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RESEARCH REPORT

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Cortical oscillations are modified by expertise in dance and music: Evidence from live dance audience

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Abstract

Over the past decades, the focus of brain research has expanded from using strictly controlled stimuli towards understanding brain functioning in complex naturalistic contexts. Interest has increased in measuring brain processes in natural interaction, including classrooms, theatres, concerts and museums to understand the brain functions in the real world. Here, we examined how watching a live dance performance with music in a real-world dance performance setting engages the brains of the spectators. Expertise in dance or music has been shown to modify brain functions, including when watching dance or listening to music. Therefore, we recorded electroencephalography (EEG) from an audience of dancers, musicians and novices as they watched the live dance performance and analysed their cortical oscillations. We compared intrabrain oscillations when participants watched the performance (with music) or listened to the music alone without the dance. We found that dancers have stronger fronto-central and parieto-occipital theta phase synchrony (4–8 Hz) than novices when watching dance, likely reflecting the effects of dance experience on motor imagery, multisensory and social interaction processes. Also, compared with novices, dancers had stronger delta phase synchrony (0.5–4 Hz) when listening to music, and musicians had stronger delta phase synchrony when watching dance, suggesting expertise in music and dance enhances sensitivity or attention to temporal regularities in movement and sound.

KEYWORDS
dance, EEG, expertise, live performance, music

Abbreviations: EEG, electroencephalography; FDR, false discovery rate; PSV, phase synchrony value.

1 | INTRODUCTION

People's ability to glean important social information from bodies in action is affected by factors including familiarity of movements, ability for motor imagery, interactions between bodies, and their number and spatial location (Calvo-Merino et al., 2005; Cross et al., 2006; Gardner et al., 2015; Menicucci et al., 2020; Wurm & Caramazza, 2019). The extrastriate body area and fusiform body area in the occipital cortex are selectively activated for the perception of human bodies, their shape, posture and movement, but not for other objects (Downing & Peelen, 2016). Further, the lateral occipito-temporal cortex activates only when observing human bodies in social interaction with each other (Abassi & Papeo, 2020; Wurm & Caramazza, 2019).

Dance and music training engages motor perception, execution and embodied interaction in a versatile manner and music and dance expertise modifies brain structure and functions (e.g., Foster Vander Elst et al., 2023; Giacosa et al., 2016; Karpati et al., 2015; Poikonen et al., 2016, 2018b). In dance, these changes are shown to occur over several brain regions including premotor, parietal, cerebellar and posterior temporal areas related to action observation and execution, as well as aesthetic appreciation (Calvo-Merino et al., 2006; Cross et al., 2009; Kirsch et al., 2015). In music, the changes are associated with the brain regions in charge of motor control and auditory processing and the connectivity between the motor networks and the auditory system (Olszewska et al., 2021 for a review).

Recently, interest has increased in measuring brain processes in real-world interactional settings, including classrooms, theatres, concerts and museums (Chabin et al., 2021; Dikker et al., 2017, 2021; Dolan et al., 2018; Tervaniemi et al., 2022) as opposed to the conventional artificial viewing situations and simplified stimuli used in isolated laboratories (e.g., Abassi & Papeo, 2020; Calvo-Merino et al., 2005; Cracco et al., 2021; Wurm & Caramazza, 2019). Brain responses evoked by complex movies, dance or music cannot be inferred easily from data collected in such artificial settings and simplified tasks (Bartels & Zeki, 2004; Jola & Grosbras, 2013; Nastase et al., 2020; Zhang et al., 2021). In addition, the co-presence and mutual relationship of the spectator and performer during a live performance cannot be incorporated in a video-recorded performance. For example, motor corticospinal excitability is shown to be enhanced in novice spectators when they watch live dance in comparison to video-recorded dance (Jola & Grosbras, 2013).

Artistic experiences, like watching dance, can create strong emotions and lasting memories. Emotional processing has been associated with lower oscillations on delta and theta frequencies (Knyazev et al., 2009). Theta synchrony is also suggested to play a crucial role in the formation of episodic memories in multisensory environments (Clouter et al., 2017). In addition, theta synchrony is central in associative memory processes for creating abstract knowledge and spatial processing, including rhythmic shifting of attention in space (Fiebelkorn & Kastner, 2019). In professional dancers, theta phase synchrony over fronto-central electrodes is shown to be enhanced in comparison to musicians and novices (Poikonen et al., 2018a). Such enhanced synchrony may arise from a combination of modified multisensory or spatial processing, and emotional or memory processes (Clouter et al., 2017; Knyazev et al., 2009; Krause et al., 2000).

Alongside theta synchrony, delta synchrony may play a role during expertise and naturalistic viewing conditions over a long time span. In addition to deep sleep, delta synchrony is associated with deep internal concentration (Harmony, 2013 for a review). Experts in mathematics and experienced meditators are shown to have enhanced large-scale delta synchrony when they engage in their discipline of expertise (Poikonen et al., 2024; Yordanova et al., 2020). Yet, it is not known whether experts in music or dance show similar brain oscillations related to deep internal concentration. On the other hand, perception of dance and music may enhance delta synchrony because the beat frequency in music typically falls in the delta range. Many studies show frequency enhancement at, and phase alignment to, the beat during listening (e.g., Cirelli et al., 2016; Doelling & Assaneo, 2021; Henry et al., 2014; Nozaradan et al., 2011).

In the current study, we investigated the influence of audio-visual expertise related to social and aesthetic full-body movement on neural responses to dance performance in a naturalistic setting. Specifically, we recorded electroencephalography (EEG) from three groups—dancers, musicians and novices who were neither dancers nor musicians—when they watched an entire live duet dance performance in a theatre. Musicians make interesting comparison groups because they have artistic and auditory expertise but no dance expertise. We had three hypotheses. First, that the dancers would have stronger intrabrain fronto-central theta phase synchrony than novices when watching live dance (consistent with Poikonen et al., 2018a). Second, that theta phase synchrony would extend to posterior electrodes because the participants were watching: (i) two dancers instead of one (Abassi & Papeo, 2020; Cracco et al., 2021) and (ii) live rather than video-recorded dance (Jola & Grosbras, 2013). Our third hypothesis was that experts in dance and music show stronger intrabrain delta phase synchrony than novices when watching live dance and listening to music (Poikonen et al., 2024; Yordanova et al., 2020).

2 | MATERIALS AND METHODS

2.1 | Participants

Altogether 20 dancers, 20 musicians and 20 people without a significant background in either music or dance (novices) participated in the experiment as audience members. Dancers and musicians were professional, students or people with an advanced-level dance/music hobby. Four dancers, two musicians and two novices were discarded because of noisy data, leaving a final sample of 13 female and 3 male dancers (14 right-handed, 2 left-handed; mean age 22.06, SD 3.87), 9 female and 9 male musicians (14 right-handed, 4 left-handed; mean age 21.61, SD 3.18) and 12 female and 6 male novices (17 right-handed, 1 left-handed; mean age 19.72, SD 1.41). The age groupings of the participants are presented in Figure 1. We were not able to calculate the sample size needed as there were no prior studies of EEG phase synchrony change during a live dance performance and therefore no information on expected variability.

Through a recruitment letter and questionnaire, participants were classified into groups (see Table S1a–c). Dancers' backgrounds varied from ballet to contemporary dance to street dance (Figure 2). Musicians' self-reported expertise varied from singing to piano to violin to saxophone (Figure 3). Several self-dancers reported expertise

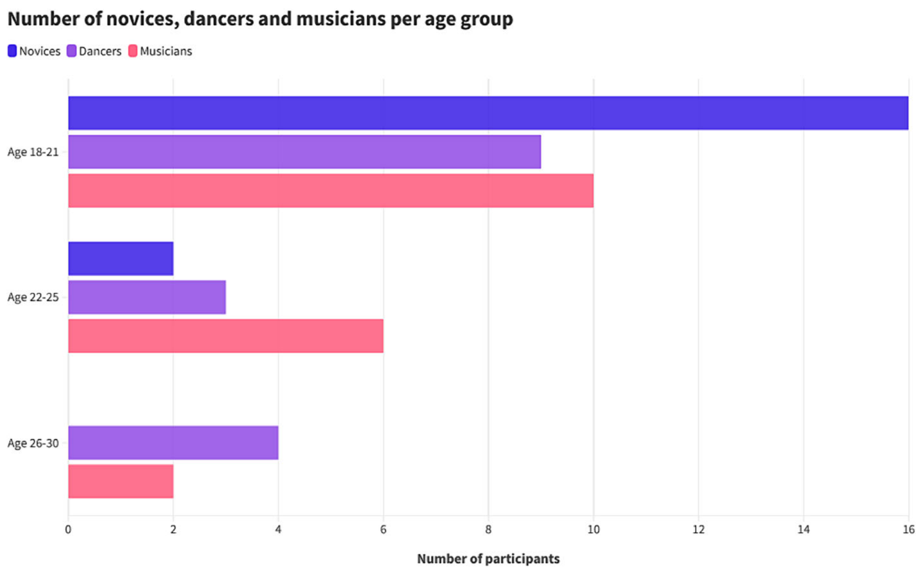

FIGURE 1 The age groupings of dancers, musicians and novices who participated in our study.

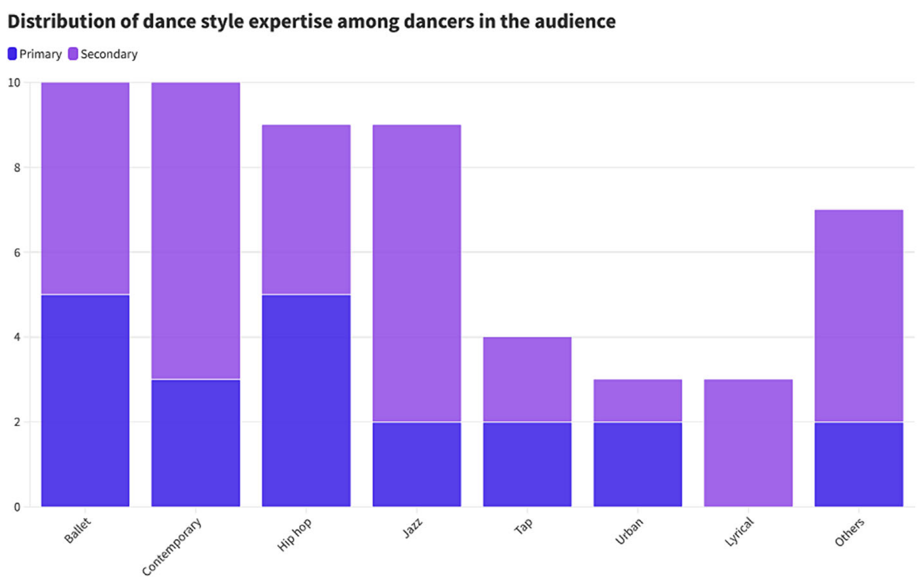

FIGURE 2 Distribution of dance style expertise among dancers in the audience, including self-reported primary and secondary dance styles.

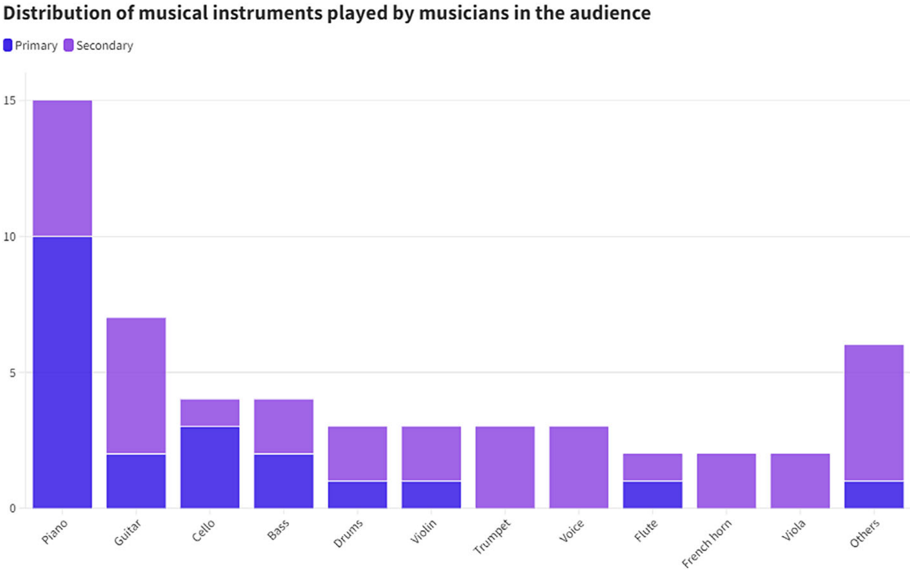

FIGURE 3 Distribution of musical instruments played by musicians in the audience, including self-reported primary and secondary instruments.

in more than one dance style and several musicians reported expertise in more than one instrument. No participants reported hearing loss or a history of neurological illnesses. Participants received a financial compensation of CAD 30 for their time. The study protocol was conducted in accordance with the Declaration of Helsinki and approved by the University of Helsinki Review Board in Humanities and Social and Behavioral Sciences and the McMaster Research Ethics Board.

Two professional dancers with backgrounds in break dance and contemporary dance, Adrian Vega and Diego Garrido, performed the dance piece. They had performed actively for several years around the world in dance festivals and theatres. They gave their consent for collecting motion capture data and video recording their performances.

2.2 | Stimuli

Audience participants experienced a 10-min live contemporary dance performance *Un ultimo recuerdo* performed by the dance artists with a pre-recorded musical accompaniment (live dance). This was followed by a presentation of only the music used in the dance performance. It was played with the theatre darkened and without any visual stimulus (music alone). The music was composed of instrumental electronic ambient sounds unfamiliar to the audience (musical excerpts from the music are added, Sound S1a for the music during slow movement [low acceleration as described in Section 2.5.1] and Sound S1b for the music during fast and large movement [high acceleration]). The dance was choreographed by the performing dancers and was unfamiliar to all participants. The inclusion of two dancers enabled an extension of our previous study, in which individuals watched solo video dance recordings (Poikonen et al., 2018a), to social aspects of dance. We also ensured that the dance piece included fast and slow parts to be able to investigate the effects of movement quantity on audience experiences. A short video of the project, including excerpts of the choreography performed can be watched here: https://vimeo.com/345086503. The entire stimulus is not openly published because the performance *Un ultimo recuerdo* is still actively presented in theatres.

2.3 | Data collection

The dancers' performances were captured with Motion Capture (Qualisys, Gothenburg, Sweden) using three sensors on each wrist of each dancer and one sensor on each outer ankle of each dancer. The sensors' locations were chosen as the most informative based on a previous dance study with 28 sensors covering the limbs, torso and head (Poikonen et al., 2018a). The Motion Capture data from the performing dancers was collected to be able to examine the effects of dance kinematics on audience responses, for example, the effects of the dancers' movement quantity on the cortical oscillations of the spectators.

Twelve EEG channels were measured from each audience participant with electrode caps by Brain Products GmbH using active EEG electrodes at a sampling rate of 500 Hz. The electrode locations (Fp1, Fp2, FCz, FC3, FC4, FC5, FC6, C3, C4, CPz, PO1 and PO2) were chosen based on previous music and dance phase synchrony results (Poikonen et al., 2018a, 2018b). Electrode impedances were below 20 kΩ at the beginning of the measurement. The beginning and end of each stimulus (live dance, music alone for each of four performance rounds, see below) was indicated with a trigger in the EEG data.

2.4 | Procedure

The study was conducted at the LIVELab at the McMaster Institute for Music and the Mind (McMaster University, Hamilton, Canada). There were four performance rounds in each of which EEG data was collected from 15 audience members (a mixture of dancers, musicians and novices). Because we were only able to collect simultaneous EEG data from a maximum of 15 participants at a time, four rounds were needed to obtain 20 participants per group. Upon arrival, participants filled out the consent form. A team of research assistants fitted the 15 participants in each group with the EEG caps, checked impedances and escorted them to their sets in the LIVELab. The researcher then welcomed them to the study and gave them their instructions. Live dance was then presented, followed by music alone. During music alone, participants were asked to listen to the music with their eyes open, although there was no visual stimulus on the stage. As functional connectivity is influenced by whether the eyes are open or closed (Costumero et al., 2020), it was important that participants' eyes were open in both live dance and music alone; the participants had their eyes open.

The dance piece was presented to the participants on the stage of the LIVELab while the participants were seated in the audience next to each other in four rows facing the stage. The participants did not have a specific task during the experiment, other than being instructed to watch and/or listen. The objective was to have live dance resemble as closely as possible the experience of a live dance performance. Both live dance and music alone were approximately 10 min in length.

Immediately after live dance and music alone, participants answered a self-reflection question: *I was immersed in watching the dance performance/listening to the music* on a 5-point scale: 1, *completely disagree*; 2, *somewhat disagree*; 3, *somewhere in between*; 4, *somewhat agree*; 5, *completely agree*. The participants indicated the most suitable self-evaluation by circling a corresponding number in a printed questionnaire document. After the experiment, participants filled in an extensive questionnaire on general demographics (gender, handedness, age and neurological illnesses) and their detailed background in music and dance. The entire procedure, including filling in questionnaires, having the EEG caps applied, experiencing live dance and music alone and debriefing lasted approximately 1.5 h.

2.5 | Data processing and analysis

2.5.1 | Movement analysis

Fast and complex movements are expected to activate the mirror neuron system and/or attentional engagement more strongly than slow and simple movements (Poikonen et al., 2018a). For these reasons, we analysed the movements of the dancers in order to identify times when there was a lot of motion and times when there was little motion in order to compare EEG responses during these two types of movement (Poikonen et al., 2018a). We extracted parts of the dance performance with high acceleration (fast full-body movements with or without physical contact with the other dancer, moving quickly in the space; the high acceleration condition as described below) and parts with low acceleration (moving in slow-motion with or without physical contact with the other dancer, lifting an arm gently, nearly still presence; the low acceleration condition as described below) measured with the motion capture system from two performing dancers on each of the four performance rounds. These were the only analyses for which the motion capture data were used. We used the MoCap Toolbox (version 1.5), which consists of MATLAB functions designed for the analysis and visualization of Motion Capture data (Burger & Toiviainen, 2013). It is designed for the extraction of features related to several movement dimensions identified in kinetics and kinematics. The toolbox can be used for the analysis of music-related movement and has been applied for capturing different movement qualities as defined in the movement theory by Laban (Laban, 1950; Luopajärvi, 2012). Each round of the dance performance was processed separately with the MoCap Toolbox to find the time points of interest related to the movement quantities during the live performances. The dance performance consisted of choreographed movements, some of which were not choreographed with precise timing to the music, for example, when walking in slow motion. Therefore, the timing of the movements during each performance was not identical across all the performance rounds but varied over a few seconds.

Acceleration was calculated for each time point and each marker in each dancer similar to previous Motion Capture studies of dance (Poikonen et al., 2018a, 2018b). Acceleration (the second temporal derivative of position) is shown to correlate well with the perceptual quantity of movement (Luck et al., 2010; Luck & Sloboda, 2008). In the movement theory of Laban, acceleration is related to one of four movement factors, *time*. The other three movement factors are *space*, *weight* and *flow* (Laban, 1950). We calculated the absolute value of acceleration for each marker for each dancer at each time point and then averaged across the right wrist, left wrist, right ankle and left ankle of both dancers at each time point. Finally, we averaged the absolute values of acceleration over 2-s segments, using a sliding window with 50% overlapping across consecutive segments. As we were interested in the excerpts with a large movement acceleration, we extracted the segments with the largest (10% of the whole Motion Capture data) and smallest (10% of the whole Motion Capture data) absolute values of acceleration to be used as a temporal reference in the synchrony analysis of the EEG data. These segments are referred to as high motion capture acceleration (high acceleration, 12 segments in total for each performance round) and low motion capture acceleration (low acceleration, 12 segments in total for each performance round), respectively. Perceptually, the epochs of high acceleration contain fast movements by both dancers such as pirouettes, vast arm and leg movements with or without physical contact with the other dancer and rapid movement in the space. Epochs of low acceleration contain simple small movements such as turning the head calmly, slow steps, or just standing with no, or minor, body movements with or without physical contact with the other dancer. The movements during low acceleration are not dance as traditionally understood, but rather embodied presence and interpretation of emotions relevant to the storyline. Importantly, the music during low acceleration and high acceleration differed drastically. Music during low acceleration was slow, meditative and atmospheric, whereas music during high acceleration was loud and intense with disharmonic sounds.

2.5.2 | EEG preprocessing

The EEG data of all the participants were first preprocessed with EEGLAB (version 2020.0; Delorme & Makeig, 2004). The average of all 12 electrodes was set as a reference. The data were high-pass filtered at 0.5 Hz and low-pass filtered at 50 Hz. Finite impulse response (FIR) filtering, based on the firls (least square fitting of FIR coefficients) MATLAB function, was used as a filter for all the data. The data were then treated with independent component analysis (ICA) decomposition with the runamica algorithm of EEGLAB (Delorme & Makeig, 2004) to detect and remove artefacts related to eye movements and blinks. ICA decomposition gives as many spatial signal source components as there are channels in the EEG data. Thus, the number of components was 12 in all the participants. Typically, one to two ICA components related to the eye artefacts were removed for each participant. Then, the data were split into the frequency bands of 0.5–4 Hz (delta), 4–8 Hz (theta), 8–13 Hz (alpha) and 13–30 Hz (beta) with high-pass and low-pass filtering using the same EEGLAB FIR filter function as above.

2.5.3 | Synchrony analyses

We calculated the phase synchrony values (PSVs) of the EEG data across all electrode pairs for each participant for each 2-s segment in each of the high acceleration and low acceleration conditions during the dance performance as defined by the motion capture analyses, described above. The PSV was calculated based on the Hilbert transformation of the phases of the data stream by an electrode pair under comparison. The Hilbert-based method, introduced by Tass et al. (1998), is widely used in phase synchrony analysis (e.g., Hong et al., 2006; Poikonen et al., 2024; Samaha et al., 2015; Wang et al., 2006). A similar method has also been used in EEG data analysis collected during continuous music and dance experiences (Bhattacharya & Petsche, 2000; Poikonen et al., 2018a, 2018b).

Each electrode was compared pairwise to all the other electrodes, resulting in 66 electrode pairs of comparison. This analysis was done separately for each of the delta, theta, alpha and beta frequency bands. Then, all of the 2-s PSVs occurring in high acceleration windows were averaged for each participant for each frequency band for each electrode pair. The same procedure was done for the low acceleration windows. Thus, for each frequency band, each participant got one PSV score for each electrode pair for each of the high acceleration and low acceleration conditions. Importantly, each performance round had its own times for high and low accelerations due to the nature of the choreography as described in the first paragraph of Section 2.5.1, and these individual time points were used for the EEG time windows of each performance.

In addition to phase synchrony between electrode pairs, we calculated amplitude power with Welch's method (Welch, 1967) for each electrode (12 electrodes in total) and each frequency band (delta, theta, alpha and beta) for the same 2-s time windows.

The same analyses were done on the EEG collected during music alone. In this case, the time points of high and low acceleration were taken from the first dance performance round, and the same time stamps were used for all the music alone rounds to ensure that for music alone the same time points were analysed for all the participants no matter which one of four performance rounds they participated in. There were only small differences in timestamps (a few second differences as discussed in the first paragraph of Section 2.5.1) for times of low and high accelerations between the four performance rounds and therefore, the music during the timestamps for low and high accelerations was very similar over the performance rounds.

2.5.4 | Statistical analyses

The statistical analyses were conducted with MATLAB version R2019b and were identical with Poikonen et al. (2018a, 2018b). Repeated-measures ANOVAs (between-subject factor group: dancers, musicians and novices; within-subject factor condition: high acceleration and low acceleration) were conducted separately for each electrode pair (66 electrode pairs) for each frequency band (delta, theta, alpha and beta). This procedure was repeated separately for dance performance and unimodal music (live dance, music alone). We also calculated repeated-measures ANOVAs for the same between-subject and within-subject factors for the amplitude power values for each electrode for each frequency band.

The multiple comparisons of group and condition were calculated with the Bonferroni-corrected critical value. In Section 3, *p* indicates the *p* values of these multiple comparisons of group and condition. The comparison of 66 electrode pairs increased the Type 1 error. Thus, the false discovery rate (FDR) was calculated for each set of 66 electrode pairs (one for each frequency band) from their *p* values of the results of the repeated-measures ANOVAs to control the expected proportion of false positives. For FDR correction, we employed a *q*-value threshold of 0.05. In Section 3, we report only the statistically significant results in which both the *p* and the pFDR are <0.05.

3 | RESULTS

3.1 | Behavioural results

For live dance, a one-way ANOVA was calculated for the self-evaluation reflection *I was immersed in watching the dance performance* with the factor group (dancers, musicians, novices). There was a significant effect of group [$F(2,49) = 8.27$, $p < 0.001$], Figure 4. Multiple comparisons revealed that dancers (mean rating = 4.69, SD = 0.48) reported feeling more immersed than novices (mean rating = 3.56, SD = 0.92) [dancers > novices, $p = 0.001$]. Musicians (mean rating = 4.17, SD = 0.92) fell between the dancers and novices but did not differ significantly from either ($p = 0.1598$, $p = 0.0720$, respectively).

3.2 | EEG results: theta band

For the theta band, during live dance, the phase synchrony was significantly stronger in dancers when compared with novices over the electrode pairs FC4–FC6 [the main factor group $F(2,49) = 3.97$, $p = 0.025$, dancers > novices $p = 0.021$], FC4–C4 [$F(2,49) = 4.19$, $p = 0.021$, dancers > novices $p = 0.020$], FC5–FC6 [$F(2,49) = 3.35$, $p = 0.043$, dancers > novices $p = 0.042$], FC6–C4 [$F(2,49) = 6.15$, $p = 0.0041$, dancers > novices $p = 0.0031$] and PO1–PO2 [$F(2,49) = 5.63$, $p = 0.0063$, dancers > novices $p = 0.0047$]. Musicians' theta phase synchrony did not differ from those of dancers or novices. The statistically significant results according to both *p* and pFDR are presented in Table 1 for the main factor group. The electrode locations of these group differences are illustrated in Figure 5. On theta band, there were no group differences during music alone. Nor were there any group differences in amplitude power (Table 2).

3.3 | EEG: delta band

For the delta band, during live dance, the phase synchrony was significantly stronger in musicians when compared with novices over the electrode pairs Fp1–Fp2, FC3–FC5, FC3–FC6, FC3–C3 and C3–CPz (Table 3 for statistics; Figure 6). In addition, during music alone, delta

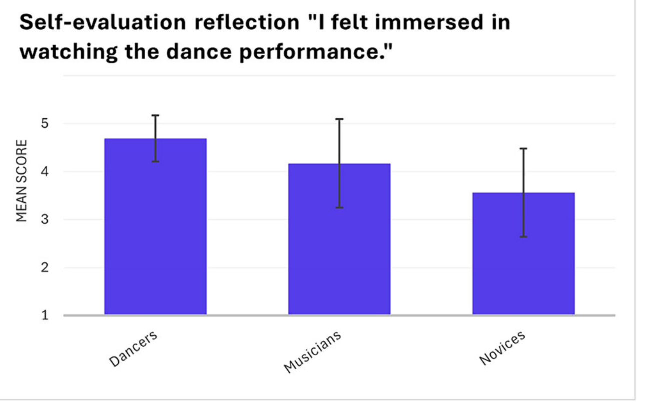

FIGURE 4 Self-evaluation reflection 'I felt immersed in watching the dance performance.' by dancers, musicians and novices in the audience on a 5-point scale: 1, *completely disagree*; 2, *somewhat disagree*; 3, *somewhere in between*; 4, *somewhat agree*; 5, *completely agree*. The self-report was filled in after watching the performance.

TABLE 1 Electrode pairs with significant synchronization differences in the main factor group (dancers, musicians, novices) during the live dance in conditions high acceleration and low acceleration over the frequency band theta (4–8 Hz). The mean values are averaged over the high and low acceleration conditions.

Electrode pair	F (2,49)	*p*	Multiple comparison (Bonferroni)	pFDR	*q*	Mean PSV dancers (standard deviation)	Mean PSV musicians (standard deviation)	Mean PSV novices (standard deviation)
FC4–FC6	3.97	0.025	Dancers > novices, $p = 0.021$	0.0024	0.0023	0.44 (0.043)	0.42 (0.044)	0.41 (0.070)
FC4–C4	4.19	0.021	Dancers > novices, $p = 0.020$	0.0026	0.0023	0.48 (0.073)	0.45 (0.052)	0.43 (0.084)
FC5–FC6	3.35	0.043	Dancers > novices, $p = 0.042$	0.0033	0.0023	0.42 (0.056)	0.39 (0.037)	0.39 (0.066)
FC6–C4	6.15	0.0041	Dancers > novices, $p = 0.0031$	0.0016	0.0012	0.44 (0.045)	0.42 (0.039)	0.40 (0.072)
PO1–PO2	5.63	0.0063	Dancers > novices, $p = 0.0047$	0.0012	0.0012	0.55 (0.061)	0.51 (0.067)	0.49 (0.088)

Abbreviations: FDR, false discovery rate; PSV, phase synchrony value.

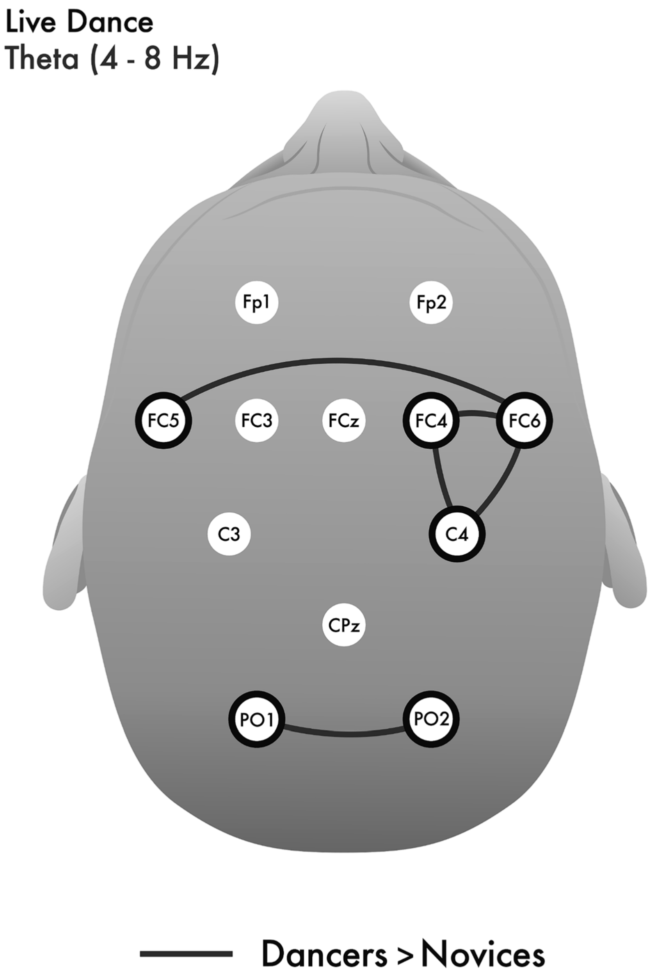

FIGURE 5 Electrode pairs showing stronger theta phase synchrony (4–8 Hz) in dancers in comparison to novices when watching live dance.

phase synchrony was significantly stronger in dancers than novices over the electrode pair FC6–C4. Further, during the music alone condition, the group*condition interactions revealed that during low acceleration, synchrony was significantly stronger in dancers than novices over the electrode pairs Fp1–PO1 and PO1–PO2 (Table 4 for statistics; Figure 7). There were no group differences in amplitude power.

3.4 | EEG: other frequency bands

For both the alpha and beta bands, there were no significant group differences during the live dance or music alone in phase synchrony or amplitude power.

4 | DISCUSSION

In the current study, dancers in the audience showed an enhanced theta phase synchrony compared with novices over the fronto-central and parieto-occipital electrodes, in line with previous work showing similar enhanced fronto-central theta synchrony in dancers watching videos of dance (Poikonen et al., 2018a). Dancers also reported greater immersion during the dance performance compared with novices. In addition, musicians showed stronger delta phase synchrony than novices when watching dance, and dancers showed stronger delta phase synchrony than novices when listening to music, especially during calm and meditative parts of the music.

Given the naturalistic context in which these data were collected, it is difficult to pinpoint a specific brain process that would solely explain the results. Rather in the following, we discuss different brain processes that likely contributed to the differences we found in dancers', musicians' and novices' brains when they watched the live dance duet and listened to the music of the dance piece. These results may further help in understanding the influence of social interaction and expertise in the perception of human bodies and actions.

TABLE 2 Amplitude power for each electrode on theta band (4–8 Hz) during live dance. There were no significant group differences in amplitude power on any frequency band during either live dance or music alone, and therefore, further amplitude power results are not reported. The mean values are averaged over the high and low acceleration conditions.

Electrode	F(2,49)	*p*	Mean value dancers (standard deviation)	Mean value musicians (standard deviation)	Mean value novices (standard deviation)
Fp1	1.17	0.32	0.34 (0.32)	0.28 (0.24)	0.58 (0.99)
Fp2	0.78	0.46	0.45 (0.52)	0.52 (0.62)	0.73 (0.95)
FCz	0.99	0.38	0.76 (2.28)	0.13 (0.11)	0.35 (0.68)
FC3	1.26	0.29	0.67 (2.04)	0.12 (0.068)	0.20 (0.17)
FC4	0.49	0.62	0.29 (0.47)	0.22 (0.43)	0.17 (0.13)
FC5	0.61	0.55	0.58 (0.90)	0.33 (0.46)	0.63 (1.14)
FC6	0.59	0.56	0.94 (3.34)	0.47 (0.77)	1.18 (1.81)
C3	0.93	0.40	0.23 (0.34)	0.11 (0.087)	1.36 (5.02)
C4	0.80	0.46	0.15 (0.22)	0.29 (0.81)	0.91 (3.11)
CPz	1.32	0.28	0.17 (0.21)	0.11 (0.049)	0.30 (0.81)
PO1	0.95	0.39	0.28 (0.23)	0.20 (0.10)	0.26 (0.17)
PO2	0.14	0.87	0.36 (0.32)	0.40 (0.67)	0.34 (0.28)

TABLE 3 Electrode pairs with significant synchronization differences in the main factor group (dancers, musicians, novices) during the live dance over the frequency band delta (0.5–4 Hz). The mean values are averaged over the high and low acceleration conditions.

Electrode pair	F (2,49)	*p*	Multiple comparison (Bonferroni)	pFDR	*q*	Mean PSV dancers (standard deviation)	Mean PSV musicians (standard deviation)	Mean PSV novices (standard deviation)
Fp1–Fp2	3.25	0.047	Musicians > novices, $p = 0.046$	0.00054	0.00028	0.43 (0.088)	0.47 (0.068)	0.41 (0.10)
FC3–FC5	3.73	0.031	Musicians > novices, $p = 0.028$	0.00090	0.00028	0.43 (0.081)	0.44 (0.045)	0.40 (0.094)
FC3–FC6	3.31	0.045	Musicians > novices, $p = 0.039$	0.00064	0.00028	0.40 (0.070)	0.42 (0.045)	0.38 (0.092)
FC3–C3	3.45	0.40	Musicians > novices, $p = 0.036$	0.00077	0.00028	0.43 (0.078)	0.45 (0.044)	0.40 (0.10)
C3–CPz	3.77	0.30	Musicians > novices, $p = 0.025$	0.0017	0.00028	0.41 (0.078)	0.44 (0.050)	0.39 (0.091)

Abbreviations: FDR, false discovery rate; PSV, phase synchrony value.

4.1 | Movement and the mirror neuron system

Attentional selection of visual body stimuli recruits both visual and somatosensory cortical regions (Arslanova et al., 2019), and action observation, motor imagery and actual movement execution activate a common network including premotor, rostral parietal and somatosensory areas (meta-analysis by Hardwick et al., 2018). Previous brain imaging studies suggest that activation of dancers' mirror neuron system is enhanced when they watch familiar dance movements but not when they watch other types of movements (Calvo-Merino et al., 2005; Cross et al., 2006) and this is reflected in alpha band responses (e.g., Pineda, 2005; Wu et al., 2016). We did not find group differences in the alpha band related to movement observation in our spectator dancers compared with musicians and novices, but we did find enhanced effects for dancers in lower frequencies, suggesting a more general effect of dance training on the brain, perhaps involving cognitive, emotional, somatosensory and/or social processing (Ramsey et al., 2021). This is in line with the fact that dancers in our audience reported versatile backgrounds, including ballet, street, contemporary and ballroom dance. Thus, most participants were not trained in the specific dance style of our study. Furthermore, our spectator dancers varied in level of dance expertise, from having dance as an advanced hobby, being a dance student or being a professional dancer, and previous studies show that level of dance expertise also influences brain functions and corticospinal activity (Calvo-Merino et al., 2005; Cross et al., 2006, 2009; Jola et al., 2012).

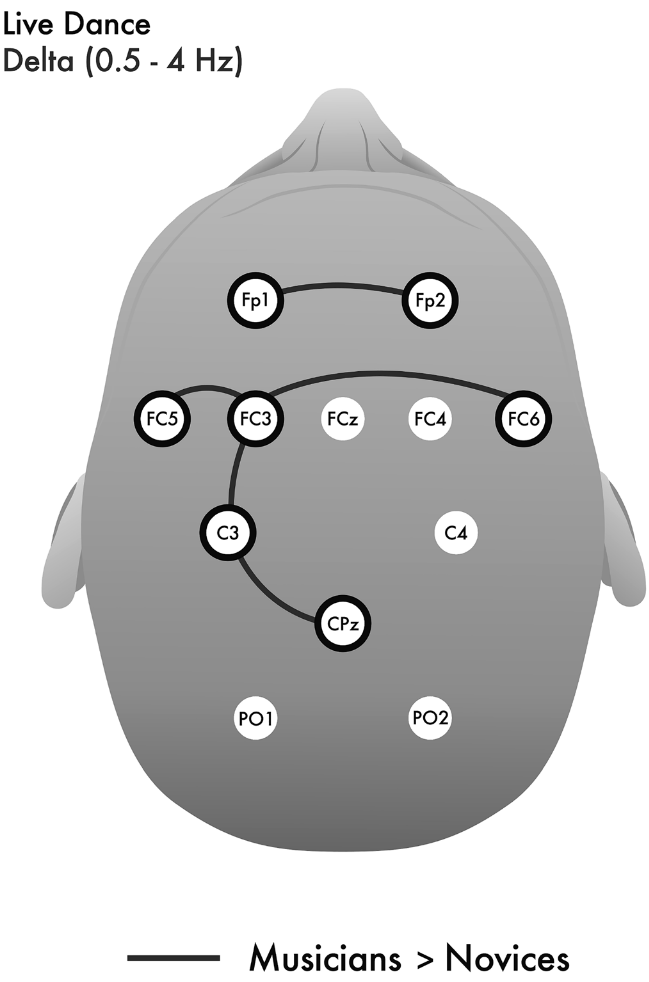

FIGURE 6 Electrode pairs showing stronger delta phase synchrony (0.5–4 Hz) in musicians in comparison to novices when watching live dance.

4.2 | Spatial awareness, multimodal integration and memory

Neural measurements of people watching continuous movies suggest the existence of chronoarchitecture, that is, neural assemblies that activate over long time spans (Bartels & Zeki, 2004; Sonkusare et al., 2019 for a review). Similarly, musical features that are context-dependent over a long musical piece are shown to activate the brain differently in comparison to rapid changes in simple musical features (Alluri et al., 2012). In our study, the spectator dancers reported feeling more immersed in watching dance in comparison to novices, which could be expected to enhance their contextual processing and activation of cerebral chronoarchitecture. Our finding of increased intrabrain fronto-central theta synchronization in dancers in comparison to novices when watching live dance is consistent with the first hypothesis outlined in Section 1, as well as with Poikonen et al. (2018a). Such theta synchrony in dancers may reflect enhanced associative and episodic memory processes and emotional responses as well as rhythmic attention shifting in space due to their dance experience. Previous studies have found increased fronto-central theta synchrony associated with activation of associative memory and memory formation for real-world stimuli (Clouter et al., 2017), exploration of novel environments (Kragel et al., 2020), multimodal interaction and attention (Wang et al., 2016), spatial awareness and rhythmic shifting of attention (Kahana et al., 1999; Ekstrom et al., 2005; Vass et al., 2016; Fiebelkorn & Kastner, 2019), sensory–motor interaction (Bland & Oddie, 2001; Zarka et al., 2014), predictive movement tim-

TABLE 4 Electrode pairs with significant synchronization differences in the main factor group (dancers, musicians, novices) and group*condition interactions in the high acceleration condition during music alone over the frequency band delta (0.5–4 Hz). There were no significant interactions in the low acceleration condition. For the group main effect, the mean values are averaged over the high and low acceleration conditions.

Electrode pair	F (2,49)	pGG	Multiple comparison (Bonferroni)	pFDR	*q*	Mean PSV dancers (standard deviation)	Mean PSV musicians (standard deviation)	Mean PSV novices (standard deviation)
Group main effect								
FC6–C4	3.27	0.046	Dancers > novices, $p = 0.041$	0.0018	0.00058	0.48 (0.070)	0.44 (0.059)	0.41 (0.11)
Group*condition interaction								
Fp1–PO1	3.27	0.046	LowAcc: dancers > novices, $p = 0.030$	0.0010	0.00031	MinAcc: 0.42 (0.045)	MinAcc: 0.39 (0.049)	MinAcc: 0.35 (0.099)
PO1–PO2	3.54	0.037	LowAcc: dancers > novices, $p = 0.011$	0.0012	0.00031	MinAcc: 0.54 (0.064)	MinAcc: 0.48 (0.064)	MinAcc: 0.44 (0.13)

Abbreviations: FDR, false discovery rate; PSV, phase synchrony value.

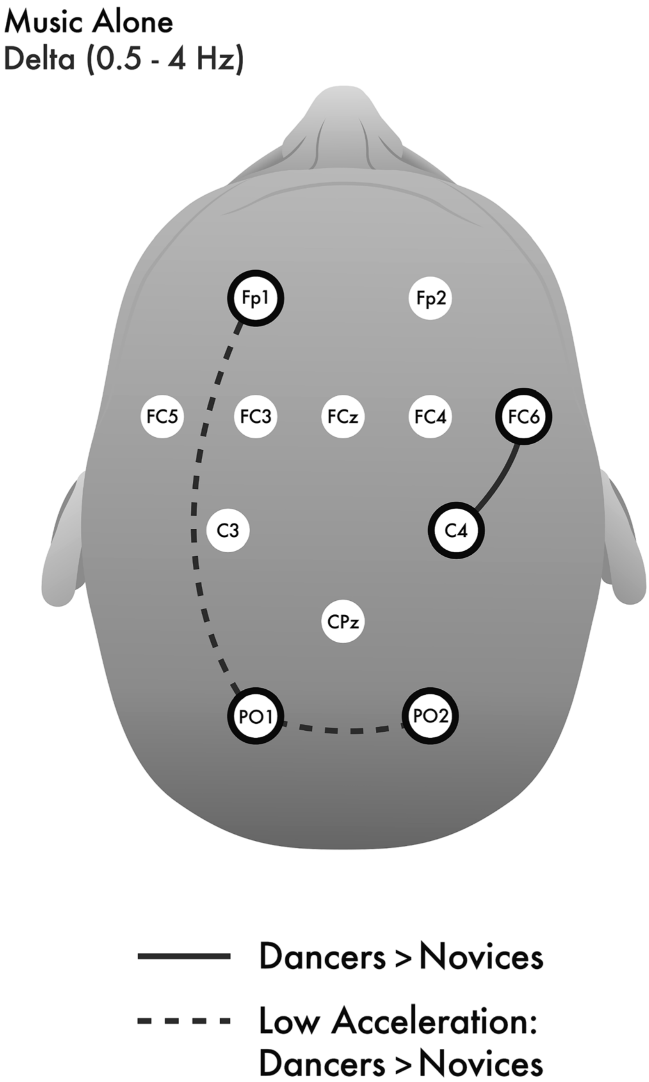

FIGURE 7 Electrode pairs showing stronger delta phase synchrony (0.5–4 Hz) in dancers in comparison to novices when listening to music alone.

ing (Arnal & Giraud Mamessier, 2012) and emotional processing (Balconi & Lucchiari, 2006; Knyazev et al., 2009; Krause et al., 2000).

Dancers' enhanced bilateral occipito-temporal theta synchronization in comparison to novices is in line with our second hypothesis and also consistent with previous findings showing that activation in this region is right-lateralized in novices but bilateral in dancers when watching dance movements (Orlandi & Proverbio, 2019). Perception of dance potentially recruits different processes in mental imagery, aesthetic evaluation and action observation in dancers compared with novices (Calvo-Merino et al., 2010), which may play a role in the enhanced parieto-occipital theta synchrony that dancers showed in our study. Further, the ability for fast motor imagery (Kurkin et al., 2023) and self-evaluation of the ability to execute dance movements (Cross et al., 2006) have been also associated with posterior theta synchrony.

4.3 | The social brain

In contrast to previous dance observation studies (e.g., Herbec et al., 2015; Jola et al., 2012; Poikonen et al., 2016), our performance included two interacting dancers. Our findings on enhanced theta synchrony in spectator dancers in comparison to novices raise the additional question of whether dancers' brains may be particularly tuned for motor and social interactions between interacting dancers (Abassi & Papeo, 2020; Cracco et al., 2021; Wurm & Caramazza, 2019). In general, neural responses are enhanced when observing collective compared with individual movements (Cracco et al., 2021). Further, the lateral occipital cortex codes two bodies in interaction in comparison to individual bodies and two bodies that are not in interaction (Abassi & Papeo, 2020). Regions in the lateral occipito-temporal cortex provide the perceptual basis for interpretations of social actions between people and interact with multiple other areas that interpret relevant action components in a situation-dependent manner (Wurm & Caramazza, 2019).

It is also possible that watching the dance performance in an audience with others contributed to the effects we saw. Some recent naturalistic study designs involve immersion in a natural environment and social attunement to other participants who are sharing the experience, in conjunction with the perceptual and cognitive experiences. For example, people move with more energy or vigour at live versus pre-recorded concerts (Swarbrick et al., 2019) and in the presence of social cues from fellow audience members (Dotov et al., 2021). It is also possible that experiencing the performance with others in the audience enhanced synchrony between people as has been shown for music (Chabin et al., 2022), but we did not have a condition where individuals experienced the performance alone, so this remains speculative.

4.4 | Rhythm and delta synchrony

In our study, musicians showed stronger fronto-centro-parietal delta phase synchrony than novices when watching dance whereas dancers showed stronger fronto-centro-parieto-occipital delta phase synchrony than novices when listening to music, especially during the slow meditative parts of the music. These results are somewhat in line with our third hypothesis that experts in dance and music would show stronger intrabrain delta phase synchrony than novices when watching live dance and listening to music (Poikonen et al., 2024; Yordanova et al., 2020), but the dance-specific and music-specific effects were not predicted. The optimal beat rate for music (centred around 2 Hz) corresponds to the rate at which tempo discrimination and motor synchronization are best (e.g., Drake et al., 2000; London, 2004; McAuley et al., 2006) and falls within the delta range. Many studies report the presence of neural oscillations at the beat frequency when listening to music (e.g., Cirelli et al., 2016; Doelling & Assaneo, 2021; Henry et al., 2014; Nozaradan et al., 2011), even in premature infants (Edalati et al., 2023), raising the speculation that temporal regularities in movement and sound are more salient to dancers and musicians than novices. On the other hand, experiencing a longer unfolding performance may create a state of internal concentration that does not emerge during short stimuli (Poikonen et al., 2024; Yordanova et al., 2020) and enhanced delta synchrony may reflect internal concentration (Harmony, 2013 for a review). For example, delta phase synchrony is shown to be enhanced when the experts are immersed in the task of their discipline (Poikonen et al., 2024; Yordanova et al., 2020). When dancers listen to music or musicians watch dance, they may enter into similar brain states of internal concentration. In particular, the far-distance cortical synchronies over delta frequency observed in our study may reflect deeper internal concentration in dancers and musicians in comparison to novices (Poikonen et al., 2024; Yordanova et al., 2020). In contrast, when dancers watch dance or musicians listen to music, they may recruit cortical processes of sustained attention with higher vigilance, which are relevant for task monitoring, working memory and motor preparation and associated with faster neural frequencies.

4.5 | Limitations, conclusions and future directions

A strength of this study is its execution in a naturalistic real performance venue. However, there is a tradeoff between naturalness and what can be done in a controlled laboratory situation (Nastase et al., 2020; Sonkusare et al., 2019; Zhang et al., 2021). The relatively small number of EEG electrodes precluded source localization, so synchronies were measured between electrodes rather than brain regions, making some interpretations more speculative. Volume conduction between nearby electrodes can also be an issue in measuring synchronies, but this is unlikely an issue here as we found expertise/novice differences in synchrony between distant electrodes. Also, the large variation in audience dancers' and musicians' backgrounds (e.g., type of dance/music training; length of training) precluded addressing some more specific questions related to the type of training and interactions between training type and style of dance and music presented. On the other hand, this variability increased the generalizability of the findings. Our sample size was also relatively small, although it was not possible to conduct a proper power calculation beforehand as the variance associated with our novel method was unknown. Also, we did not collect extensive qualitative data on the individual differences in spectators experiences or in personality traits, which have been shown to influence the experience of watching dance (Jola et al., 2014; Rose et al., 2022).

In sum, the results indicated that expertise in dance leads to greater neural synchronization in theta frequencies over the fronto-central and parieto-occipital electrodes compared with novices, likely reflecting real-world experience combining multisensory, cognitive, aesthetic, motor imagery and social interaction processes. Expertise also led to greater synchronization in the delta band, for musicians when viewing dance and for dancers when listening to music, suggesting that expertise affects sensitivity to the temporal structure of the movement in dance and sound in music. In the future, it would be valuable to compare movement execution to movement observation and to investigate other physiological signals, such as heart rate and eye movements, that might also reflect expertise/novice processing differences.

AUTHOR CONTRIBUTIONS

Hanna Poikonen: Conceptualization; methodology; investigation; funding acquisition; formal analysis; writing—original draft. **Mari Tervaniemi:** Funding acquisition; writing—review and editing. **Laurel Trainor:** Resources; funding acquisition; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial interests.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ejn.16525.

DATA AVAILABILITY STATEMENT

The data and code for this study will be openly published in 2025 after our research group has finished our ongoing data analyses aiming for further publications. Until then, the data and codes can be received by requesting them from the corresponding author. There is no preregistration for this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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