# Musical groove modulates motor cortex excitability: A TMS investigation

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ABSTRACT

Groove is often described as a musical quality that can induce movement in a listener. This study examines the effects of listening to groove music on corticospinal excitability. Musicians and non-musicians listened to high-groove music, low-groove music, and spectrally matched noise, while receiving single-pulse transcranial magnetic stimulation (TMS) over the primary motor cortex either on-beat or off-beat. We examined changes in the amplitude of the motor-evoked potentials (MEPs), recorded from hand and arm muscles, as an index of activity within the motor system. Musicians and non-musicians rated groove similarly. MEP results showed that high-groove music modulated corticospinal excitability, whereas no difference occurred between low-groove music and noise. More specifically, musicians' MEPs were *larger* with high-groove than low-groove music, and this effect was especially pronounced for on-beat compared to off-beat pulses. These results indicate that high-groove music increasingly engages the motor system, and the temporal modulation of corticospinal excitability with the beat could stem from tight auditory–motor links in musicians. Conversely, non-musicians' MEPs were *smaller* for high-groove than low-groove music, and there was no effect of on- versus off-beat pulses, potentially stemming from suppression of overt movement. In sum, high-groove music engages the motor system, and previous training modulates how listening to music with a strong groove activates the motor system.

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## 1. Introduction

Music and movement are intimately entwined. Music is produced by movements of an instrumentalist; and in turn, music can induce movements in a listener. When music 'feels right', listeners might want to tap their feet, bob their heads, or even break into unbridled dance. Movement induction is strongly related to the musical rhythm. The tight linkage between movement and auditory rhythm is highly apparent in groove music. Groove is often described as a musical quality that makes us want to move with the rhythm or beat (e.g., Iyer, 2002; Janata, Tomic, & Haberman, 2012; Madison, 2006; Pressing, 2002; Waadeland, 2001). Burgeoning areas of research explore the musical factors that promote groove, the auditory–motor neural links that underlie movement induction, and how training can modulate these auditory–motor links. However, the interplay between these research

areas, the neural response to groove, and how groove utilizes these auditory–motor neural links still remain unknown. In this study, we addressed these questions directly by investigating how the perception of high- vs. low-groove music modulates the excitability of the motor control system in musicians and non-musicians as probed by transcranial magnetic stimulation.

The close connection between groove and movement has been established by ethnomusicologists and music cognition researchers (e.g., Iyer, 2002; Janata et al., 2012; Madison, 2006; Pressing, 2002; Waadeland, 2001). The concept of groove is widely understood to relate primarily to how music "makes you want to move" and is also associated with a strong beat, pleasure, and enjoyment (Janata et al., 2012). When participants are asked to rate a song's groove, the ratings are highly consistent between individuals (Janata et al., 2012; Madison, 2006), indicating that listeners "know a good groove when they hear it" (Zbikowski, 2004). While the term "groove" could be more associated with musical styles that cultivate danceable rhythms such as soul and R&B (Janata et al., 2012), groove ratings emerged consistently across a wide range of styles suggesting that groove reflects psychological factors independent of musical style (Madison, 2006). Similar phenomena to groove might be captured by more genre-specific terms such as "swing" in jazz, the "push" in polka, or Hodeir's (1956) more

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general "vital drive" (Keil, 1995), which evoke the quality or feeling that makes music come alive and induce movement (Butterfield, 2010).

In addition to consistent subjective understanding, groove has recently been shown to affect movement. After establishing groove ratings for many musical examples, Janata et al. (2012) showed that the high groove songs yielded more accurate movement synchrony in a tapping task, and induced more spontaneous movement such as foot tapping. This underscores that groove is largely a phenomenon of sensorimotor coupling (Janata et al., 2012), and that groove reflects the music's "efficiency for entrainment" (Madison, Gouyon, Ullén, & Hörnström, 2011).

### 1.1. Musical aspects of groove

Many musical factors relate to groove, but most generally, groove is strongly linked to rhythm and timing. In many forms of music, groove is predominantly shaped by drums (or percussion) and bass (Butterfield, 2010; Iyer, 2002; Keil, 1995; Pressing, 2002). Musicians have developed many techniques to promote groove, and some specific musical features are thought to underlie groove and movement induction. One key factor in groove is a repetitive rhythm that can increase engagement and attention (Pressing, 2002) and improve the ability to predict and synchronize with a beat (Madison et al., 2011). Perfect predictability, however, can undermine the groove, and many musicians (and drum machines) purposefully introduce subtle deviations within a rhythmic structure to increase groove (Danielsen, 2006; Prögler, 1995). Expressive timing deviations or "microtiming" (e.g., Desain & Honing, 1993) can highlight musical structure and imply motion (e.g., Iyer, 2002), and are a commonly discussed factor in groove (e.g., Iyer, 2002; Keil, 1995; Naveda, Gouyon, Guedes, & Leman, 2011; cf. Madison et al., 2011). For example, ensemble musicians often purposely play slightly apart from each other in time (Keil, 1995), with one player consistently leading by some tens of milliseconds (Butterfield, 2010; Friberg & Sundström, 2002; Prögler, 1995). Slightly asynchronous onsets can create a sense of collective participation (Iyer, 2002; Waadeland, 2001), and have been shown to improve movement synchrony for musically trained participants (Hove, Keller, & Krumhansl, 2007).

The rhythmic structure of a groove is typically hierarchical and contains subdivisions that can serve to reinforce the beat (Madison et al., 2011), and improve synchronization precision (Repp, 2003). The right amount of rhythmic complexity is important for groove; rhythms that are too simple or too complex are unlikely to groove (Witek, Clarke, Wallentin, Kringelbach, & Vuust, 2011). Syncopation is another important component of groove (Holm & Isaksson, 2010); and musicians "enjoy" syncopated rhythms more than unsyncopated rhythms (Keller & Schubert, 2011).

Groove has also been shown to depend on sonic factors of music. Madison et al. (2011) examined acoustic features of many songs and could quantitatively establish that beat density and beat salience were strong predictors of groove. Another recent study found that highly rhythmic periodicities, clear pulses, and energy in low frequency bands were especially powerful for inducing movement in participants (Burger et al., 2012). The musical convention that the bass and the bass drum often set the musical beat might stem from the propensity for low-frequencies to induce movement or give timing cues. Low tones also generate a vestibular response (Todd, 2001), and the vestibular system has been shown to play an important role in perceiving musical rhythm (Trainor, Gao, Lei, Lehtovaara, & Harris, 2009).

Finally, groove can be facilitated by playing at a tempo that affords easy synchronization (Madison et al., 2011). Tempi of dance music have a very clear peak around 120 bpm (Moelants, 2002), which aligns with spontaneous tapping and preferred movement tempo (e.g., Fraisse, 1982; MacDougall & Moore, 2005), making it both easy to synchronize with and energizing. In Janata et al. (2012), higher groove ratings occurred for songs in the faster category (mean tempo = 115.6 bpm) than the slower category (mean tempo = 90.8 bpm). And in a recent fMRI study, tempo strongly influenced aesthetic ratings of rhythms, and listening to rhythms at a participant's preferred tempo increasingly activated his or her motor-related brain areas (Kornysheva, von Cramon, Jacobsen, & Schubotz, 2010). These preferred tempo effects suggest enhanced sensorimotor simulation of the beat and that auditory–motor resonance is key for groove.

### 1.2. Auditory-motor links and music

Experimental evidence indicates that listening to music is tightly linked to neural processes associated with the motor system (for a review see Zatorre, Chen, & Penhune, 2007). Numerous fMRI investigations have shown that perception of auditory rhythms without actual movement activates motor regions, including premotor cortices, supplementary motor areas (SMA), and the basal ganglia (Bengtsson et al., 2009; Chen, Penhune, & Zatorre, 2008; Chen, Zatorre, & Penhune, 2006; Grahn & Brett, 2007; Kornysheva et al., 2010; Schubotz, Friederici, & von Cramon, 2000). For example, simply listening to an auditory rhythm, as well as tapping along with that rhythm, similarly activate areas of the SMA and premotor cortex (Chen et al., 2008). Such activity in motor regions suggests that temporal features of music might induce people to "tune in to its beat" (cf. Kornysheva et al., 2010). Thus, the musical factors that contribute to groove – including rhythm, timing, sonic features, and tempo – may do so by directly engaging movement via auditory–motor links.

Fine-grained temporal correlations between dynamic aspects of auditory rhythms and activity in the brain have been observed using experimental methodologies with high temporal resolution including EEG (e.g., Nozaradan, Peretz, Missal, & Mouraux, 2011) and MEG (e.g., Fujioka, Trainor, Large, & Ross, 2012). The temporal dynamics of music can be observed in motor regions during passive listening. For instance, using MEG, Popescu, Otsuka, and Ioannides (2004) showed that when listening to music, the time course of motor-related areas (lateral premotor areas, SMA, and somatomotor areas) correlated with the fine temporal structures of the sound, indicating the synchronization of external and internal rhythms.

Combined transcranial magnetic stimulation (TMS) and electromyography (EMG) methodologies offer another approach to investigate the precise temporal dynamics of such sensorimotor processes and moreover to localize observed effects at the motor level. Delivering single-pulse TMS over primary motor cortex (M1) and using EMG to measure the resulting response in contralateral muscle activity (a motor evoked potential, MEP) gives a measure of corticospinal excitability at the time of pulse. The amplitude of a MEP is known to be influenced by activity in other cortical motor regions – including premotor and the supplementary motor areas (Guillot & Collet, 2010) – and therefore this index can be used to make direct inferences about the excitability of the human motor system with high temporal resolution. For example, Wilson and Davey (2002) used TMS pulses in time with music to examine how listening to a song with a strong beat modulated the MEPs in ankle flexor and extensor muscles. No difference in MEPs was observed for on-beat vs. off-beat TMS pulses when participants relaxed and listened to music (cf. Cameron, Stewart, Pearce, Grube, & Muggleton, 2012). However correlations between the antagonist muscles were lower during music trials than white noise trials, possibly indicating that corticospinal excitability of the flexor and extensor were time-locked to the music, but out of phase (Wilson & Davey, 2002).

**Table 1**
The 8 musical clips and their respective groove rating (based on Janata et al. (2012)), vocals, meter signature, beats per minute (BPM) and absolute peak dB level. High- and low-groove songs were selected as pairs matched as closely as possible in terms of instrumentation, meter signatures, and tempo. The high-groove and low-groove matched pairs are Superstition/Cheeseburger in Paradise, Look-Ka Py Py/Ray Dawn Balloon, Bad Tune/Bryter Layter and If I Ain't Got You/Yes I Am (indicated by superscript symbols).

| Song name | Artist | Groove[a] | Vocals | Meter | BPM | Peak (dB) |
|---|---|---|---|---|---|---|
| Superstition[#] | Stevie Wonder | High | Male | 4/4 | 101 | −1 |
| Look-Ka Py Py[+] | The Meters | High | None | 4/4 | 87 | −1 |
| Bad Tune[$] | Earth, Wind and Fire | High | None | 4/4 | 118 | −1 |
| If I Ain't Got You[~] | Alicia Keys | High | Female | 6/8 | 41 | −1 |
| Cheeseburger in Paradise[#] | Jimmy Buffett | Low | Male | 4/4 | 140 | −1 |
| Ray Dawn Balloon[+] | Trey Anastasio | Low | None | 4/4 | 80 | −1 |
| Bryter Layter[$] | Nick Drake | Low | None | 4/4 | 119 | −1 |
| Yes I Am[~] | Melissa Etheridge | Low | Female | 6/8 | 53 | −1 |

[a] Based on Janata et al. (2012).

**Table 2**
Mean ratings of groove, liking and familiarity. Possible values range from 0 to 127.

| Song name | Groove rating (SD) | Groove rating (Janata et al., 2012) | Liking | Familiarity |
|---|---|---|---|---|
| Superstition | 120.5 (13.6) | 108.7 | 101.1 | 57.5 |
| Look-Ka Py Py | 94.9 (33.3) | 92.5 | 94.5 | 30.5 |
| Bad Tune | 86.9 (41.3) | 86.2 | 89.7 | 35.3 |
| If I Ain't Got You | 70.5 (36.6) | 98.7 | 91.0 | 90.0 |
| Cheeseburger in Paradise | 93.7 (27.6) | 48.6 | 87.1 | 43.5 |
| Ray Dawn Balloon | 34.0 (31.3) | 38.5 | 77.9 | 22.3 |
| Bryter Layter | 38.5 (31.6) | 40.4 | 65.8 | 26.3 |
| Yes I Am | 45.9 (35.9) | 40.2 | 74.7 | 46.9 |

**Table 3**
Mean MEPs for each condition for each individual participant. Instrument names are abbreviated: piano = pno; percussion = perc; guitar = gtr; vocals = voc; saxophone = sax.

| Expertise | Instruments | Mean MEP high-groove | Mean MEP low-groove | Mean MEP noise |
|---|---|---|---|---|
| Musician | pno, perc | 1.083 | .953 | 1.042 |
| Musician | pno, gtr, voc, perc | .578 | .470 | .292 |
| Musician | pno, gtr, voc, perc | .515 | .422 | .396 |
| Musician | pno | .473 | .399 | .449 |
| Musician | pno | .324 | .250 | .286 |
| Musician | gtr, pno | .326 | .328 | .276 |
| Musician | pno, sax | .927 | .969 | .721 |
| Non-musician | | .764 | .980 | .784 |
| Non-musician | | .552 | .678 | .765 |
| Non-musician | | .294 | .417 | .340 |
| Non-musician | | 1.438 | 1.542 | 1.531 |
| Non-musician | | 1.527 | 1.578 | 1.616 |
| Non-musician | | .788 | .801 | .860 |
| Non-musician | | .613 | .612 | .604 |
| Non-musician | | .708 | .684 | .707 |

Most of the aforementioned studies showing tight auditory–motor coupling were observed in non-musicians. Long-term musical training can further strengthen auditory–motor coupling. Behavioral and neuroimaging investigations have shown that the musician's brain develops multiple sensorimotor associations between sensory and motor areas, as a result of musical training (e.g., Bangert & Altenmüller, 2003; Bangert et al., 2006; D'Ausilio et al., 2006; Drost, Rieger, Brass, Gunter, & Prinz, 2005; Haslinger et al., 2005; Haueisen & Knösche, 2001; Lahav, Saltzman, & Schlaug, 2007). In an MEG study Haueisen and Knösche (2001) compared motor activations in pianists and non-pianists while listening to piano pieces. They found an increase of activity in motor cortex in pianists, but not in non-pianists. This result indicates that musicians develop tight auditory–motor links through training.

In the present experiment, we investigated whether musical groove utilizes auditory–motor links and modulates motor cortex excitability. Musicians and non-musicians listened to commercially available high- and low-groove music (as previously assessed by Janata et al., 2012) while receiving single-pulse TMS over the left primary motor cortex (M1). MEPs were recorded from muscles of the right hand and the right forearm, and their amplitude was examined to assess corticospinal excitability. We hypothesized that listening to high-groove music would increase corticospinal excitability more than listening to low-groove music or spectrally matched noise, as high-groove music is known to induce movement and entrain the listener. Moreover, given the evidence for especially strong audio-motor coupling in musicians, we examined potential differences between musicians' and non-musicians' response to groove music.

## 2. Method

### 2.1. Participants

Fifteen adults (8 female) participated in the experiment (mean age = 25.1, SD = 2.9). One additional participant was excluded due to a technical failure. Seven participants (4 female) were musicians

with musical performance experience ranging from 8 to 18 years ($M = 13.4$ years, $SD = 4.2$). Their starting age ranged from 4 to 12 years ($M = 7.0$, $SD = 2.3$). Most musicians had experience playing multiple instruments; all seven had piano training, and other instruments were guitar, saxophone, and percussion (see Table 3 for details). The 8 remaining participants (4 female) were non-musicians who had no musical training. The experiment was run in Leipzig, Germany, and all participants were German speakers. All participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). A Mann–Whitney test revealed no significant difference of laterality quotient between musicians and non-musicians, $z = -.78$, $p = .433$. The mean time of listening to music did not differ between musicians ($M = 8.4$ h/ week, $SD = 6.2$) and non-musicians ($M = 6.5$ h/week, $SD = 3.8$), $t(13) = .72$, $p = .483$. Both musicians and non-musicians reported that they usually dance more often than once a month, but less often than once a week. The experiment was approved by the local ethics committee. Participants gave informed consent and were paid for participating. They were naïve with regard to the purpose of the study.

## 2.2. Musical stimuli

Four high-groove and four low-groove songs clips were selected from over 150 songs that were recently rated on groove (Janata et al., 2012). The song clips were free 30-s previews available from the iTunes Music Store (www.apple.com/itunes) from the genres pop, rock and soul. High- and low-groove songs are shown in Table 1, and were selected as pairs matched as closely as possible in terms of instrumentation, meter signatures, and tempo (which did not significantly differ between categories, $z = -.58$, $p > .5$). Additionally, the clips were equated in loudness using the Software Nuendo (Steinberg, Hamburg, Germany), so that the peak dB levels were at $-1$ dB.

As a control condition, eight noise clips were created with the same frequency spectrum profile as a corresponding song. The noise clips contained no beat-like structure or temporal modulation (other than the narrow-band filter characteristics of the frequency envelope). A pre-study with 9 participants (3 female, 6 male; mean age = 24.6 years, $SD = 2.6$) established the subjective equal loudness of the noise compared to the songs. Stimuli were presented over Sennheiser IE 6 in-ear headphones (Sennheiser, Wedemark-Wennebostel, Germany).

The overall loudness of the song and noise clips during the TMS experiment was adjusted to be loud and clear but still comfortable. To ensure that the stimuli were pleasant, prior to the experiment, participants were asked about stimuli loudness; as a result, loudness was turned down slightly for four participants and was not adjusted further during the experiment. Additionally, at the end of the entire experimental session, participants rated the global perceived loudness of music and noise on a 7-point Likert-scale (1 = much too quiet; 7 = much too loud). Subjective ratings showed that participants judged the loudness to be comfortable for both noise ($M = 4.13$; $SD = .35$) and music ($M = 4.33$; $SD = .62$), with no difference between the two, $t(14) = -1.15$, $p = .271$. The stimuli were not audible to the experimenters, who were blind to the experimental conditions.

## 2.3. TMS and EMG recordings

Focal single TMS pulses (Magstim 200, Whitland, UK; 70 mm figure-of-eight stimulation coil) and EMG recordings were combined in order to measure corticospinal excitability. We examined changes in MEP amplitudes, which were measured simultaneously from right hand (first dorsal interosseous, FDI) and right forearm (extensor carpi radialis, ECR) muscles, as previous studies investi-

gating motor representations of music have commonly recorded MEPs from FDI (e.g., Giovannelli et al., 2013; Novembre, Ticini, Schütz-Bosbach, & Keller, 2012) and ECR (e.g., D'Ausilio et al., 2006; Novembre et al., 2012).

The EMG signal was recorded using Ag/AgCl surface electrodes placed in a belly-tendon montage. A ground electrode was placed on the back of the right hand. The signal was amplified 1000 times, band-pass filtered (10–1000 Hz) with a mains hum notch filter at 50 Hz and digitized at 5 kHz.

TMS was delivered over the left M1, which was identified by moving the coil over the left motor cortex while sending pulses with constant time interval (of 6 s) and constant intensity until the optimal scalp position (i.e., which elicited maximal MEP amplitudes from both right FDI [hand] and ECR [forearm] muscles) was identified and marked with a pencil. For two participants it was not possible to identify a scalp position that would reliably elicit MEPs from both ECR and FDI muscles (this was presumably related to structural–functional individual differences). Hence, for these participants, MEPs were only recorded from ECR.

The intensity of the stimulation was set at 120% of each individual motor threshold, which was defined as the lowest intensity at which 5 out of 10 TMS pulses produced MEPs with an amplitude greater than 50 μV. The stimulation intensity ranged from 37% to 58% ($M = 44.47$, $SD = 6.56$) of the maximum stimulator output. MEP amplitudes were constantly monitored visually.

## 2.4. Procedure

Participants sat in a cushioned seat with armrests. The right armrest was adjusted to ensure that the muscles were relaxed. A green fixation cross appeared on screen during presentation of auditory stimuli, and it turned white during the 3 s between trials. Participants were instructed to sit relaxed. They were explicitly instructed not to move while listening to the auditory stimuli; this was monitored and corroborated by the two experimenters in the room, and was empirically confirmed by looking at the muscle activity prior to each pulse (see below).

Each presentation of a 30-s audio clip was accompanied by four TMS pulses. Metrical positions of pulses alternated within each clip between on-beat and off-beat (counterbalanced in order between clips). On-beat pulses were delivered on the beat (i.e., on the quarter notes in 4/4 clips and on the eighth notes in the 6/8 clips); and off-beat pulses were delivered between the beats (i.e., on the eighth notes in the 4/4 clips, and on the sixteenth notes in 6/8 clips). The inter-pulse interval was approximately 6 s ($SD = 307$ ms). The first pulse in a trial started either approximately 5 or 7 s into the trial in order to avoid stimulating on the same beats on every presentation of a music clip. Each participant received 48 pulses for each of the experimental conditions (high-groove, low-groove, spectrally matched noise), resulting in a total of 144 pulses through the entire experiment.

The experiment consisted of three blocks, each containing the 12 auditory stimuli in random order (4 high-groove songs, 4 low-groove songs, 4 spectrally matched noise recordings). Noise recordings were counterbalanced between subjects, so that each participant heard only 4 noise recordings (2 high- and 2 low-groove spectrally matched noise recordings). The blocks lasted 7 min each, and were separated by short breaks.

After the TMS experiment, participants rated all 8 music clips first in terms of familiarity, then liking, then groove (which was defined as "an aspect of music that makes you want to move"). They could start and stop the currently rated clip individually by pressing the space bar of a computer keyboard. A mouse was used to adjust a horizontal slider on a computer screen corresponding to their rating. Low ratings (on the left) and high ratings (on the right)

ranged in value from 0 to 127, respectively, but participants could not see these numerical values.

The entire experiment, including preparation, music listening, and questionnaires lasted approximately 80 min per participant.

## 2.5. Data processing

The absolute distance between the maximum and minimum MEP values (peak-to-peak) – within a time window between 10 ms and 80 ms after the TMS pulse – was calculated separately for both muscles. To control for actual movement, the mean pre-pulse EMG activity in the 50 ms window prior to a TMS pulse was calculated after taking the absolute value of all samples in this window. If this pre-pulse EMG mean was larger than .075 µV (indicating movement), or if an MEP was more than 3 standard deviations from the mean MEP for each participant, muscle, condition and block, that MEP was excluded (.57% of total MEPs). MEPs from spectrally matched high-groove noise and low-groove noise were collapsed, as an ANOVA with the factors noise (high-groove noise/low-groove noise), muscle (FDI/ECR) and expertise (musicians/non-musicians) revealed no main effect of noise and no interactions ($ps > .2$).

Since an ANOVA with the factors muscle (FDI[hand]/ECR[forearm]), condition (high-groove/low-groove/noise) and expertise (musicians/non-musicians) revealed no main effect or interactions of muscle (all $ps > .1$), the mean MEP of both muscles was used as the main dependent variable (for the two participants whose FDI could not be stimulated, ECR data were used). The noise condition was used as a baseline to normalize the high- and low-groove conditions. Thus we subtracted the mean MEP in the noise condition from the mean MEP in the high-groove and low-groove conditions for each participant.

To ensure that possible differences observed in MEP amplitudes were not preceded by a difference in the EMG signal, mean pre-pulse EMG activity was calculated for each MEP (after having filtered out the large pre-pulse EMG trials that would stem from actual movement). Mean pre-pulse EMG was calculated by averaging the absolute values of all samples in the 50 ms window before a pulse. The EMG data were normalized with the noise condition as a baseline using the same procedure used for the MEPs: pre-pulse EMG activity of the noise condition was subtracted from pre-pulse EMG activity of the high- and low-groove conditions.

Additionally – although groove is a complex musical feature resulting from the interplay of many factors – as an exploratory step to identify audio features that might differ between high- and low-groove music, we extracted a set of audio features from the music clips using Matlab's (Mathworks, Natick, MA) MIR toolbox (Lartillot & Toiviainen, 2007). The audio features we extracted were: event density (the number of note onsets per second); pulse clarity (strength of the beats); fluctuation (rhythmic periodicity); low energy (measure of dynamics in percentage of less-than-average energy); spectral flux (distance between the spectrum of successive frames); and sub-band spectral flux in eight frequency bands.

## 3. Results

### 3.1. Subjective ratings

Every high-groove clip was rated higher than the matched low-groove clip in the groove rating and in the liking rating. Mean ratings of groove, liking, and familiarity are shown in Table 2. With exception of the songs "Cheeseburger in Paradise" and "If I Ain't Got You", the ratings of the present study aligned very well with the ratings of Janata et al. (2012). Groove ratings significantly cor-
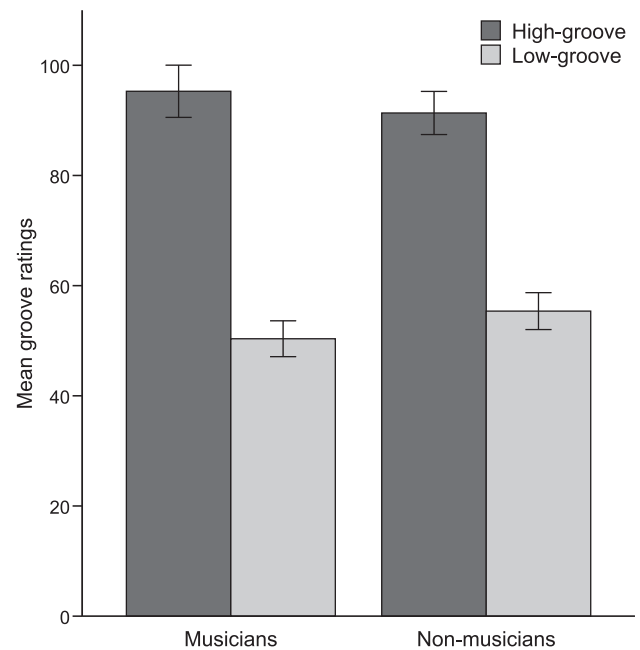


**Fig. 1.** Mean groove ratings of musicians and non-musicians. Error bars represent ±.5 SE.

related with liking ratings in both musicians and non-musicians, $r(53) = .37$, $p = .005$, and $r(61) = .55$, $p < .001$, respectively. Groove rating and familiarity correlated in non-musicians, $r(61) = .32$, $p = .012$, but not in musicians, $r(53) = .22$, $p = .114$.

An ANOVA on the groove ratings with the factors groove category (high-groove/low-groove) and expertise (musicians/non-musicians) revealed a main effect of groove category, $F(1, 13) = 30.97$, $p < .001$, $\eta_p^2 = .70$, indicating that the perceived groove ratings for high-groove clips were indeed higher than for low-groove clips (see also Fig. 1). Significant main effects of groove category in the same direction were also found in separate ANOVAs on liking ratings, $F(1, 13) = 5.67$, $p = .033$, $\eta_p^2 = .30$, and on familiarity ratings, $F(1, 13) = 13.25$, $p = .003$, $\eta_p^2 = .51$. No between-subject effects and no interactions between musicians and non-musicians occurred for groove ratings, liking, or familiarity.

### 3.2. MEPs

Normalized MEPs of high- and low-groove clips are shown for musicians and non-musicians in Fig. 2. A clear difference in high-groove MEPs can be observed between musicians and non-musicians. High- and low-groove clips affected the MEPs of musicians and non-musicians differently, as indicated by a significant interaction between groove category and expertise in the 2 × 2 ANOVA, $F(1, 13) = 13.55$, $p = .003$, $\eta_p^2 = .51$. For musicians, high-groove clips produced *larger* MEPs than low-groove clips, $t(6) = 2.67$, $p = .037$; whereas for non-musicians, high-groove clips produced *smaller* MEPs than low-groove clips, $t(7) = -2.66$, $p = .032$. The main effect of expertise was significant, $F(1, 13) = 5.09$, $p = .042$, $\eta_p^2 = .28$, indicating that musicians showed larger overall MEPs than non-musicians when listening to music (relative to the noise baseline). The main effect of groove category was not significant $F(1, 13) = .14$, $p = .718$, $\eta_p^2 = .01$, due to the opposite effects observed for musicians and non-musicians. Table 3 displays MEPs by condition of each individual participant.

We next compared the mean MEPs between the groove categories and spectrally matched noise ($y = 0$, in Fig. 2) using t-tests. In musicians, high-groove clips produced *larger* MEPs than noise, $t(6) = 2.86$, $p = .029$, whereas low-groove clips did not show a
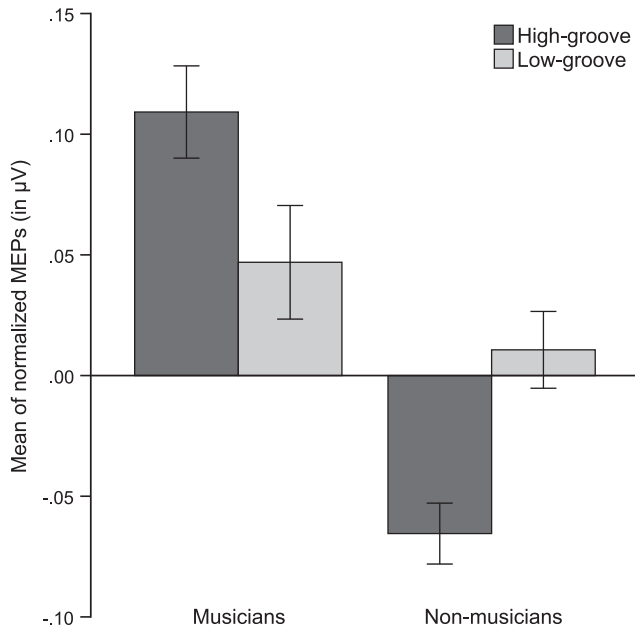
**Fig. 2.** Normalized MEPs of musicians and non-musicians. $Y = 0$ represents the mean MEP size during listening to spectrally matched noise clips. Error bars represent ±.5 SE.

significant difference, $t(6) = 1.00$, $p = .357$. In non-musicians, high-groove clips produced *smaller* MEPs than noise, $t(7) = -2.60$, $p = .036$, and again, low-groove clips did not differ from noise, $t(7) = .34$, $p = .748$. Therefore, high-groove clips, and not low-groove, lead to a concrete modulation of corticospinal excitability.

In order to examine the high- versus low-groove MEP differences between musicians and non-musicians, we compared musicians' and non-musicians' MEPs for each song clip individually. Results for each independent samples t-test on the normalized MEPs are shown by song in Table 4. For every high-groove clip, a significant difference occurred between musicians and non-musicians, with musicians having larger MEPs. Conversely, for the low-groove clips, no significant differences in MEPs occurred between musicians and non-musicians.

Finally, possible effects of on- and off-beat pulses were examined. Two separate ANOVAs with the factors beat (on-/off-beat) and groove category (high-/low-groove) were performed on mean MEPs for musicians and non-musicians. There was no main effect of beat for musicians, $F(1,6) = .10$, $p = .768$, $\eta_p^2 = .02$, or for non-musicians, $F(1,7) = 1.11$, $p = .328$, $\eta_p^2 = .14$. However in musicians, the interaction between beat and groove category approached significance, $F(1,6) = 5.87$, $p = .052$, $\eta_p^2 = .50$, indicating that on-beat and off-beat MEPs tended to differ between high- and low-groove conditions. Follow-up t-tests showed that on-beat MEPs were larger for high-groove clips than for low-groove clips, $t(6) = 2.79$,

$p = .031$, whereas off-beat MEPs did not differ, $t(6) = .35$, $p = .738$ (see Fig. 3). Thus, the musicians' modulation of motor excitability mirrored the beat structure. Interestingly, in non-musicians no on-beat/off-beat differences between high- and low-groove clips were evident in the interaction, $F(1,7) = .24$, $p = .638$, $\eta_p^2 = .03$.

### 3.3. Pre-pulse EMG activity

Mean pre-pulse EMG activity is shown for musicians and non-musicians in Fig. 4. For the non-musicians, pre-pulse EMG differed between high- and low-groove clips, with higher activity associated with high-groove clips $t(7) = 2.39$, $p = .048$. Musicians, however, showed no significant difference in pre-pulse EMG activity for high- and low groove clips, $t(6) = .53$, $p = .616$. Further analysis comparing high- or low-groove and noise were not significant for musicians or non-musicians ($ps > .3$).

### 3.4. Audio features

Separate Mann–Whitney tests revealed significant differences between high- and low-groove clips (with higher values for high-groove music clips) for spectral flux, $z = -2.02$, $p = .043$, and sub-band flux in the low frequency bands: band 1 [20–100 Hz], $z = -2.02$, $p = .043$, and band 3 [216–467 Hz], $z = -2.02$, $p = .043$, (a similar trend occurred in band 2 [100–216 Hz], $z = -1.44$, $p = .149$). Sub-band flux in mid- and high-frequency bands did not differ between groove categories, nor did the other extracted audio features ($ps > .2$).

### 4. Discussion

Groove has been established as a musical quality associated with movement induction (e.g., Iyer, 2002; Janata et al., 2012; Madison, 2006; Pressing, 2002; Waadeland, 2001). This study provides direct evidence of neural modulation of the motor system while listening to high-groove music, but not low-groove music. High-groove clips modulated corticospinal excitability more than low-groove and noise clips for both musicians and non-musicians. As expected, musicians showed a higher excitability for high-groove clips compared to low-groove clips and noise. Two musical training effects were observed: (1) corticospinal excitability with high-groove clips was higher in musicians than in non-musicians, whereas no difference between groups was found for low-groove clips; and (2) excitability was affected by on- versus off-beats in musicians, but not in non-musicians. Rather unexpectedly, non-musicians showed lower corticospinal excitability for high-groove clips than for low-groove clips and noise, despite higher subjective groove ratings for the high-groove clips. Additionally, for the non-musicians, the high-groove clips elicited higher pre-pulse EMG activity than low-groove clips.

**Table 4**
Independent samples t-tests comparing musicians' and non-musicians' normalized MEPs for the 8 song clips.

| Song name | $t(13)$ | $p$ (Two-tailed) | Mean difference | SE difference |
|---|---|---|---|---|
| Superstition[a] | 2.74 | .017[*] | .178 | .065 |
| Look-Ka Py Py[a] | 3.39 | .005[**] | .187 | .055 |
| Bad Tune[a] | 2.85 | .014[*] | .112 | .039 |
| If I Ain't Got You[a] | 2.47 | .028[*] | .222 | .090 |
| Cheeseburger in Paradise | 0.54 | .598 | .030 | .055 |
| Ray Dawn Balloon | −0.56 | .589 | −.027 | .049 |
| Bryter Layter | 1.01 | .330 | .110 | .108 |
| Yes I Am | 0.36 | .725 | .036 | .100 |

[a] High-groove song clips.
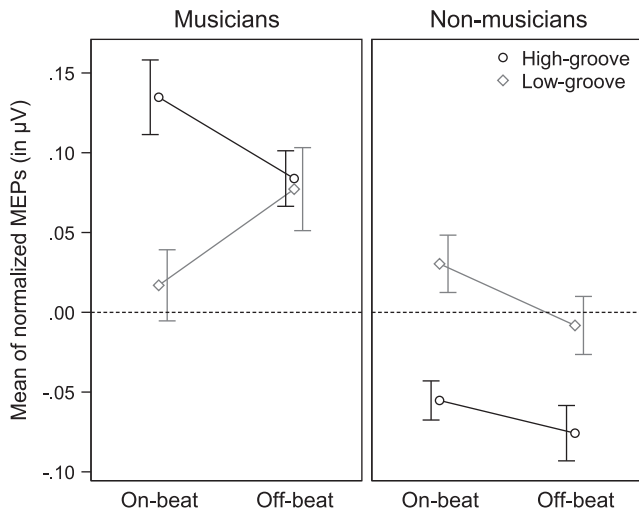[*] $p < .05$.
[**] $p < .01$.

**Fig. 3.** Normalized high-groove and low-groove MEPs of on- and off-beat TMS pulses in musicians and non-musicians. *Y* = 0 represents the mean MEP size during listening to spectrally matched noise clips. Error bars represent ±.5 SE.
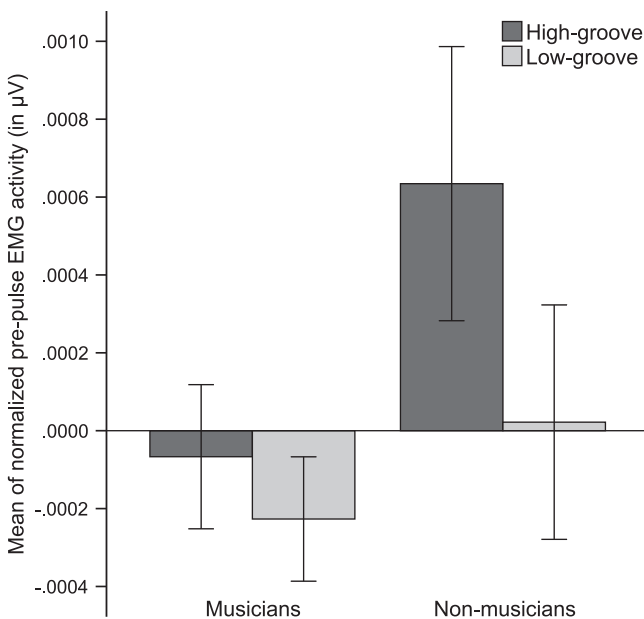


**Fig. 4.** Pre-pulse EMG activity of musicians and non-musicians for high- and low-groove clips. *Y* = 0 represents the mean pre-pulse EMG activity during listening to spectrally matched noise clips. Error bars represent ±.5 SE.

The musical stimuli in the current study had been previously established as high- or low-groove in a recent study by Janata et al. (2012). In the current study, the subjective groove ratings of the high-groove clips were indeed rated higher than matched low-groove clips, indicating the robustness of the groove construct. Groove ratings here aligned well with Janata et al. (2012), with the exception of the music clips "Cheeseburger in Paradise" and "If I Ain't Got You." Differences in ratings for these two music clips may be due to effects of enculturation and context. Participants in Janata et al. (2012) rated 148 music clips (compared to only 8 in our study), and thus they maybe developed better defined groove categories. Regardless, in line with previous studies of Janata et al. (2012) and Madison (2006), the participants in the current study had highly consistent subjective ratings of groove. Groove ratings were also associated with likeability, as well as a modulation of motor system activity (relative to baseline). Groove

ratings were associated with familiarity only for the non-musicians, and unlikely drive the effect (as many unfamiliar songs were rated high in groove in Janata et al. (2012)); future work however should consider familiarity when selecting stimuli. More interesting is the connection between likeability and motor system modulation. While we cannot discern the causal direction of the likeability/motor system effects, other work suggests a possible role of the motor system in aesthetic appreciation (e.g., Calvo-Merino, Jola, Glaser, & Haggard, 2008; Cross & Ticini, 2012).

In musicians, motor system activity, as measured by MEPs, was consistent with their groove ratings: High-groove music elicited larger MEPs than low-groove music and noise. Motor system activity did not differ between low-groove music and noise. High-groove clips positively modulated the corticospinal excitability in musicians, and the extent of corticospinal excitability aligned with the subjective ratings of "wanting to move to the music." This result is in line with other studies that describe groove as a phenomenon of sensorimotor coupling (Janata et al., 2012) and the music's "efficiency for entrainment" (Madison et al., 2011).

More detailed analyses of MEPs in musicians showed that the difference in motor excitability between high- and low-groove music is driven by differences related to the fine-grained temporal dynamics of the music. On-beat MEPs were larger for high-groove than low-groove music, whereas off-beat MEPs were nearly identical for high- and low-groove music. This provides evidence that the corticospinal excitability of musicians is related to the temporal dynamics of music. Activity in motor-related brain areas was shown to correlate with dynamic aspects of a solo piano piece (Popescu et al., 2004); and motor excitability was recently found to be influenced by metrical structure (Cameron et al., 2012). However, one must note that these studies tested only participants with little to no musical experience, and that musicians might show even stronger effects.

Through musical training, musicians shape their sensory and motor representations and develop strong auditory–motor links (e.g., Bangert & Altenmüller, 2003; Bangert et al., 2006; D'Ausilio et al., 2006; Drost et al., 2005; Haslinger et al., 2005; Haueisen & Knösche, 2001; Lahav et al., 2007). After many years of training auditory–motor connections, simply hearing music can activate the motor system (e.g., Haueisen & Knösche, 2001). Musicians' motor systems were highly activated when listening to the high-groove music, and the motor system's modulation in time with the music could stem from the well-trained auditory–motor links. All participants trained on instruments requiring hand movements, the area where the modulation of excitability was observed. However, this effect is surely not limited to the hand and arm areas of M1; increased corticospinal excitability likely extends throughout large parts of the motor system including premotor and supplementary motor regions.

In addition to automatic auditory–motor coupling, the current results could also relate to musicians' advantages in auditory encoding and rhythm processing. Mismatch negativity (MMN) investigations have shown that musicians are more sensitive in encoding rhythmic regularities than non-musicians (van Zuijen, Sussman, Winkler, Näätänen, & Tervaniemi, 2005; Vuust, Ostergaard, Pallesen, Bailey, & Roepstorff, 2009), and that MMNs elicited by music can be enlarged by auditory–motor training (Lappe, Herholz, Trainor, & Pantev, 2008). Additionally, musicians have faster and larger brainstem responses to auditory stimuli than non-musicians, indicating a more precise subcortical representation of timing (Musacchia, Sams, Skoe, & Kraus, 2007). Together, musicians' advantages in rhythm processing and auditory encoding could contribute to the musical rhythm's increased modulation of motor excitability.

The musicians' increased corticospinal excitability in time with the music might also relate to more efficient motor control. During

motor tasks, piano players have lower motor cortical activations than non-musicians, indicating musicians' greater functional efficiency within cortical motor areas (Jäncke, Shah, & Peters, 2000; Krings et al., 2000). Functional efficiency of the motor systems might relate to the control of a motor action threshold, which differentiates imagined or prepared movement from executed movement. In general, imagined and executed movements share similar neural networks (e.g., Gerardin et al., 2000; Jeannerod & Frak, 1999), but differ in whether commands are sent to effectors. Imagined or simulated movement have been shown to increase MEPs, indicating sub-threshold motor system activity (Fadiga et al., 1999; Hashimoto & Rothwell, 1999; Kasai, Kawai, Kawanishi, & Yahagi, 1997). Thus, musicians' increased MEPs while listening to high-groove music (especially on the beat) are consistent with increased motor simulation. Musicians often use motor simulation, for example in ensemble performance (Keller, 2008; Keller, Knoblich, & Repp, 2007; Novembre et al., 2012), and this experience might allow them to decouple the covert simulation system from the overt execution system. Additionally, musicians' more efficient motor system would enable simulation without overt movement as they can presumably approach the motor action threshold without "overstepping" it.

The non-musicians' decrease in MEPs in high-groove was rather surprising given that (1) their subjective groove ratings (i.e., how much the music "made them want to move") was significantly higher for the high-groove clips, and (2) other studies show that non-musicians have increased motor system activation in time with a musical beat (e.g., Popescu et al., 2004). Given that the non-musicians reported that the high-groove songs "made them want to move," it is likely that they wanted to move, but in order to follow the "do not move" instructions, they needed to suppress movement. In line with this idea of movement suppression, a recent study using facilitatory paired-pulse TMS showed that passive reading of positive sentences related to hand actions (e.g., "I grab the handle") were associated with corticospinal suppression, compared to negative hand action related sentences (e.g., "I don't grab the handle") (Liuzza, Candidi, & Aglioti, 2011). Additionally, there is evidence that the non-musicians' below-baseline MEPs for high-groove clips may reflect a suppression of movements. Sohn, Dang, and Hallett (2003) showed that corticospinal excitability is suppressed during the imagination of suppressing TMS-induced hand movements (negative motor imagery) compared to a control condition without imagination. It is possible that, although non-musicians potentially show beat-specific modulations, such modulations are not observable when the motor system is inhibited. If this was the case, then the lack of excitability in response to high-groove and the lack of beat-modulation would be due to non-musicians' inability to motorically represent *groove* music without causing an actual movement.

Non-musicians' higher pre-pulse EMG activity for high-groove compared to low-groove was rather unexpected. The excitability of M1 typically increases with voluntary muscle contraction (e.g., Hess, Mills, & Murray, 1987; Ugawa, Terao, Hanajima, Sakai, & Kanazawa, 1995). However, the non-musicians' increase of EMG activity during high-groove music might also reflect the inhibition of movement, as during a go/no-go task, the peak rate of change of EMG (reflecting the gain of the corticomotor pathway) was higher for no-go (inhibition) trials than for go trials (Coxon, Stinear, & Byblow, 2007). Thus, higher pre-pulse EMG activity with high-groove music in non-musicians may relate to an attempt to combat the urge to move by contracting antagonistic pairs of extensor and flexor muscles. The role of inhibition was not directly tested here, but could be examined by measuring cortical silent periods evoked by single-pulse TMS or short-interval intracortical inhibition (SICI) probed by double-pulse TMS. Additional future work could examine the precise time-course of corticospinal excitability relative to

the beat by adding pulses slightly before and after the beats, and looking for potential individual or between-group differences.

The qualitative difference between musicians' and non-musicians' motor system activity while listening to high-groove music is noteworthy because the vast majority of previous work on perceptual and cognitive effects of music has shown only quantitative differences between musicians and non-musicians. This may suggest that musicians and non-musicians use experience-based auditory–motor links differently when processing music under specific circumstances.

Finally, the exploratory analysis of audio features revealed significant differences between high- and low groove clips in spectral flux, especially in the low-frequency bands. Null effects of other audio features, such as event density (which have previously been shown to correlate with groove ratings (Madison et al., 2011; cf. Witek et al., 2011)), could in part stem from the small number of clips examined in the present study. Regardless, the current results align well with research showing a correlation between spectral flux and the perceived energy or "activity" of the audio signal (Alluri & Toiviainen, 2009), and that energy in low frequency bands is a key feature of movement induction (Burger et al., 2012). Low-frequency tones have been shown to create vestibular responses (Todd, 2001), which are important in perceiving musical rhythm (Trainor et al., 2009), and may be especially powerful in movement induction and timing. The differences in spectral flux in low-frequency bands between high- and low-groove clips possibly relate to the MEP results. However, more studies with naturalistic music clips (or parametric manipulation of factors) would be needed to further investigate the influence of acoustic and rhythmic features of music on corticospinal excitability.

In conclusion, our study demonstrates that high-groove music modulates the motor system activity differently for musicians and non-musicians, and that modulations of the motor system in musicians are aligned with the beat during high-groove music. The human motor system is involved in rhythm processing (e.g., Zatorre et al., 2007); and the current results suggest that the degree of motor involvement relates to the temporal and sonic features of musical groove. Music engages on many levels – cognitive, emotional, social (Huron, 2006) – and auditory–motor coupling is one of the most direct ways that music can capture a listener. The current study shows that groove is a musical quality that is especially powerful at activating the motor system via auditory–motor coupling. High-groove music and its power to induce movement can facilitate movement synchrony between individuals. Close interpersonal synchrony is thought to have an adaptive function (Merker, 1999; Merker, Madison, & Eckerdal, 2009), and can create strong prosocial effects (e.g., Hove & Risen, 2009). People all over the world are motivated to synchronize their movements to a shared musical rhythm in social contexts (Clayton, Sager, & Will, 2005; Koelsch, 2010; Overy & Molnar-Szakacs, 2009). The study of groove and its ability to engage the motor system gives further insights into this pervasive social and musical phenomenon.

## Acknowledgments

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