Age:Rhythm:Peak3	-0.060	-0.091	-0.029	

Age:Rhythm:Peak4	-0.091	-0.122	-0.059	
Tempo:Rhythm:Peak0	-0.142	-0.174	-0.110	
Tempo:Rhythm:Peak2	-0.064	-0.096	-0.032	0.014
Tempo:Rhythm:Peak3	-0.110	-0.141	-0.078	
Tempo:Rhythm:Peak4	-0.088	-0.120	-0.057	
Age:Tempo:Rhythm:Peak0	0.022	-0.022	0.066	
Age:Tempo:Rhythm:Peak2	0.072	0.028	0.116	0.005
Age:Tempo:Rhythm:Peak3	0.115	0.071	0.160	
Age:Tempo:Rhythm:Peak4	0.143	0.098	0.187	

Table 6. Follow-up t-test results for neural activity amplitudes at meter-related frequencies comparing age groups at each peak and condition including t-statistic, p-value and Cohen's d effect size.

Peak	Condition	t-statistic	p-value	Effect size
BF	Non-syncopated - Slow	1.532	0.127	0.163
CR	Non-syncopated - Slow	7.642	0.000	0.764
H1	Non-syncopated - Slow	4.538	0.000	0.476
H2	Non-syncopated - Slow	-2.711	0.007	-0.286
H3	Non-syncopated - Slow	-4.789	0.000	-0.503
BF	Syncopated - Slow	-3.122	0.002	-0.334
CR	Syncopated - Slow	4.488	0.000	0.476
H1	Syncopated - Slow	0.048	0.962	0.005
H2	Syncopated - Slow	-2.309	0.022	-0.249
H3	Syncopated - Slow	-0.470	0.639	-0.051
BF	Non-syncopated - Fast	4.770	0.000	0.495
CR	Non-syncopated - Fast	1.115	0.266	0.118
H1	Non-syncopated - Fast	2.894	0.004	0.309
H2	Non-syncopated - Fast	-0.762	0.447	-0.083
H3	Non-syncopated - Fast	-3.918	0.000	-0.410
BF	Syncopated - Fast	4.612	0.000	0.486
CR	Syncopated - Fast	8.011	0.000	0.798
H1	Syncopated - Fast	7.141	0.000	0.729
H2	Syncopated - Fast	-2.243	0.026	-0.240

H3 Syncopated - Fast -4.289 0.000 -0.449

Table 7. Follow-up t-test results for meter-related peak frequencies comparing BF and CR for each age group and condition including t-statistic, p-value and Cohen's d effect size.

Age	Condition	t-statistic	p-value	Effect size
Younger	Non-syncopated - Slow	-15.359	0.000	-1.285
Younger	Syncopated - Slow	-4.734	0.000	-0.501
Older	Non-syncopated - Slow	-10.873	0.000	-0.995
Older	Syncopated - Slow	1.694	0.092	0.178
Younger	Non-syncopated - Fast	-11.996	0.000	-1.096
Younger	Syncopated - Fast	-7.690	0.000	-0.775
Older	Non-syncopated - Fast	-10.816	0.000	-0.991
Older	Syncopated - Fast	-9.809	0.000	-0.919

Table 8. Follow-up t-test results for meter-related peak frequencies comparing BF and H3 for each age group and condition including t-statistic, p-value and Cohen's d effect size.

Age	Condition	t-statistic	p-value	Effect size
Younger	Non-syncopated - Slow	11.834	0.000	1.085
Younger	Syncopated - Slow	3.745	0.000	0.401
Older	Non-syncopated - Slow	0.812	0.417	0.086
Older	Syncopated - Slow	-0.135	0.893	-0.014
Younger	Non-syncopated - Fast	10.044	0.000	0.962
Younger	Syncopated - Fast	10.286	0.000	0.979
Older	Non-syncopated - Fast	3.954	0.000	0.409
Older	Syncopated - Fast	-1.407	0.160	-0.148

Table 9. Summary of maximally fitted multiple linear regression model predicting spectral amplitude at meter-related frequency peaks over multiple electrode montages, including coefficient, Wald 95% confidence intervals and R^2 for each predictor (where there are multiple levels, R^2 is given for the predictor as a whole). Random effects and coefficients for all channel predictors account for < 0.00 of model variation, and are therefore not reported.

Predictor	Coefficient	2.5%	98.5%	R^2
(Intercept)	0.218	0.186	0.250	0.0280319
Age	-0.077	-0.122	-0.032	0.0000035
Tempo	-0.027	-0.063	0.009	0.0018315
Rhythm	-0.110	-0.147	-0.073	0.0000014
Peak0	-0.223	-0.258	-0.188	
Peak2	-0.154	-0.190	-0.119	0.0505123
Peak3	-0.183	-0.219	-0.148	
Peak4	-0.131	-0.166	-0.095	
Ring1	-0.020	-0.056	0.016	
Ring2	-0.056	-0.090	-0.021	0.0039672
Ring3	-0.079	-0.113	-0.044	
PTA	-0.001	-0.002	0.001	-0.0000017
Age:Tempo	0.068	0.018	0.118	0.0000158
Age:Rhythm	0.054	0.003	0.106	0.0000103
Tempo:Rhythm	0.091	0.041	0.141	0.0009352
Age:Peak0	0.056	0.007	0.106	
Age:Peak2	0.058	0.009	0.108	0.0020063
Age:Peak3	0.096	0.047	0.146	
Age:Peak4	0.124	0.075	0.173	
Tempo:Peak0	0.103	0.053	0.153	
Tempo:Peak2	0.008	-0.042	0.058	0.0040778
Tempo:Peak3	0.034	-0.016	0.085	
Tempo:Peak4	0.032	-0.018	0.082	
Rhythm:Peak0	0.168	0.118	0.218	
Rhythm:Peak2	0.064	0.014	0.115	0.0107487
Rhythm:Peak3	0.099	0.049	0.149	
Rhythm:Peak4	0.098	0.048	0.148	
Age:Ring1	0.000	-0.049	0.050	
Age:Ring2	0.032	-0.016	0.080	0.0000157
Age:Ring3	0.028	-0.020	0.076	
Tempo:Ring1	-0.006	-0.057	0.045	0.0000192

Tempo:Ring2	-0.008	-0.057	0.041	
Tempo:Ring3	-0.005	-0.055	0.044	
Rhythm:Ring1	0.009	-0.042	0.060	
Rhythm:Ring2	0.034	-0.015	0.084	0.0003398
Rhythm:Ring3	0.046	-0.003	0.095	
Peak0:Ring1	0.026	-0.025	0.077	
Peak2:Ring1	0.007	-0.044	0.058	
Peak3:Ring1	0.015	-0.036	0.067	
Peak4:Ring1	0.018	-0.033	0.069	
Peak0:Ring2	0.048	-0.002	0.097	
Peak2:Ring2	0.033	-0.016	0.083	0.0013441
Peak3:Ring2	0.048	-0.001	0.097	
Peak4:Ring2	0.041	-0.008	0.091	
Peak0:Ring3	0.049	-0.000	0.098	
Peak2:Ring3	0.049	0.000	0.099	
Peak3:Ring3	0.069	0.020	0.118	
Peak4:Ring3	0.061	0.011	0.110	
Age:Tempo:Rhythm	-0.106	-0.176	-0.037	0.0024413
Age:Tempo:Peak0	-0.079	-0.149	-0.009	
Age:Tempo:Peak2	-0.052	-0.122	0.017	0.0012833
Age:Tempo:Peak3	-0.077	-0.147	-0.007	
Age:Tempo:Peak4	-0.077	-0.147	-0.008	
Age:Rhythm:Peak0	0.013	-0.057	0.082	
Age:Rhythm:Peak2	-0.029	-0.099	0.041	0.0013572
Age:Rhythm:Peak3	-0.060	-0.130	0.010	
Age:Rhythm:Peak4	-0.091	-0.161	-0.021	
Tempo:Rhythm:Peak0	-0.142	-0.213	-0.071	
Tempo:Rhythm:Peak2	-0.064	-0.135	0.007	0.0041286
Tempo:Rhythm:Peak3	-0.110	-0.180	-0.039	
Tempo:Rhythm:Peak4	-0.088	-0.159	-0.017	
Age:Tempo:Ring1	0.015	-0.056	0.085	
Age:Tempo:Ring2	0.051	-0.016	0.119	0.0000577
Age:Tempo:Ring3	0.030	-0.038	0.098	
Age:Rhythm:Ring1	0.002	-0.069	0.072	
Age:Rhythm:Ring2	-0.020	-0.088	0.048	0.0000470
Age:Rhythm:Ring3	-0.018	-0.086	0.050	
Tempo:Rhythm:Ring1	-0.006	-0.078	0.066	0.0002310

Tempo:Rhythm:Ring2	-0.026	-0.096	0.043	
Tempo:Rhythm:Ring3	-0.048	-0.117	0.022	
Age:Peak0:Ring1	-0.029	-0.099	0.042	
Age:Peak2:Ring1	0.008	-0.063	0.078	
Age:Peak3:Ring1	-0.006	-0.077	0.064	
Age:Peak4:Ring1	-0.019	-0.090	0.051	
Age:Peak0:Ring2	-0.155	-0.223	-0.087	
Age:Peak2:Ring2	-0.025	-0.093	0.043	0.0006946
Age:Peak3:Ring2	-0.053	-0.121	0.015	
Age:Peak4:Ring2	-0.057	-0.125	0.011	
Age:Peak0:Ring3	-0.113	-0.181	-0.045	
Age:Peak2:Ring3	-0.013	-0.081	0.055	
Age:Peak3:Ring3	-0.042	-0.110	0.026	
Age:Peak4:Ring3	-0.072	-0.140	-0.005	
Tempo:Peak0:Ring1	-0.010	-0.083	0.062	
Tempo:Peak2:Ring1	0.013	-0.059	0.086	
Tempo:Peak3:Ring1	0.002	-0.070	0.075	
Tempo:Peak4:Ring1	-0.005	-0.077	0.068	
Tempo:Peak0:Ring2	-0.008	-0.078	0.061	
Tempo:Peak2:Ring2	0.020	-0.050	0.089	0.0008020
Tempo:Peak3:Ring2	-0.002	-0.072	0.067	
Tempo:Peak4:Ring2	-0.005	-0.074	0.065	
Tempo:Peak0:Ring3	0.008	-0.062	0.077	
Tempo:Peak2:Ring3	0.018	-0.052	0.087	
Tempo:Peak3:Ring3	-0.008	-0.077	0.062	
Tempo:Peak4:Ring3	-0.016	-0.086	0.053	
Rhythm:Peak0:Ring1	-0.045	-0.117	0.028	
Rhythm:Peak2:Ring1	0.010	-0.062	0.083	
Rhythm:Peak3:Ring1	-0.008	-0.080	0.065	
Rhythm:Peak4:Ring1	-0.011	-0.084	0.061	
Rhythm:Peak0:Ring2	-0.081	-0.151	-0.011	0.0002211
Rhythm:Peak2:Ring2	-0.008	-0.078	0.061	
Rhythm:Peak3:Ring2	-0.034	-0.103	0.036	
Rhythm:Peak4:Ring2	-0.021	-0.090	0.049	
Rhythm:Peak0:Ring3	-0.116	-0.185	-0.046	
Rhythm:Peak2:Ring3	-0.006	-0.076	0.063	
Rhythm:Peak3:Ring3	-0.045	-0.114	0.025	

Rhythm:Peak4:Ring3	-0.036	-0.106	0.034	
Age:Tempo:Rhythm:Peak0	0.022	-0.077	0.121	
Age:Tempo:Rhythm:Peak2	0.072	-0.027	0.171	0.0042622
Age:Tempo:Rhythm:Peak3	0.115	0.017	0.214	
Age:Tempo:Rhythm:Peak4	0.143	0.044	0.241	
Age:Tempo:Rhythm:Ring1	-0.002	-0.102	0.098	
Age:Tempo:Rhythm:Ring2	-0.041	-0.137	0.055	0.0001699
Age:Tempo:Rhythm:Ring3	0.012	-0.084	0.108	
Age:Tempo:Peak0:Ring1	0.045	-0.055	0.144	
Age:Tempo:Peak2:Ring1	-0.020	-0.120	0.079	
Age:Tempo:Peak3:Ring1	-0.008	-0.107	0.092	
Age:Tempo:Peak4:Ring1	-0.004	-0.103	0.096	
Age:Tempo:Peak0:Ring2	0.094	-0.002	0.190	
Age:Tempo:Peak2:Ring2	-0.066	-0.162	0.030	0.0004681
Age:Tempo:Peak3:Ring2	-0.032	-0.128	0.064	
Age:Tempo:Peak4:Ring2	-0.038	-0.134	0.058	
Age:Tempo:Peak0:Ring3	0.087	-0.009	0.183	
Age:Tempo:Peak2:Ring3	-0.027	-0.123	0.069	
Age:Tempo:Peak3:Ring3	-0.021	-0.117	0.075	
Age:Tempo:Peak4:Ring3	-0.004	-0.100	0.092	
Age:Rhythm:Peak0:Ring1	0.044	-0.056	0.144	
Age:Rhythm:Peak2:Ring1	-0.012	-0.112	0.088	
Age:Rhythm:Peak3:Ring1	0.003	-0.096	0.103	
Age:Rhythm:Peak4:Ring1	0.013	-0.087	0.112	
Age:Rhythm:Peak0:Ring2	0.201	0.105	0.297	
Age:Rhythm:Peak2:Ring2	0.017	-0.079	0.113	0.0001993
Age:Rhythm:Peak3:Ring2	0.051	-0.045	0.147	
Age:Rhythm:Peak4:Ring2	0.026	-0.070	0.121	
Age:Rhythm:Peak0:Ring3	0.195	0.099	0.291	
Age:Rhythm:Peak2:Ring3	0.004	-0.091	0.100	
Age:Rhythm:Peak3:Ring3	0.032	-0.064	0.128	
Age:Rhythm:Peak4:Ring3	0.045	-0.050	0.141	
Tempo:Rhythm:Peak0:Ring1	0.057	-0.045	0.160	
Tempo:Rhythm:Peak2:Ring1	-0.012	-0.114	0.091	
Tempo:Rhythm:Peak3:Ring1	0.010	-0.092	0.112	0.0001993
Tempo:Rhythm:Peak4:Ring1	0.008	-0.095	0.110	
Tempo:Rhythm:Peak0:Ring2	0.101	0.002	0.199	

Tempo:Rhythm:Peak2:Ring2	0.002	-0.096	0.101	
Tempo:Rhythm:Peak3:Ring2	0.043	-0.056	0.141	
Tempo:Rhythm:Peak4:Ring2	0.013	-0.086	0.111	
Tempo:Rhythm:Peak0:Ring3	0.163	0.065	0.262	
Tempo:Rhythm:Peak2:Ring3	0.012	-0.086	0.111	
Tempo:Rhythm:Peak3:Ring3	0.068	-0.030	0.167	
Tempo:Rhythm:Peak4:Ring3	0.035	-0.063	0.134	
Age:Tempo:Rhythm:Peak0:Ring1	-0.079	-0.220	0.062	
Age:Tempo:Rhythm:Peak2:Ring1	0.015	-0.126	0.156	
Age:Tempo:Rhythm:Peak3:Ring1	-0.003	-0.144	0.138	
Age:Tempo:Rhythm:Peak4:Ring1	-0.010	-0.151	0.131	
Age:Tempo:Rhythm:Peak0:Ring2	-0.180	-0.316	-0.044	
Age:Tempo:Rhythm:Peak2:Ring2	0.056	-0.080	0.191	0.0011185
Age:Tempo:Rhythm:Peak3:Ring2	0.009	-0.126	0.145	
Age:Tempo:Rhythm:Peak4:Ring2	0.034	-0.102	0.170	
Age:Tempo:Rhythm:Peak0:Ring3	-0.264	-0.399	-0.128	
Age:Tempo:Rhythm:Peak2:Ring3	-0.004	-0.140	0.131	
Age:Tempo:Rhythm:Peak3:Ring3	-0.026	-0.162	0.110	
Age:Tempo:Rhythm:Peak4:Ring3	-0.037	-0.173	0.098	

Supplementary Materials 2 – Tapping analysis

In these supplementary materials, analysis of the tapping data is presented. Stimuli and procedure are as described in the main manuscript.

Mean inter-tap interval (ITI) was calculated for each participant and each condition and is plotted in Figure S1, where error bars represent standard deviation. Mean (standard deviation) ITIs for slow non-syncopated, fast non-syncopated, slow syncopated and fast syncopated were 781.1 (186.1), 400.34 (97.2), 791.4 (193.2) and 434.1 (135.7) respectively. A mixed effects multiple linear regression model predicting ITI with *tempo*, *rhythm* and *age* as fixed effects found a significant effect of tempo, but not of rhythm or age (see Table 1), nor are there any significant interactions between the predictors. More specifically, ITIs in response to fast stimuli were shorter than slow stimuli.

Together, Figure and Table 1 show that the majority of participants tapped at a metrical grouping of 4 events (800ms for the slow tempo and 400ms for the fast tempo). A few participants also tapped at a faster rate (grouping of 2 events).

Table 1. Summary of predictors from the maximally fitted multiple linear regression model predicting ITI including coefficient, Wald 95% confidence intervals and R^2 for each predictor (where there are multiple levels, R^2 is given for the predictor as a whole).

Predictor	Coefficient	2.5%	98.5%	R^2
Intercept	1464.3	838.6	2098.9	-
Tempo	-530.3	-829.9	-230.7	-.001
Rhythm	-263.3	-638.0	111.5	.00
Age	-198.4	-594.9	198.1	.00
Tempo:Rhythm	127.2	-65.5	319.8	.00
Tempo:Age	90.8	-98.8	280.5	.00
Rhythm:Age	175.0	-60.3	410.2	.00
Tempo:Rhythm:Age	-74.5	-195.0	46.0	.00
Random effects				
Intercept	21134			
Fast Nonsyncopated	14652			
Slow Syncopated	27363			.67
Fast Syncopated	26364			
Residual	19469

Figure S1. Mean ITI for each participant for slow (A) and fast (B) tempi and non-syncopated and syncopated rhythms, divided by age group. Error bars represent standard deviation.