Neural entrainment facilitates duplets:

Frequency-tagging differentiates musicians and non-musicians when they tap to the beat

Celma-Miralles, A.^{1,2,*}; Kleber, B.A.¹; Toro, J.M.^{2,3}; Vuust, P.¹

1- Center for Music in the Brain, Department of Clinical Medicine, Aarhus University & The

Royal Academy of Music Aarhus/Aalborg, Aarhus/Aalborg, Denmark

2- Center for Brain and Cognition, Universitat Pompeu Fabra, Barcelona, Spain

3- Institució Catalana de Recerca i Estudis Avançats, Barcelona, Spain

*Corresponding Author: a.celma.miralles@clin.au.dk

Dept. of Clinical Medicine, Health, Aarhus University Universitetsbyen, 3 (1710), 8000 Aarhus
C, Denmark

ABSTRACT

Motor coordination to an isochronous beat improves when it is subdivided into equal intervals. Here, we study if this subdivision benefit (i) varies with the kind of subdivision, (ii) is enhanced in individuals with formal musical training, and (iii), is an inherent property of neural oscillations. We recorded electroencephalograms of musicians and non-musicians during: (a) listening to an isochronous beat, (b) listening to one of 4 different subdivisions, (c) listening to the beat again, and (d) listening and tapping the beat with the same subdivisions as in (b). We found that tapping consistency and neural entrainment in condition (d) was enhanced in non-musicians for duplets (1:2) compared to the other types of subdivisions. Musicians showed overall better tapping performance and were equally good at tapping together with duplets, triplets (1:3) and quadruplets (1:4), but not with quintuplets (1:5). This group difference was reflected in enhanced neural responses in the triplet and quadruplet conditions. Importantly, for all participants, the neural entrainment to the beat and its first harmonic (i.e. the duplet frequency) increased after listening to each of the subdivisions (c compared to a). Since these subdivisions are harmonics of the beat frequency, the observed preference of the brain to enhance the simplest subdivision level (duplets) may be an inherent property of neural oscillations. In sum, a tapping advantage for simple binary subdivisions is reflected in neural oscillations to harmonics of the beat, and formal training in music can enhance it.

KEYWORDS: beat perception, subdivision benefit, neural entrainment, sensorimotor synchronization, EEG frequency-tagging

Highlights

- The neural entrainment to periodic sounds only differs between musicians and non-musicians when they perform a predictive sensorimotor synchronization task.
- After listening to a subdivided beat, the frequencies related to the beat and its first harmonic are enhanced in the EEG, likely stabilizing the perception of the beat.
- There is a natural advantage for binary structures in sensorimotor synchronization, observed in the tapping of duplets by non-musicians, which can be extended to other subdivisions after extensive musical training.

Introduction

The ability to precisely predict future events is fundamental to human survival by representing a main principle to guide brain processing and a prerequisite for sensorimotor synchronization (Friston, 2010). To optimally process temporal events, our brain generates predictions and expectations that are compared with the perceptual input to improve future predictions (Koelsch, Vuust & Friston, 2019). Dividing and structuring time in smaller units improves the brain's ability to predict and, as a consequence, to enhance the precision of our actions. Hence, when temporal events are subdivided into smaller periodic events, sensorimotor synchronization (henceforth, SMS) is less variable (Repp, 2003; Repp, 2010; Repp and Dogget, 2007). This phenomenon, known as the subdivision benefit, may be fundamental to our ability to synchronize with each other in music, dance or sports (Damm et al., 2020; Solberg & Jensenius, 2019) and could contribute to movement rehabilitation (Schaefer, 2014; Nombela, et al., 2013; Bek et al., 2020). Previous research has studied the neural oscillations underlying the beat and its slower metrical grouping (Nozaradan, 2014). Here, we apply frequency-tagging to the neural entrainment to subdivisions in order to understand the mechanisms underlying the SMS advantage at the faster metrical level of the beat. In addition, we will take into account the role of musical training in auditory motor coupling, which requires the highly accurate processing of temporal events, leading to improved synchronized performance with others or with a periodic metronome.

SMS refers to the coordination of a motor action with an external physical rhythm, which can emerge intentionally or spontaneously (e.g., when people listen to music and start tapping the foot). It reflects the generation of temporal expectations based on the identification of a prominent beat within a metrical hierarchy (Vuust & Witek, 2014; Large, 2008). This happens because rhythms are perceived in relation to an evenly-paced pulse (i.e. the beat) that is organized into

meters —hierarchical levels establishing referential points at faster (i.e. subdivisions) and slower rates (London, 2012; Honing, 2012)— thus creating differentially-accented patterns. While many behavioral studies have focused on SMS to the beat, few of them focused on the subdivisions (see the reviews by Repp, 2005; and Repp & Su, 2013). Finger-tapping paradigms allow to study the accuracy and the variability between taps predicting a beat (e.g. Dalla Bella et al., 2017; Iversen & Patel, 2008). These paradigms have revealed two major effects of subdivisions on tapping: (i) the filled duration illusion (Buffardi, 1971; Thomas & Brown, 1974; Wearden, Norton, Martin & Montford-Bebb, 2007) and (ii) the subdivision benefit (Repp, 2003). That is, adding metrical subdivisions to continuous beats increases the perceived duration of an interval and reduces tapping variability (Repp 2010; Repp & Doggett 2007). These psychophysical effects were found in both musicians and non-musicians performing continuation-tapping paradigms and perceptual judgment tasks (Repp, 2008, Repp & Bruttomesso, 2009). The presumed mechanisms are that subdivisions can reduce the underestimation of inter-onset intervals ----the cause of the negative mean asynchronies due to taps that anticipate the beat (Wohlschläger & Koch, 2000)— and improve the prediction of future events. The subdivision benefit could also have great potential for improving the beneficial effects of periodic musical stimulation on motor control in people with impaired coordination (e.g., Parkinson’s disease, Damm et al., 2020).

Subdivision benefits in musicians and non-musicians have been found for distinct subdivision ratios and tempi (e.g. 1:2, 1:3, 1:4; in Repp, 2008; and Zendel, Ross & Fujioka, 2011). Repp (2003) showed that tapping variability decreased when the taps were subdivided by evenly paced sounds. Zendel, Ross and Fujioka (2011) found that negative mean asynchronies decreased when subdivision tones occurred between constant inter-tapping intervals (ITIs). Interestingly, the synchronization of musicians was better than non-musicians when they tapped to the beat of

subdivisions ranging from 1:2 to 1:9 ratios (Repp, 2007). That is, non-musicians' tapping synchronization was reduced for all uneven subdivisions, while musicians showed the slowest synchronization for the quintuplets (1:5), which are scarce in Western music. In contrast, there was a general SMS advantage for binary subdivisions compared to ternary and uneven subdivisions. Similarly, tapping synchronization improves when participants imagine an antiphase beat (i.e. 1:2, the duplet) or tap to every other sound (2:1, binary meter) (Repp & Dogget, 2007; Repp, 2010b). Importantly, binary subdivisions are present in most cultures around the world (Savage et al., 2015), emerge spontaneously in iterated learning paradigms (Ravignani, Delgado & Kirby, 2016), and could arise from the interaction of categorical perception with timing scalar properties (Ravignani, Thompson, Lumaca & Grube, 2018). Together, these findings suggest that both musical training and binary meters may interact with the neural processing of the subdivisions and the related SMS advantage.

We can study this SMS advantage through neural entrainment to subdivisions using frequency-tagging (Nozaradan, 2014), a method that consists of converting steady-state evoked potentials (SSEPs) —neural activity frequency-locked and phase-locked to the stimuli — into amplitudes on the frequency dimension. This is based on the neural resonance theory of rhythm (Large & Snyder, 2009), which states that beat perception arises from the entrainment of populations of neurons “resonating” to the frequency of the beat, which in turn produces higher-order oscillations at the frequency of harmonics (i.e. subdivisions) and subharmonics (i.e. metrical groupings). Higher-order oscillations in EEG/MEG recordings reflect the integration of exogenous (bottom-up) and endogenous (top-down) processes underlying the perception and prediction of the beat and its metrical grouping (Nozaradan et al., 2011; Fujioka, Zendel & Ross, 2010; Stupacher et al., 2016; Celma-Mirallès, de Menezes & Toro, 2016). In fact, neural entrainment is not just a

reflection of the physical signal (Pretto, Deiber & James, 2018) but involves the selection and enhancement of relevant frequencies of the signal, such as the beat of complex syncopated rhythms (Nozaradan, Peretz & Keller, 2016; Tal et al., 2017), the periodic pulses of naturalistic musical excerpts (Tierney & Kraus 2015), and the syntactic levels of linguistic phrases (Ding et al., 2017).

This work has mainly focused on beat perception and synchronization at the slower metrical level (Nozaradan, 2014; Fujioka, Ross & Trainor, 2015; Vuust & Witek, 2014; Cirelli et al., 2016) and dealt with subdivisions only indirectly, as complex auditory stimuli inherently make use of faster metrical levels. For instance, subdivisions are found in syncopations (Tal et al., 2017) and polyrhythms (Stupacher, Wood & Witte, 2017; Vuust et al., 2006), rhythmic patterns can be grouped by 2 or 3 (Nozaradan, Peretz & Mouraux, 2012), and sequences can be organized into binary metrical levels, which can elicit mismatch negativities (Honing, Bower & Háden, 2014; Vuust et al., 2005) or metrically-differentiated ERPs (Brochard et al., 2003). Even tapping to every other sound following a binary meter could be conceived as tapping to the beat of very slow duplets (Nozaradan, Zerouali, Peretz & Mouraux 2015).

The present study focuses on the natural frequency range of the subdivision and its processing in the brain by directly targeting the neural underpinnings of the subdivisions. Using frequency tagging of the EEG, we study the subdivision benefit in the brain and compare the neural responses between musicians and non-musicians. We expect that binary subdivisions would produce more consistent tapping performances than non-binary subdivisions in both musicians and non-musicians, and that this improvement will be reflected in the frequency-tagged amplitudes related to the beat and its harmonics. We also hypothesize that musically-trained participants would tap more consistently than musically-naïve participants across subdivisions, especially with triplets (as in Repp, 2007). Finally, we predict positive correlations between finger-tapping

performances and the neural amplitudes of the participants (as in Nozaradan, Peretz & Keller, 2016). Thus, the comparison of the amplitudes across tasks and participants can reveal the presence of neural advantages in relation to particular subdivisions, differences between the listening and the tapping tasks (perceptual versus SMS), and the extent to which they depend on use-dependent brain plasticity (i.e. musical training).

MATERIALS and METHODS

Participants

Thirty-one healthy volunteers (22 female, mean age: 23.39 ± 3.21 , age range: 19-35) participated in this study after providing written informed consent. Sixteen of them pursued (at least) ten years of formal training in music and/or extensive musical practice (henceforth, *musicians*). The other fifteen participants pursued less than two years of basic music training, if any, (henceforth, *non-musicians*). No one of them reported any hearing, psychiatric or neurological disorder. To validate the two groups, participants performed the rhythmic discrimination of the Musical Ear Test (Wallentin et al., 2010), which revealed that the scores for musicians ($M = 79.57$, $SE = 1.65$) were higher than the scores of non-musicians ($M = 66.28$, $SE = 1.88$; $t_{(29)} = 5.33$, $p < .001$). The ethical board of Aarhus University Hospital approved all the procedures.

Auditory Stimuli

The stimuli consisted of isochronous sequences of tones, in which a periodic beat was subdivided into duplets (1:2), triplets (1:3), quadruplets (1:4) and quintuplets (1:5). The beat frequency was set at 1.25 Hz because previous research revealed that it easily elicits steady-state evoked potentials and allowed all subdivisions to fall within the ecological range of beat perception

(London, 2012). We created a 30 ms-pure tone at the pitch frequency of 659 Hz, whose amplitude was shaped from 0 to 1 with a sinusoidal bell curve (see Figure 1). To create each auditory rhythm, we presented this sound at distinct inter-onset intervals (IOI). There were five different rhythmic sequences that lasted 20 seconds, the beat (25 sounds presented at 1.25 Hz, IOI = 800 ms), the duplets (50 sounds at 2.5 Hz, IOI = 400 ms), the triplets (75 sounds presented at 3.75 Hz, IOI = 266 ms), the quadruplets (100 sounds presented at at 5 Hz, IOI = 200 ms), and the quintuplets (125 sounds presented at at 6.25 Hz, IOI = 160 ms). For the practice trials, we used shorter sound sequences that lasted 6.4 seconds, in which the sounds that did not occur at the beat frequency – those that created each subdivision rhythm and occupied offbeat positions – were reduced 50% in their amplitude. All the auditory stimuli were created in Matlab 2019b (MathWorks) and presented binaurally through in-ear headphones at a comfortable hearing level, by using Psychtoolbox.

Paradigm

After signing the informed consent form, participants comfortably sat in the silent room and went through two tasks. First, they performed the rhythmic part of the Musical Ear Test (Wallentin et al., 2010). In this behavioral test, participants had to listen to 52 pairs of rhythmic sequences and answer in a paper form whether they were identical or different. Secondly, the EEG setting was prepared and the scalp electrodes were positioned. During the EEG paradigm, participants were facing a screen, which displayed the self-spaced experimental instructions, alerts to take 2 breaks (after approximately 15 minutes each), and a fixation cross to keep the eyes quiet during the tasks. A tapping midi device was located close to their hand in front of them. In the beginning, participants were presented with short practice trials and the experimenter instructed them when to tap the beat of the distinct subdivisions. Every auditory trial consisted of four parts, in which participants had to: (1) listen to an isochronous beat, (2) listen to one of the four

subdivisions, (3) listen to the beat again, and (4) listen to the same subdivision while tapping the beat (see Figure 1). The fixation cross was converted into a count-down from 3 to 1, just before the tapping task, to prepare participants. After eight practice trials, the experiment started, and participants listened to the actual trials presented 9 times in a pseudo-randomized order. This order was counterbalanced across participants and aimed to avoid consecutive repetitions of the same trial. During the two breaks, the experimenter responded to the participants' comments and checked the quality of the EEG recordings.

---- Figure 1 about here ----

EEG recordings

We recorded each participant's electroencephalographic signal using the BrainVision Analyzer Software package (BrainVision Recorder 2.1, Gilching, Germany), with a BrainAmp amplifier (Brain Products GmbH, Germany) and a 32-electrodes actiCap (Fp1, Fp2, F3, F4, C3, C4, P3, P4, F7, F8, T7, T8, P7, P8, Fz, Cz, Pz, FC1, FC2, CP1, CP2, FC5, FC6, CP5, CP6, TP9, TP10, Oz) placed on the scalp following the International 10/20 system. Two electrodes were placed on the left and right mastoid (RM and LM). Horizontal and vertical eye movements were monitored using two electrodes placed on the right eye: at the infra-orbital ridge and at the outer canthus (EogV and EogH). The signal was recorded with reference to the FCz channel. All electrode impedances were kept below 20 k Ω . The signals were amplified and digitized at a sampling rate of 1000 Hz, with an online low cut-off of 10 seconds and high cut-off of 1000 Hz.

EEG analyses

We pre-processed the EEG recordings using BrainVision Analyzer 2.1 (Brain Products GmbH). We interpolated any channel that appeared very noisy or flat from the surrounding channels via spherical spline interpolation. Subsequently, all channels were re-referenced to a common average-reference, which gave us back the channel FCz for following analyses. We preprocessed the EEG signal using a zero-phase Butterworth filter to remove slow drifts in the recordings with a notch filter at 50 Hz, a high pass filter at 0.1 Hz (with order 8) and a low pass filter at 30 Hz (with order 8). We automatically detected offline whether the EEG activity crossed a maximal allowed voltage step of 50 $\mu\text{V}/\text{ms}$, a maximal allowed difference of voltage of $\pm 100 \mu\text{V}$ or a voltage lower than 0.5 μV , and marked it as bad intervals within $\pm 200 \text{ ms}$. We removed the eye blinks and clear muscular movements from the signal by using the Ocular Correction ICA function, which was based on the EEG data free of bad intervals. Finally, we segmented the filtered EEG data based on task and subdivision rhythm, and exported the nine 20-second trials into European Data Format. All further analyses were performed in Matlab, SPSS (version 19, IBM) and R Studio software (version R-3.6.2).

We removed the first 1.6 seconds of each 20-second sequence, to discard the evoked potentials related to the onset of the stimuli (and any changes across tasks), taking into account that steady-state evoked potentials require some repetitions to appear (Nozaradan et al, 2011). To attenuate neural activities non-phase-locked to the stimuli or to the motor task, we averaged the EEG epochs for each participant and condition across the nine trials. We applied a fast Fourier transform (zero-padded to the next power of 2: 2^{15}) and got the signal's amplitude (in μV) over a frequency range from 0 to 500 Hz and a bin frequency resolution of 0.0305 Hz. These amplitudes may represent the sum of the neural activity induced by the processing of the physical stimuli and

some background noise or spontaneous activity. To increase the signal-to-noise ratio, we subtracted from each frequency bin the averaged amplitude of the two surrounding non-adjacent frequency bins, that is, from -0.153 to -0.122 Hz and from 0.122 to 0.153 Hz. We assume that, if no steady-state evoked potentials are present, all the frequencies of the spectra may vary similarly (Nozaradan, 2014). Therefore, after the subtraction of the means of adjacent frequency bins, each frequency peak should randomly tend towards zero. To discover the presence of peaks related to beat and its subdivisions in the frequency spectra, all participants' magnitudes centered at our frequencies of interest were averaged across the scalp and submitted to *t*-tests against zero. In an additional analysis (see Supplementary Figure 3), we firstly applied the fast Fourier transform to each trial and afterwards the trial average to control for the possibility that the neural entrainment to the beat of the subdivision could be phase-locked to another sound of each subdivision group (e.g. the second sound of the duplet).

The Supplementary Table 1 reports the *t*- and *p*-values of all the peaks and their harmonics for each frequency and subdivision. For all four subdivisions, *t*-tests against zero revealed that there were SSEPs elicited at all frequencies (all $p < .001$) during the listen-to-the-beat tasks. Similarly, during the listen-to-the-subdivision and the tapping-to-the-beat tasks there were SSEPs elicited at the frequencies related to each subdivision (all $p < .001$). Interestingly, there was a peak at 1.25 Hz for quadruplets during the listen-to-the-subdivision task ($p < .044$) and for all subdivisions during the tapping-to-the-beat task (all $p \leq .002$). If the Bonferroni correction is applied to the sixteen tests comprised in each frequency, the alpha drops to the conservative level of significance $p < .003$, still above the *p*-values of the peaks reported here. Thus, several peaks appeared in the frequency spectra of the beat and its four subdivisions, centered at 1.25, 2.5, 3.75, 5 and 6.25 Hz (see Figure 2).

--- Figure 2 about here ---

For each target frequency, the amplitudes of the peaks were submitted to three-way Mixed Design ANOVAs. First, we compared at each frequency (1.25, 2.5, 3.75, 5, 6.25 Hz) how the perception of beat was affected by listening to distinct subdivisions. Five three-way mixed design ANOVAs were applied to the peak magnitudes with the within-factors Task (Pre-Subdivision, Post-Subdivision) and Rhythm (Duplets, Triplets, Quadruplets, Quintuplets), and the between-factors Group (Musicians, non-Musicians). Second, we compared at each frequency of interest how the perception of the subdivision was affected by the tapping to the beat. Five three-way mixed design ANOVAs were run again, but using the within-factor Task (Subdivision, Tapping). When the assumption for sphericity was violated, we corrected the degrees of freedom using Greenhouse-Geisser estimates of sphericity. When significant effects and/or interactions appeared, we applied *post hoc* two-tailed *t*-tests with the Bonferroni correction (with significance level at $p < .05$).

In addition, to compare the effects of the subdivision on the perception of beat across frequencies, we subtracted the PreSubdivision amplitudes from the PostSubdivision ones. We also subtracted the Subdivision amplitudes from the Tapping ones, to account for the effects of tapping on the perception of the subdivision across frequencies. The obtained “values” were analyzed in two separated three-way mixed design ANOVAS, with the within-factors Frequency (1.25, 2.5, 3.75, 5, 6.25 Hz) and Rhythm (Duplets, Triplets, Quadruplets, Quintuplets), and the between-factors Group (Musicians, non-Musicians), followed by corrected *post hoc* comparisons.

Behavioral analyses

First, we calculated the ITIs of the finger-tapping responses, and cleaned out the double-taps by removing the second tap of two consecutive taps within ITIs below 150 ms. Next, we corrected the timings for an approximate recording delay of 20 ms. Finally, we converted the finger-tapping responses into a common angular scale in radians by multiplying the value of each tap by 2π and dividing it by the beat IOI (i.e. 800 ms). For each subject, trial and subdivision rhythm, we calculated the mean resultant vector and its length by using the Matlab Toolbox for Circular Statistics (Berens, 2009). The angular direction of the mean resultant vector indicates the position of the taps (i.e. phase) in relation to an isochronous beat, while the length of the mean resultant vector is indirectly related to the variance between taps, and reflects how concentrated the taps are around the mean angular direction. An Omnibus test revealed that the angular directions of all participants were not uniformly distributed around the circle ($p < .001$), but that they occurred in specific directions. Circular V-tests showed the mean vector directions of both musicians and non-musicians pointed towards 0° , corresponding to the beat “onset”, for all rhythm subdivisions ($p < .001$), except for quintuplets in non-musicians ($p = .105$). To account for the effects of the subdivision rhythm and the musical training, we ran a robust circular two-factor ANOVA known as Harrison-Kanji test (Berens, 2007). To provide evidence of unequal group directions across groups, we compared musicians’ and non-musicians’ angular directions for every subdivision rhythm using Watson-Williams tests, circular analogues of two-sample t -tests. To test the consistency of the taps, we run on the mean vector length a Mixed-Design Anova, with the within factor Subdivision rhythm (duplet, triplet, quadruplet, quintuplet) and the between-factor Musical training (musicians, non-musicians), followed by the Bonferroni-corrected post hoc t -tests.

RESULTS

Steady-state Evoked Potentials related to the beat and its subdivisions

First, we analyzed how listening to distinct subdivisions affected the neural entrainment to the beat. The analyses of variance showed that there was a significant effect of Task on the peak magnitudes centered at 1.25, 2.5 and 6.25 Hz (all $p \leq .021$, see Table 1a). The *post hoc* pairwise comparisons revealed that the peaks at 1.25 Hz ($M_{pre} = 0.09$, $SE = .014$, $M_{post} = 0.11$, $SE = .012$, $MD = 0.02$, $p = .021$) and 2.5 Hz ($M_{pre} = 0.04$, $SE = .006$, $M_{post} = 0.05$, $SE = .006$, $MD = 0.01$, $p = .019$) increased in amplitude after listening to subdivisions. In contrast, the amplitudes at 6.25 Hz decreased after listening to the subdivisions ($M_{pre} = 0.03$, $SE = .003$, $M_{post} = 0.02$, $SE = .003$, $MD = 0.01$, $p = .018$). The absence of any interaction may indicate that these increases of the peaks of the beat and its first harmonic occurred after listening to all subdivision rhythms in both musicians and non-musicians (see Figure 3).

--- Table 1 about here ---

--- Figure 3 and 4 about here ---

Subsequently, we studied how tapping to the beat affected the neural entrainment to the beat and its subdivision. The analyses of variance revealed multiple main effects and interactions across the five frequencies (see Table 1b). Importantly, we found a significant interaction between Task and Musical training across all frequencies (all $p \leq .005$), as well as between Task and Subdivision rhythm (all $p \leq .029$, except at 5 Hz). The latter interaction also depended on Musical training at 1.25 and 2.5 Hz (all $p \leq .005$). The *post hoc* pairwise comparisons revealed three main findings (see Figure 4). First, musicians' amplitudes were greater than non-musicians' amplitudes in the tapping task (see Table 2). This was true for all subdivisions at 3.75, 5 and 6.25 Hz, for

triplets and quadruplets at 1.25 and 2.5 Hz, and for duplets at 2.5 Hz. Second, the amplitudes in the tapping task were generally greater than the amplitudes in the listening task (see Table 2 and Table 3). This effect was mainly found in musicians across all subdivisions and frequencies (except for quintuplets at 2.5 Hz, $p = .065$), and only found in non-musicians for duplets and triplets at 1.25 Hz (see Table 2). Besides, the increase due to tapping seems to be non-significant for quintuplets at 3.75 and 6.25 Hz, and for duplets at 6.25 Hz (see Table 3). Third, the amplitudes at the frequency of each subdivision were higher than the amplitudes at frequencies unrelated to the subdivision for both musicians and non-musicians during listening and tapping (see Table 4). Interestingly, the amplitudes related to quintuplets were smaller at 4 Hz for all participants during both tasks, at 3.75 Hz in the tapping task, and at 1.25 and 2.5 Hz in the tapping task, but only in musicians. Finally, at 1.25 Hz, non-musicians had higher amplitudes when they tapped to the beat of duplets, compared to quadruplets and quintuplets.

--- Table 2, 3, and 4 about here ---

Peak increases across frequencies and subdivision rhythms

For the Post-Pre subtraction, the ANOVA showed a main effect of Frequency (see Table 1c). The *post hoc* pairwise comparisons (depicted in Figure 5a) indicated that the increases at 1.25 Hz ($M = .019$, $SE = .008$) were greater than the increases at 5 Hz ($M = -.004$, $SE = .003$, $MD = .023$, $p = .023$), and that the increases at 2.5 Hz ($M = .008$, $SE = .003$) were greater than the increases at 3.75 Hz ($M = -.005$, $SE = .003$, $MD = .013$, $p = .021$), 5 Hz ($M = -.004$, $SE = .003$, $MD = .012$, $p = .014$), and 6.25 Hz ($M = -.005$, $SE = .002$, $MD = .013$, $p = .025$). For the Tap-Sub subtraction, the ANOVA revealed a significant interaction between Frequency, Rhythm and Music (see Table 1c). The *post hoc* pairwise comparisons (see Figure 5b) showed that, in non-musicians, the increases at 1.25 Hz were larger for duplets than in quadruplets ($p = .015$), while in musicians, the

increases at 1.25, 2.5 and 3.75 Hz were larger for duplets, triplets and quadruplets compared to quintuplets (all $p \leq .038$), the increases at 5 Hz were larger for triplets compared to quadruplets and quintuplets (all $p \leq .033$) and the increases at 6.25 Hz were smaller for quintuplets compared to triplets and quadruplets (all $p \leq .013$).

--- Figure 5 about here ---

Finger-tapping responses

The Harrison-Kanji test on the mean angular directions of the taps revealed an effect of musical training ($F_{(1, 123)} = 13.11, p < .001$) and an effect of subdivision rhythm ($F_{(3, 123)} = 3.29, p = .023$), but no interaction between them ($F_{(3, 123)} = 1.65, p = .181$). The post-hoc Watson-Williams tests revealed that there were differences between musicians and non-musicians ($F_{(1, 123)} = 5.55, p < .020$), but no differences between the four conditions (all $p > .05$). However, when musicians' and non-musicians' angular directions were compared for every subdivision rhythm using Watson-Williams tests, differences between them appeared for the quintuplet rhythm ($p = .005$). Besides, the angular directions during the tapping to the quintuplets were not different from the other subdivisions in musicians (all $p > .05$), while they were different from triplets ($p = .025$) and quadruplets ($p = .038$), but not duplets ($p = .073$), in non-musicians (see Figure 6a). The Mixed-Design Anova on the mean vector length (i.e. tapping consistency) revealed a main effect of Subdivision rhythm ($F_{(1.63, 47.28)} = 69.05, p < .001$), a main effect of Musical training ($F_{(1, 29)} = 23.80, p < .001$) and an interaction between them ($F_{(1.63, 47.28)} = 4.22, p = .027$). The subsequent Bonferroni-corrected post hoc t -tests (see Figure 6b) revealed that tapping consistency was larger for musicians than for non-musicians at all subdivisions (all $p < .001$) except quintuplets ($p = .083$). For non-musicians, duplets ($M = .725, SE = .045$) were higher than triplets ($M = .595, SE = .050$), quadruplets ($M = .599, SE = .048$) and quintuplets ($M = .330, SE = .057$, all $p \leq .002$), and

quintuplets were smaller than duplets, triplets and quadruplets (all $p \leq .002$). For musicians, only quintuplets ($M = .472$, $SE = .055$) were smaller than duplets ($M = .974$, $SE = .044$), triplets ($M = .957$, $SE = .048$) and quadruplets ($M = .936$, $SE = .047$, all $p < .001$).

--- Figure 6 about here ---

Correlations between MET, tapping and neural entrainment

For every subdivision rhythm, we computed Spearman's rank correlation coefficients to assess the relationship between the consistency in tapping and the discriminatory abilities obtained in the MET. There was a positive correlation between the two variables, for duplets ($\rho = 0.53$, $p = .002$), for triplets ($\rho = 0.57$, $p < .001$), and for quadruplets ($\rho = 0.5$, $p = .004$), but not for quintuplets ($\rho = 0.34$, $p = .058$; see Supplementary Figure 1). However, these positive correlations disappeared when we split participants into musicians and non-musicians (all $p > .05$), suggesting that musicians had more consistent taps and higher scores in MET than non-musicians.

To assess the effect of the synchronized tapping on the perception of each subdivision, we computed Spearman's rank correlations between the consistency in tapping to each subdivision rhythm and the increases of the EEG amplitudes (i.e. tapping – listening to subdivision) at all frequencies. At 1.25 Hz, positive correlations were found for duplets ($\rho = 0.57$, $p = .001$), triplets ($\rho = 0.69$, $p < .001$) and quadruplets ($\rho = 0.52$, $p = .003$), but not for quintuplets ($\rho = 0.06$, $p = .750$). At 2.5 Hz, positive correlations were found for duplets ($\rho = 0.53$, $p = .003$), triplets ($\rho = 0.79$, $p < .001$), quadruplets ($\rho = 0.61$, $p < .001$) and quintuplets ($\rho = 0.58$, $p < .001$). At 3.75 Hz, positive correlations were found for duplets ($\rho = 0.60$, $p < .001$), triplets ($\rho = 0.45$, $p = .012$) and quadruplets ($\rho = 0.66$, $p < .001$), but not for quintuplets ($\rho = 0.18$, $p = .32$). At 5 Hz, positive correlations were found not for duplets ($\rho = 0.4$, $p = .028$), triplets ($\rho = 0.66$, $p < .001$) and

quintuplets ($\rho = 0.59$, $p < .001$), but not for quadruplets ($\rho = 0.16$, $p = .390$). Finally, at 6.25 Hz, positive correlations were found for duplets ($\rho = 0.44$, $p = .014$), triplets ($\rho = 0.47$, $p = .008$) and quadruplets ($\rho = 0.39$, $p = .032$); but not for quintuplets ($\rho = 0.14$, $p = .460$). The more consistent the tapping to the beat was, the greater the amplitude increases at the beat-related frequencies (see Supplementary Figure 2).

Since we found an increase at the frequency of the beat and its first harmonic after listening to all four subdivisions, we decided to explore whether these increases could relate to a better performance in tapping. Again, we computed Spearman's rank correlations between the consistency in tapping to each subdivision rhythm and the increases of the EEG amplitudes (i.e. post – pre listening to subdivision) at 1.25 and 2.5 Hz. However, no correlations were found (all $p > .05$). This indicates that the increased entrainment to the beat does not produce better tapping responses.

DISCUSSION

We found enhancement of neural entrainment indicated by the SSEPs in musicians compared to non-musicians when they tap along with a subdivided beat, but not when they merely listen to it. For both groups, neural entrainment was greater in the tapping than in the listening conditions. For non-musicians, both neural entrainment and tapping responses reflected an advantage for binary subdivisions. That is, non-musicians tapped more consistently to the beat of the duplets compared to all other subdivisions, thus reinforcing the simplest 1:2 temporal ratios. In contrast, musicians performed highly consistently across all subdivisions, except for the quintuplets, which reduced tapping performance similar to non-musicians. Importantly, for both groups of participants, the

neural entrainment to the beat and its first harmonic—i.e. the binary subdivisions—increased after listening to any type of subdivision, even if these were not binary. This indicates that despite the brain’s preference for the simplest binary subdivision, musicians may be able to compensate for any disadvantage when tapping along with other subdivisions.

Neural entrainment increases during tapping

Our main finding is that SMS increases the neural entrainment to the beat and its harmonics. However, these increases vary as a function of musical training and the number of subdivisions. For example, when musicians tapped to the beat of the subdivision, their amplitudes increased across frequencies and subdivision rhythms (see Figure 4b), but became smaller at higher frequencies and faster rhythms. This could mean that musicians were able to improve their temporal predictions with an increased number of events, except for the quintuplets (Figure 5b). This was not the case for non-musicians, who only showed neural increases for duplets and triplets at the frequency of the beat. It is interesting to point out that these two subdivisions correspond to the smallest integer ratios found across cultures (Savage et al., 2015), and appear when adult and child non-musicians reproduce rhythms (Drake, 1998).

Another finding was that the EEG amplitudes of musicians and non-musicians only differed during the sensorimotor task, at the beat frequency, and not for all subdivisions. This may reflect the effect of years of extensive musical practice involving rhythmic synchronization. It seems that differences in the neural entrainment between musicians and non-musicians during listening may only occur when top-down perceptual tasks are required, such as keeping a mental pulse (Stupacher, Wood and Witte, 2017), building a metrical structure (Celma-Miralles and Toro, 2019) or performing SMS tasks (Lenc, Keller, Varlet and Nozaradan, 2020). Furthermore, the

neural entrainment to the beat of duplets and quintuplets was not different between the two groups. This suggests a default advantage for SMS with duplets, which may become overshadowed in highly trained musicians, as well as a general disadvantage for SMS with the less common quintuplets. That is, regardless of musical training, the tapping consistency of quintuplets decreased and elicited less neural entrainment across frequencies, perhaps due to its scarce presence in the Western music tradition and the fast tempo of the quintuplets' IOIs.

Neural entrainment increases after listening to the subdivisions

Another relevant finding is that after listening to any kind of subdivision, the frequency-tagged peaks increased at the frequency of the beat and its first harmonic. We speculate that these two increases reflect a stabilization of the neural entrainment to the frequency of the beat and its smaller integer ratio, the duplex (1:2). This would be in line with the small integer ratio bias in timing (discussed in Ravignani, Thompson, Lumaca and Grube, 2018; also see Mathias, Zamm, Ross, Gianferrara, and Palmer, 2020), and could explain the presence of duplets in all musical idioms (Savage et al., 2015). On the other hand, these increases could also reflect attentional demands during the preparation of the tapping to the beat. In the study by de Pretto, Deiber and James (2018), attentional demands during SMS were related to a stronger activation in the bilateral middle/posterior cingulate gyrus, which is involved in attention-related motor control (Vogt, 2009; Leech and Sharp, 2014), for the first harmonic compared to the beat frequency. However, this difference disappeared in passive listening. More evidence comes from Tierney and Kraus (2014), who connected increases at the beat frequency and its first harmonic to the attentional processing of an accentuated beat within a metrical grid. Further research should therefore disentangle the role of attention during preparation of the motor task from the cognitive processes that enhance the beat based on its simplest binary subdivision (1:2 ratio).

The binary subdivision advantage and musical training

The neural entrainment to the duplets was not different between musicians and non-musicians, despite the fact that non-musicians tapped more consistently to the beat of the duplets than to the beat of any other subdivision. The existence of a general SMS advantage for duplets, as outlined above, may perhaps be related to common binary-structured actions, such as bipedal walking. Preferences for binary structures can be found in the predisposition of young infants to easily process duple meter (Bergeson and Trehub, 2005) or in the automatic grouping led by the “tick-tock” effect (Brochard et al., 2003). Binary groupings (1:2 and 2:1) also emerge from iterated learning paradigms in which non-musicians listen to chaotic auditory sequences and transmit the rhythmic patterns from one generation to another during repetition (Ravignani, Delgado and Kirby, 2016). Together, this suggests that binary structures exist already in early stages of development and do not require musical training to emerge. It implies that our musically-naïve participants benefited from listening to duplets in the tapping task, whereas this effect disappears in musically-trained participants due to the training of SMS to triplets and quadruplets. Indeed, the increases of musicians’ neural entrainment to the tapping of triplets and quadruplets may reflect the brain’s adaptation to music playing (Zatorre, Chen and Penhune, 2007; Chen, Penhune and Zatorre, 2008), which boosts the coupling of auditory and motor areas to optimize temporal predictions (Morillon and Baillet, 2017; Damm et al., 2020).

Limitations of this study

While listening to the subdivision, the neural entrainment to the frequency of the beat was generally missing across all but the quadruplets subdivisions, which showed a peak significantly distinct from zero. We can therefore not exclude the possibility that participants could have entrained to the subdivisions as faster beat sequences. That is, without a clear bottom-up cue

signaling the “strong” beat (Farrokh, 2018), participants may have anchored the downbeat of the subdivision at distinct positions within the subdivision rhythm, and the average of trials may have neutralized the distinctly phase-locked SSEPs. Additional frequency analyses, with FFT prior to averaging the trials, showed peaks at the frequency of the beat for triplets and quadruplets (Supplementary Figure 3). An absence of peaks at the beat frequency of duplets and quintuplets could indicate two things: the IOI of duplets was comfortable enough in tempo to be perceived as a “new beat” substituting the previous beat (IOI=800 ms). Likewise, the IOI of quintuplets could have been too short to precisely keep the cyclical downbeat by top-down projections. However, this does not affect our main findings, as neural entrainment to the beat was present in the tapping condition for all subdivisions. In fact, when analyzing tapping performance together with the neural responses underlying the predictive SMS task, most of the increases of the amplitudes correlated with the consistency of taps across frequencies and subdivisions (similar to Nozaradan, Peretz & Keller, 2016), which supports the behavioral relevance of our results. Further research should take into account some acoustic manipulations to signal the downbeat of the subdivision in order to avoid timing confusions in the grouping of the rhythms.

CONCLUSIONS

When we listen to music, our brain automatically entrains to the underlying periodicities of its rhythms. The main pulse that we synchronize to is the beat, which can be divided into faster, evenly-paced subdivisions. The present work studied the neural underpinnings of processing two binary subdivisions (duplets and quadruplets) and two non-binary subdivisions (triplets and quintuplets). We found that neural entrainment to the beat and its first harmonic (the frequency of the duplets) increased after listening to any of the subdivisions, likely stabilizing the perception of the beat, which could account for an enhanced tapping performance. While non-musicians’ neural

entrainment only increased during the tapping to the beat for duplets and triplets, musicians' amplitudes increased for all subdivisions and beyond the frequency of the beat. In general, musicians had better finger-taps predicting the beat within the auditory subdivision. Moreover, while both groups tapped to the beat of quintuplets with less consistency, non-musicians tapped to the beat of duplets more consistently. Based on these data, we provide novel evidence for the existence of a neural “default” SMS advantage for duplets (1:2), the simplest binary subdivision of the beat that is present in the majority of cultures. Our results also support evidence for neural and behavioral sensorimotor differences related to formal training in music. The demonstrated binary subdivision advantage may also be relevant for clinical applications by improving the beneficial effects of periodic musical stimulation in patients with movement disorders.

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TABLES

a) Listening to PreSubdivision versus PostSubdivision																	
frequencies		Task				Rhythm				Task*Rhythm				Music			
		df	F	p	η^2	df	F	p	η^2	df	F	p	η^2	df	F	p	η^2
1.25 Hz		1,29	5.93	.021	.170	2,3,67.5	1.43	.246	.047	3,87	1,28	.285	.042	1,29	0.26	.613	.009
	*Music	1,29	0.14	.708	.005	2,3,67.5	0.64	.555	.022	3,87	0.48	.695	.016				
2.5 Hz		1,29	6.18	.019	.176	3,87	1.05	.375	.035	2,4,70.6	0.15	.896	.005	1,29	0.02	.901	.001
	*Music	1,29	0.63	.433	.021	3,87	0.92	.434	.031	2,4,70.6	2.33	.094	.074				
3.75 Hz		1,29	3.03	.093	.094	3,87	0.48	.697	.016	3,87	1.32	.272	.044	1,29	1.08	.308	.036
	*Music	1,29	1.19	.285	.039	3,87	0.55	.650	.019	3,87	0.27	.851	.009				
5 Hz		1,29	2.18	.151	.070	3,87	2.99	.035	.094	3,87	1.16	.332	.038	1,29	0.06	.806	.002
	*Music	1,29	1.30	.263	.043	3,87	1.27	.291	.042	3,87	0.66	.582	.022				
6.25 Hz		1,29	6.24	.018	.177	3,87	1.45	.234	.048	3,87	0.29	.833	.010	1,29	0.00	.984	.000
	*Music	1,29	2.99	.094	.094	3,87	1.49	.224	.049	3,87	1.71	.170	.056				
b) Listening to Subdivision versus Tapping																	
1.25 Hz		1,29	58.97	<.001	.670	2,3,68.1	15.84	<.001	.353	2,3,65.9	13.87	<.001	.324	1,29	15.15	.001	.343
	*Music	1,29	15.05	.001	.342	2,3,68.1	5.33	.005	.155	2,3,65.9	5.44	.005	.158				
2.5 Hz		1,29	41.60	<.001	.589	1,9,55.1	91.90	<.001	.760	2,2,63.2	17.97	<.001	.383	1,29	20.7	<.001	.416
	*Music	1,29	24.51	<.001	.458	1,9,55.1	3.28	.047	.102	2,2,63.2	9.59	<.001	.249				
3.75 Hz		1,29	40.88	<.001	.585	1,8,51.0	81.55	<.001	.738	3,87	8.66	<.001	.230	1,29	14.08	.001	.327
	*Music	1,29	21.37	<.001	.424	1,8,51.0	1.51	.233	.049	3,87	1.50	.221	.049				
5 Hz		1,29	14.52	.001	.334	1,9,55.7	72.68	<.001	.715	2,1,61.2	1.58	.213	.052	1,29	12.84	.001	.307
	*Music	1,29	9.70	.004	.251	1,9,55.7	1.62	.209	.053	2,1,61.2	1.17	.320	.039				
6.25 Hz		1,29	5.16	.031	.151	1,6,45.1	53.28	<.001	.648	2,5,71.6	3.43	.029	.106	1,29	3.66	.066	.112
	*Music	1,29	9.43	.005	.245	1,6,45.1	0.31	.681	.011	2,5,71.6	2.36	.090	.075				
c) Differences in amplitudes between conditions																	
subtraction		Frequency				Rhythm				Frequency*Rhythm				Music			
		df	F	p	η^2	df	F	p	η^2	df	F	p	η^2	df	F	p	η^2
Post-Pre		1,7,50.2	7.53	.002	.206	3,87	0.55	.649	.019	6,6,190	1.07	.382	.036	1,29	1.51	.230	.049
	*Music	1,7,50.2	0.01	.991	.000	3,87	0.38	.770	.013	6,6,190	1.11	.359	.037				
Tap-Sub		2,0,58.7	28.80	<.001	.498	2,1,61.3	32.16	<.001	.526	5,5,158.2	6.33	<.001	.179	1,29	38.89	<.001	.573
	*Music	2,0,58.7	7.78	.001	.212	2,1,61.3	12.87	<.001	.307	5,5,158.2	3.14	.008	.098				

Table 1. Main effects and interactions of EEG frequency-tagged amplitudes. Degrees of Freedom, F-statistic, *p*-value and η^2 effect size of the 3-way Mixed Design ANOVAs for the comparisons of (a) the listening to the beat before and after the subdivision (amplitudes at each frequency), (b) the listening to the subdivision passively or while tapping to the beat (amplitudes at each frequency), and (c) the subtraction of peak amplitudes across frequencies (differences in the listening-to-the-beat and the-listening-to-the-subdivision conditions). All the interactions with the between-factor “Musical training” are reported in a second line below the within-factors main effects and interactions. Significant *p*-values appear in bold.

			Listening	Tapping	Mean Diff. (Tap - Listen)
1.25 Hz	Duplets	Non-Musicians	M = .016 SE = .010	M = .116 SE = .031	MD = .100 $p = .004$
		Musicians	M = .005 SE = .009	M = .194 SE = .030	MD = .189 $p < .001$
		Mean Diff. (M - nonM)	MD = -.011 $p = .422$	MD = .078 $p = .079$	
	Triplets	Non-Musicians	M = .007 SE = .010	M = .071 SE = .027	MD = .063 $p = .030$
		Musicians	M = .006 SE = .009	M = .232 SE = .027	MD = .226 $p < .001$
		Mean Diff. (M - nonM).	MD = -.002 $p = .911$	MD = .161 $p < .001$	
	Quadruplets	Non-Musicians	M = .012 SE = .012	M = .048 SE = .023	MD = .035 $p = .165$
		Musicians	M = .023 SE = .012	M = .220 SE = .023	MD = .197 $p < .001$
		Mean Diff. (M - nonM)	MD = .011 $p = .533$	MD = .172 $p < .001$	
	Quintuplets	Non-Musicians	M = -.002 SE = .007	M = .022 SE = .018	MD = .024 $p = .194$
		Musicians	M = -.003 SE = .007	M = .064 SE = .017	MD = .066 $p = .001$
		Mean Diff. (M - nonM)	MD = .000 $p = .986$	MD = .042 $p = .096$	
2.5 Hz	Duplets	Non-Musicians	M = .119 SE = .017	M = .149 SE = .027	MD = .030 $p = .257$
		Musicians	M = .121 SE = .016	M = .302 SE = .026	MD = .181 $p < .001$
		Mean Diff. (M - nonM)	MD = .002 $p = .923$	MD = .153 $p < .001$	
	Triplets	Non-Musicians	M = .011 SE = .006	M = .028 SE = .019	MD = .017 $p = .406$
		Musicians	M = -.002 SE = .006	M = .152 SE = .019	MD = .155 $p < .001$
		Mean Diff. (M - nonM)	MD = -.013 $p = .149$	MD = .124 $p < .001$	
	Quadruplets	Non-Musicians	M = .014 SE = .008	M = .033 SE = .022	MD = .019 $p = .382$
		Musicians	M = .011 SE = .008	M = .166 SE = .021	MD = .155 $p < .001$
		Mean Diff. (M - nonM)	MD = -.002 $p = .824$	MD = .133 $p < .001$	
	Quintuplets	Non-Musicians	M = -.002 SE = .006	M = -.001 SE = .009	MD = .001 $p = .947$
		Musicians	M = .005 SE = .005	M = .023 SE = .009	MD = .019 $p = .065$

		<i>Mean Diff. (M - nonM)</i>	MD = .006 <i>p</i> = .395	MD = .024 <i>p</i> = .068	
3.75 Hz		Non-Musicians	M = .019 SE = .003	M = .029 SE = .008	MD = .010 <i>p</i> = .228
		Musicians	M = .015 SE = .003	M = .078 SE = .008	MD = .063 <i>p</i> < .001
		<i>Mean Diff. (M - nonM)</i>	MD = .003 <i>p</i> = .459	MD = .050 <i>p</i> < .001	
5 Hz		Non-Musicians	M = .025 SE = .003	M = .028 SE = .005	MD = .003 <i>p</i> = .631
		Musicians	M = .032 SE = .003	M = .057 SE = .005	MD = .025 <i>p</i> = .005
		<i>Mean Diff. (M - nonM)</i>	MD = .006 <i>p</i> = .198	MD = .029 <i>p</i> = .029	
6.25 Hz		Non-Musicians	M = .022 SE = .004	M = .019 SE = .006	MD = -.003 <i>p</i> = .582
		Musicians	M = .022 SE = .004	M = .041 SE = .006	MD = .019 <i>p</i> = .001
		<i>Mean Diff. (M - nonM)</i>	MD = .000 <i>p</i> = .939	MD = .022 <i>p</i> = .011	

Table 2. Post hoc comparisons of the interaction Task*Music. At each frequency of interest (and subdivision, when needed), neural amplitude means (M) and standard errors (SE) are reported for each group and task. Mean differences (MD) and *p*-values between the Listening and the Tapping tasks are reported in the right column, while mean differences and *p*-values between musicians and non-musicians appear below every group division.

		Listening	Tapping	<i>Mean Diff. (Tap - Listen)</i>
3.75 Hz	Duplets	$M^2 = -.004$ $SE = .003$	$M^2 = .050$ $SE = .007$	$MD = .054$ $p < .001$
	Triplets	$M^3 = .072$ $SE = .009$	$M^3 = .111$ $SE = .010$	$MD = .038$ $p = .002$
	Quadruplets	$M^4 = -.001$ $SE = .003$	$M^4 = .046$ $SE = .007$	$MD = .047$ $p < .001$
	Quintuplets	$M^5 = .001$ $SE = .003$	$M^5 = .008$ $SE = .005$	$MD = .007$ $p < .219$
6.25 Hz	Duplets	$M^2 = .009$ $SE = .007$	$M^2 = .011$ $SE = .004$	$MD = .002$ $p = .792$
	Triplets	$M^3 = .000$ $SE = .003$	$M^3 = .017$ $SE = .006$	$MD = .017$ $p = .001$
	Quadruplets	$M^4 = .000$ $SE = .002$	$M^4 = .000$ $SE = .002$	$MD = .017$ $p = .009$
	Quintuplets	$M^5 = .079$ $SE = .009$	$M^5 = .075$ $SE = .008$	$MD = -.003$ $p = .512$

Table 3. Post hoc comparisons of the main effect of Task at 3.75 and 6.25 Hz. Neural amplitude means (M) and standard errors (SE) are reported for each task at each subdivision rhythm. Mean differences (MD) and *p*-values between the Listening and the Tapping tasks are reported in the right side.

		Listening			Tapping		
		Rhythm 1	Rhythm 2	Mean Diff. (R1 - R2)	Rhythm 1	Rhythm 2	Mean Diff. (R1 - R2)
1.25 Hz	Non-Musicians	M ² = .016 SE = .010	M ³ = .007 SE = .010	MD = .009 <i>p</i> = 1	M ² = .116 SE = .031	M ³ = .071 SE = .027	MD = .046 <i>p</i> = .280
			M ⁴ = .012 SE = .012	MD = .004 <i>p</i> = 1		M ⁴ = .048 SE = .023	MD = .069 <i>p</i> = .005
			M ⁵ = - .002 SE = .007	MD = .019 <i>p</i> = .950		M ⁵ = .022 SE = .018	MD = .095 <i>p</i> = .044
		M ³ = .007 SE = .010	M ⁴ = .012 SE = .012	MD = -.005 <i>p</i> = 1	M ³ = .071 SE = .027	M ⁴ = .048 SE = .023	MD = .023 <i>p</i> = 1
			M ⁵ = - .002 SE = .007	MD = .010 <i>p</i> = 1		M ⁵ = .022 SE = .018	MD = .049 <i>p</i> = .581
		M ⁴ = .012 SE = .012	M ⁵ = - .002 SE = .007	MD = .015 <i>p</i> = 1	M ⁴ = .048 SE = .023	M ⁵ = .022 SE = .018	MD = .026 <i>p</i> = 1
	Musicians	M ² = .005 SE = .009	M ³ = .006 SE = .009	MD = .000 <i>p</i> = 1	M ² = .194 SE = .030	M ³ = .232 SE = .027	MD = -.037 <i>p</i> = .539
			M ⁴ = .023 SE = .012	MD = -.018 <i>p</i> = .931		M ⁴ = .220 SE = .023	MD = -.026 <i>p</i> = .964
			M ⁵ = - .003 SE = .007	MD = .008 <i>p</i> = 1		M ⁵ = .064 SE = .017	MD = .130 <i>p</i> = .002
		M ³ = .006 SE = .009	M ⁴ = .023 SE = .012	MD = -.018 <i>p</i> = .747	M ³ = .232 SE = .027	M ⁴ = .220 SE = .023	MD = .012 <i>p</i> = 1
			M ⁵ = - .003 SE = .007	MD = .008 <i>p</i> = 1		M ⁵ = .064 SE = .017	MD = .168 <i>p</i> < .001
		M ⁴ = .023 SE = .012	M ⁵ = - .003 SE = .007	MD = .026 <i>p</i> = .464	M ⁴ = .220 SE = .023	M ⁵ = .064 SE = .017	MD = .156 <i>p</i> < .001
		Listening			Tapping		
2.5 Hz	Non-Musicians	M ² = .119 SE = .017	M ³ = .011 SE = .006	MD = .108 <i>p</i> < .001	M ² = .149 SE = .027	M ³ = .028 SE = .019	MD = .121 <i>p</i> < .001
			M ⁴ = .014 SE = .008	MD = .105 <i>p</i> < .001		M ⁴ = .033 SE = .022	MD = .116 <i>p</i> < .001
			M ⁵ = - .002 SE = .006	MD = .121 <i>p</i> < .001		M ⁵ = - .001 SE = .009	MD = .150 <i>p</i> < .001
		M ³ = .011 SE = .006	M ⁴ = .014 SE = .008	MD = -.003 <i>p</i> = 1	M ³ = .028 SE = .019	M ⁴ = .033 SE = .022	MD = -.005 <i>p</i> = 1
			M ⁵ = - .002 SE = .006	MD = .013 <i>p</i> = .882		M ⁵ = - .001 SE = .009	MD = .029 <i>p</i> = .972
		M ⁴ = .014 SE = .008	M ⁵ = - .002 SE = .006	MD = .016 <i>p</i> = .588	M ⁴ = .033 SE = .022	M ⁵ = - .001 SE = .009	MD = .034 <i>p</i> = .766

	Musicians	M ² = .121 SE = .016	M ³ = - .002 SE = .006	MD = .124 <i>p</i> < .001	M ² = .302 SE = .026	M ³ = .152 SE = .019	MD = .150 <i>p</i> < .001
			M ⁴ = .011 SE = .008	MD = .110 <i>p</i> < .001		M ⁴ = .166 SE = .021	MD = .136 <i>p</i> < .001
			M ⁵ = .005 SE = .005	MD = .117 <i>p</i> < .001		M ⁵ = .023 SE = .009	MD = .279 <i>p</i> < .001
		M ³ = - .002 SE = .006	M ⁴ = .011 SE = .008	MD = -.014 <i>p</i> = .532	M ³ = .152 SE = .019	M ⁴ = .166 SE = .021	MD = -.014 <i>p</i> = 1
			M ⁵ = .005 SE = .005	MD = -.007 <i>p</i> = 1		M ⁵ = .023 SE = .009	MD = .129 <i>p</i> < .001
		M ⁴ = .011 SE = .008	M ⁵ = .005 SE = .005	MD = .007 <i>p</i> = 1	M ⁴ = .166 SE = .021	M ⁵ = .023 SE = .009	MD = .143 <i>p</i> < .001
			Listening			Tapping	
3.75 Hz	All	M ² = - .004 SE = .003	M ³ = .072 SE = .009	MD = -.076 <i>p</i> < .001	M ² = .050 SE = .007	M ³ = .111 SE = .010	MD = -.060 <i>p</i> < .001
			M ⁴ = - .001 SE = .003	MD = -.002 <i>p</i> = 1		M ⁴ = .046 SE = .007	MD = .004 <i>p</i> = 1
			M ⁵ = .001 SE = .003	MD = -.004 <i>p</i> = 1		M ⁵ = .008 SE = .005	MD = .043 <i>p</i> < .001
		M ³ = .072 SE = .009	M ⁴ = - .001 SE = .003	MD = .074 <i>p</i> < .001	M ³ = .111 SE = .010	M ⁴ = .046 SE = .007	MD = .064 <i>p</i> < .001
			M ⁵ = .001 SE = .003	MD = .072 <i>p</i> < .001		M ⁵ = .008 SE = .005	MD = .103 <i>p</i> < .001
		M ⁴ = - .001 SE = .003	M ⁵ = .001 SE = .003	MD = -.002 <i>p</i> = 1	M ⁴ = .046 SE = .007	M ⁵ = .008 SE = .005	MD = -.039 <i>p</i> < .001
				All: Listening and Tapping			
5 Hz	All	M ² = .050 SE = .004	M ³ = .014 SE = .003	MD = .037 <i>p</i> < .001			
			M ⁴ = .074 SE = .006	MD = -.024 <i>p</i> = .001			
			M ⁵ = .003 SE = .003	MD = .048 <i>p</i> < .001			
		M ³ = .014 SE = .003	M ⁴ = .074 SE = .006	MD = -.061 <i>p</i> < .001			
			M ⁵ = .003 SE = .003	MD = .011 <i>p</i> = .002			
		M ⁴ = .074 SE = .006	M ⁵ = .003 SE = .003	MD = .072 <i>p</i> < .001			
		Listening			Tapping		
6.25 Hz	All	M ² = .009 SE = .007	M ³ = .000 SE = .003	MD = .009 <i>p</i> = 1	M ² = .011 SE = .004	M ³ = .017 SE = .006	MD = -.006 <i>p</i> = .623
			M ⁴ = .000 SE = .002	MD = .009 <i>p</i> = 1		M ⁴ = .000 SE = .002	MD = -.006 <i>p</i> = .503
			M ⁵ = .079 SE = .009	MD = -.070 <i>p</i> < .001		M ⁵ = .075 SE = .008	MD = .064 <i>p</i> < .001
		M ³ = .000	M ⁴ = .000	MD = .000	M ³ = .017	M ⁴ = .000	MD = .000

		SE = .003	SE = .002	$p = 1$	SE = .006	SE = .002	$p = 1$
			M ⁵ = .079 SE = .009	MD = -.078 $p < .001$		M ⁵ = .075 SE = .008	MD = -.058 $p < .001$
		M ⁴ = .000 SE = .002	M ⁵ = .079 SE = .009	MD = -.079 $p < .001$	M ⁴ = .000 SE = .002	M ⁵ = .075 SE = .008	MD = -.058 $p < .001$

Table 4. Post hoc comparisons of the main effect and interactions related to the Subdivision rhythms.

At each frequency of interest (and participants' group, when required), neural amplitude means (M) and standard errors (SE) are reported for the Listening and the Tapping tasks. Mean differences (MD) and p -values are reported in the right side of every task column. M2 stands for duplets, M3 stands for triplets, M4 stands for quadruplets, M5 stands for quintuplets.

FIGURES

Figure 1. Our stimuli, paradigm and main neural entrainment. The top left section depicts our 30-ms sound used to create the beat, the duplets, the triplets, the quadruplets and the quintuplets. A variable range of tempi and differences in amplitude were used for the training, while a constant tempo (IOI=800 ms, $f = 1.25$ Hz) and amplitude were used for the study. The bottom part depicts our paradigm, which involves four tasks for every auditory sequence: (1) listen to the beat, (2) listen to the subdivision, (3) listen to the beat, and (4) listen to the same subdivision while tapping to the beat. The neural entrainment of all participants averaged is depicted for each task as topographies at each frequency of interest. The top right section shows musicians and non-musicians' differences between listening and tapping to the subdivisions at the beat frequency. Notice the greater increases in musicians for all subdivisions. This is also evident in the topographies, which show the averaged neural entrainment for all subdivisions at 1.25 Hz.

Figure 2. Frequency amplitudes of musicians and non-musicians for each task and subdivision. The red line stands for musicians' mean, while the blue line stands for non-musicians mean at each task (rows) and subdivision (columns). The triangles signal the frequencies of the beat and its harmonics: black for the beat (f), cyan for the duplet ($2f$), red for the triplet ($3f$), blue for the quadruplet ($4f$), pink for the quintuplet ($5f$). At the task 4, tapping to the beat while listening to the subdivision, topographies showing the amplitudes at 1.25Hz are represented for all participants. * stands for $p < .05$; ** stands for $p < .01$; *** stands for $p < .001$.

EEG frequency-tagged amplitudes during the listen-to-the-beat

Figure 3. Peak amplitudes at each frequency of interest during the listening to the beat (task 1 and 3). The bars depict before (in white) and after (in gray) listening to the subdivision. * stands for $p < .05$

EEG frequency-tagged amplitudes during the listen-to-the-subdivision:

a) without tapping

b) with tapping

Figure 4. Peak amplitudes at each frequency of interest and subdivision during the listening to the subdivisions (a) without tapping (task 2) and (b) with tapping to the beat (task 4). The bars depict musicians (in white) and non-musicians (in gray). * stands for $p < .05$; *** stands for $p < .001$

EEG frequency-tagged amplitude differences (a) after listening to subdivisions and (b) when tapping to the beat of the subdivisions

Figure 5. Amplitude increases across frequencies. Amplitude differences (a) between Task3-Task1, when participants listened to the beat, and (b) between Task4-Task3, when non-musicians (first row) and musicians (second row) listened to the distinct subdivisions. * stands for $p < .05$; ** stands for $p < .01$; *** stands for $p < .001$

Figure 6. Tapping responses for each group and subdivision. The rose-plots (a) represent non-musicians' and musicians' tapping accuracy for duplets, triplets, quadruplets and quintuplets. The downbeat of the subdivision should be located close to 0°. The bar graph (b) represents non-musicians' and musicians' tapping consistency for duplets, triplets, quadruplets and quintuplets. * stands for $p < .05$; ** stands for $p < .01$; *** stands for $p < .001$