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Body Movement Selectively Shapes the Neural Representation of Musical Rhythms

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Abstract

It is increasingly recognized that motor routines dynamically shape the processing of sensory inflow (e.g., when hand movements are used to feel a texture or identify an object). In the present research, we captured the shaping of auditory perception by movement in humans by taking advantage of a specific context: music. Participants listened to a repeated rhythmical sequence before and after moving their bodies to this rhythm in a specific meter. We found that the brain responses to the rhythm (as recorded with electroencephalography) after body movement were significantly enhanced at frequencies related to the meter to which the participants had moved. These results provide evidence that body movement can selectively shape the subsequent internal representation of auditory rhythms.

Keywords

musical-rhythm processing, auditory perception, body movement, sensorimotor integration, EEG, neuronal entrainment, steady-state evoked potentials

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To gather data from the environment, people most often explore it through movement, and these exploratory movements are thought to shape the processing of sensory inflow (Schroeder, Wilson, Radman, Scharfman, & Lakatos, 2010). Because exploratory movements are often rhythmic in nature, it has been suggested that the shaping of perception by movement involves some kind of neural entrainment. This is easily conceivable for vision, somatosensation, or olfaction—in which eye, head, finger, or sniffing movements are directly involved in sensory exploration. How movement might shape perception in the auditory system is less straightforward (Schroeder et al., 2010).

To provide evidence of rhythmic motor shaping of audition, we took advantage of a specific context: music. Getting entrained to music is a universal human behavior that strikingly illustrates how auditory perception can be linked to action patterns (Leman, 2007; Phillips-Silver, Aktipis, & Bryant, 2010). Notably, while musical rhythms make people move, movement can, in turn, shape the perception of musical rhythms. Although this idea has long been considered an axiom in music theory and education (Jaques-Dalcroze, 1920), behavioral evidence has been provided only recently: Phillips-Silver and Trainor (2005, 2007, 2008) have shown that movements performed concurrently with rhythmic sound patterns can, at least momentarily, modulate the perception of musical meter (i.e., the perception of nested temporal periodicities, as in a waltz, which has three beats per meter). However, the manner in which the brain builds a neural representation of musical rhythms and how movements might shape this neural representation remain largely unknown.

To explore this phenomenon, we used an approach based on the electroencephalographic (EEG) recording of steady-state evoked potentials (SSEPs) to identify the neural entrainment to musical rhythm (Nozaradan, Peretz,

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Missal, & Mouraux, 2011; Nozaradan, Peretz, & Mouraux, 2012b). This approach allows one to objectively capture the neural activities elicited by musical rhythms in the form of multiple SSEPs observed in the EEG spectrum at frequencies corresponding to the rhythm envelope (Nozaradan et al., 2012b). These SSEPs have been shown to be selectively enhanced at meter-related frequencies, even when those frequencies were not prominent in the spectrum of the sound envelope (Nozaradan et al., 2012b); this finding indicates that these neural activities do not merely reflect the physical structure of the sound envelope but, instead, reflect an internal representation of the perceived meter (Large, 2008).

In the current research, we used SSEPs to capture the changes in the neural dynamics of perceived metric structure occurring both after and before body movements thought to induce implicit auditory-motor modulation. EEGs were recorded while participants listened to an ambiguous rhythm, before and after a body-movement session designed to disambiguate the perception of this rhythm by favoring a specific meter (e.g., two beats per measure vs. three beats per measure; Phillips-Silver & Trainor, 2005, 2007, 2008). When comparing the EEGs recorded after and before body movement, we predicted that we would find enhanced SSEPs at frequencies corresponding to the metric interpretation induced implicitly during the movement session, even though participants did not move or focus attention on the metric structure during the EEG recording. Such a finding would provide direct evidence that rhythmic body movements selectively shape the neural representation of musical rhythms.

Method

Experiment 1

Participants. Fourteen healthy volunteers (8 females, 6 males; all right-handed; mean age = 23 years, *SD* = 4) took part in Experiment 1 after providing written informed consent. Only nonmusicians (but with some experience in Western music as amateur listeners or dancers) were asked to participate, as nonmusicians would not be expected to be aware of the theoretic structure of the polyrhythm and of the meter induced by the body movements. None had prior experience with the rhythm task used in the present experiment. They had no history of hearing, neurological, or psychiatric disorder, and none were taking any medication at the time of the experiment. The experiment was approved by the local ethics committee.

Auditory stimulus. The stimulus consisted of a rhythmic pattern lasting 1.2 s, looped continuously for 33 s. The rhythmic patterns consisted of alternating intervals of sound (a 990-Hz pure tone of 200-ms duration with a 10-ms rise and 10-ms fall) and silence, as illustrated in Figure 1a. The auditory stimuli were created using Audacity software (Version 1.2.6; http://audacity.sourceforge.net/) and presented binaurally through earphones (BeyerDynamic DT 990 PRO, Heilbronn, Germany) at a comfortable hearing level, using E-Prime software (Version 2.0; Schneider, Eschman, & Zuccolotto, 2001). Pure tones were used to ensure that the frequency content of the sounds used as unitary events did not interfere with the frequencies of interest. Moreover, rhythmic presentation of pure tones has been shown to elicit SSEPs with significant signal-to-noise ratios (Nozaradan et al., 2012b). The rhythmic pattern used in the experiment was metrically ambiguous, as it could induce the perception of a ternary meter as well as of a binary meter (i.e., a subdivision of the rhythmic pattern by three or by two, or *hemiola* in music; Phillips-Silver & Trainor, 2005, 2007, 2008).

Experimental conditions. The rhythmic pattern was presented in three successive sessions (Fig. 1b). In each session, the 33-s auditory stimulus was repeated 11 times (each repeat constituted 1 trial). The onset of each pattern was preceded by a 3-s period between the time the participant pressed a button to begin the trial and the appearance of the stimulus. The experimenter remained in the recording room with the participant at all times to monitor compliance to the procedure and instructions.

The first session (the before-movement session) was structured as follows. During the first 10 trials, participants were asked to listen carefully to the stimulus in order to detect very short accelerations of tempo (creating by decreasing the duration of two successive events by 10 ms, i.e., each event was 190 ms). These accelerations were inserted six times at random positions in two of the trials within the session. The participants were instructed to report the change in tempo at the end of each trial. This task ensured that participants focused on the temporal aspects of the presented sound. The two trials containing the tempo changes were excluded from further analyses.

During the 11th trial of the first session, participants were asked to perform a tapping task. The tapping was performed using the right hand: Participants made small up and down movements of the hand starting from the wrist joint, while keeping the forearm and elbow fixed on an armrest. When tapping, the fingers of the tapping hand came briefly in contact with the armrest (Nozaradan et al., 2012b; Nozaradan, Zerouali, Peretz, & Mouraux, 2013). The tapping movements were recorded using an accelerometer placed on the tapping hand. Participants were instructed to tap freely to the rhythm, in the way that seemed the most natural for them. This allowed us to obtain a relative indication of their perception of beat

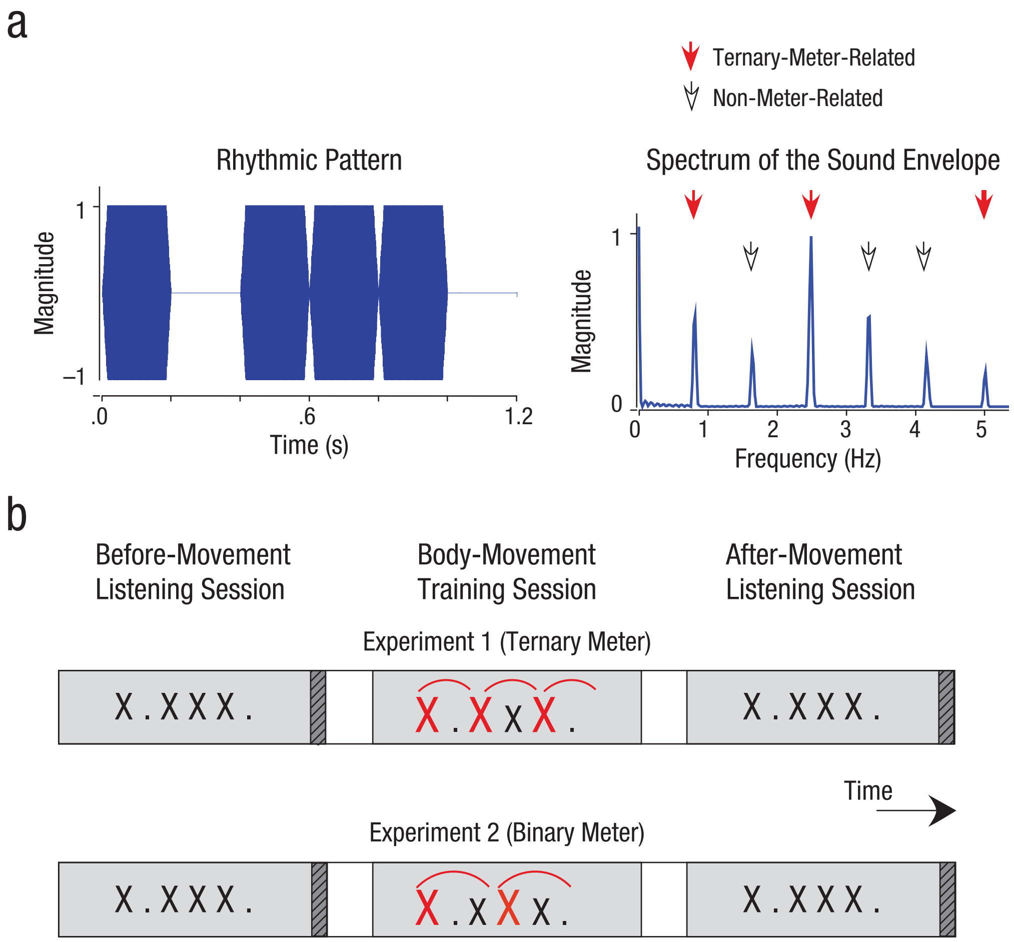

Fig. 1. Experimental paradigm. Participants listened to a rhythmic pattern consisting of a succession of sounds (pure 990-Hz tone with a 10-ms rise and 10-ms fall) and silences (a), each lasting 200 ms. This rhythmic pattern was metrically ambiguous, as it could induce the perception of a ternary meter as well as the perception of a binary meter. The spectrum of the sound envelope shows that the rhythmic pattern contained a series of six equidistant peaks, which can be classified as related or unrelated to a ternary-metric interpretation of the rhythm. Each experiment had three sessions (b). In the before-movement session (10 trials), participants listened to the rhythmic pattern (cross: 200-ms tone, dot: 200-ms silence) looped across 33 s. They were instructed to detect very short accelerations of tempo in two of the trials interspersed within the session. During the 11th trial (dark gray bar), participants were asked to tap with their right hand along with the rhythm. In the movement-training session, participants were trained to move according to a ternary-metric interpretation (Experiment 1) or a binary-metric interpretation (Experiment 2), represented by the crosses and curves. The after-movement listening session was identical to the before-movement listening session.

and meter as induced by the rhythmic pattern, without suggesting explicitly to the participants that some beat and meter periodicities could be perceived from the pattern. Moreover, participants were asked to start tapping as soon as they heard the first sound of the trial and to maintain their movement as consistently as possible throughout the tapping trial.

During the second session (the body-movement-training session), participants were asked to move their body (clap the hands, bob the head, tap the foot, sway the torso) isochronally according to a ternary-metric interpretation of the rhythmic pattern (i.e., a subdivision of the rhythmic pattern by three, as represented in Fig. 1). This training was performed continuously while participants listened to the rhythmic pattern during 11 trials. To entrain participants to these movements, the experimenter demonstrated a similar movement. This training session purposely involved multiple parts of the body as well as multisensory cues for meter induction (visual, auditory, and vestibular) because (a) we aimed to optimize the effect of the movement as measured in the third session, and (b) this training resembled the complexity and natural variability of movements performed on rhythms in ecological musical contexts.

The third session of the experiment (the after-movement session) was identical to the before-movement session. Comparison of performance during the tapping trial of the before- and after-movement sessions provided an indication of the possible changes in perception of beat and meter.

Finally, at the end of the experiment, participants were asked to describe their general feeling about the rhythm and to report whether they noticed any change in the meter of the rhythm subsequent to movement training, either while listening to the rhythm or while tapping to it. To ensure that the movement-training sessions were guided accurately, we enlisted the participation of an expert professional musician with 20 years of violin- and piano-playing experience and a high level of music education.

EEG recording. In the before-movement and after-movement sessions, participants were comfortably seated in a chair with their head resting on a support. They were instructed to relax, avoid any unnecessary head or body movement, and keep their eyes fixated on a point displayed on a computer screen in front of them. The EEG was recorded using 64 Ag-AgCl electrodes placed on the scalp according to the international 10-10 system (Waveguard64 cap, Cephalon A/S, Norresundby, Denmark). Vertical and horizontal eye movements were monitored using four additional electrodes, one placed on the outer canthus of each eye and one above and one below the left orbit. Electrode impedances were kept below 10 kΩ. The signals were amplified, low-pass filtered at 500 Hz, digitized using a sampling rate of 1,000 Hz, and referenced to an average reference (64-channel high-speed amplifier, Advanced Neuro Technologies, Enschede, The Netherlands).

Hand-movement recording. Movements of the hand were measured using a three-axis accelerometer (MMA7341L, Pololu Robotics & Electronics, Las Vegas, NV) attached to the hand dorsum. The signals generated by the accelerometer were digitized using three additional bipolar channels of the EEG system.

Sound-pattern analysis. To determine the frequencies at which SSEPs were expected to be elicited in the recorded EEG signals, we extracted the temporal envelope of the 33-s sound pattern using a Hilbert function, which yielded a time-varying estimate of the instantaneous amplitude of the sound envelope, as implemented in the MIRToolbox (Lartillot & Toiviainen, 2007). The obtained waveforms were then transformed in the frequency domain using a discrete Fourier transform (Frigo & Johnson, 1998), which yielded a frequency spectrum of envelope magnitude (Bach & Meigen, 1999). We determined that the frequencies of interest were greater than or equal to 5 Hz, that is, the frequency corresponding to the 200-ms period of the unitary event of the pattern. As shown in Figure 1a, the envelope spectrum of the pattern consisted of six distinct frequencies ranging from 0.84 Hz (corresponding to the pattern duration) to 5 Hz (corresponding to the unitary-event duration) with an interval of 0.84 Hz. According to a ternary-metric interpretation of the rhythmic pattern (as induced by the body-movement-training session) and to music theory concerning polyrhythms (London, 2004), these frequencies could be classified in three ternary-meter-related frequencies (0.84 Hz, 2.5 Hz, and 5 Hz, corresponding to the frequency of the measure, the ternary beat, and the unitary event, respectively) and three non-meter-related frequencies (1.6 Hz, 3.3 Hz, and 4.2 Hz).

We then computed z scores using the magnitude of the peaks obtained at each of the six frequencies in the spectrum of the pattern envelope, as follows: $z = (x - \mu)/\sigma$, where μ and σ correspond to the mean and standard deviation, respectively, of the magnitudes of the six peaks (Nozaradan et al., 2012b). This procedure allowed us to assess which frequencies stood out relative to the entire set of frequencies.

EEG analysis. The continuous EEG signals recorded before and after the movement session were filtered using a 0.1-Hz high-pass Butterworth zero-phase filter to remove slow drifts in the recorded signals. Epochs lasting 32 s were obtained by segmenting the recordings from +1 to +33 s relative to the onset of the auditory stimulus. The EEG recorded during the 1st s of each epoch was removed to discard the transient auditory evoked potentials related to the onset of the stimulus (Nozaradan, 2013; Nozaradan et al., 2011; Nozaradan, Peretz, & Mouraux, 2012a; Nozaradan et al., 2012b). These EEG-processing steps were carried out using Analyzer software (Version 1.05; Brain Products, Gilching, Germany). Artifacts produced by eye blinks or eye movements were removed from the EEG signal using a validated method based on an independent component analysis (Jung et al., 2000) that utilized the runica algorithm (Bell & Sejnowski, 1995; Makeig, 2002).

For each participant and condition, EEG epochs were averaged across trials. The time-domain-averaging procedure was used to enhance the signal-to-noise ratio of EEG activities time locked to the patterns. The obtained average waveforms were then transformed in the frequency domain using a discrete Fourier transform (Frigo & Johnson, 1998), which yielded a frequency spectrum of signal amplitude (µV) ranging from 0 to 500 Hz with a frequency resolution of 0.031 Hz (Bach & Meigen, 1999). This procedure allowed us to assess the appearance of frequency components in the EEG elicited by the frequency components of the sound patterns and induced beat and meter percept (Nozaradan et al., 2012b). The deliberate choice of computing Fourier transforms of long-lasting epochs was justified by the fact that it improves the frequency resolution of the obtained EEG spectra. This concentrates the magnitude of the SSEPs in a narrow frequency band and, thereby, enhances their signal-to-noise ratio. Furthermore, this is required to disentangle nearby SSEPs in the EEG frequency spectrum (Regan, 1989).

These EEG-processing steps were carried out using Letswave 5 (Institute of Neuroscience, University of Louvain; www.nocions.webnode.com/letswave), MATLAB (The MathWorks, Natick, MA), and EEGLAB (Swartz Center for Computational Neuroscience, University of California San Diego). Within the obtained frequency spectra, signal amplitude may be expected to correspond to the sum of (a) stimulus-induced SSEPs and (b) unrelated residual background noise due to, for example, spontaneous EEG activity, muscle activity, or eye movements. Therefore, to obtain valid estimates of SSEP magnitude, we removed the contribution of this noise by subtracting, at each bin of the frequency spectra, the average amplitude measured at neighboring frequency bins (two frequency bins ranging from −0.15 to −0.09 Hz and from +0.09 to +0.15 Hz relative to each frequency bin).

The validity of this subtraction procedure relies on the assumption that in the absence of an SSEP, the signal amplitude at a given frequency bin should be similar to the signal amplitude of the mean of the surrounding frequency bins (Mouraux et al., 2011; Nozaradan et al., 2011; Nozaradan et al., 2012a, 2012b; Nozaradan et al., 2013). This subtraction procedure is important (a) to assess the scalp topographies of the elicited SSEPs, as the magnitude of the background noise is not equally distributed across scalp channels, and (b) to compare the amplitude of SSEPs elicited at distinct frequencies, as the background-noise magnitude may be unequally distributed across the frequency spectrum. The magnitude of the SSEPs was then estimated by taking the maximum noise-subtracted amplitude measured in a range of three frequency bins centered over the expected SSEP frequency, based on the spectrum of the sound envelope. This range of frequencies allowed us to account for possible spectral leakage because the discrete Fourier transform did not estimate signal amplitude at the exact frequency of any of the expected SSEPs (Nozaradan et al., 2011; Nozaradan et al., 2012a, 2012b).

Topographical distribution of SSEPs. For each SSEP frequency, topographical maps were computed by spherical interpolation using the EEG frequency spectra obtained in the before- and after-movement sessions. These topographical maps were averaged across meter-related frequencies and non-meter-related frequencies.

Statistical analyses. To exclude any electrode-selection bias, we selected a pool of electrodes of interest as follows. Normalized topographical maps obtained for each participant, condition, and frequency were averaged to select the five electrodes exhibiting the maximum SSEP amplitudes (electrodes Fz, F1, F2, F3, and F4, i.e., predominantly located over fronto-central areas). Notably, because the pool of electrodes was determined on the basis of the scalp distribution of the spectrum averaged across the two conditions, this procedure did not bias our results toward finding a difference between the two conditions.

A 2 (meter: ternary-meter-related vs. non-meter-related) × 2 (session: before training vs. after training) repeated measures analysis of variance (ANOVA) was conducted on mean SSEP magnitude. Paired samples t tests were used to perform post hoc pairwise comparisons of the magnitude of the SSEPs measured before and after movement training. The significance level was set at $p < .05$.

In addition, as for the sound-pattern analysis, the amplitudes of the SSEPs obtained at the expected frequencies were expressed as z scores, using the mean and standard deviation of the magnitudes obtained across the different peaks, to assess how each of the different SSEPs stood out relative to the entire set of SSEPs and relative to the z scores obtained from the sound-pattern envelope (Nozaradan et al., 2012b). To assess specifically whether SSEPs elicited at ternary-meter-related frequencies (0.84 Hz, 2.5 Hz, and 5 Hz) were selectively enhanced, we compared the average of the z scores representing SSEP amplitude at ternary-meter-related frequencies with the average of the z scores representing these same frequencies in the sound-pattern envelope, using a one-sample t test (Nozaradan et al., 2012b). A similar procedure was used to compare the magnitude of SSEPs and the magnitude of the sound envelope at non-meter-related frequencies. The significance level was set at $p < .05$.

Hand-movement analysis. The hand-movement analysis was based on previous work showing that the frequency spectrum of the vertical-axis acceleration signal can be used reliably to assess the dynamics of repeated hand tapping, appearing as clear peaks at the hand-tapping frequency and its harmonics (Nozaradan et al., 2013). In the current study, this approach was preferred to an approach based on an estimation of intertap latencies because participants were instructed to tap freely to the rhythm in the way that seemed the most natural for them.

The vertical-acceleration signals recorded for each participant and tapping session were segmented from +0 to +33 s according to the sound onset. The discrete Fourier transforms (Frigo & Johnson, 1998) were then computed. The same 2 × 2 ANOVA that was used to compare mean SSEP magnitude was used to compare these magnitudes. Paired-samples *t* tests were used to perform post hoc pairwise comparisons of the magnitudes measured in the two sessions. The significance level was set at $p < .05$.

Experiment 2

Fourteen participants (10 females, 4 males; all right-handed; mean age = 25 years, *SD* = 7) took part in Experiment 2. None of these participants took part in Experiment 1 (to avoid possible persistent effect of the movement trained in Experiment 1, which could have interfered in Experiment 2). Experiment 2 was identical to Experiment 1, except that during the body-movement-training session, participants were trained to move to a binary-metric interpretation of the rhythm instead of a ternary-metric interpretation (Fig. 1b).

Notably, although the rhythm used in these two experiments can be considered ambiguous because it can be interpreted according to a ternary or a binary meter, the structure of the rhythm itself is likely to favor a ternary interpretation, as suggested by the distribution of the acoustic energy in the envelope of the rhythm. For this reason, the binary-meter body-movement training performed in Experiment 2 was not expected to necessarily shape the auditory processing in the form of a selective enhancement of SSEPs at corresponding binary-meter frequencies. Rather, it was expected to prevent shaping the auditory processing toward a ternary-metric interpretation. The aim of Experiment 2 was thus to examine whether the enhancement of ternary-meter-related SSEPs observed in Experiment 1 was due to the body movements being performed according to a ternary meter or simply to continuously listening to this rhythm throughout three sessions, independently of the metric of the body movement. To achieve this aim, we applied the same statistical analysis as in Experiment 1, comparing ternary-meter-related and nonrelated SSEPs before and after the binary-movement session.

However, we also tested whether the binary-movement session affected the SSEPs at binary-meter-related frequencies. According to a binary-metric interpretation of the rhythmic pattern, the SSEPs could be classified in three meter-related frequencies (0.84 Hz, 1.6 Hz, and 5 Hz, corresponding to the frequency of the measure, the binary beat, and the unitary event, respectively) and three non-meter-related frequencies (2.5 Hz, 3.3 Hz, and 4.2 Hz). A 2 (meter: binary-meter-related vs. non-meter-related) × 2 (session: before training vs. after training) repeated measures ANOVA was conducted on mean SSEP magnitude. Paired-samples *t* tests were used to perform post hoc pairwise comparisons of the magnitude of the SSEPs measured between the two sessions. The significance level was set at $p < .05$. The same statistical analyses were used to compare the magnitude of the peaks appearing in the spectrum of the vertical axis of the accelerometer.

Results

Sound-pattern analysis

The envelope spectrum of the rhythm was unequally distributed along the frequencies of interest. Indeed, the magnitude of the peaks appearing at ternary-meter-related frequencies stood out relatively to the other frequencies. Although the rhythm we used is theoretically ambiguous (both a binary and a ternary meter can be induced from it), the predominance of ternary-meter-related frequencies suggests that this rhythm is physically biased toward favoring a ternary-meter interpretation.

Self-reports of rhythm perception

At the end of Experiments 1 and 2, participants reported that they did not notice a difference in beat and meter before versus after the movement session. None of the participants reported that the body-movement-training session induced a specific metric interpretation of the rhythm (this was asked by the experimenter while clapping the ternary or binary rhythm at the moment of the self-report) or changed their tapping performance.

However, about half of the participants in both Experiments 1 and 2 reported a qualitative change in their perception of the sound, which they described as "more pleasant" or "more rhythmic," after the movement-training session. Moreover, in Experiment 2, most participants reported that they felt uncomfortable performing the movement according to the binary meter.

Detection task

During the before- and after-movement sessions, participants correctly detected all targets in both experiments. In Experiment 1, the median number of false alarms was 7 (interquartile range: 3.5–9.5). In Experiment 2, the median number of false alarms was 8 (interquartile range: 4.0–9.5). The number of correct detections did not differ significantly before and after the movement session in Experiment 1, $t(13) = 2.83$, $p = .21$, and Experiment 2, $t(13) = 3.26$, $p = .34$. Similarly, the number of false alarms was not significantly different before and after the movement session in Experiment 1, $t(13) = 2.83$, $p = .21$, and Experiment 2, $t(13) = 3.26$, $p = .34$.

Steady-state evoked potentials

In both experiments, each of the six frequencies constituting the envelope spectrum of the rhythmic pattern elicited an SSEP before and after the movement-training session (Figs. 2 and 3). The scalp topography of the elicited SSEPs was, on average, maximal over fronto-central regions and symmetrically distributed over the two hemispheres (Fig. 3). Moreover, as shown in Figure 3, the scalp topography of meter-related and non-meter-related frequencies recorded before and after the movement-training session did not differ substantially.

Experiment 1. The repeated measures ANOVA used to examine SSEP magnitude in Experiment 1 revealed a significant main effect of meter, $F(2, 27) = 36.39$, $\eta^2 = .73$, $p < .0001$; a significant main effect of session, $F(2, 27) = 7.73$, $\eta^2 = .37$, $p = .01$; and a significant interaction between meter and session, $F(2, 27) = 10.43$, $\eta^2 = .44$, $p = .007$, which indicates that meter-related and non-meter-related SSEPs were not similarly affected by the movement-training session. Post hoc pairwise comparisons showed that the amplitudes of meter-related SSEPs were significantly enhanced compared with the amplitudes of non-meter-related SSEPs, both before, $t(13) = 3.7$, $p = .002$, and after, $t(13) = 6.53$, $p < .0001$, the movement-training session (Figs. 2a and 2b). Most important, the amplitude of meter-related SSEPs was significantly greater after than before the movement-training session, $t(13) = 3.63$, $p = .003$, whereas there was no significant difference in the amplitude of the non-meter-related SSEPs recorded after and before movement, $t(13) = 0.26$, $p = .79$.

In the before-movement session, the standardized estimates of the SSEP amplitudes obtained at meter-related and non-meter-related frequencies were not significantly enhanced compared with the standardized estimates of the sound envelope at the corresponding frequencies, $t(13) = 0.31$, $p = .76$, and $t(13) = 0.31$, $p = .76$, respectively. This suggests that there was no clear selective enhancement of neural entrainment related to the meter. In contrast, in the after-movement session, the standardized estimates of SSEP amplitudes were significantly enhanced at meter-related frequencies, $t(13) = 3.47$, $p = .004$, and reduced at non-meter-related frequencies, $t(13) = 3.47$, $p = .004$, which suggests that the movement-training session resulted in the emergence of a selective enhancement of neural entrainment at frequencies related to the meter, as in Nozaradan et al. (2012b).

Experiment 2. Contrasting with the results of Experiment 1, results of the repeated measures ANOVA used to compare the magnitude of ternary-meter-related and non-meter-related SSEPs before and after the movement-training session revealed a significant main effect of meter, $F(2, 27) = 16.78$, $\eta^2 = .56$, $p = .001$, but no significant effect of session, $F(2, 27) = 0.65$, $\eta^2 = .04$, $p = .43$, and no significant interaction between meter and session, $F(2, 27) = 0.01$, $\eta^2 = .001$, $p = .89$. These findings indicate that the movement-training session did not significantly affect meter-related and non-meter-related SSEPs in Experiment 2, either by inducing an enhancement or a diminishment of the ternary-meter-related SSEPs (Figs. 2c and 2d). There was no significant diminishment of these SSEPs after the binary movement.

In the before-movement session, the standardized estimates of the SSEP amplitudes obtained at meter-related, $t(13) = 0.11$, $p = .91$, and non-meter-related, $t(13) = 0.11$, $p = .91$, frequencies were not significantly enhanced compared with those of the sound envelope at the corresponding frequencies. This suggests that, as in Experiment 1, there was no selective enhancement of neural entrainment at frequencies related to the ternary meter before movement training. In the after-movement session, the standardized estimates of ternary meter-related SSEPs were also not significantly enhanced compared with the standardized estimates of the sound envelope at corresponding frequencies, $t(13) = 0.21$, $p = .83$. There was also no enhancement of non-meter-related SSEPs, $t(13) = 0.21$, $p = .83$. This suggests that in Experiment 2, the movement-training session did not result in the emergence of a selective enhancement of neural entrainment at frequencies related to the ternary meter.

The repeated measures ANOVA used to compare SSEP magnitude revealed a significant main effect of meter, $F(2, 27) = 11.73$, $\eta^2 = .47$, $p = .005$, but no significant effect of session, $F(2, 27) = .65$, $\eta^2 = .04$, $p = .43$, and no significant interaction between meter and session, $F(2, 27) = 1.47$, $\eta^2 = .10$, $p = .24$. Taken together, the results of Experiment 2 indicate that the selective enhancement of the ternary-meter-related SSEPs observed in Experiment 1 after body movement was likely due to the metric of the body movement, as such an enhancement was not observed after participants moved according to a different metric interpretation.

Hand-tapping movement

Experiment 1. The analysis on hand tapping in Experiment 1 was performed on 13 participants, as the data of 1 participant were unavailable because of a technical problem during the experiment. As shown in Figure 4a, there was a difference in the tapping performed before and after the movement session. The repeated measures ANOVA conducted on vertical-acceleration signals revealed a significant main effect of meter, $F(2, 25) = 20.57$, $\eta^2 = .63$, $p = .001$; no effect of session, $F(2, 25) = 2.59$, $\eta^2 = .17$, $p = .13$; and a significant interaction between meter and session, $F(2, 25) = 9.67$, $\eta^2 = .44$,

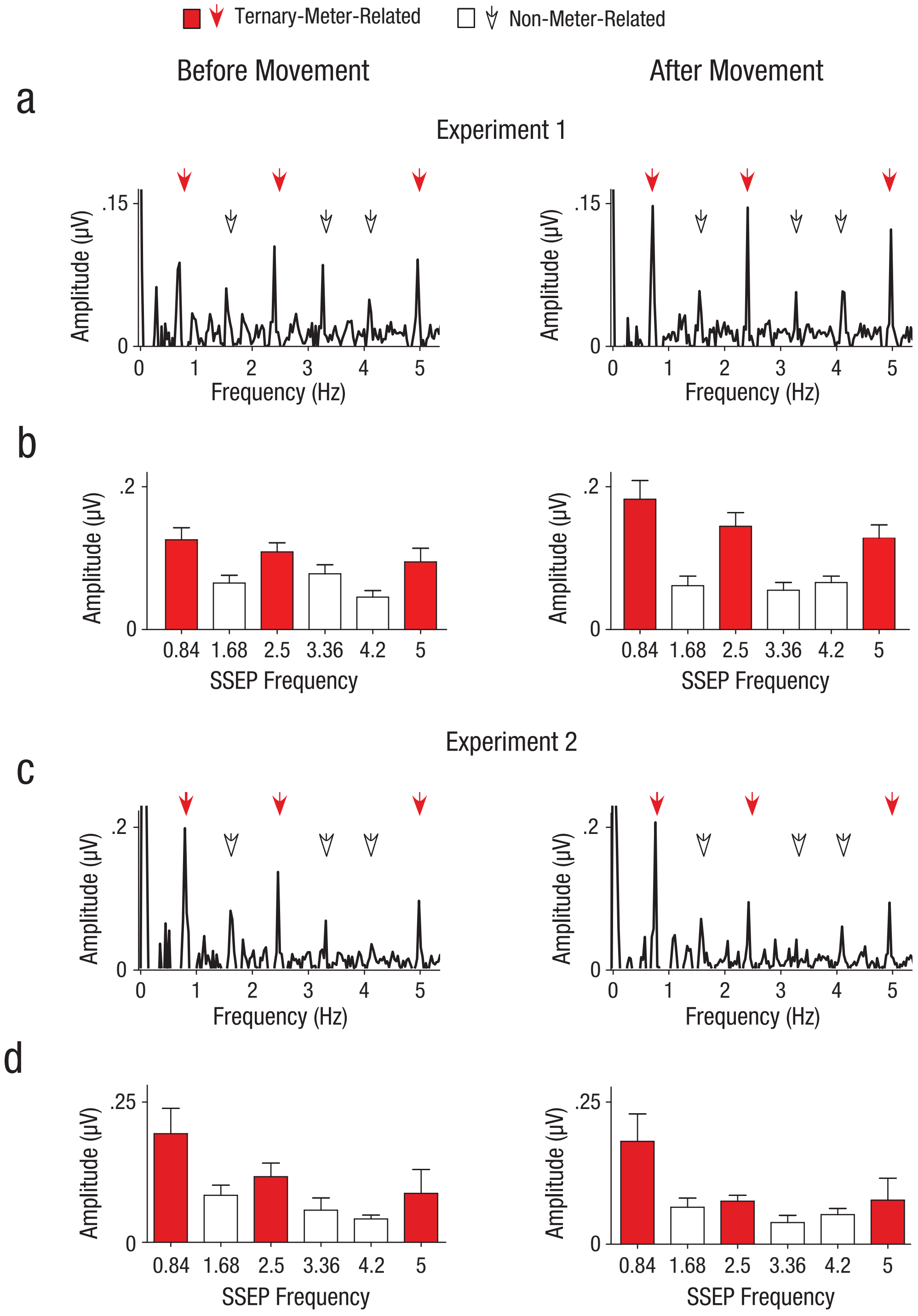

Fig. 2. Ternary-meter-related and non-meter-related steady-state evoked potentials (SSEPs) obtained before (left column) and after (right column) the ternary-movement-training session (Experiment 1) and binary-movement-training session (Experiment 2). For both experiments, the waveforms (a, c) show electroencephalographic spectra averaged across participants and across electrodes Fz, F1, F2, F3, and F4. Ternary-meter-related frequencies and non-meter-related frequencies are indicated. The bar graphs (b, d) show mean amplitude of the SSEPs at each meter-related or non-meter-related frequency of interest. Error bars indicate standard errors of the mean.

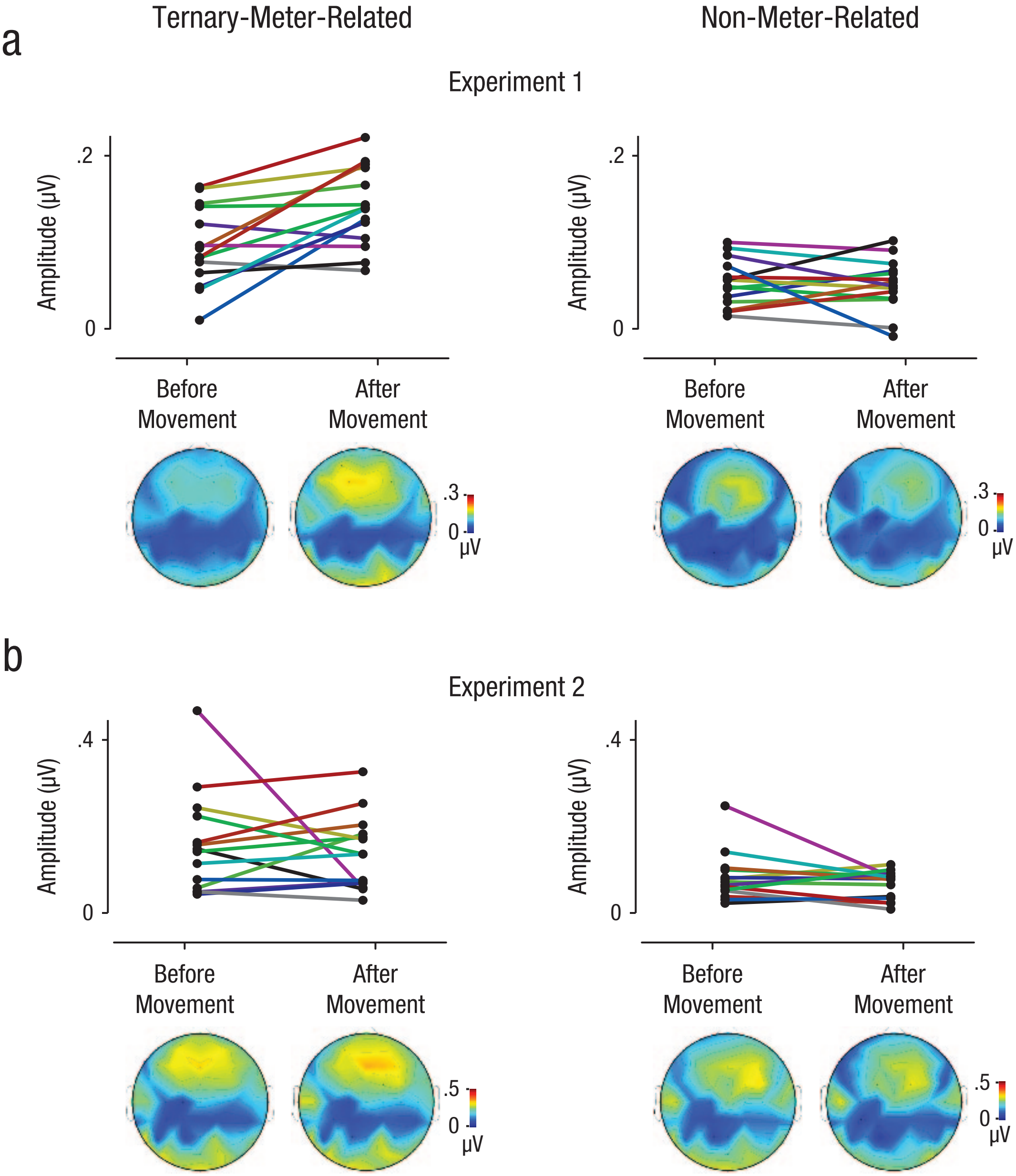

Fig. 3. Group-level average amplitude and scalp topography of ternary-meter-related (left column) and non-meter-related (right column) steady-state evoked potentials obtained before and after the movement-training session for each participant (colors across left and right plots correspond to the same participants). Results are shown separately for (a) Experiment 1 (ternary-movement-training session) and (b) Experiment 2 (binary-movement-training session).

p = .009. Post hoc pairwise comparisons showed that the magnitudes at meter-related frequencies were significantly greater than the magnitudes at non-meter-related frequencies after the movement-training session, $t(12)$ = 3.93, p = .001, but not before the movement-training session, $t(12)$ = 1.21, p = .24 (Fig. 4). Moreover, the magnitude at meter-related frequencies was significantly greater after than before the movement-training session, $t(12)$ = 3.08, p = .008, whereas there was no significant difference in the magnitudes at the non-meter-related frequencies recorded before and after movement, $t(12)$ = 0.88, p = .39. Taken together, these results indicate that participants tended to tap according to a ternary-metric interpretation of the rhythmic pattern (increased magnitude at meter-related frequencies) after the body-movement session compared with before and, hence, that the movement-training session exerted an effect on rhythm production.

Experiment 2. The hand-tapping analysis for Experiment 2 was performed on 13 participants, as the data of

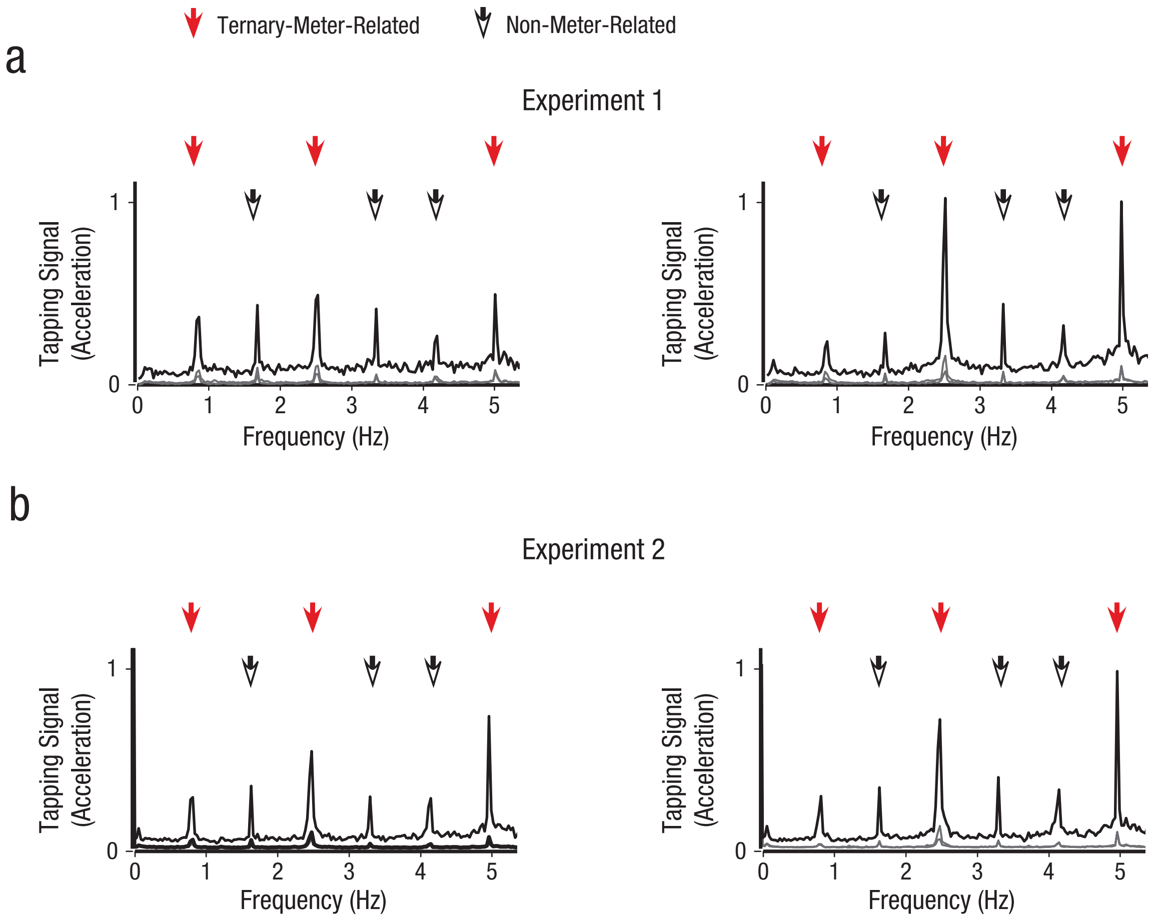

Fig. 4. Mean spectra of hand-tapping movement performed before (left column) and after (right column) the movement-training sessions in (a) Experiment 1 and (b) Experiment 2. Results for the vertical axis are in bold; results for the anteroposterior axis and transverse axis (combined) are shown beneath the results for the vertical axis. The arrows indicate ternary-meter-related frequencies and non-meter-related frequencies.

1 participant were unavailable because of a technical problem during the experiment. In contrast with the results of Experiment 1, findings from the repeated measures ANOVA conducted on vertical-acceleration signals in Experiment 2 revealed a significant main effect of meter, $F(2, 25) = 37.87$, $\eta^2 = .77$, $p < .0001$, but no significant effect of session, $F(2, 25) = 3.92$, $\eta^2 = .26$, $p = .7$, and no interaction between meter and session, $F(2, 25) = 2.29$, $\eta^2 = .17$, $p = .15$ (Fig. 4b). These results indicate that in Experiment 2, participants did not consistently tap according to a ternary-metric interpretation of the rhythmic pattern after the body-movement session.

The repeated measures ANOVA on binary-meter-related and non-meter-related frequencies revealed no significant main effect of meter, $F(2, 25) = 2.35$, $\eta^2 = .17$, $p = .15$, no significant main effect of session, $F(2, 25) = 3.92$, $\eta^2 = .26$, $p = .7$, and no significant interaction between meter and session, $F(2, 25) = 0.29$, $\eta^2 = .026$, $p = .6$.

Discussion

The present study explored the interactions between perception and movement by taking advantage of the strong sensorimotor coupling inherent to musical-rhythm perception and production. One of the most intriguing phenomena related to musical rhythm and meter is that it powerfully compels one to move (Janata, Tomic, & Haberman, 2012). In turn, body movements shape rhythm perception (Phillips-Silver & Trainor, 2007, 2008).

Here, we showed that the SSEPs elicited by listening to an ambiguous auditory rhythm that can be perceived either as a binary or a ternary meter are significantly enhanced at the frequencies corresponding to a ternary-metric interpretation after body-movement training using this metric interpretation. In contrast, these SSEPs were not enhanced after body-movement training using a binary-metric interpretation. Taken together, these results constitute direct evidence that the neural entrainment to musical rhythms is not only determined by acoustic features of the rhythmic sounds but is also, at least in the context of an ambiguous rhythm—shaped by the previous experience of body movement (Phillips-Silver & Trainor, 2007, 2008).

Both in Experiment 1 and in Experiment 2, the magnitude of ternary-meter-related SSEPs was significantly greater than the magnitude of unrelated SSEPs before the movement-training session, which indicates an a priori bias toward a ternary-metric structure. However, when SSEP magnitudes were compared with the magnitudes of the corresponding frequencies in the spectrum of the sound envelope, ternary-meter-related SSEPs were not greater in the before-movement session, which suggests that the a priori bias toward ternary-meter-related frequencies resulted from the fact that such frequencies were prominent in the sound envelope itself. Building on recent results on neural-entrainment mechanisms to musical rhythms (Nozaradan et al., 2012b), we suggest that the lack of enhancement before movement may be related to the metric ambiguity of the rhythm, which did not elicit a stable perception of meter. This result is also consistent with tapping performance before the movement-training session, which did not show any significant relative enhancement at meter-related frequencies. The selective enhancement of the ternary-meter-related SSEPs compared with the sound envelope appeared only in the after-movement session of Experiment 1, not in Experiment 2. Taken together, these results indicate that there was no significant difference in the a priori metric interpretation across the two groups, but that the difference appeared specifically after the ternary-movement session.

In contrast, selective enhancement of the ternary-meter-related SSEPs compared with the sound envelope appeared only after ternary-body-movement training. This reshaping of the EEG spectrum can be interpreted as evidence of a metric disambiguation of the rhythm, involving neural mechanisms selecting meter-relevant frequencies identified by the body movements. Again, this selective entrainment to meter-related frequencies was reflected in the behavioral measures, which showed improved consistency of tapping at ternary-meter-related frequencies (Fig. 4).

It could be hypothesized that the selective enhancement of the SSEPs subsequent to ternary body movement would occur similarly after moving the body according to any distinct metric interpretation. In other words, the selective neural entrainment could emerge subsequent to nonspecific repeated body movement performed to any rhythm, or could even arise from the repeated listening of this rhythm across three sessions, independently of the body-movement temporal pattern. However, the results of the second experiment demonstrate that this was not the case. Indeed, no significant enhancement of the magnitude of ternary-meter-related SSEPs was observed after participants moved their bodies according to a binary-metric interpretation. Furthermore, there was also no enhancement of tapping at ternary-meter-related frequencies.

Of interest, there was an asymmetry between the effect of the ternary- and binary-movement experiments. Although the rhythm used in the present study can be considered ambiguous because it can be interpreted according to a ternary or a binary meter, the stronger priming effect of moving one's body to a ternary meter than to a binary meter could result from the distribution of the acoustic energy in the envelope of the rhythm, favoring the ternary-metric interpretation. Also, this asymmetry could result from other features of the rhythm, such as the tempo chosen for the rhythm presentation (London, 2004), or from perceptual and cultural biases toward the grouping of acoustic events by two (corresponding to the ternary meter in the present study) in Western subjects (Brochard, Abecasis, Potter, Ragot, & Drake, 2003). Hence, the shaping of the neural entrainment to the rhythm by previous movement could be limited to specific interpretations of the stimulus. Namely, the selective enhancement appeared at congruent frequencies between the sound structure and the movement.

The asymmetry between the two metrical interpretations could appear discrepant with previous findings (Phillips-Silver & Trainor, 2005, 2007, 2008). This could be explained by the different methods used to capture the effect. In previous experiments performed with adults (Phillips-Silver & Trainor, 2007, 2008), the metrical interpretation was evaluated on the basis of an explicit behavioral outcome asked to the participants (a forced choice between two differently accented versions of the rhythmic pattern, either binary or ternary). In these studies, as in the current experiments, participants were never instructed to recall or match the movement experience. However, in the current experiments, there was no explicit outcome requested from the participants regarding the metrical interpretation, either during the listening or the tapping trials, in contrast with previous studies. Also, as EEG samples only a fraction of the elicited electrocortical activity, one should be cautious when interpreting a lack of effect of binary movement on SSEP magnitudes. Future studies using, for example, intracerebral recordings of auditory- and motor-cortex activity could help clarify this question. Finally, the relative discomfort reported by participants when performing the binary-movement training could have contributed to the difference between the effects of binary- and ternary-movement priming and could also explain the differences reported in previous studies using this rhythm (Phillips-Silver & Trainor, 2008).

The movement training performed in the present experiments purposely involved multiple parts of the body (the head, the torso, the hands and feet) as well as multisensory cues for meter induction. Having participants move multiple parts of their bodies allowed us to optimize the effect of movement on auditory perception as measured with EEG after the training and also to mimic the complexity and natural variability of movements performed to rhythms in ecological musical contexts (Burger, Saarikallio, Luck, Thompson, & Toiviainen, 2012; Wallin, Merker, & Brown, 2000). Whether the observed shaping of the EEG activities resulted from a change in the transformation of the sound by the auditory system or whether a distinct interconnected auditory-motor network contributed to our observations remain to be investigated.

In addition, it remains an open question what components of body movement were most responsible for the reshaping of the neural entrainment to the rhythm and whether such a reshaping could be obtained using inputs other than body movement, such as auditory accents. For example, this reshaping could be the result of vestibular input. Indeed, previous behavioral studies have observed that metric encoding of a rhythm can be biased by passive motion of the head, which suggests that vestibular input may play a key role in rhythm perception (Phillips-Silver & Trainor, 2008; Todd & Cody, 2000). The enhancement of meter-related frequencies could also reflect a cross-modal process of dynamic attending.

According to the dynamic-attending model of rhythm perception (Jones & Boltz, 1989; Large & Jones, 1999), the perception of meter would result from a dynamic process in which the perceived meter leads to a periodic modulation of attention as a function of time (Brochard et al., 2003; Fujioka, Zendel, & Ross, 2010; Grube & Griffiths, 2009; Iversen, Repp, & Patel, 2009; Schaefer, Vlek, & Desain, 2010; Snyder & Large, 2005). This view is in agreement with models of perceptual selection describing attention as a neural process by which the brain enhances the representation of task relevant inputs (Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008). Such a perceptual selection through dynamic attending is usually embedded in active motor routines, such as the one performed in the present study (Patel & Iversen, 2014; Schroeder et al., 2010). Similar mechanisms of perceptual enhancement through rhythmic priming could be envisioned within (Desain & Honing, 2003) and across distinct types of stimuli, as such rhythmic priming has been observed to shape subsequent speech processing (Cason & Schön, 2012).

Taken together, our results show that the recording of SSEPs to capture the shaping of rhythm perception by movement constitutes a promising approach to investigating the fundamental mechanisms underlying movement-perception integration in adults and even in infants, as it does not require any explicit behavioral outcome.

Author Contributions

B. Chemin and S. Nozaradan developed the study concept. All authors contributed to the study design. Testing and data collection were performed by B. Chemin and S. Nozaradan. B. Chemin and S. Nozaradan analyzed the data. All authors interpreted the results and wrote the manuscript. All authors approved the final version of the manuscript for submission.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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