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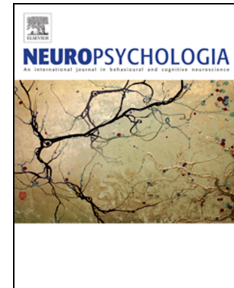
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Prolonged exposure to highly rhythmic music affects brain dynamics and perception

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Abstract

Rhythmic stimulation is a powerful tool to improve temporal prediction and parsing of the auditory signal. However, for long duration of stimulation, the rhythmic and repetitive aspects of music have often been associated to a trance state. In this study we conceived an auditory monitoring task that allows tracking changes of psychophysical auditory thresholds. Participants performed the task while listening to rhythmically regular and an irregular (scrambled but spectrally identical) music that were presented with an intermittent (short) and continuous (long) type of stimulation. Results show that psychophysical auditory thresholds increase following a Continuous versus Intermittent stimulation and this is accompanied by a reduction of the amplitude of two event-related potentials to target stimuli. These effects are larger with regular music, thus do not simply derive from the duration of stimulation. Interestingly, they seem to be related to a frequency selective neural coupling as well as an increase of network connectivity in the alpha band between frontal and central regions. Our study shows that the idea that rhythmic presentation of sensory stimuli facilitates perception might be limited to short streams, while long, highly regular, repetitive and strongly engaging streams may have an opposite perceptual impact.

Keywords

Temporal prediction, trance, regular streams, neural entrainment

Introduction

During the last decade, the scientific literature has clearly shown the power of music in modifying the neural activity: the endogenous rhythmic neural activity synchronizes with the rhythmic structure of music, a phenomenon often described as neural entrainment (Large, 2008; Nozaradan et al., 2011; Doelling & Poeppel, 2015; Haegens & Golumbic, 2018). Importantly, this stimulus to brain coupling is not limited to the auditory system, but propagates to the motor system and beyond (Chen et al., 2008; Grahn & Brett, 2007; Fujioka et al., 2012; Grahn, 2012).

Rhythmic stimulation seems a powerful tool to improve temporal prediction and parsing of the auditory signal (Schön & Tillmann, 2015). Indeed, short duration of rhythmic stimulation seems to have a facilitatory effect on auditory processing (Jones et al., 2002; Nozaradan et al., 2016), including speech (Przybylski et al., 2013; Kotz & Gunter, 2015; Cason et al., 2015a, 2015b; Bedoin et al., 2016; Chern et al., 2017; Falk et al., 2017; Gould et al., 2017) and these effects extend to visual perception (Escoffier et al., 2010; Bolger et al., 2014; Miller et al., 2013).

However, for long durations of stimulation, the rhythmic and repetitive aspects of percussive music have often been described by ethnologists as strongly associated to the fulfillment of a trance state: a transient and non-pathological modification of the state of consciousness often accompanied by a narrowing of awareness of immediate surroundings (De Martino, 1988; Rouget, 1980). More commonly, long-lasting music listening may induce a feeling of alienation, of being somewhere else. Under this perspective, music listening may alter, to a certain extent, the default level of consciousness and, in turn, perception and cognition.

While neuroscience research on trance and even more on music and trance is scarce, the neuroscience literature on other types of altered states of consciousness is substantial. Research on hypnosis has shown a change of hearing thresholds during the hypnotic state with larger effects for participants with high hypnotic susceptibility (Crawford et al., 1979; Facco et al., 2014).

Similar results have been obtained with event-related potentials, in particular with the mismatch negativity (MMN) and P300. While the MMN is governed by a pre-attentive sensory memory mechanism, the P300 is generated when participants need to attend/discriminate stimuli (Näätänen, 1990, Polich and Kok, 1995). A reduction or vanishing of the mismatch negativity (MMN) and P300 have been obtained during sleep (Campbell & Colrain, 2002; Strauss et al., 2015). Finally, the amplitude of the MMN and P300 are reduced in clinical conditions of altered consciousness (e.g. coma, vegetative state) compared to

healthy individuals (Naccache et al., 2005; Kotchoubey et al., 2005; Fischer et al., 2008; Lugo et al., 2016).

Our study questions the well-accepted claim that rhythmic presentation of sensory stimuli facilitates perception, by hypothesizing that such claim might only be valid for short streams with low rhythmic engagement, while long, highly regular, repetitive and strongly engaging streams will have an opposite perceptual impact. At these aims we conceived an auditory monitoring task that would allow to track changes in the psychophysical auditory threshold. Participants listened to a regular and an irregular music excerpt and had to detect an auditory target presented at different intensity levels around the auditory threshold. The test was run twice with an intermittent (short) and continuous (long) duration of music stimulation. Because this task is an auditory selective attention task, it should generate a P300 in correspondence to target detection, indicating a context updating of the auditory environment (Polich and Kok, 1995). The positive component should be preceded in our task by a processing negativity to attended tones (targets) that has also been referred to as negative difference (Nd), peaking between 200 and 400ms following stimulus onset (Hillyard et al., 1973; Hansen & Hillyard, 1980; Alain & Arnott, 2000). In our task a negative difference could also be interpreted as an object-related negativity, thought to index concurrent sound segregation (Alain et al., 2001).

We hypothesized that, compared to a short auditory stimulation, an over-long rhythmic stimulation, by inducing an absorptive state of consciousness (Herbert, 2012; Gingras et al., 2014; Hove & Stelzer, 2018), would induce an increase in the psychophysical perceptual auditory thresholds and a reduction of event-related responses. Importantly this effect should be mostly visible using regular music compared to irregular music stimulation and should be related to neural entrainment. In other words, we hypothesized an interaction between duration of stimulation and regularity of the music; whereas the alternative scenario of no interaction (a similar effect of duration of stimulation across regular and irregular music) may be simply explained by a fatigue effect.

Material and Methods

Participants

Twenty-two right-handed participants (9 males, average age: 26-year-old) were recruited for this experiment. They all had normal hearing threshold as tested by a preliminary audiometry. None of the participants was a musician (range of years of practice: 0-7, mean: 2). Participants signed an informed consent form and received 20 euros for their participation. The study was approved by the local ethics review board.

Stimuli

The regular stimulus was a 30s excerpt of trance music, a sub-genre of electronic music, taken from *Dark Side of My Room* by Extrawelt with a highly regular beat at 2.15Hz. The irregular stimulus was designed by time-domain scrambling the regular stimulus, in order to preserve the spectral content over longer time scales, but removing the structure at shorter timescales (here the rhythmic structure, see Figure 1). More precisely, the algorithm takes the original rhythmic stimulus, chops it into a set of short windows (500 ms with 50 ms overlap), tapers them using a Hann window, shuffles them (over a radius of 3.7 s), then re-overlaps them.

This results in a stimulus that is still clearly recognizable as music but that has a highly irregular temporal structure. The two excerpts were repeated in a loop to fit the duration of the different testing sessions (a short version of regular and irregular stimuli is presented as Supplementary Material). Participants were required to perform an auditory psychophysical detection task on target auditory stimuli inserted on top of the music. The target stimulus was the sound produced by the music instrument triangle (musical percussion instrument, with a high frequency range), lasting approximately 500ms, with a sharp attack and fast decay. In order to minimize possible differential masking effects of music across regular and irregular conditions, targets were presented on strictly identical acoustic background. This was possible thanks to the highly repetitive nature of the music that presented, every 3700ms, the same sound. In order to ensure an identical acoustic background in the regular and irregular conditions, starting 100ms before the target onset and during a window of 600ms the music excerpt was not touched by the shuffling algorithm. Moreover, besides this stringent acoustic control forcing identical context to targets in the regular and irregular conditions, the absolute time of target presentation with the respect to the start of the music was also strictly identical across conditions.

The software Presentation (Neurobehavioural systems) was used to program the experiment. A sound Blaster X-Fi Xtreme Audio, an amplifier Yamaha P2040 and Yamaha loudspeakers (NS 10M) were used for sound presentation. All sound stimuli were presented at 22050 Hz sample rate and 16 bits resolution. Music excerpts were presented at ~85 dBA in order to approach (safely) the sound full immersion experienced when listening to this type of music in social contexts (parties, disco, ~100dBA).

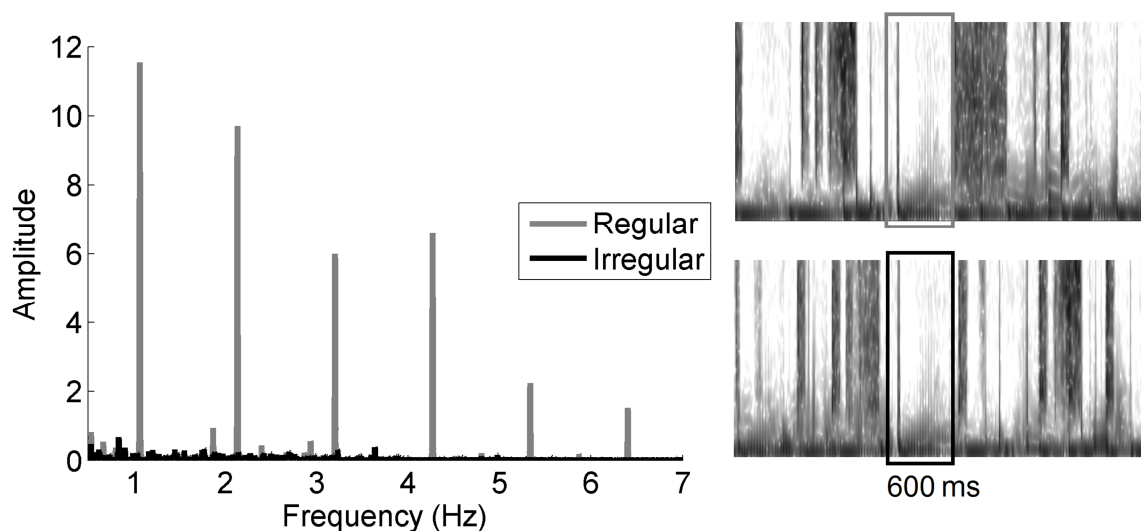


Figure 1. Left: Power spectral density (PSD) of the envelope of the regular and irregular stimuli. Peaks represent the regularity of the temporal structure. The amplitude is in arbitrary units. Right: Time-frequency representation of ~3 seconds of the regular (top) and irregular stimuli. The rectangular frames indicate the musical section used to present the target sound that were not affected by the scrambling procedure.

Experimental design

Target stimuli were mixed at different intensity levels with the musical stimuli and participants were asked to press a button whenever they heard the target sound (triangle). As detailed above, targets were presented always in correspondence of the same musical context, repeating every 3700ms. This allowed to keep the intensity level of the musical context exactly the same across all target presentations. However, the target stimulus was not presented every 3700ms and those instances without the target stimulus (50%, randomly distributed) were considered catch trials. This prevented participants to predict target presentations.

First, for every participant a quick estimate of the threshold for the target stimulus was measured, for both the regular and irregular musical context, using a staircase procedure (2dB step). This allowed also participants to become familiar with the task and the different levels of the target stimulus. Then, for each participant, five levels of intensity of the target stimulus were chosen in such a way that the highest level was 6 dB above the average threshold level of the participant. The intensity of four remaining levels was decreased by 2 dB steps.

Then the proper experiment began. The musical context could be either regular or irregular and the type of the stimulation could be Intermittent or Continuous. In the Intermittent stimulation condition, we used three blocks of 3 minutes each, separated by a very short break (~20 s). In the Continuous condition, the psychoacoustic test was run without breaks (9 minutes) and it was also preceded by 6 extra minutes of listening to the same music (see Figure 2). The target was presented 15 times at each intensity level in each of the four conditions (ie 75 times in each condition). The order of the four conditions was counterbalanced. The four conditions were separated by a five minutes break.

Importantly, if the effects we measure were uniquely driven by the duration of stimulation possibly inducing a stronger drowsiness, we should observe the same effects independently of the rhythmic structure of the stimuli.

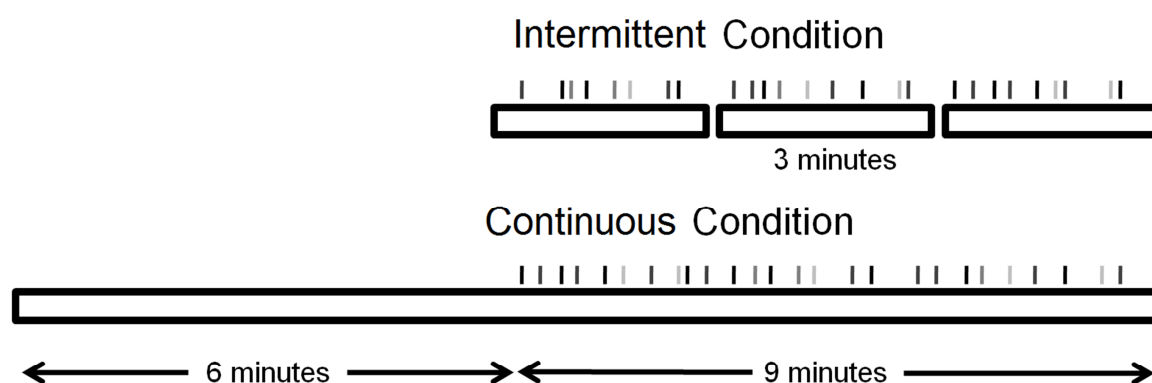


Figure2. Schematic view of the experimental design describing the Intermittent and Continuous type of stimulation (black boxes). The small vertical traits indicate the presentation of some of the target sound at different levels of intensities (light grey to dark).

Signal processing and statistical analyses

EEG signal was recorded at 1 kHz using a BrainAmp amplifier and 32 pre-amplified channels mounted following the 10-10 international system (Fp1, Fp2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, TP9, CP5, CP1, CP2, CP6, TP10, P7, P3, Pz, P4, P8, PO9, O1, Oz, O2, PO10). The reference electrode was set at Fcz while the ground was set in front of AFz. Impedances were kept below 25 kOhms. Signal processing was done using EEGLAB (Delorme & Makeig, 2004, version 12.0.2), Fieldtrip (Oostenveld et al., 2011, version 2014.11.16) and custom Matlab scripts. Continuous data were filtered using a high-pass filter (0.4 Hz, 12 dB/octave) and major artifacts rejected by eye. Independent Component Analysis (ICA, EEGLAB) was used on continuous data (24 components) to remove physiological

artifacts such as eye-blinks and muscular activity. Four components/subject were rejected on average. Average reference was then computed. For the ERP analysis, data were segmented into 1.1s epochs starting 100ms before the presentation of the target stimulus. Further rejection of remaining artifacts was done on the basis of visual inspection of each epoch and was always lower than 10% of the total number of epochs in a given condition.

Statistical analyses were run using a Region of Interest approach for two ERP components (Nd and P3 for target minus catch trials). In order to prevent a data selection bias, the ROIs were defined on the basis of the topography of the average of all conditions (excluding catch trials), by selecting the electrodes most representative of each ERP component (hierarchical clustering analysis using Statistica 7.1). The ROI for the Nd comprised Fz, FC1, FC2, C3, Cz, C4, CP1, CP2, Pz (see Figure 4), and was temporally defined as the mean value \pm 20ms around the peak. The ROI for the P3 comprised Cp1, Cp2, P3, Pz, P4, O1, Oz, O2 (see Figure 5) and was temporally defined as the mean value \pm 100ms around the peak.

A three-way repeated-measure analysis of variance was used to analyze behavioral and electrophysiological responses with Duration of Stimulation (Intermittent, Continuous), Intensity (5 levels) and Rhythmicity (Regular, Irregular) as within subject factors. The d' index was used as dependent variable in the behavioral analysis, while mean amplitudes were used as dependent variable in the ERP analysis. Greenhouse-Geisser correction for sphericity was used when appropriate.

Inter-trial coherence (ITC) was computed to verify that there would be a stronger coupling to the temporal structure of the Regular compared to the Irregular Music, thus in the 1 to 5Hz range (see Figure 1). This was strongly expected insofar as the temporal structure of irregular music was disrupted by the shuffling procedure. More interestingly, this analysis allows testing whether the strength of the coupling would be affected by the Type of Stimulation (Intermittent and Continuous). Data were segmented into 7.4s epochs starting 3.7s before the onset of each target. In other words, segments comprised two full measures of music to allow accurate frequency resolution (0.2Hz). In order to measure the phase coupling across trials we computed the ITC between 0.2 and 7 Hz using a discrete FFT and Hanning tapering (EEGLAB function `newtimef`). This frequency range was defined on the basis of the PSD of the envelope of the musical stimuli. Frequency peaks were defined on the average ITC values of all conditions (including catch trials) using the "findpeak" function of Matlab. Importantly, ITC peaks precisely corresponded to the main peaks visible in the PSD of the stimuli (2.15 and 4.3 Hz). Values at a frequency peak (e.g. 4.3 Hz) were then divided by the average value of two lower and two higher neighbors (e.g., for 4.3 Hz: 4, 3.9, 4.6, 4.7 Hz). The validity of this procedure relies on the assumption that, in absence of stimulation, the signal amplitude at a given frequency should be similar to the signal

amplitude of the mean of the surrounding frequencies (Nozaradan et al., 2011, 2012). Thus, this normalization ensures that ratios greater than one actually indicate the presence of stimulus induced specific frequency peaks and most importantly it allows to compare the strength of stimulus to brain coupling in different conditions (eg Continuous vs Intermittent). The ROI for the ITC analysis was defined using a similar approach to the one described for the ERPs (average across all conditions, including catch trials) and resulted in a ROI comprising Fz, FC1, FC2, C3, Cz, C4, CP1, CP2. Statistical analyses were run on normalized peak values to verify whether values were significantly greater than one (presence or absence of a peak). Then a model including Type of Stimulation (Intermittent and Continuous) as within subject factor was used.

In order to assess the influence of the independent variables at the level of network dynamics we computed the functional connectivity between electrode pairs using an approach that minimizes the effect of common sources (volume conduction and common reference). At this aim, data were epoched as for the ITC analyses. We then computed the cross-spectral density using a multitapering frequency transformation based on Slepian sequences as tapers (using Fieldtrip `freqanalysis` function). Connectivity measures were estimated using a debiased estimator of the weighted phase lag index (wPLI, using Fieldtrip `connectivity` analysis function). The phase lag index estimates to what extent the phase leads and lags between signals from two sensors are not equiprobable. In the weighted PLI the contribution of the observed phase leads and lags is weighted by the magnitude of the imaginary component of the cross-spectrum, reducing the sensitivity to volume conduction (common input) and uncorrelated noise sources (see Vinck et al., 2011 for technical details). By contrast with the ITC analysis, we did not hypothesize that changes in connectivity would be limited to the frequency range of the envelope of the musical stimuli. On the contrary, these changes may take place in a higher frequency range (Nakatani et al., 2005). The metrics were thus computed across all electrode pairs between 0.4 and 40Hz. Statistical analyses were run across all frequency bands to test differences induced by Stimulation type. Then, a model including Type of Stimulation and Rhythmicity as within subject factor was used in significant frequency bands.

Results

To investigate whether the duration and regularity of auditory streams were critical factors leading to a music-induced sensory facilitation or hindrance, we first analyzed three classical markers of the quality of sensory processing: d' , Nd and P300. We then performed spectral

and connectivity analyses to investigate possible modulatory effects on neural entrainment and network level synchrony.

Psychophysical measures

The repeated-measures ANOVA (Type of Stimulation * Intensity * Rhythmicity) on the d' showed, as expected, a very strong influence of the intensity level of the target on sensitivity (main effect of intensity: $F(4,84)=309$, $\eta^2=0.93$, $p<0.001$, see Figure 3). As expected participants were very accurate at high intensity levels while their performance was very poor at low intensity levels. Importantly, during the Continuous stimulation condition, sensitivity was lower compared to Intermittent stimulation ($F(1,21)=5.2$, $\eta^2=0.2$, $p=0.03$) and this effect depended upon the intensity levels (Type of Stimulation by Intensity interaction: $F(4,84)=6.06$, $\eta^2=0.24$, $p<0.001$). Post-hoc tests (Tukey) showed a significantly reduced sensitivity during the Continuous compared to Intermittent condition only at intensity levels of +6 and +2 dB SL ($p<0.001$, $p=0.001$, respectively). While the Rhythmicity factor did not reach significance as a main effect or in interaction with the other factors, planned comparisons of the type of stimulation by rhythmicity interaction ($F(1,21)=1.34$, $\eta^2=0.06$, $p=0.2$) showed a reduced sensitivity following Continuous stimulation with regular music and not with irregular music (regular: mean 2.38, $se=0.1$; irregular: mean=2.68, $se=0.1$, Fisher test: $p=0.01$). This difference was not significant following Intermittent stimulation (regular: mean 2.4, $se=0.1$; irregular: mean = 2.5, $se=0.12$, $p=0.27$).

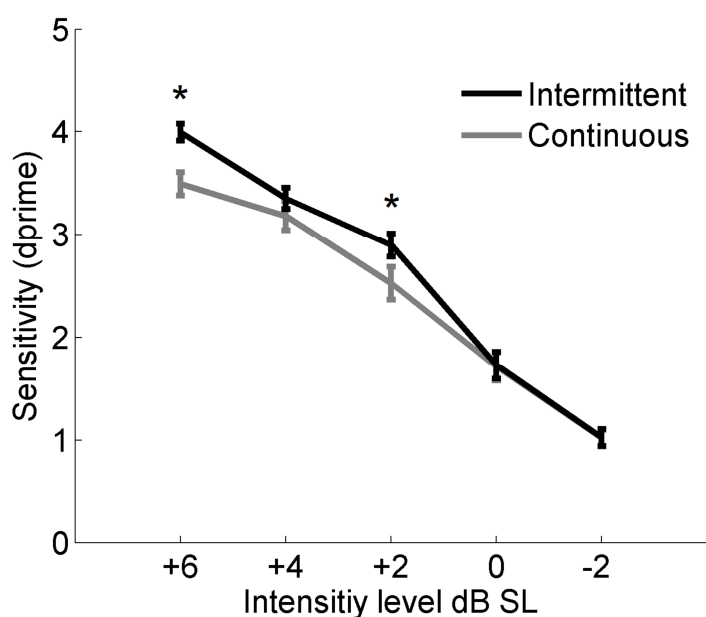


Figure 3. Mean sensitivity (d') as a function of the intensity level of the target and the type of stimulation (Intermittent and Continuous). Error bars represent the standard error from the mean.

Electrophysiological measures

Analyses on the Nd (same ANOVA as for behavior) showed, as expected, a reduction of the Nd amplitude with decreasing intensity level of the targets (main effect of intensity: $F(4,84)=3.4$, $\eta^2=0.14$, $p=0.012$). Strikingly, the Nd amplitude was smaller during rhythmic regular stimulation compared to irregular stimulation (main effect of Rhythmicity, $F(1,21)=12.8$, $\eta^2=0.38$, $p=0.001$) and this was only visible during the Continuous and not during the Intermittent condition (see Figure 4) and most clearly for the two highest intensity levels (interaction between Rhythmicity, Type of Stimulation and Intensity, $F(4, 84)=2.6$, $\eta^2=0.11$, $p=0.04$, post-hoc test $p=0.003$ & $p<0.001$).

Analyses on the P300 also showed a reduction of the P300 amplitude with decreasing intensity level of the targets (main effect of intensity: $F(4,84)=3.4$, $\eta^2=0.14$, $p=0.012$). Importantly, the P300 amplitude was smaller during the Continuous compared to the Intermittent condition (main effect of Type of Stimulation, $F(1,21)=4.4$, $\eta^2=0.17$, $p=0.04$) and this was most prominent with the Regular music (interaction between Rhythmicity, Type of Stimulation and Intensity, $F(4,84)=5.3$, $\eta^2=0.36$, $p<0.001$, see Figure 5).

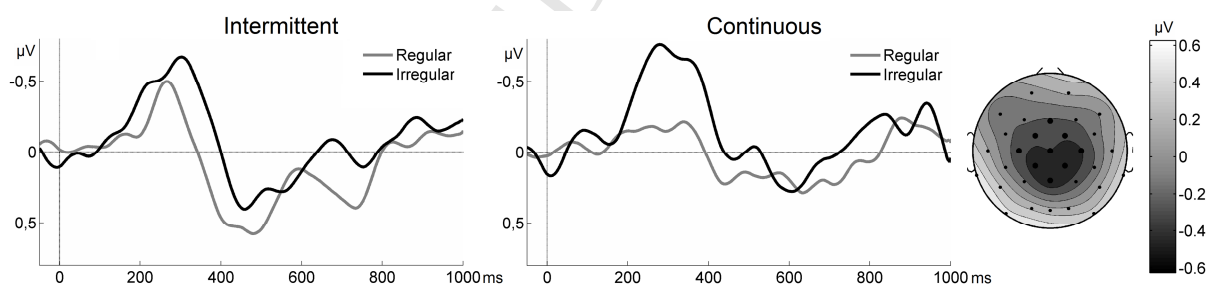


Figure 4. Mismatch negativity like effect (target minus catch trials) during the Intermittent and Continuous conditions with Regular and Irregular music. The plots represent the mean activity across 9 electrodes (in μV). Right panel: topography showing the Nd spatial distribution averaged across all conditions (in μV). Larger dots indicate the electrodes averaged in the plots and included in the ROI.

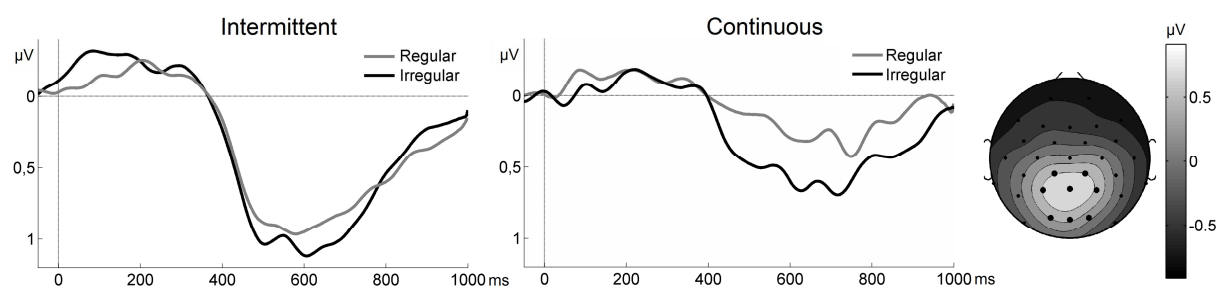


Figure 5. P3 during the Intermittent and Continuous conditions with Regular and Irregular music. The plots represent the mean activity across 8 electrodes (in μV). The topography shows the P3 spatial distribution averaged across all conditions (in μV). Larger dots indicate the electrodes averaged in the plots and included in the ROI.

Inter-trial coherence analyses

As expected, no significant peaks were visible in the ITC for the irregular music because the shuffling destroyed the temporal structure of the stimulus (one sample t-test, always $t(21) < 0.7$, $p > 0.45$). By contrast, both Intermittent and Continuous conditions showed an ITC peak at 4.3 Hz to the Regular Music ($t(21) = 2.6$, $p = 0.01$; $t(21) = 4.9$, $p < 0.001$, respectively, see Figure 6A). The peak normalized values were significantly higher for the Continuous Regular condition compared to the Intermittent Regular condition for both the 4.3 and 2.15 Hz peaks ($\eta^2 = 0.3$, $t(21) = 2.95$, $p = 0.008$, $\eta^2 = 0.2$, $t(21) = 2.3$, $p = 0.03$, respectively, see Figure 6B).

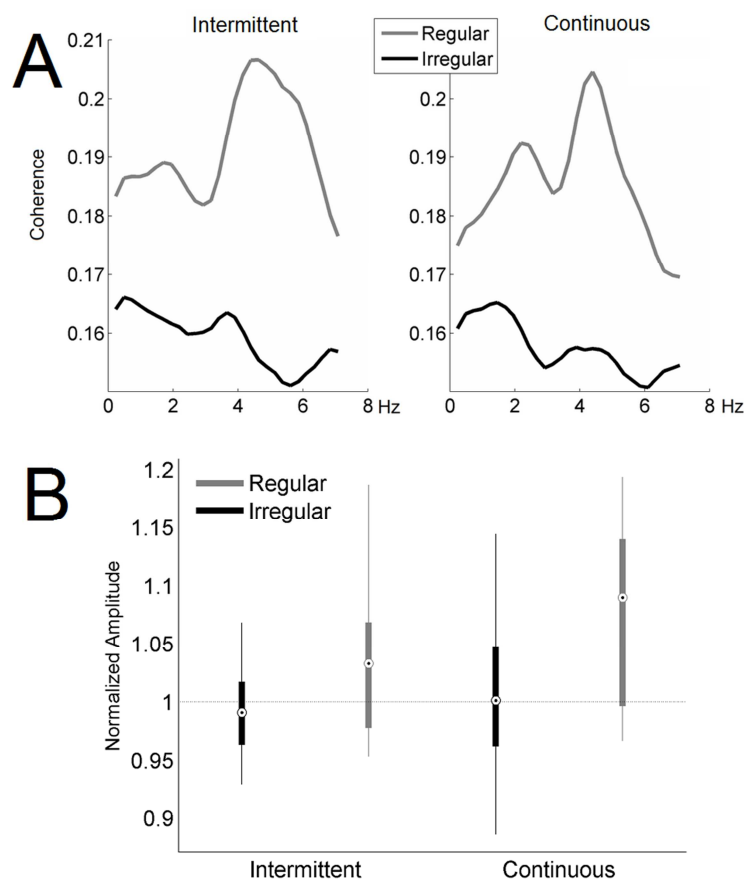


Figure 6. A. Inter-trial coherence averaged across 8 electrodes representing the level of entrainment of the neural signal to the Regular and Irregular stimuli during Intermittent and Continuous conditions. The two clear peaks (2.15 and 4.3Hz) visible when listening to the Regular music precisely correspond to the periodicities present in the musical stimulus (see Figure 1). The peaks are narrower in the Continuous condition compared to the Intermittent and absent with the Irregular music. B. Boxplot of normalized peak values for the 4.3 peak (ratios between the peak and the neighboring values). Values for the Irregular Conditions are not different from 1 showing absence of a peak. Larger ratios for the Regular music in the Continuous compared to the Intermittent condition are due to a sharper peak.

Connectivity analyses

Analyses across frequencies showed a modification of connectivity only in the alpha band in the Continuous compared to the Intermittent condition. A two-way repeated measure ANOVA in the alpha band showed significantly stronger connectivity during the continuous stimulation condition (main effect of stimulation, $\eta^2=0.19$, $F(1,21)=5.1$, $p=0.03$) essentially driven by the regular rhythm (Stimulation by Regularity interaction, $\eta^2=0.23$, $F(1,21)=6.2$, $p=0.02$). Indeed, post-hoc testing showed that only the regular continuous condition induced stronger

connectivity in the alpha band compared to the regular intermittent condition ($p=0.003$). Importantly this effect was significant between the frontal and central regions only ($p=0.03$) and thus differed from the typical occipital alpha-band topography (Figure 7).

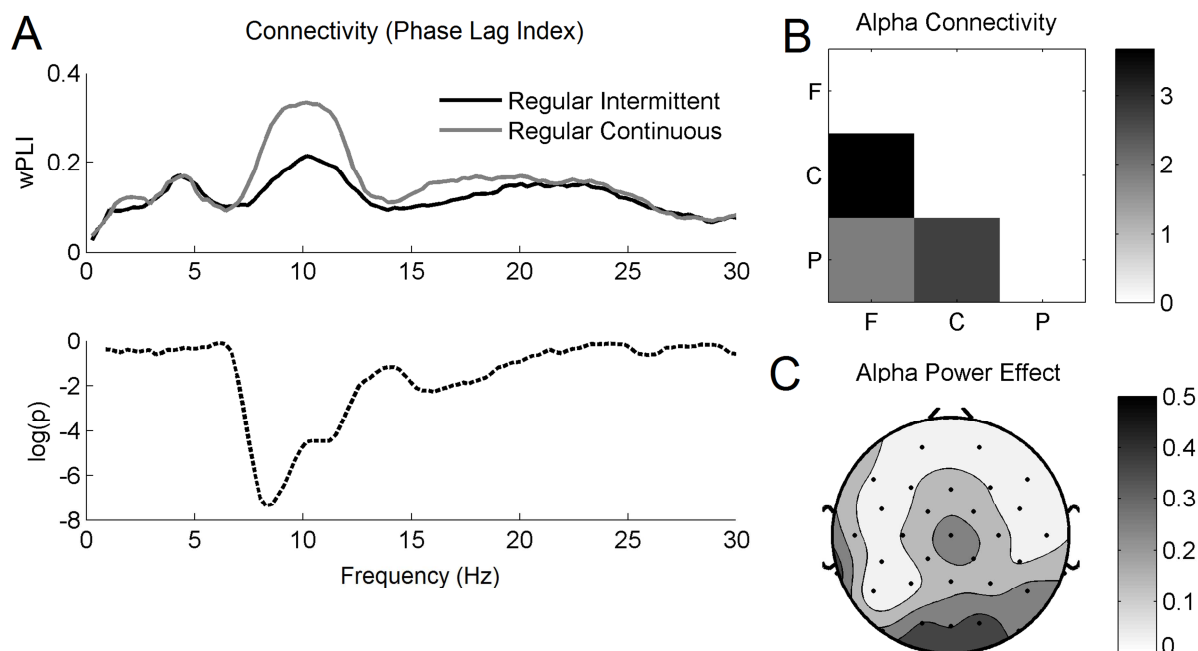


Figure 7. A. Top: Frequency-resolved unbiased weighted phase lag index during Regular Intermittent and Regular Continuous conditions. Bottom: Log of the p values assessing differences across frequencies between the two conditions (Wilcoxon signed-rank). B. Significance of the connectivity between frontal (F), central (C) and posterior (P) electrodes. Gray scale represents negative log of p values. C. Topography of the differences in alpha power between Regular Continuous and Regular Intermittent conditions (in μV).

Discussion

Our study demonstrates three key findings. First, a long-lasting, strongly metrical and highly predictable musical stimulation reduces the sensitivity of the auditory system to detect a target sound. Second, this effect is not simply a habituation effect because it is modulated by the temporal rhythmic structure of the musical stimulus: the sensitivity index as well as the amplitude of the Nd & P300 components were more strongly affected in the Continuous and Regular stimulation condition. In other words, while previous studies have shown a habituation effect of ERP components (reduced amplitude) following long stimulation (Budd et al., 1998; Ravden et al., 1999; McGee et al., 2001), in the present results the hypothesis of an effect simply driven by habituation or fatigue does not account for the differences engendered by the rhythmicity and regularity of the stimulus. Finally, a potential neural correlate explaining the music-induced modulation of the auditory thresholds is the

sharpness of the EEG frequency profile, namely the level of precision of brain to stimulus coupling, as well as the strength of the intracortical functional connectivity.

Overall, these findings directly compete with the general claim that rhythmic stimulation facilitates sensory processing (see Haegens & Golumbic, 2018 for a critical review). They rather suggest that highly rhythmic and repetitive over-long auditory streams, by reducing the complexity of the brain dynamics, degrade auditory processing. Furthermore, they put into question the general idea that neuronal entrainment by providing differential excitability states as a mechanism of selection has always a beneficial impact on cognitive processing (Schroeder & Lakatos, 2009; Arnal & Giraud, 2012). For instance, in the auditory domain, regular stimuli induce a greater sensitivity to changes in pitch (Jones et al., 2002; Morillon et al., 2016), intensity (Geiser et al., 2012), and duration (Barnes and Jones, 2000; McAuley and Jones, 2003). These findings have also been extended to visual targets (Bolger et al., 2014; Miller et al., 2013) including visual word and face recognition (Escoffier et al., 2010; Brochard et al., 2013) and working memory (Cutanda et al., 2015). Interestingly, rhythmic stimulation can have an effect that seem to last beyond the duration of the rhythmic stimulus (McAuley & Henry, 2010; Cason et al., 2015a; Falk et al., 2017) and this has been used to promote rhythmic stimulation in the rehabilitation of different types of motor (Thaut et al., 2015; Dalla Bella et al., 2015) and language skills (for a review see Schön and Tillmann, 2015).

Our results stand in contrast to these previous claims by showing that listening to a highly rhythmical and repetitive auditory stimulus, for a sufficiently long duration, induces an increase in synchronization of brain oscillatory activity but that this is accompanied by a decreased sensitivity to auditory targets, possibly due to a reduction of the level of brain rhythms complexity. This apparent contradiction between previous and our current findings can be possibly solved by taking into account the duration and quality of the auditory stimulation. Previous studies showing a facilitatory effect of rhythmic entrainment on information processing have used a rhythmic stimulation of a short duration (< 1 minute) and did not test, to our knowledge, the potential effect of longer durations of stimulation. A further difference relies on the previous use of highly controlled and simple stimuli with a low level of rhythmic engagement. By contrast the style of music we used in this study, trance techno music, is a highly engaging and extremely rhythmical and repetitive stimulus. Both stimulus features, duration and rhythmic engagement, possibly play a role in pushing the stimulus to a high level of brain coupling. Moreover, that these features may play a key role in changing the facilitatory effect into a deleterious effect well fits with the ethnomusicological literature showing a preference of long, rhythmic, repetitive (and thus predictable) strongly engaging music during trance rituals (Becker-Blease, 2004, Szabó, 2006). While by no means we are

claiming here that our participants entered a trance-state that requires a particular social context difficult to reproduce under experimental conditions, the important point here is that the use of stimuli similar to those described by ethnomusicology as being used in trance rituals reduces the sensitivity of the auditory system. This reduction is accompanied by changes in brain oscillatory dynamics. Because many rituals contexts use very monotonous drumming to induce trance, a direct comparison of strongly engaging music and monotonous drumming could be an interesting future direction.

Overall our results point to a bistable state induced by rhythmic stimulation. On one side, intrinsic brain oscillations can entrain to the temporal structure of a stimulus amplifying relevant inputs and suppressing irrelevant ones (Schroeder & Lakatos, 2009). In standard conditions this would produce a reasonable amount of synchronization of a local network and a facilitatory effect. On the other side, when the same neural dynamics enter an extreme rhythmic mode the excessive amount of synchronization of a generalized network have deleterious effects. Interestingly, in patients with epileptic seizures, loss of consciousness is accompanied by an increase in long-distance synchronization in thalamo-cortical systems (Arthuis et al., 2009). Similarly, during progressive sedation, the amplitude of stimulus-related responses to median nerve stimulation diminishes while coherence of ongoing frontal alpha activity increases, pointing to a possible link between hypersynchronous activity and loss of consciousness (Supp et al., 2011).

While synchronization between brain distant areas is thought to be an essential mechanism for conscious perception (Dehaene & Changeux, 2011; Naci et al., 2014; Fries, 2015), these changes in neural synchronization are transient and of short duration, of the order of a few hundreds of milliseconds (Melloni et al., 2007). In patients with seizures inducing loss of consciousness, the cortico-cortical synchronization is extremely strong, prolonged and stable, lasting several seconds, pointing to a deleterious effect of excessive long-distance synchronization (Koch et al. 2016). Interestingly, epileptiform discharges can be induced in generalized epilepsy via repetitive and rhythmic presentation of both flashes and auditory stimuli (Hogan & Sundaram, 1989). A recent work using fMRI showed that prolonged listening to rhythmic drumming engenders an increased connectivity between the posterior cingulate cortex and the dorsal anterior cingulate and the insula (Hove et al., 2015). These areas are respectively part of the network involved in internally oriented cognitive states and the control network. This network reconfiguration, possibly mediated by entrainment, may thus be at the origin of changes in awareness with the internal and external world.

Bridging the two apparently rather distant domains, music-induced trance and epilepsy, it could be that prolonged listening to regular, repetitive and extremely marked rhythms may induce a particularly strong and stable thalamo-cortical and cortico-cortical coupling that may

be assimilated to what is observed during certain types of seizures, although to a much lesser extent. This reminds of certain rituals used with patients with psychogenic non-epileptic seizures in the South of Italy until the 60's that used extremely rhythmical and unbridled music to induce loss of consciousness (that was supposed to free the patient from the disease, De Martino & Zinn, 2015). Our data show that prolonged listening to highly rhythmical music induces a stronger coupling at the periodicities present in the music (Figures 6) and an increased functional connectivity in the alpha-band between frontal and central regions (Figure 7) compared to an intermittent listening of the same music. In particular, the greater sharpness of the frequency coupling profile following prolonged listening seems to indicate that the longer the listening, the more brain activity becomes tightly coupled to the temporal structure present in the music. Although it remains to be further explored, the level of stimulus induced cortical entrainment may be a good candidate to explain the dissociative states that can be induced by prolonged listening to highly rhythmical and repetitive music. Particularly high levels of rhythmic entrainment may be accompanied by an excessive connectivity limiting intracortical communication and resulting in impoverished perceptual processing.

Finally, it is commonly acknowledged that music listening, under ecological conditions, can induce mind absorption and dissociative states (Herbert, 2011, 2012). Interestingly, the alteration of consciousness while listening to drumming is similar to the alterations experienced in hypnosis (Szabó, 2006). Repetitive drumming has been reported to induce specific subjective experiences such as heaviness, decreased heart rate and dreamlike experience (Gingras et al., 2014). Such similarity between music listening and hypnotic experience is underlined by the fact that highly suggestible individuals show a greater experiential involvement with music compared to low suggestible participants (Snodgrass and Lynn, 1989). Interestingly, similarly to our findings using rhythmic music stimulation, research assessing the effects of hypnosis on the perception of external stimuli has shown a general dampening-down effect on visual activity as indexed by reduced amplitude of electrophysiological components (Raz et al., 2005). A reduction of the P300 amplitude has been observed following hypnotic procedures to visual and somatosensory target stimuli, especially in highly susceptible individuals (Spiegel, et al., 1985; Spiegel, et al., 1989; Lamas & Valle-Inclán, 1998). The effect on P300 amplitude is particularly strong when using an obstructive hypnotic procedure ("preventing" to perceive) and has been observed with both auditory and visual stimuli (Barabasz et al, 1999; Jensen et al, 2001). These effects on electrophysiological component can be accompanied, as in our results, by modifications in the behavior indicating a reduced connection with the external world, indexed for instance by a reduction of word fluency and reaction times in tasks assessing executive functions

(Gruzelier and Warren, 1993; Kallio et al, 2001; Virta et al., 2015). Recently, Hove and colleagues, in a follow-up EEG study of the fMRI study cited above, showed that shamanic practitioners had reduced brain responses to sounds during drumming-induced trance. This is very similar to what we described and suggests a link between repetitive music, trance induction and disengagement from the sensory environment (Hove et al. 2017, Hove & Stelzer, 2018).

In conclusion, the present study showed that, in contrast with stimulation of shorter duration and less engaging stimuli, highly rhythmic stimulation of sufficiently long and continuous duration induces a decrease of sensitivity of the auditory system and possibly of other sensory channels. This goes along with a high level of synchronization of the neuronal system to the temporal structure of the auditory stimulus. In light of the ethnomusicological research on the use of music to induce trance, this effect can be interpreted in terms of an alteration of the level of consciousness and may be possibly mediated by an increase in functional connectivity in the alpha band.

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Long-lasting rhythmic musical stimulation reduces the sensitivity of the auditory system

This effect is modulated by the temporal rhythmic structure of the musical stimulus

Stimulus-brain coupling and functional connectivity are potential explanatory mechanisms

ACCEPTED MANUSCRIPT

Credit

Cosima Lanzilotti : Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Visualization; Writing - original draft; Writing - review & editing

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