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„Pupillary Sensitivity to Musical Groove“

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ABSTRACT

The capacity to entrain movement to rhythmic auditory stimulation is universally found in humans, but apparently rare in other species. One way to study this link between movement and music is to look at the variation in how music evokes a desire to move. This variation is captured by the concept groove: high-groove music stimulates a strong desire to move, whereas low-groove music does not. Here, we aim to determine the effects of groove on the nervous system and the modulation of those effects by frequency content and metrical structure (absent actual movement). We do this in a series of psychophysiological experiments examining the pupillometric response of listeners hearing: (1) excerpts of real music varying in groove; (2) frequency filtered excerpts of real music; and (3) drum loops varied in bass frequency content and syncopation. Our results demonstrate stronger pupil dilation in response to high- vs. low-groove music, and stronger effect for high-frequency content vs. low-frequency content in filtered high-groove music. Further, we find modulation of pupillary responses by frequency content and metrical structure, as well as sex differences in these effects. These findings suggest that the link between movement and music in our species is supported by the capacity of high-groove music to stimulate central and peripheral arousal. Applying the techniques developed here in other developmental stages, cultures or species should allow us to determine whether they exhibit similar sensitivities, thus providing insight into the biological foundations of music.

ZUSAMMENFASSUNG

Unsere Kapazität sich zu rhythmisch-akustischer Stimulierung zu bewegen finden wir in jeder Kultur ausgeprägt, ist jedoch im Tierreich eine rare Fähigkeit. Eine Möglichkeit diesen Zusammenhang zwischen Bewegung und Musik zu studieren, ist sich die Variation in der Fähigkeit von Musik uns zum Bewegen zu bringen anzuschauen. Diese Variation wird durch den Begriff Groove definiert; während hoher Groove uns zum Tanzen bringt, ist bei niedrigem Groove der Gegenteil der Fall. In dieser Arbeit wird die Auswirkung von Groove in Musik auf das Nervensystem untersucht und die Beeinflussung dieses Effekts durch Frequenz und metrische Faktoren. Hierzu messen wir Pupillenerweiterung als Korrelat zu Aktivität des Nervensystem in Reaktion auf (1) Musik mit hohen und niedrigen Groove; (2) Frequenz gefilterte Musik mit hohen Groove und (3) Drum-Loops, mit hohen und tiefen Frequenzen und hohen und schwachen Anteilen von Synkopen. Unsere Resultate zeigen, dass hoher Groove zu einer größeren Pupillenerweiterung führt und dass hohe Frequenzen wichtig für diesen Effekt sind. Außerdem finden wir einen Einfluss von Frequenz- und metrischen Manipulation auf die Pupillenerweiterung und Geschlechtsunterschiede in diesen Effekten. Die Resultate deuten darauf hin, dass der stimulierende Effekt von hohen Groove in Musik, zum Teil durch die Aktivierung des peripheren und zentralen Nervensystems erklärt werden kann. Überdies bietet die Methode von Pupillometrie Möglichkeiten zur Anwendung in anderen Kulturen, Entwicklungsstadien und Tierarten, was uns letztendlich helfen kann, die biologischen Wurzeln von Musik besser zu verstehen.

INTRODUCTION

Humans can hardly help but tap, sway and bob their head in response to rhythmic sound. In no other species is this capacity for rhythmic auditory-motor coupling so widely expressed and flexibly realized (Ravignani, Bowling, & Fitch, 2014) and the fact that we find music and dance in every culture, suggests biological underpinnings to this phenomenon. Importantly, not all music evokes the same subjective sense of wanting to move. This variation is captured by the concept groove, with high-groove music stimulating a strong desire to move, whereas low-groove music does not (Madison, 2006; Janata, Tomic, & Haberman, 2012). Previous studies have demonstrated that perceptual ratings of groove are highly consistent across listeners (Cronbach's alpha = 0.8-0.9; Janata et al., 2012; Madison, 2006). Further, music perceived as high in groove is positively correlated self-reported ease and measured accuracy when tapping along to the beat, as well as more spontaneous rhythmic movement (Janata et al., 2012). Consistent with this findings, neuroimaging studies have demonstrated that rhythmic music engages not only auditory but also motor pathways and increases coupling between the them, even in the absence of actual movement (Chen, Penhune, & Zatorre, 2008; Chen, Zatorre, & Penhune, 2006; Grahn & Rowe, 2009). This raises the possibility that groove can be systematically manipulated to study this link between music and movement on a neurobiological level (Stupacher, Hove, Novembre, Schütz-Bosbach, & Keller, 2013).

Recent work has highlighted the importance of key acoustic and metrical parameters associated with the perceived amount of groove in musical pieces. Prominently among them are the presence of strong low frequencies and syncopation. With respect to the former, bass drums are used in many different musical genres to demarcate strong metrical locations (Large, 2000). Dynamic bass activity is correlated with groove ratings of music, and manipulations that increase bass energy in synthetic drum patterns result in higher groove ratings (Jan Stupacher, Hove, & Janata, 2016). Furthermore, it has been shown that people tend to move more actively and exhibit more entrainment with louder bass drums in dance music (Van Dyck et al., 2013), and that lower frequency instruments support greater sensitivity to timing deviations than higher frequency instruments in music (Hove, Marie, Bruce, & Trainor, 2014; Stupacher et al., 2016). Regarding metrical properties, syncopation has been implicated to play a key role in groove, as it features frequently in genres that emphasize groove, such as funk, soul and hip-hop (Butler, 2006). Syncopation is a technique, which systematically violates the rhythmic expectation of a listener (Witek, Clarke, Wallentin, Kringelbach, & Vuust, 2014). Technically, it is defined as the omission of events at metrically strong (expected) locations and the sounding of events at metrically weak (unexpected) locations (Longuet-Higgins & Lee, 1984). Studies using synthetic drum patterns suggest that syncopation is associated with groove via an inverted U-shaped function, with high and low levels of syncopation being perceived as less groovy than moderate levels of syncopation (Sioros, Miron, Davies, Gouyon, & Madison, 2014; Witek, Clarke, Kringelbach, & Vuust, 2014).

Building on this research, we examined whether differences in musical groove are associated with differential effects on the nervous system, as well as the extent to which such effects may be dependent on bass and syncopation. We used pupillometry to assess the effects on the nervous system. Pupil size is governed by the autonomous nervous system, with sympathetic activation stimulating dilation and parasympathetic activation stimulating contraction. Beyond responding to light, pupil dilation has been observed in response to a variety of cognitive factors (e.g., effort, working memory, language processing and pain; reviewed in Andreassi, 2007). Pupillometry has also been effectively applied to studies of music. In 1954, (Slaughter, 1954) reported that 'stimulating' music evoked higher pupil dilation than 'sedative' music. More recently, (Gingras, Marin, Puig-Waldmüller, & Fitch, 2015) found that pupil dilation was correlated with perceived arousal in response to short excerpts of romantic period piano trios. Likewise, (Weiss, Trehub, Schellenberg, & Habashi, 2016) found that the pupil dilates more in response to vocal melodies compared to the same melodies played by a piano. Finally, (Laeng, Eidet, Sulutvedt, & Panksepp, 2016) found that acute pupil dilation can be used to detect the occurrence of music-induced chills.

Here we examine the relationship between pupil size and groove across three experiments. In experiment 1, we presented listeners with excerpts of real (i.e., commercially available) music differing in groove to test whether high-groove music stimulates stronger pupil dilation than low-groove music. In experiment 2, we presented listeners with frequency filtered versions of the high-groove music excerpts from experiment 1 to test whether low or high frequency content is more effective at stimulating pupil dilation. In experiment 3, we presented listeners with custom-designed drum loop stimuli to test the effects of systematic variation in frequency content and syncopation.

METHODS

Subjects. Thirty-two adults (16 males and 16 females; mean age = 24, range = 20-32) participated in this study in exchange for monetary compensation. Individuals had taken weekly music and/or dance lessons for an average of 5.4 years (*SD* = 4.9), and amount of musical training was not significantly different between males and females (M_{male}=6.4, M_{female}=4.5; *U*=84.5, *p*=0.3927). All participants were naïve to the research questions. The experiments were approved by the University of Vienna Ethics Committee.

Apparatus. Pupillometric data was collected using an SR Research EyeLink 1000 head-supported infrared optical eye-tracking system. All stimuli were presented over Beyerdynamic DT-770 headphones (Pro/80 Ohm; 5Hz-35KHz frequency response) connected to an Apple Mac Mini computer (model 4.1) running OSX 10.11.6. A computer monitor was used solely to display a fixation cross during trials and a countdown during rest periods. Stimulus presentation and the recording of pupillometric data were controlled by custom Matlab (version R2015a; Mathworks, 2015) code written using functions from the Psychophysics (v3.0.14) and Eyelink Toolbox extensions (Brainard, 1997; Cornelissen, Peters, & J., 2002; Pelli, 1997).

Procedure. Upon entering the lab, subjects received a brief explanation of the experimental procedure and provided written informed consent. They were then seated in front of the eye-tracker with their heads placed on the chin-rest. The height of the seat was adjusted as required and example stimuli similar to those used in the experiments (see below) were briefly played so that the subject could adjust the volume to a comfortable level, which was then maintained for the rest of the session. Volume levels did not differ systematically between males and females volume levels did not differ systematically between males and females (U = 258, Z = 1.44, p = 0.148). The three pupillometry experiments were run in two blocks, with an opportunity for a short break in between. Block one consisted of experiment 3 (drum patterns) and block two consisted of experiment 1 (music) immediately followed by experiment 2 (filtered music; see below for details). The decision to start with the relatively simple drum patterns and end with more dynamic musical stimuli was made to mitigate subject boredom and fatigue in later stages of the experimental session. Each block began with a calibration of the eye-tracking system followed by two practice trials that used the example stimuli mentioned above. Trials lasted 50 seconds: 10 seconds of silence followed by 40 seconds of stimulus playback. During trials, subjects were instructed to minimize blinking and focus on a gray fixation cross presented against a black background at the center of the computer monitor. Between trials, a 40-second countdown was presented on the monitor and subjects were encouraged to rest their eyes in preparation for the next trial. After completing the pupillometry experiments, subjects took a brief computerized survey in which they heard each stimulus a second time and provided ratings of groove, arousal, familiarity and preference (Supplementary Figure 1). Finally, participants were paid 10 Euros and debriefed. An experimental session lasted approximately 45 minutes.

Stimuli. The stimuli in experiment 1 were created from excerpts of commercially available music previously rated for groove in Janata et al. (2012). Eight instrumental excerpts, closely matched for tempo, were selected: four with relatively high-groove ratings and four with relatively low-groove ratings (Table 1). Excerpts were obtained by downloading the original track from the iTunes music store (AAC compression, sampling rate = 44100 Hz, bit rate = 260-293 kbps) and extracting the 30-second window used in (Janata et al., 2012). Once extracted, each excerpt was extended to 40-seconds by identifying a time-point within the last 5 seconds at which the content could be looped without disrupting the beat. One-second linear ramps were then applied to the start and end of each stimulus to create 'fade-in' and 'fade-out' effects. Finally, the amplitude of each stimulus was adjusted so that all had approximately the same average sound pressure level as measured using a RION NL-62 sound level meter (set to dBA; RION, Tokyo, JP). Looping was performed in Logic Pro X (version 10.2.0; (Apple, 2013)). Fades and amplitude adjustments were made in Matlab and then saved as .wav files for presentation (sampling rate = 44100, bit depth = 16). All subjects heard all eight stimuli in randomized order, making it possible to compare the effects of high- vs. low-groove within-subjects.

Table 1. REAL MUSIC STIMULI

Track Name	Artist	Tempo (BPM)	Mean Groove Rating
HIGH GROOVE STIMULI			
Sco-mule (DJ Logic remix)	Bernie Worrell, Chris Wood, Gov't Mule and John Scofield	120	93.9
Bad tune	Earth, Wind and Fire	118	86.2
Outa-space	Billy Preston	115	90.9
Look ka py py	The Meters	87	92.5
LOW GROOVE STIMULI			
Beauty of the sea	The Gabe Dixon Band	120	32.1
Bryter layter	Nick Drake	119	40.4
Druid fluid	Yo-Yo Ma, Mark O'Connor and Edgar Meyer	115	38.1
Ray dawn ballon	Trey Anastasio	80	38.5

Groove ratings are from Janata et al. 2012, and were collected on a scale from 0-127 (Janata et al. 2012); BPM = Beats Per Minute

The stimuli in experiment 2 were filtered versions of the four high-groove stimuli from experiment 1. The filter type, a first-order Butterworth filter, was selected because its relatively gradual roll-off (-6dB per octave) retained some energy in the stop band, preserving some of the character of the original stimulus but emphasizing content in the pass band. This filter was applied to each original stimulus twice: once as a low-pass filter to create a version emphasizing low-frequency energy, and once as a high-pass filter to create a version emphasizing high-frequency energy. Both applications used a cutoff frequency of 300 Hz. Finally, one-second linear ramps were applied to the start and end of each stimulus, amplitudes were adjusted to approximately the same mean sound pressure level, and the results were saved as .wav files following the procedures described above. Filtering was also performed in Matlab (functions: 'butter.m' and 'filtfilt.m'). Unlike experiment 1, experiment 2 was conducted between-subjects with half of the subjects hearing only the low-pass stimuli and the other half hearing only the high-pass stimuli (both groups half male). This decision was made to mitigate potential order effects resulting from repeated exposure to highly similar stimuli.

The stimuli in experiment 3 were four synthesized drum patterns designed to cross manipulations of frequency content and metrical structure. Each drum pattern consisted of samples of three drum types (high-hat, snare and kick) from the “Portland Kit” instrument in Logic Pro X. These samples were arranged to create two-bar drum patterns in 4/4 time played at 100 BPM (total duration = 4.8 seconds). The number of hits on each drum type was the same across patterns. Frequency content was manipulated by altering the pitch of the snare and kick drums (J. Stupacher, Hove, & Janata, 2016). In the ‘low-drums’ patterns, the original drum samples were used (peak frequencies at 40 Hz and 135 Hz respectively). In the ‘high-drums’ patterns, the snare and kick drums were pitch-shifted up using the ‘Inspector’ and ‘Transpose’ functions in Logic Pro X (new peak frequencies at 135 and 228 Hz respectively). The amplitude of the shifted samples was adjusted to achieve comparable loudness with the original samples using the ‘loudness for impulsive sounds’ model in the Loudness Toolbox extension for Matlab (function: ‘Loudness_LMIS.m’; (Boullet, 2005)). Structure was manipulated by shifting the onset time of snare and kick hits. In the ‘straight’ patterns (Supplementary Figure 2A), all hits occurred at relatively strong metrical locations resulting in a pattern with no syncopation (polyphonic syncopation score = 0; (Witek, Clarke, Kringelbach, & Vuust, 2014b)). In the ‘syncopated’ patterns (Supplementary Figure 2B), multiple hits occurred at weak metrical locations before omissions at stronger locations, resulting in a level of syncopation near the top of the U-shaped curve reported by (Witek, Clarke, Wallentin, et al., 2014) (polyphonic syncopation score = 41). These manipulations resulted in four patterns: straight low-drums, straight high-drums, syncopated low-drums, and syncopated high-drums. Each pattern was looped ~8 times to create a 40-second stimulus with linear fades were applied to first and last second. The results were saved as .wav files for presentation.

Analysis of Pupil Size. The diameter of the left pupil and the x-y position of the subject's gaze on the computer monitor were collected continuously throughout each trial (sampling rate = 1000 Hz). This data was processed offline in Matlab to remove artifacts introduced by blinks and visual fixations away from the cross. During blinks, the eye-tracker loses the pupil and records an arbitrary value. These samples were identified and removed including a 50 ms buffer immediately before and after (Gingras et al., 2015). Fixations away from the cross were identified as samples with x-y coordinates located outside a circular region centered on the fixation cross. These samples were also excluded along with a 50 ms buffer immediately before and after. In accordance with other pupillometric studies, the gaps introduced by these procedures were linearly interpolated and the resulting continuous traces were smoothed using a low-pass filter (4 Hz) to remove jitter (Sirois & Brisson, 2014). The smoothed trace from each trial was then baseline-normalized by dividing each sample by the mean calculated over a one-second baseline immediately preceding stimulus onset. Trials in which more than 50% of the data was excluded (either during baseline or stimulus playback) were excluded from further analyses, resulting in the loss of 25 out of 512 trials (4.8%). When an experimental condition included more than one stimulus (experiments 1 and 2), average pupillary responses were calculated within subject prior to statistical analyses.

Statistics. Experimental effects on pupil size were evaluated for statistical significance in two ways. In the first approach, comparisons were made using standard hypothesis tests (Wilcoxon signed-rank tests in experiments 1 and 3, Mann-Whitney U tests in experiment 2) to compare distributions of individual subject means calculated over time periods in which pupil size was maximally differentiated between experimental conditions, as approximated by visual inspection of the average traces (see Figures 1-3). In the second approach, experimental effects were assessed using linear mixed effects (LME) models to predict baseline-normalized pupil size as a function of effects of interest over the full 40 seconds of stimulation (as represented by averages calculated every 100 ms). All LME models included fixed effects for the experimentally manipulated factors (groove in experiment 1, frequency content in experiment 2, metrical structure and frequency content in experiment 3), listener sex, the interactions between these variables, time since stimulus onset (0-4000 in 100 ms steps), and a random (intercept) effect for subject (ID# 1-32). The same effect structures were also used to model responses to the survey questions. All statistics were performed in RStudio (v1.0.153; (Rs. Team, 2015)). The 'wilcox.test' function from package 'stats' (v3.3.3) was used to conduct Wilcoxon sign-rank and Mann-Whitney U tests (R. C. Team, 2015); the 'lmer' function from package 'LME4' (v1.1-13) was used to build models (Bates, Mächler, Bolker, & Walker, 2015); the 'anova' function from package 'car' (v2.1-5) was used to assess the significance of fixed effects in LME models (Fox, Friendly, & Weisberg, 2013); the 'contrast' function from package 'lsmeans' was used to conduct post-hoc comparisons for significant interactions (Length, 2016); all *p* values reported in association with post-hoc contrasts were corrected using the Bonferroni method (for 6 tests in experiment 1, and 28 tests in experiment 3); finally, the 'effects' function from package 'effects' (v4.0-0) was used to plot interactions (Fox, 2003).

RESULTS

Experiment 1: High- vs. Low-Groove Music. The average pupillary response to the high- and low-groove music stimuli are shown in Figure 1A. In general, the pupillary response to the onset of musical stimulation was characterized by a sharp initial increase in size followed by a gradual decline. High-groove stimuli evoked stronger dilation than low-groove stimuli on average, with the difference being most pronounced over a time window from 0-15 seconds post onset. Comparison of individual subject means calculated over this period indicated a statistically significance difference, M_{HighG}=104.9% (*SD*=4.9%) vs. M_{LowG}=102.7% (*SD*=3.8%), *W*=149, *p*=0.0315. Comparison of individual subject means calculated over the remaining 25 seconds showed greater similarity between responses, M_{HighG}=100.4% (*SD*=4.9%) vs. M_{LowG}=100.0% (*SD*=5.7%), *W*=304, *p*=0.4545.

The LME model analysis showed similar results. Groove was a significant predictor of pupil dilation, $\chi^2(1)=456.6$, p<0.0001, with the response to high-groove music estimated to be 0.56% stronger than the response to low-groove music on average over the entire 40 seconds of stimulation (β=0.0056, *SE*=0.0008). The interaction between groove and listener sex was also a significant predictor, $\chi^2(1) = 131.0$, p < 0.0001 (Figure 1B). Post-hoc analyses showed that both males and females responded more strongly to high-groove music than low-groove music (*ts* = 22.7 and 13.3 respectively, *ps*<0.0001), but that the difference was larger for males than females, $\beta_{\text{male}} = 0.018$ vs. $\beta_{\text{female}} = 0.011$ (*SEs*=0.00080). Finally, pupil size was predicted to decrease with time post stimulus onset at a rate of ~0.2% per second, β=-0.00019, *SE*=$2.4\text{x}10^{-6}$, $\chi^2(1)=5599.1$, p<0.0001.

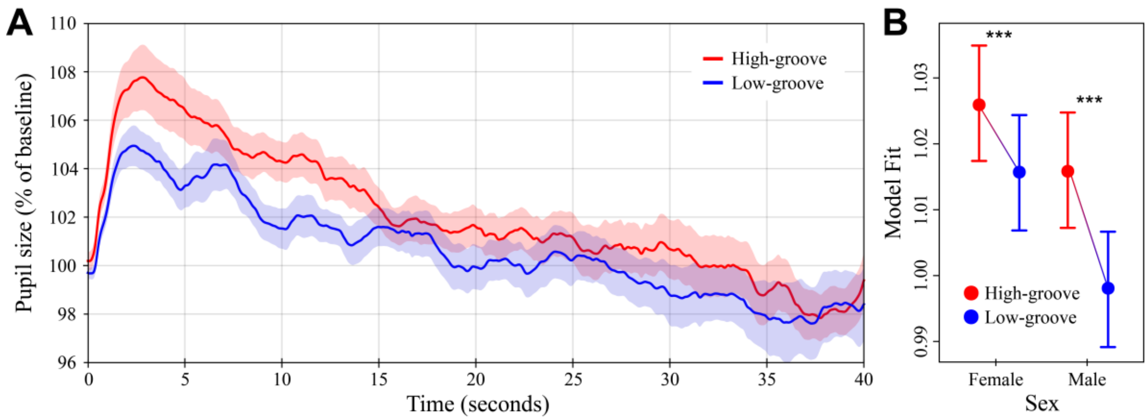

Figure 1. Pupil dilation as a function of groove in music. (A) Colored lines depict average baseline normalized pupil size over time in response to high- and low-groove music stimuli (N=32 for each line). Stimulus onset occurred at 0 seconds and lasted until 40 seconds. (B) LME model predictions for baseline normalized pupil size showing the significant two-way interaction between groove and sex (see main text). *** $p < 0.0001$. Error bars (shaded and lines) represent ±1 SEM.

Experiment 2: Filtered High-Groove Music. The average pupillary response to the high- and low-pass filtered versions of the high-groove music stimuli from experiment 1 are shown in Figure 2A. The overall pattern of pupil dilation was similar to that observed previously, albeit with lower maxima and a more rapid initial decline in response to the low-pass stimuli. High-pass stimuli evoked stronger dilation than the low-pass stimuli on average, with the difference again being most pronounced over a time window from ~0-15 seconds post stimulus onset. Comparison of individual subject means calculated over this period indicated a statistically significance difference, M_{highP}=102.8% (SD=3.2%) vs. M_{lowP}=99.7% (SD=3.5%), U=205, p=0.0275. As in experiment 1, comparison of individual subject means calculated over the remaining 25 seconds showed greater similarity between responses, M_{highP}=97.6% (SD=7.2%) vs. M_{lowP}=95.2% (SD=6.1%), U=230, p=0.2067.

The LME model analysis showed similar results. Frequency content was a marginally significant predictor of pupil dilation, with the response to high-pass stimuli estimated to be 1.6% stronger than the response to low-pass stimuli on average over the entire 40 seconds of stimulation,

β=0.016 (SE=0.023), $\chi^2(1)$=2.89, p=0.0890. The relationship between frequency content and sex resembled that observed between groove and sex in experiment 1, but did not attain significance, β_{male}=0.037 vs. β_{female}=0.016 (SEs=0.023), $\chi^2(1)$=0.46, p=0.4991 (cf. Figures 1B and 2B). Listener sex alone, however, was determined to be a significant predictor, with females exhibiting stronger responses than males overall, β=0.034 (SE = 0.023), $\chi^2(1)$=7.6, p=0.0058 (Figure 2B). Finally, pupil size was predicted to decrease with time post stimulus onset at a rate equal to that found in experiment 1, β=-0.0002/100 ms (SE=3.5x10^{-6}), $\chi^2(1)$=4158.3, p<0.0001.

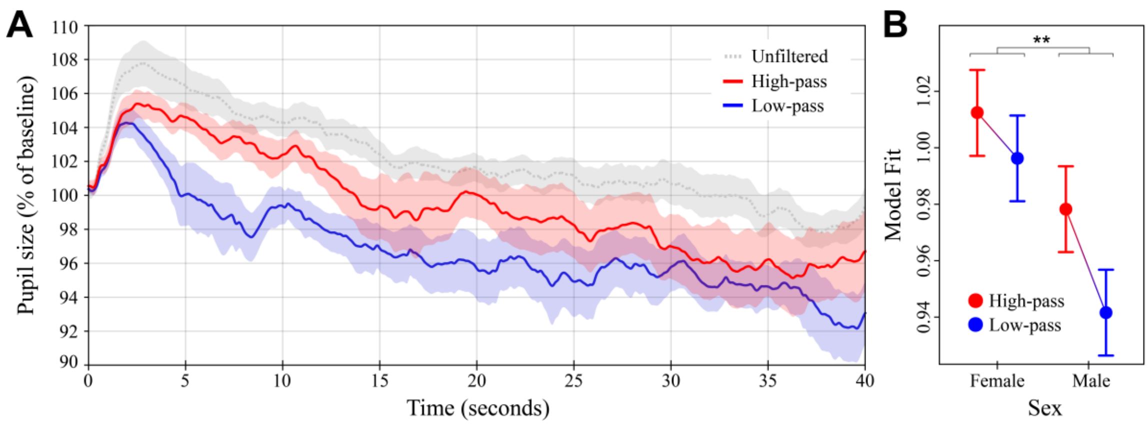

Figure 2. Pupil dilation as a function of filtered high-groove music. (A) Colored lines depict average baseline normalized pupil size over time in response to high- and low-pass filtered versions of the high-groove stimuli from experiment 1 (N=16 for each line). The gray line depicts the response to the original high-groove stimuli (from experiment 1) for comparison. Stimulus onset occurred at 0 seconds and lasted until 40 seconds. (B) Average pupil size for males and females in response to high- and low-pass filtered stimuli as predicted by the LME model (see main text). (C) LME model predictions for baseline normalized pupil size showing the significant main effect of sex (see main text). Error bars (shaded and lines) represent ±1 SEM. ** p < 0.01.

Experiment 3: Drum Patterns. The average pupillary responses to the drum pattern stimuli are shown in Figure 3A. The general pattern of pupil dilation was similar to that observed in experiments 1 and 2 albeit with lower maxima and more rapid declines. Unlike experiments 1 and 2, however, no obvious differences between conditions were apparent in the average responses. Comparison of individual subject means calculated over time windows from 0-15 and 16-40 seconds post onset failed to show any statistically significant differences. The biggest difference in the 0-15 window was between responses to the straight high- and low-drum patterns, $M_{straightHigh}$=101.8% (*SD*=4.6%) vs. $M_{straightLow}$=99.9% (*SD*=6.2%), *W*=183, *p*=0.1299. Likewise, the biggest difference in the 16-40 second window was between responses to the straight low-drum and syncopated low-drum patterns, $M_{straightLow}$=94.3% (*SD*=7.1%) vs. $M_{syncLow}$=97.2% (*SD*=9.2%), *W*=181, *p*=0.1207.

Here, the LME model analysis proved particularly useful in deciphering the results. Interpretation of the independent effects of metrical structure, frequency content and listener sex on pupil dilation was complicated by their involvement in a significant three-way interaction, $\chi^2(1)=1279.4$, p<0.0001 (Figure 3B). Post-hoc analyses indicated that males and females reacted differently to structure depending on frequency. The biggest difference occurred between males responding to the low-drum patterns, with the model predicting 4.7% stronger dilation in response to the syncopated vs. straight pattern on average, $\beta=0.047$ (*SE*=0.0013), *t*(47561.2)=35.9, *p*<0.0001. Females showed an opposite (albeit much weaker) difference, with the model predicting 0.47% weaker dilation in response to the syncopated pattern on average, $\beta=-0.0047$ (*SE*=0.0015), *t*(47567.6)=-3.2, p=0.0381. Complicating matters further, both male and female differences were reversed in response to the high-drum patterns, with the model predicting 3.3% weaker dilation for males responding to the syncopated vs. straight pattern on average, $\beta=-0.033$ (*SE*=0.0013), *t*(47563)=-47.34, p < 0.0001; and 1.4% stronger dilation for females responding to the syncopated pattern on average, $\beta=0.014$ (*SE*=0.0014), *t*(47563.2)=10.08, *p*<0.0001. Finally, in keeping with the results of experiments 1 and 2, pupil size was predicted to decrease with time post stimulus onset at a rate of -0.24% per second, $\beta=-0.00024$ ($SE = 3.0\text{x}10^{-6}$), $\chi^2(1)=5820.5$, p<0.0001.

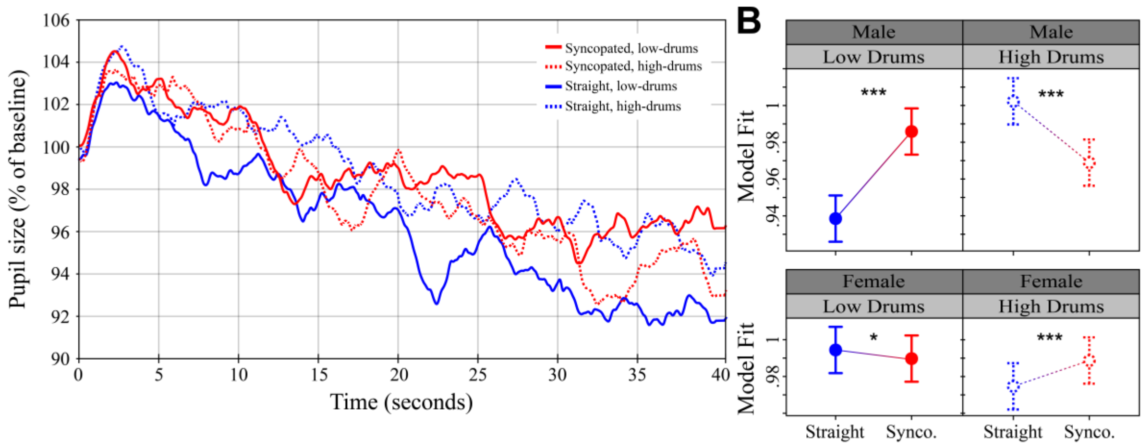

Figure 3. Pupil dilation as a function of metrical structure and frequency content in synthetic drum patterns. (A) Colored lines depict average baseline normalized pupil size over time in response to the four drum patterns crossing manipulations of metric structure (straight vs. syncopated) and frequency content (high- vs. low-drums; N = 32 for each line). Stimulus onset occurred at 0 seconds and playback lasting until 40 seconds. (B) LME model predictions for baseline normalized pupil size showing the significant three-way interaction between structure, frequency and sex (see main text). Error bars (shaded and lines) represent ±1 SEM. * p < 0.05, *** p < 0.0001.

Survey Results. The results of the survey are shown in Figure 4. For the stimuli used in experiment 1 (left panel), LME modeling of the survey responses confirmed that the high-groove stimuli were rated as higher in groove than the low-groove stimuli, β=49 (*SE*=8.2), $\chi^2(1)$=76.4, *p*<0.0001, as well as more arousing, β=52.4 (SE=8.1), $\chi^2(1)$=100.7, *p*<0.0001, and more familiar β=22.0 (SE=7.5), $\chi^2(1)$=26.9, *p*<0.0001. Additionally, groove and listener sex interacted in predicting ratings of arousal, $\chi^2(1)$=4.5, *p*=0.0339, with post-hoc comparisons indicating that male responses to high-groove stimuli tended to be stronger than female responses to high-groove stimuli, β=25.4 (*SE*=9.5), *t*(71.3)=2.67, *p*=0.0563.

For the stimuli used in experiment 2 (Figure 4, middle panel), LME modeling of the survey responses showed marginally significant effects of frequency content on groove and familiarity ratings. The high-pass stimuli tended to be rated as higher in groove than the low-pass stimuli, β=28.3 (*SE*=21.2), $\chi^2(1)$=3.2, *p*=0.0730, and the low-pass stimuli tended to be rated as more familiar than the high-pass stimuli, β=22.4 (*SE*=18.5), $\chi^2(1)$=3.5, *p*=0.0619. A significant effect of listener sex was found for arousal ratings, with males rating the stimuli as more arousing than females overall, β=15.1 (*SE*=15.7), $\chi^2(1)$=4.2, p=0.0402.

For the stimuli used in experiment 3 (Figure 4; right panel), LME modeling of the survey responses showed significant effects of structure for all four questions. Ratings of the syncopated patterns were higher for groove, β=63.5 (*SE*=13.3), arousal β=41.4 (*SE*=11.0), familiarity, β=49.3 (*SE*=14.1), and preference, β=47.1 (*SE*=11.1), χ^2s(1)=72.5, 34.2, 53.3 and 70.8 respectively, *ps*<0.0001). Frequency content also affected survey responses, with low-drum patterns receiving marginally higher ratings for groove, β=4.4 (*SE*=13.3); $\chi^2(1)$=3.0, p=0.0811, and significantly higher ratings for preference, β=12.0 (*SE*=11.5), $\chi^2(1)$=4.5, p=0.0329, in opposition to the effects of frequency content observed in experiment 2. Finally, a marginally significant interaction was found between frequency content and listener sex in predicting arousal ratings, $\chi^2(1)$=3.8, p=0.0523, reflecting the tendency of males to rate low-drum patterns as more arousing than high-drum patterns, β=18.1 (*SE*=7.8). However, post-hoc analysis of this difference did not survive Bonferroni correction, $t(90.0)$=2.3, p=0.1299.

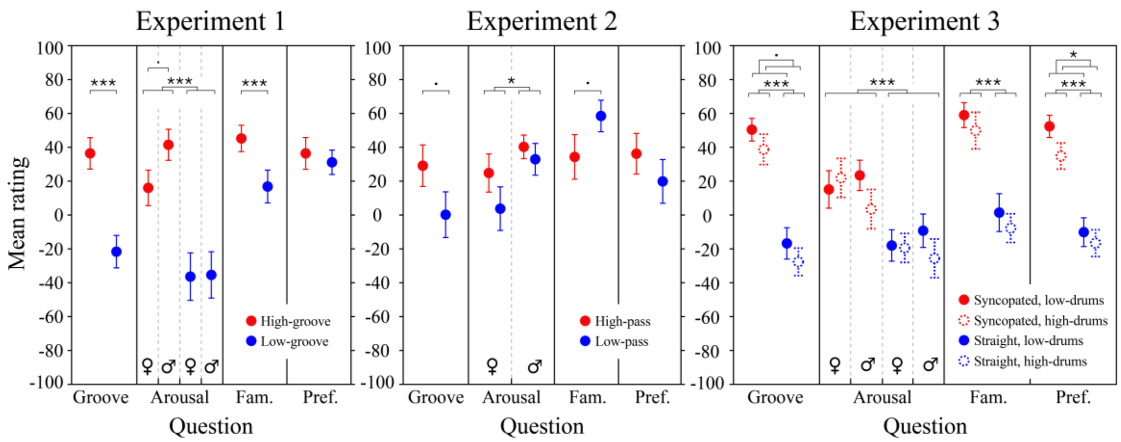

Figure 4. Survey results. Mean groove, arousal, familiarity, and preference ratings for the stimuli in experiments 1, 2, and 3. Each data point represents an average rating calculated across subjects. Error bars represent ±1 SEM. For experimental conditions comprising multiple stimuli (high- and low-groove in experiment 1, high- and low-pass in experiment 2), ratings were averaged within subjects before averaging across subjects. Male and female responses are shown separately when the corresponding LME model analysis predicted an effect of sex, or an interaction including sex. *** $p < 0.0001$, * $p < 0.05$, . $p < 0.09$. In experiment 1, the p-value associated with the post-hoc comparison of female and male arousal ratings for high-groove stimuli was corrected for 6 tests using the Bonferroni method. In experiment 3, the lower row of statistical brackets describes effects of structure, and the upper row describes effects of frequency (see main text).

DISCUSSION

In experiment 1 we tested the effect of groove in musical stimuli reliably rated as high- or low-groove on pupil size. The results showed that the high-groove stimuli evoked significant stronger pupil dilation than low-groove music. Interestingly, these differences emerged rapidly increasing to a delta of almost 3%, were maintained at ~2% for almost 15 seconds, after which they dropped to similar levels for the remaining 25 seconds. Over the whole 40 seconds the LME analysis predicted a significant difference of 0.6%. Importantly, these results cannot be explained on the basis of tempo or loudness, as these factors were controlled between high- and low-groove stimuli. Comparison of the average intensity contours of the high- and low-groove stimuli further confirms that local differences in intensity between conditions are unlikely to account for these effects (Supplementary Figure 3A). Another interesting observation was that the effects of groove on pupil size interacted with the sex of the listener, such that males showed a greater difference in response between the low-groove and high-groove stimuli than females. Comparison of the pupillary and survey results shows an overall consistent pattern. In addition high-groove music evoking stronger pupil dilation, those stimuli were also perceived by participants to evoke a stronger desire to move, greater arousal and familiarity. The familiarity ratings are unlikely to account for the stronger dilation, as we do not find a consistent pattern of higher familiarity eliciting stronger pupil dilation across experiments. Also, none of the participants reported that they know the songs. Consistent with the sex difference in the pupillary response, males also perceived a greater difference between high- and low-groove stimuli. Taken together, these findings show that high-groove music stimulates physiological arousal to a degree that can be detected using pupillometry, with males exhibiting greater sensitivity to differences in groove.

In experiment 2 we used high-pass and low-pass filtered versions of the high-groove stimuli from experiment 1 to test the effects of high- and low-frequency content on pupil dilation.

Contrary to our expectations based on the common association between groove and bass, we found stronger pupillary reactions to the high-pass stimuli than the low-pass stimuli. Specifically, differences were once again most pronounced over a window from approximately 2-15 seconds, resulting in significant stronger dilation by a delta of ~2% of high-pass stimuli, while a trend for stronger dilation by a delta of 1.6% was predicted by the LME analysis over the whole 40 seconds ($\chi^2(1)=2.89$, $p=0.0890$). A reason why the LME does not approach significance here could be that in contrast to experiment 1 we opted in experiment 2 for a between-subject, exposing only half of the participants to the high-pass and the other half to the low pass stimuli (thus halving the sample size) to mitigate boredom and fatigue in later stages of the experimental session. Still, combined with the significant mean differences, we find those results convincing and will discuss them further. The effect of high-pass stimuli eliciting stronger dilation compared to low-pass is unlikely to be explained by differences in the overall loudness of the stimuli, as this factor was controlled between conditions (Supplemental Figure 3B). Consistent with experiment 1, pupil dilation interacted with the listener's sex, such that female pupil dilation was predicted to be ~4.4% stronger overall. The survey data shows a similar pattern to the observed pupillary responses, as high-pass stimuli also tended to be rated as higher in groove than low-pass stimuli. Listener sex was again found to affect ratings of arousal, but the effect was opposite to that observed in the pupillary responses, with males rating the stimuli as more arousing overall. Taken together, these results indicate the importance of high frequency content in the stimulating effect of high-groove music, with females exhibiting greater dilation to both high-pass and low-pass filtered stimuli. This complements previous studies that have emphasized the importance of low frequency content in groove by showing that both low and high frequency bands play important roles in the physiological effects of high-groove music. Indeed, the full spectrum stimuli were the most effective at stimulating pupil dilation, although an alternative explanation could be that this difference is the result of an order effect, as the unmanipulated high-groove stimuli were always presented first (in experiment 1). In hindsight, counterbalancing the high-groove and low-groove stimuli of experiment 1 and the band-pass filtered high-groove stimuli of experiment 2 to exclude the possibility of the order effect and exposing the participants to all band-pass filtered stimuli to increase sample size would have been more sensible. Another important caveat regarding the general importance of high frequency-content is that, the low-pass filtering applied here attenuated midrange and high frequencies, which carry important musical qualities/information such as melody and syncopation. Therefore the effect of high-pass stimuli evoking greater dilation compared to low-pass stimuli may not be specific to frequency per se, because it could also remove structural elements contained within those bands that may be critical in the stimulating effect of high-groove music.

In experiment 3 we used synthetic drum loop stimuli in which we could carefully control frequency content and metrical structure to thus test the effects of these key factors on pupil dilation. Interpreting the results of this experiment is complicated by a three-way interaction between metrical structure, frequency content and listener sex. In response to low-drum patterns, male pupil dilation was predicted to be stronger to the syncopated pattern, whereas female pupil dilation was predicted to be stronger to the straight pattern; and this pattern was reversed in response to the high-drum patterns. The largest of these differences was between males reacting to the low-drum syncopated and straight patterns. This difference provides evidence for a role of syncopation in the physiologically stimulating effects of groove and is consistent with perceptual studies related groove and syncopation (Witek, Clarke, Wallentin, et al., 2014), as well as the actual use of syncopation to enhance groove in music (Pressing, 2002). Surprisingly, females tended to react in the opposite way, showing stronger dilation to the straight pattern. The survey data showed significant higher groove, arousal, familiarity, and preference for the syncopated drum patterns, with the low-drum patterns being preferred over the high-drum patterns. In sum, the results of experiment 3 show that pupil dilation is modulated by frequency content and metrical structure, with the effects of frequency content being more pronounced for straight patterns than syncopated patterns and different between males and females. However, the present results are conflicting and do not reveal straightforward effects of frequency and metrical manipulations, suggesting a complex interplay between those factors and call for further studies to elucidate the role of frequency manipulations and syncopation on eliciting pupil dilation in music.

GENERAL DISCUSSION

Although there are several studies showing that rhythm perception engages auditory and motor regions of the brain, this is the first study showing pupillary sensitivity to differences in groove. Interestingly, recent studies have shown that pupil dilation correlates very closely to the firing rate of the locus coeruleus (LC), a brainstem nucleus that constitutes the largest group of noradrenergic neurons in the central nervous system (Samuels & Szabadi, 2008). This suggests that the effect of high-groove music on our species is supported by the capacity of stimulating central and peripheral arousal, which can be measured using pupillometry. Thus, pupillometry can provide an objective physiological measure of the connection between music and movement. This comes with several advantages over traditional self-report methods used to study groove. First, physiological measures are robust to demand characteristics (Nichols & Maner, 2008) as pupil dilation is not under voluntarily control. Second, when conducting research in non-Western and/or non-English-speaking populations, which are of particular interest when investigating the biological foundation of musicality, physiological measures avoid problems due to cultural differences in task interpretation, response style and/or language translation. Third, for interspecific comparative research, physiological measures can be directly applied with results that may be compared to humans in a relatively straightforward fashion. This is particularly compelling because there is evidence that a small number of other species, including several species of parrots, elephants one sea lion and one chimpanzee (Ravignani et al., 2014) exhibit the ability to perceive and entrain to a beat and thus may also be susceptible to the effects of groove.

Further, our results show that high-frequency energy in high-groove music stimulates stronger pupil dilation than low-frequency energy. This suggests that high-frequencies play an important role in stimulating the physiological arousal associated with groove, which complements previous studies highlighting the importance of low frequencies for groove (Hove et al., 2014;

Jan Stupacher et al., 2016; Todd & Cody, 2000; Van Dyck et al., 2013). However, further studies are necessary to disentangle the role of acoustic elements within those frequency bands and the general role of frequency content for the stimulating effect of high-groove music.

Finally, we found greater sensitivity to the differences in the frequency content and metrical structure among males despite stronger overall reactions among females. Existing evidence for sex differences in response to music are few and mixed. Nater et al. (2006) e.g., showed sex differences in psychophysiological reactivity patterns to music, such that females displayed elevated responses to arousing and unpleasant (metal) music compared to relaxing and pleasant (renaissance) music, whereas males did not. Gingras et al. (2015) found that males tend to have stronger pupillary reactions in response to short excerpts of classical music compared to females. Our findings stand in contrast to these results, which might be due to methodological differences between our and these studies. Nater et al., (2006) used a set of two long 10-minute stimuli that differed on the valence (pleasing and aversive) and arousal (relaxing and arousing) dimension, controlled for hormonal contraceptives and measured heart rate, skin conductance and finger temperature, while Gingras et al., (2015) used a large set of short, 6-second piano stimuli and measured pupil dilation. On the other hand, in our study we selected our music stimuli on the basis of groove and did not screen female participants for hormonal contraceptives. Another possibility could be that our sample of 32 young, western participants, who were mostly students, is not representative of males and females across socioeconomic background and cultures. Moreover, when contrasting males and females in a small sample, differences can arise because of variables that are very indirectly shaped by biological sex (e.g. determined by gender or culture); a problem that is very relevant when studying sex differences humans. Therefore, we parsimoniously refrain from interpreting the sex differences found here as biological differences until further studies using larger and more cultural and socioeconomic diverse samples confirm or refute them.

CONCLUSION

The experiments reported here demonstrate pupillary sensitivity to groove in music, as well as stronger effects of high-frequency content in high-groove music. Further, we find modulation of pupillary responses by frequency content and metrical structure, as well as sex differences in these effects. These results shed light on the link between music and movement by showing that high-groove music is an effective stimulus of central and peripheral arousal. Finally, we establish pupillometry as an effective method for studying the link between music and movement that can be extended across cultures, developmental stages, and other species to investigate the biological foundations of musicality.

REFERENCES

Andreassi, J. L. (2007). *Psychophysiology: human behavior and physiological response* (5th ed.). Mahwah, NJ: Lawrence Erlbaum Associates, Inc., Publishers.

Apple. (2013). Logic Pro X. Cupertino, CA: Apple Inc.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 48.

Boullet, I. (2005). *La soni des sons impulsionnels: perception, measures et modeles*. l'Universite de la Mediterrannee Aix-Marseille II.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Butler, M. J. (2006). *Unlocking the groove: Rhythm, meter, and musical design in electronic dance music*. Bloomington, IN: Indiana University Press.

Chen, J. L., Penhune, V. B., & Zatorre, R. J. (2008). Listening to musical rhythms recruits motor regions of the brain. *Cerebral Cortex*, *18*(12), 2844–2854. https://doi.org/10.1093/cercor/bhn042

Chen, J. L., Zatorre, R. J., & Penhune, V. B. (2006). Interactions between auditory and dorsal premotor cortex during synchronization to musical rhythms. *NeuroImage*, *32*(4), 1771–1781. https://doi.org/10.1016/j.neuroimage.2006.04.207

Cornelissen, F. W., Peters, E., & J., P. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments & Computers*, *34*, 613–617.

Fox, J. (2003). Effect Displays in R for Generalised Linear Models. *Journal of Statistical Software*, *8*(15), 27.

Fox, J., Friendly, M., & Weisberg, S. (2013). Hypothesis tests for multivariate linear models using the car package. *The R Journal*, *5*(1), 39–52.

Fujioka, T., Trainor, L. J., Large, E. W., & Ross, B. (2012). Internalized Timing of Isochronous Sounds Is Represented in Neuromagnetic Beta Oscillations. *Journal of Neuroscience*, *32*(5), 1791–1802. https://doi.org/10.1523/JNEUROSCI.4107-11.2012

Gingras, B., Marin, M. M., Puig-Waldmüller, E., & Fitch, W. T. (2015). The Eye is Listening: Music-Induced Arousal and Individual Differences Predict Pupillary Responses. *Frontiers in Human Neuroscience*, *9*(November), 1–12. https://doi.org/10.3389/fnhum.2015.00619

Grahn, J. A., & Rowe, J. B. (2009). Feeling the Beat: Premotor and Striatal Interactions in Musicians and Nonmusicians during Beat Perception. *Journal of Neuroscience*, *29*(23), 7540–7548. https://doi.org/10.1523/JNEUROSCI.2018-08.2009

Hove, M. J., Marie, C., Bruce, I. C., & Trainor, L. J. (2014). Superior time perception for lower musical pitch explains why bass-ranged instruments lay down musical rhythms. *Proceedings of the National Academy of Sciences*, *111*(28), 10383–10388. https://doi.org/10.1073/pnas.1402039111

Janata, P., Tomic, S. T., & Haberman, J. M. (2012). Sensorimotor coupling in music and the psychology of the groove. *Journal of Experimental Psychology. General*, *141*(1), 54–75. https://doi.org/10.1037/a0024208

Laeng, B., Eidet, L. M., Sulutvedt, U., & Panksepp, J. (2016). Music chills: The eye pupil as a mirror to music's soul. *Consciousness and Cognition*, *44*, 161–178. https://doi.org/10.1016/j.concog.2016.07.009

Large, E. W. (2000). On synchronizing movements to music. *Human Movement Science*, *19*(4), 527–566. https://doi.org/10.1016/S0167-9457(00)00026-9

Length, R. V. (2016). Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software*, *69*, 1–33.

Longuet-Higgins, H. C., & Lee, C. S. (1984). The Rhythmic Interpretation of Monophonic Music. *Music Perception: An Interdisciplinary Journal*, *1*(4), 424–441. https://doi.org/10.2307/40285271

Madison, G. (2006). Experiencing groove induced by music: Consistency and phenomenology, *Music Perc*(24), 201–208. https://doi.org/10.1525/mp.2006.24.2.201

Mathworks. (2015). Matlab. Natick, MA: The Mathworks Inc.

Nater, U. M., Abbruzzese, E., Krebs, M., & Ehlert, U. (2006). Sex differences in emotional and psychophysiological responses to musical stimuli. *International Journal of*

Psychophysiology, *62*(2), 300–308. https://doi.org/10.1016/j.ijpsycho.2006.05.011

Nichols, A. L., & Maner, J. K. (2008). The good-subject effect: investigating participant demand characteristics. *The Journal of General Psychology*, *135*(2), 151–165. https://doi.org/10.3200/GENP.135.2.151-166

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10,* 437–442.

Pressing, J. (2002). Black Atlantic Rhythm: Its Computational and Transcultural Foundations. *Music Perception*, *19*(3), 285–310.

Ravignani, A., Bowling, D. L., & Fitch, W. T. (2014). Chorusing, synchrony, and the evolutionary functions of rhythm. *Frontiers in Psychology*, *5*. https://doi.org/10.3389/fpsyg.2014.01118

Samuels, E., & Szabadi, E. (2008). Functional Neuroanatomy of the Noradrenergic Locus Coeruleus: Its Roles in the Regulation of Arousal and Autonomic Function Part I: Principles of Functional Organisation. *Current Neuropharmacology*, *6*(3), 235–253. https://doi.org/10.2174/157015908785777229

Sioros, G., Miron, M., Davies, M., Gouyon, F., & Madison, G. (2014). Syncopation creates the sensation of groove in synthesized music examples. *Frontiers in Psychology*, *5*. https://doi.org/10.3389/fpsyg.2014.01036

Sirois, S., & Brisson, J. (2014). Pupillometry. *Wiley Interdisciplinary Reviews: Cognitive Science*, *5*(6), 679–692. https://doi.org/10.1002/wcs.1323

Slaughter, F. E. (1954). The effect of stimulative and sedative types of music on normal and abnormal subjects as indicated by pupillary reflexes. *Music Therapy*, 246–248.

Stupacher, J., Hove, M. J., & Janata, P. (2016). Audio Features Underlying Perceived Groove and Sensorimotor Synchronization in Music. *Music Perception: An Interdisciplinary Journal*, *33*(5), 571–589. https://doi.org/10.1525/mp.2016.33.5.571

Stupacher, J., Hove, M. J., & Janata, P. (2016). Audio Features Underlying Perceived Groove and Sensorimotor Synchronization in Music. *Music Perception: An Interdisciplinary Journal*, *33*(5), 571–589. https://doi.org/10.1525/mp.2016.33.5.571

Stupacher, J., Hove, M. J., Novembre, G., Schütz-Bosbach, S., & Keller, P. E. (2013). Musical groove modulates motor cortex excitability: A TMS investigation. *Brain and Cognition*, *82*(2), 127–136. https://doi.org/10.1016/j.bandc.2013.03.003

Team, R. C. (2015). *R: A language and environment for statistical computing [Internet]. Vienna, Austria: R Foundation for Statistical Computing; 2014*.

Team, Rs. (2015). RStudio: integrated development for R. *RStudio, Inc., Boston, MA URL Http://Www. Rstudio. Com*.

Todd, N. P., & Cody, F. W. (2000). Vestibular responses to loud dance music: a physiological basis of the "rock and roll threshold"? *The Journal of the Acoustical Society of America*, *107*(1), 496–500.

Van Dyck, E., Moelants, D., Demey, M., Deweppe, A., Coussement, P., & Leman, M. (2013). The Impact of the Bass Drum on Human Dance Movement. *Music Perception: An Interdisciplinary Journal*, *30*(4), 349–359. https://doi.org/10.1525/mp.2013.30.4.349

Weiss, M. W., Trehub, S. E., Schellenberg, E. G., & Habashi, P. (2016). Pupils dilate for vocal or familiar music. *Journal of Experimental Psychology. Human Perception and Performance*, *42*(8), 1061–1065. https://doi.org/10.1037/xhp0000226

Witek, M. A. G., Clarke, E. F., Kringelbach, M. L., & Vuust, P. (2014a). Effects of Polyphonic Context, Instrumentation, and Metrical Location on Syncopation in Music. *Music Perception: An Interdisciplinary Journal*, *32*(2), 201–217. https://doi.org/10.1525/mp.2014.32.2.201

Witek, M. A. G., Clarke, E. F., Kringelbach, M. L., & Vuust, P. (2014b). Effects of Polyphonic Context, Instrumentation, and Metrical Location on Syncopation in Music. *Music Perception: An Interdisciplinary Journal*, *32*(2), 201–217. https://doi.org/10.1525/mp.2014.32.2.201

Witek, M. A. G., Clarke, E. F., Wallentin, M., Kringelbach, M. L., & Vuust, P. (2014). Syncopation, body-movement and pleasure in groove music. *PLoS ONE*, *9*(4). https://doi.org/10.1371/journal.pone.0094446

SUPPLEMENTARY

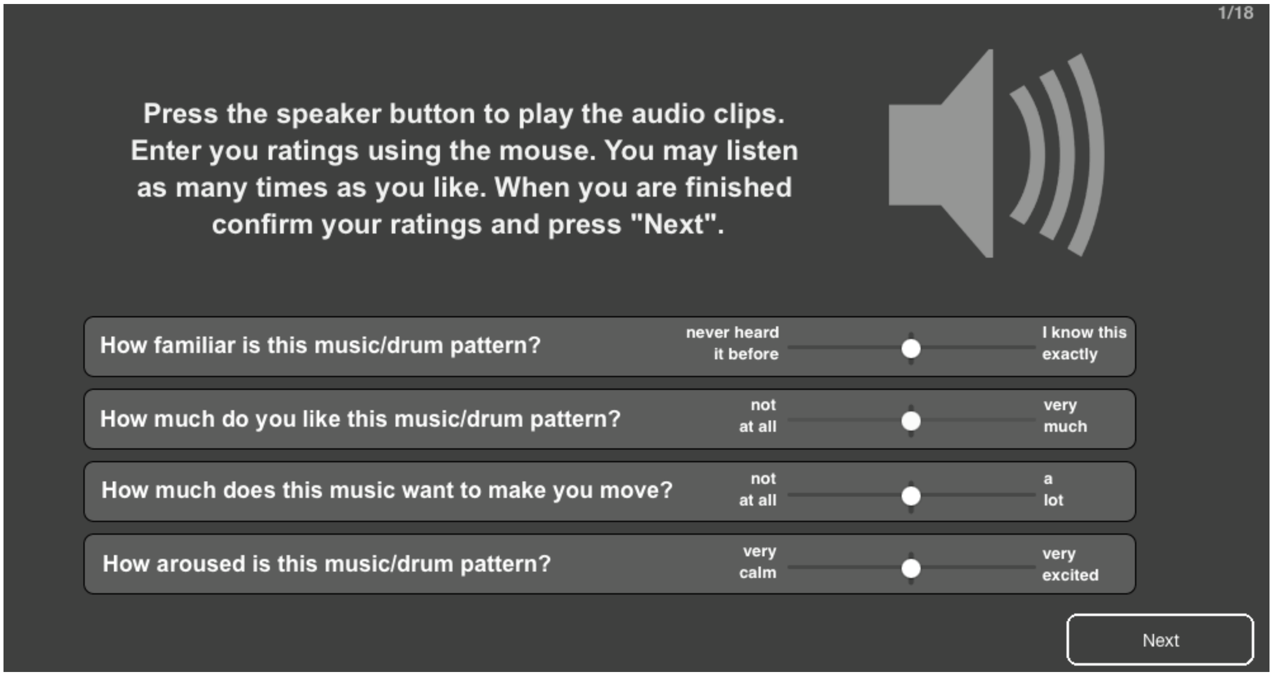

Figure S1. Computerized Survey. A screenshot of the computerized survey subjects completed after the eye-tracking phase of the experiment.

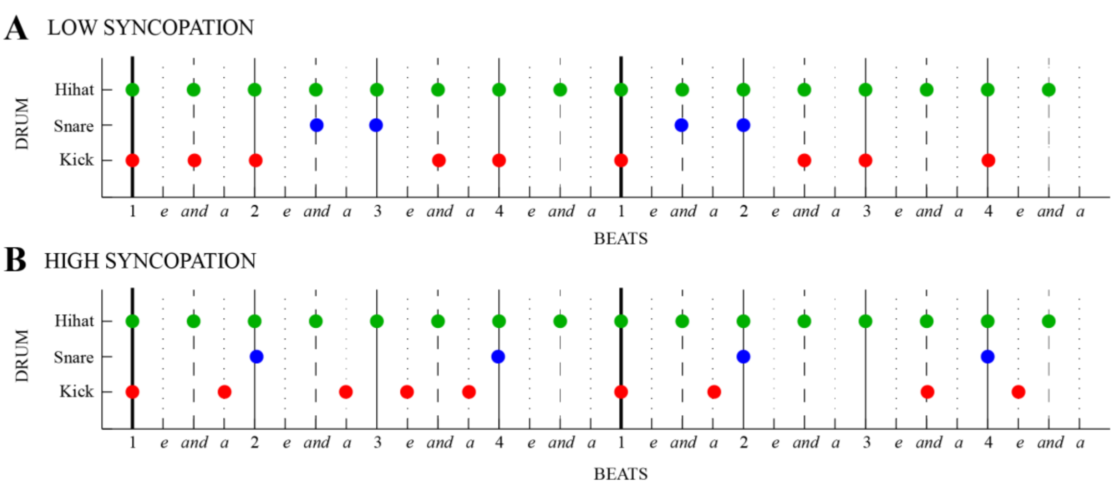

Figure S2. Straight and syncopated drum patterns. Diagrams of the low (A) and high (B) syncopation drum patterns showing the onset of each drum event. Hihat events are shown in green, snare events in blue, and kick event in red. The style of vertical lines depicts the metrical strength of each position (thick > thin > dashed > dotted).

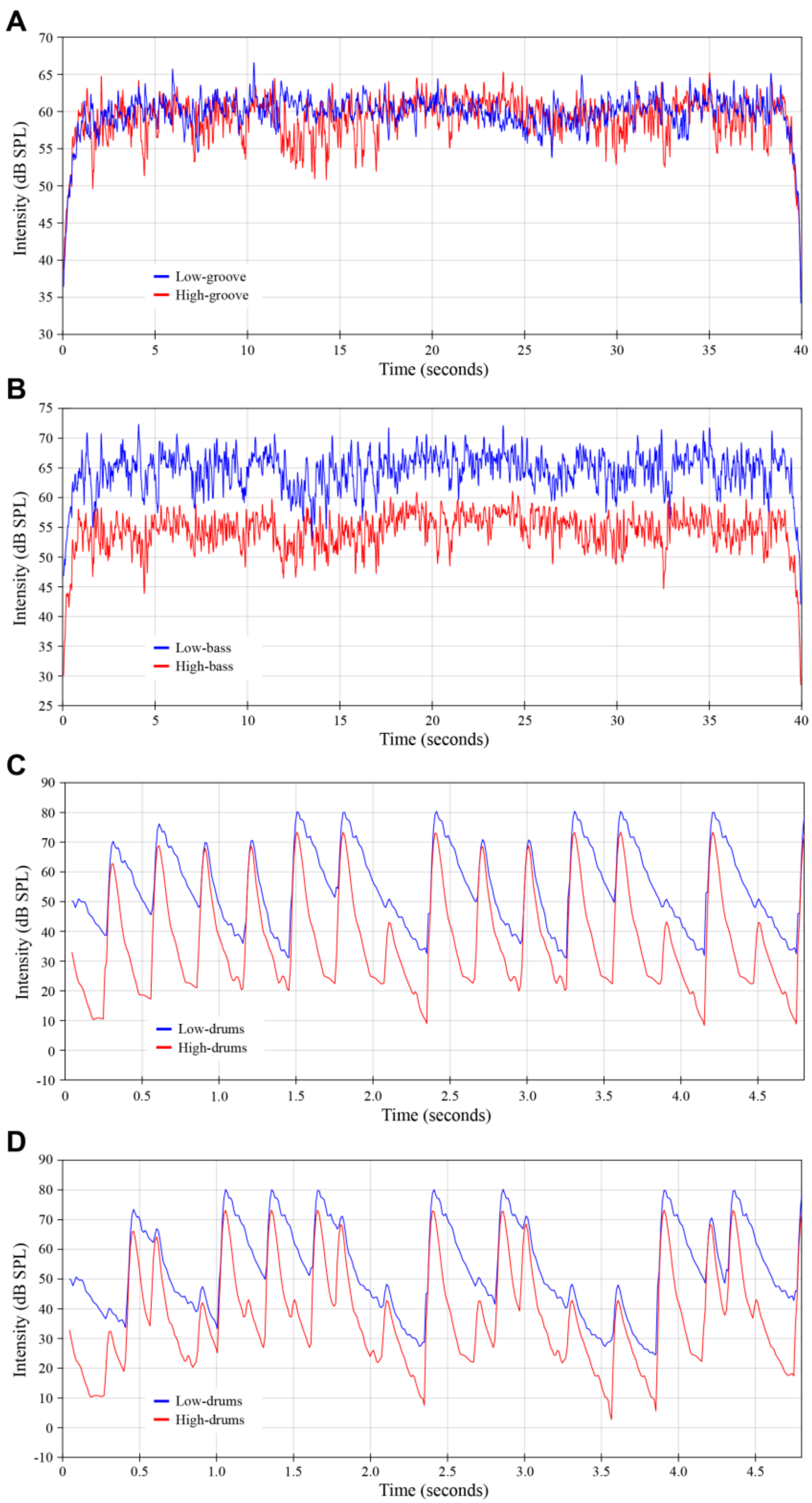

Figure S3. Average intensity traces. (A) Average intensity (dB SPL) in high- (red) and low-groove (blue) excerpts. (B) Average intensity (dB SPL) in high- (red) and low-pass (blue) filtered high-groove excerpts. (C) Average intensity (dB SPL) in straight high- (red) and low-drums (blue) excerpts. (D) Average intensity (dB SPL) in syncopated high- (red) and low-drums (blue) excerpts.