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Title: Dance on Cortex : Enhanced Theta Synchrony in Experts when Watching a Dance Piece

Year: 2018

Version:

Please cite the original version:

Poikonen, H., Toiviainen, P., & Tervaniemi, M. (2018). Dance on Cortex : Enhanced Theta Synchrony in Experts when Watching a Dance Piece. *European Journal of Neuroscience*, 47(5), 433-445. <https://doi.org/10.1111/ejn.13838>

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Article type : Research Report

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Dance on Cortex: Enhanced Theta Synchrony in Experts when Watching a Dance Piece

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Keywords: EEG, expertise, dance, music, phase synchrony

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/ejn.13838

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Abstract

When watching performing arts, a wide and complex network of brain processes emerge. These processes can be shaped by professional expertise. When compared to laymen, dancers have enhanced processes in observation of short dance movement and listening to music. But how do the cortical processes differ in musicians and dancers when watching an audio-visual dance performance?

In our study, we presented the participants long excerpts from the contemporary dance choreography of *Carmen*. During multimodal movement of a dancer, theta phase synchrony over the fronto-central electrodes was stronger in dancers when compared to musicians and laymen. In addition, alpha synchrony was decreased in all groups during large rapid movement when compared to nearly motionless parts of the choreography. Our results suggest an enhanced cortical communication in dancers when watching dance and, further, that this enhancement is rather related to multimodal, cognitive and emotional processes than to simple observation of dance movement.

Introduction

Understanding the cerebral processes in perception, cognition and emotion has advanced rapidly over the past decades. Knowledge of the anatomy and function of the brain is becoming more and more precise due to the remarkable development in the brain imaging technology. Over the past decade, the focus of brain research has turned from artificial stimuli constructed for laboratory conditions to the usage of real-life stimuli, such as art house cinema (Kauttonen et al., 2015), feature films (Hanke et al., 2014; Nummenmaa et al., 2012) and scenes of social interaction (Nummenmaa et al., 2014; Wilbers et al., 2012).

In functional magnetic resonance imaging (fMRI), these naturalistic stimuli are vastly in use also in music studies. Processing of individual musical features extracted during listening to a musical piece was studied by Alluri and colleagues (2012). The influence of music on cognitive and emotional processes has been studied (Blood and Zatorre, 2001; Burunat et al., 2014; Salimpoor et al., 2011; Wilkins et al., 2014), evidence indicating that music activates memory pathways of hippocampus and emotional processes in the limbic system. In addition, music activates movement pathways involving motor-related cortices, basal ganglia and cerebellum (Chen et al., 2009 for a review). Professional background in music has been shown to modify music evoked processes not only in auditory areas but also in prefrontal cortex, limbic system and motor regions (Herholtz and Zatorre, 2012 for a review).

Listening to music activates movement-related brain regions, as does visual observation of movement. Rizzolatti and colleagues (1996; 2001 for a review) discovered the mirror neuron system which is activated when the primate was either conducting or watching someone else conducting the same movement. Ever since, based on the mirror neuron system, a wide range of movement studies have been made also in humans. The expertise in movement was studied by Calvo-Merino and colleagues (2005) who showed simple ballet and capoeira movements to professional ballet dancers and capoeira practitioners in an fMRI scanner. In dancers, the bilateral premotor cortex, intraparietal sulcus, right superior parietal lobe and left posterior superior temporal sulcus had higher activation during watching the movement of specialization when compared to the untrained capoeira movements. Consistently, the premotor areas of dancers have been shown to be more active when compared to laymen during dance observation (Karpati et al., 2015 for a review).

In electroencephalography (EEG), continuous music has been used in the research of event-related potentials (ERPs) (Poikonen et al., 2016a; 2016b) and cortical synchrony

(Bhattacharya and Petsche, 2000). Our previous paper (Poikonen et al., 2016b) suggested professional dancers practise to modify the early cortical processing of changes in a musical feature whereas Bhattacharya and Petsche (2000) suggested professional background in music to increase inter-regional gamma synchrony during listening to a musical piece. Changes in cortical synchrony in different frequency bands has been linked to preparation, execution, perception and imagination of movement, as well as to the intention of it (Ewen et al., 2015; Tomassini et al., 2015; Zarka et al., 2014; Cevallos et al., 2015 for a review). However, these studies were based on the movement of a part of the body, such as hands, or simple whole-body movement, such as walking. The duration of movements was short and the movements were concrete actions rather than abstract movement. In addition, there was no emotional content in the movement. Since it is known that music as a unique form of rhythmic and aesthetic auditory stimulus evokes a great amount of cortical and subcortical processes, we wanted to combine it with a motor-visual artistic stimulus – dance. In addition to being in unison with music, dance is continuous complex movement involving the whole body and thus a naturalistic upgrade to the conventional movement research.

We chose long excerpts from the composition *Carmen* with a contemporary dance choreography. In addition to such a multisensory stimulus, the excerpts of the choreography transmit an evolving storyline with varying emotional content. The choreography was interpreted by a real dancer and by a stick figure constructed from the motion capture data collected during the actual performance. The recognition of the emotions expressed by the whole body is improved in full-light display when compared to a point light display (Ross et al., 2012). In addition, emotions are better recognized when interpreted by female dancers (Van Dyck et al., 2014). Thus, the multimodal performance of the real female dancer is a unique condition to evoke emotional processes in the brain. We assumed her performance to evoke stronger emotional processes than the dancing stick figure. The emotional intensity

interpreted by the dancer during the minor movement does not transmit with the stick figure and, thus, looks more like a static image, losing the anthropomorphist depth of the moving character. The movement quantity was the same in the real dancer and the stick figure, and therefore, we assumed both to decrease alpha synchrony when dancing rapidly (Hobson and Bishop, 2016).

To provide a general view into the cortical synchrony evoked by watching dance, we compared delta (1-4 Hz), theta (4-8 Hz), alpha (8-13 Hz), beta (13-30 Hz) and gamma (30-48 Hz) phase synchrony in professional dancers, professional musicians and participants without professional training in music or dance. Alpha and beta band have been associated with motor processes (Hobson and Bishop, 2016; Pineda, 2005; Pavlidou et al., 2014) whereas theta band, and its coupling to gamma band, are linked to several cognitive and affective functions (Krause et al., 2000; Kahana, 2006; Canolty and Knight, 2010). In addition, both theta and alpha band are modified during attentional and multimodal processing (Mathewson et al., 2011; van Driel et al., 2014; Wang et al., 2016).

In our study, we separated large dynamic movement from almost motionless presence, which were both important elements of the choreography. In this aspect, our study takes further the study of Hobson and Bishop (2016) in a naturalistic setting. They noticed that a still image from the video of human movement presented right before the actual movement video was the most robust baseline condition for mu power suppression over central electrodes, which is associated to the activation of the mirror neuron system. Based on their study, and the review by Pineda (2005), we hypothesized alpha synchrony to decrease during High Acceleration when compared to Low Acceleration in the central electrodes. Posterior alpha suppression is associated with the attentional processes, especially in the visual domain (Niedermeyer and da Silva, 2005). We expected the dance movement to catch attention more strongly than a nearly still body and, therefore, the alpha synchrony to also

decrease in posterior electrodes. We also assumed dancers would process the dance stimulus differently when compared to musicians and laymen (Calvo-Merino et al., 2005; Orgs et al, 2008; Pilgrim et al., 2010). Bangert and colleagues (2006) suggested a distinct musicianship-specific network which co-activates during piano melody and mute key presses in pianists in areas involved with auditory sensory motor integration. We considered that dance training could also shape perception in unimodal and multimodal conditions. We were interested whether this kind specification would be measurable with the phase synchrony of EEG.

With EEG, Jäncke (2012) has already shown how functional coupling between the auditory and premotor cortex varies during piano playing in professional pianists. Also, Bangert and Altenmuller (2003) showed with EEG that musical training triggers instant plasticity and that there is an audio-motor interface in the brain for the mental representation of the keyboard. Similar mental representations could be created for movement and music during the dance training. In expertise, not only the brain processes of production, but also the processes of perception enhance. In addition, dance training includes a lot of watching fellow dancers developing dance perception *per se*. However, we did not expect the differences in experts' brain activity during continuous dance to be necessarily related to the actual perception of movement but reflecting also other cognitive and affective qualities which develop during professional dance training.

Methods

Participants

20 professional musicians, 20 professional dancers and 20 people without a professional background in either music or dance participated in the experiment. However, two participants from each group were discarded from the data analysis for the following reasons.

EEG data in the resting state was not recorded from two dancers, one musician and one participant in the control group. Therefore, their data could not be used in the data analysis.

In addition, one musician and one participant in the control group had too many either missing or noisy EEG channels and, thus, we excluded them from the analysis.

Thus, in the groups of musicians and the laymen there were 13 female and 5 male participants and in dancers 12 female and 6 male participants. The background of the participants was screened by a questionnaire of music and dance related to both professional and every-day level. The background of the participants is presented in detail in Table 1. Both dancers and musicians were asked to have a degree or be currently studying in a university of arts or in a university of applied sciences. However, this could not be applied to three street dancers due to the lack of formal education in this dance style in Finland. We estimated that their level of training was equivalent to the formal training. Professional background of musicians varied from singing to various instruments, such as piano, violin or saxophone. The professional background of dancers was versatile from ballet and contemporary dance to street dance. Several musicians reported expertise in more than one instrument and several dancers in more than one dance style.

The age of the participants ranged from 21 to 31 years (mean 25.6 years) among musicians, from 23 to 40 years (mean 29.2 years) among dancers and from 20 to 37 years (mean 25.0 years) among laymen. Two participants in each of three groups included in the data analysis were left-handed. No participants reported hearing loss or history of neurological illnesses. The experiment protocol was conducted in accordance with the Declaration of Helsinki and approved by the University of Helsinki review board in the humanities and social and behavioural sciences. All participants provided written informed consent. Since the participants were not informed about the possibility to share data with

researchers outside the research team, for ethical reasons, we are unable to make data publicly available.

Stimuli

Audiovisual excerpts of *Carmen* composed by Bizet-Shchedrin were used as stimuli. The version of the composition used was performed by Moscow Virtuosi Chamber Orchestra and published by Melodiya, Moscow 1987. Many participants reported being familiar with the composition. The dance choreography of *Carmen* was based on the contemporary dance choreographed by Mats Ek. However, the female contemporary dancer who performed the dance excerpts for our research purposes, had an artistic freedom to create solo versions to suit her own expression. Thus, the dance choreography was not familiar to any of the participants. In addition, no dancer reported in being familiar with Mats Ek's choreography. The dancer's performance was captured with Motion Capture (Qualisys, Gothenburg, Sweden).

The total length of the stimulus was approximately 15 minutes, which was cut to 20 trials, the duration of each trial being between 15 and 63 seconds (44.5 seconds on average). Music without visual stimulus (Music), silent dance (Dance), dance and music as an audio-visual entity (Dance & Music) and a dancing stick figure with music (Stick Figure) were presented to the participants. In Figure 1, there is a still image from the choreography presented by a real dancer and a stick figure. Music, silent dance and audio-visual dance were presented in a random order whereas the stick figure was always presented as the last stimulus set. During the presentation of music only, the participants were advised to listen to the music with their eyes open although there was no visual stimulus on the screen. The excerpts were chosen from the composition based on their musical and emotional versatility

and variability in the movement dynamics. The emotional content interpreted by both music and movement varied significantly, some excerpts transmitting a joyful atmosphere, others anger or devastating sadness.

Equipment and procedure

The stimuli were presented to the participants with the Presentation 14.0 program. Each set of trials contained 20 excerpts of the same sensory modality/modalities and these sets were presented in a random order via a monitor and headphones with the intensity of 50 decibels above the individually determined hearing threshold. The distance of the monitor from the participant was 110 cm. The participants were advised to listen to the music with their eyes open and watch the dance video as still as possible. Before the data analysis, we randomly inspected the data (about one third of the whole data) and did not find signs of closed eyes (no long periods lacking eye blinks, no strong continuous alpha wave). The playback of each trial was launched by the researcher. From time to time, between the stimuli, the researcher had a short conversation with the participant via microphone to make sure the participant felt comfortable during the test procedure. The total length of the experiment material was 60 minutes. With pauses and conversations based on the individual needs of each participant, the whole test session lasted about 70-80 minutes.

The data were recorded using BioSemi electrode caps with active 128 EEG channels and 4 external electrodes placed at the tip of the nose, left and right mastoids and under the right eye. The offsets of the active electrodes were kept below 25 millivolts at the beginning of the measurement and the data were collected with a sampling rate of 1024 Hz. The beginning and the end of each trial was marked with a trigger into the EEG data.

Data processing and analysis

The extraction of movement qualities with MoCap Toolbox

We used MoCap Toolbox (version 1.1) to computationally extract the movement qualities. MoCap Toolbox is a set of MATLAB functions designed for the analysis and visualization of Motion Capture data (Burger and Toiviainen, 2013) and is used for the extraction of different features related to various movement dimensions identified in kinetics and kinematics. The toolbox is mainly used for the analysis of music-related movement and has been applied for capturing different movement qualities defined in movement theory by Laban (Laban, 1950; Luopajarvi, 2012).

We were interested in rhythmical movement with continuous and overlapping flow of newly initiated movements since the changes in the cortical synchrony are generally found within a couple of seconds after observing the initiation of movement. We hypothesized that with the nonstop flow of newly initiated movements, the synchronous processes would differ the most from the condition in which the movement is minor or absent. The second temporal derivative of position, which indicates movement acceleration, is shown to correlate well with the perceptual quantity of movement (Luck and Sloboda, 2008; Luck et al., 2010). In the movement theory of Laban, acceleration is related to the movement factor of time, the other three movement factors being space, weight and flow (Laban, 1950). Acceleration was calculated by MoCap Toolbox for each time point and each selected marker by time-differencing the velocity scalar, which is the norm of the three-dimensional velocity vector, obtained by calculating the first time derivative of the location of the marker. Subsequently, we calculated the absolute value of acceleration for each data point before averaging the values of the markers in right and left elbow and right and left knee. Then, we averaged the absolute values of acceleration over the segments of 5 seconds with 50% overlapping in each consecutive segment. Since we were interested in the excerpts with a large movement

variability, 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 as High Motion Capture Acceleration (High Acceleration) and Low Motion Capture Acceleration (Low Acceleration), respectively. Perceptually, the epochs of High Acceleration contain large fast movements such as jumps, pirouettes, vast arm and leg movements and moving rapidly 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. The movements during Low Acceleration are not dance as such but rather embodied presence and interpretation of emotions relevant for the storyline.

Preprocessing

The EEG data of all the participants were first preprocessed with EEGLAB (version 12.0.2.5b; Delorme and Makeig, 2004). The external electrodes of the left and the right mastoid were set as a reference. The data were high-pass filtered at 1 Hz and low-pass filtered at 60 Hz. Finite impulse response (FIR) filtering, based on the firfilt (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 runica algorithm of EEGLAB (Delorme and 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 128 in 18 participants. In the remaining 36 participants, some noisy channels from each were removed in preprocessing and therefore less than 128 ICA components were decomposed in them. Typically, 1 to 3 ICA components related to the eye artefacts were removed. Noisy EEG data channels of the aforementioned 36 participants were interpolated. After the

interpolation, the data were split to the frequency bands of 4-8 Hz (theta), 8-13 Hz (alpha), 13-30 Hz (beta) and 30-48 Hz (gamma) with high-pass and low-pass filtering. In addition, the frequency band 1-4 Hz was extracted for the rest EEG, and the stimuli of Dance & Music and Stick Figure, but not for the unimodal stimuli of Music or Dance.

Procedure of the synchrony analyses

We calculated the phase synchrony values (PSVs) of the EEG data to the same 5-second segments as were defined before as High Acceleration and Low Acceleration. 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; Wang et al., 2006; Samaha et al., 2015). A similar method has also been used in EEG data analysis with continuous music stimuli (Bhattacharya and Petsche, 2000).

We conducted the synchrony analysis over the 12 electrodes of C29 (Fp1), C16 (Fp2), C23 (FCz), D3 (FC3), C3 (FC4), D11 (FC5), B30 (FC6), D19 (C3), B22 (C4), A3 (CPz), A17 (PO1) and A30 (PO2) (the 128-channel BioSemi EEG cap; Figure 1) so that each electrode was compared pairwise to all the other ones resulting in 66 electrode pairs of comparison. This analysis was made separately for each frequency band of delta, theta, alpha, beta and gamma. Due to noisy or lacking electrodes during the EEG recording, the value for the electrode C16 was interpolated over the surrounding electrodes during the preprocessing of the EEG data for two dancers, a musician and a participant in the control group. Similarly, the electrode D11 was interpolated for one musician. All the PSVs of the 5-second segments correlated with High Acceleration were averaged over each participant and each stimulus condition. The same procedure was used for the segments correlated with Low Acceleration.

Thus, for each condition, each participant got a unitary PSV for each electrode pair for both High Acceleration and Low Acceleration. In addition, PSV was calculated over the 60-second rest EEG data, during which the participant sat quietly, with eyes open, in a dark and silent EEG laboratory. Also, PSV was calculated over the 60-second rest EEG data with eyes closed. Similarly to the stimulus data, the data of the rest EEG were segmented with 5 seconds and 50% overlapping of the two consecutive segments separately for the eyes open and eyes closed condition. For each participant, the rest PSVs calculated for the 5-second segments were averaged as a unitary PSV value for each electrode pair for both eyes open and eyes closed condition.

The statistical analyses were conducted with MATLAB version R2016a. The normal distribution of the PSVs were tested with the Shapiro-Wilk test. In the statistical analysis, repeated measures ANOVA (between subject factor Group: Dancers, musicians and laymen; within subject factor Condition: Eyes Open and Eyes Closed for the resting state and High Acceleration and Low Acceleration for Music, Dance, Dance & Music and Stick Figure) was conducted separately for each electrode pair (66 electrode pairs), each frequency band (theta, alpha, beta and gamma) and each stimulus (rest, Music, Dance, Dance & Music, Stick Figure). The main effects for the factor Group and Condition, and the Group*Condition interaction were calculated with the Greenhouse-Geisser (GG) adjustment. In Results, these results are referred to with p_{GG} indicating the Greenhouse-Geisser adjusted p values of the repeated measures ANOVA. The multiple comparisons of Group and Condition were calculated with the critical value of Bonferroni. In Results, 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, False Discovery Rate (FDR) was calculated for each set of 66 electrode pairs from their p_{GG} values of the results of the repeated measures ANOVA to

control the expected proportion of false positives. For FDR correction, we employed a q -value threshold of 0.05.

In the results section, we report only the statistically significant results in which both the p_{GG} and the p_{FDR} are $<.05$. According to the repeated measures ANOVA, there were some significant Group*Condition interactions. However, after applying the multiple comparison with the critical value of Bonferroni, these results did not remain significant and, thus, are not reported in this paper. On the delta band, there were no significant group differences during resting state, Music & Dance or Stick Figure stimuli, and thus the results on delta band are not reported either.

Results

On **theta band**, during the Dance & Music stimulus, the synchrony was significantly stronger in dancers when compared to musicians over the electrode pairs FC3-FC4 (the main factor Group $F(2,51)=5.67$, $p_{GG}=.0060$, Dancers > Musicians $p=0.0044$), FC4-FC5 ($F(2,51)=10.28$, $p_{GG}=.00018$, Dancers > Musicians $p=0.00032$), FCz-FC3 ($F(2,51)=7.65$, $p_{GG}=.0012$, Dancers > Musicians $p=0.00078$) and FCz-FC5 ($F(2,51)=8.26$, $p_{GG}=.00078$, Dancers > Musicians $p=0.0020$). Over the electrode pairs FC4-FC5 and FCz-FC5 also the laymen differed from the dancers (Dancers > Laymen $p=0.0023$ and Dancers > Laymen $p=0.0039$, respectively). The statistically significant results according to both p_{GG} and p_{FDR} are presented in Table 2 for the main factor Group. The electrode locations of these group differences are illustrated in Figure 2. On theta band, there were no further group differences during the stimuli of rest, Music, Dance or Stick Figure.

On the **alpha, beta or gamma bands** there were no significant group differences during any stimuli.

On **alpha band**, however, there were several differences in the main factor Condition.

During the Dance stimulus, the main factor Condition provided statistically significant results at the following electrode pairs FC6 – FC4, FC6 – FCz, FC4 – FCz, FC4 – FC3, FC3 – Fp1, FC3 – Fp2, FC5 – Fp1, FC5 – Fp2 and Fp1 – Fp2 indicated *Low Acceleration > High Acceleration*. In contrast, for the electrode pairs FC3 – C3 and FC5 – C3 the main factor Condition was statistically significant for *High Acceleration > Low Acceleration*.

During the Dance & Music stimulus the main factor Condition provided statistically significant results at the following electrode pairs CPz – C3, CPz – PO1, C4 – FC4, C4 – FCz, C4 – FC3, C4 – Fp2, FC6 – FC4, FC6 – FCz, FC6 – FC3, FC6 – Fp1, FC6 – Fp2, FC6 – PO1, FC4 – FCz, FC4 – FC3, FC4 – Fp1, FC4 – Fp2, FC4 – PO1, FCz – PO1, FC3 – Fp1, FC3 – Fp2, FC3 – PO1, FC3 – PO2, FC5 – Fp1, FC5 – Fp2, FC5 – PO2, C3 – Fp1, Fp1 – Fp2, Fp1 – PO2, Fp2 – PO1, Fp2 – PO2 and PO1 – PO2 indicated *Low Acceleration > High Acceleration*.

During the Stick Figure stimulus, the main factor Condition provided statistically significant results at the following electrode pairs FC6 – Fp1, FC4 – FCz, FC4 – Fp1, FC4 – PO1, FCz – PO1, FC3 – PO2 and Fp1 – Fp2 indicated *Low Acceleration > High Acceleration*. These results for the main factor Condition during Dance, Dance & Music and Stick Figure stimuli are presented in detail in Table 3 and illustrated in Figure 3.

Discussion

Here, we asked how cortical processes differ in musicians and dancers when watching an audio-visual dance performance. To this end, we provided the participants with long excerpts from the contemporary dance choreography of *Carmen*. We found out that theta phase

synchrony in the fronto-central electrodes was increased in dancers during Dance & Music stimulus when compared to musicians and laymen. In addition, alpha phase synchrony decreased on several electrode pairs during strong dynamic movement when compared to the nearly motionless parts of the choreography. This desynchronization emerged the strongest during Dance & Music but some desynchronization was also observed during the stimuli of Dance and Stick Figure. Even if differences in the brain structure (Li et al., 2014; Hänggi et al., 2010; tentatively reviewed by Karpati et al., 2015) and resting state connectivity (Li et al., 2015) have been shown in professional dancers and musicians when compared to laymen, in our study the cortical synchrony in rest did not differ between dancers, musicians and laymen. Furthermore, we found no group differences during the stimuli of Music, Dance or Stick Figure on any of the frequency bands studied. Bhattacharya and Petsche (2000) reported enhanced gamma synchrony in musicians when compared to laymen when listening to whole musical pieces, eyes closed. Our research did not extend their result during listening to music, eyes open.

Alpha synchrony in the perception of movement

In alpha synchrony, we noticed differences related to the movement quantity similarly in dancers, musicians and laymen. Alpha desynchrony is generally associated with increased attention or motor processes via activation of the mirror neuron system (Pineda, 2005; Hobson and Bishop, 2016). We found a clear decrease in the alpha synchrony over several electrode pairs across the brain during High Acceleration when compared to Low Acceleration. The differences in the synchrony on the alpha band are most likely related to the lower-level sensory-motor, and attentional processes related to the amount of movement perceived. These results are in line with our hypotheses: Increased movement quantity and

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elevated attention due to the movement decrease alpha synchrony on central and posterior electrodes, respectively (Niedermeyer and da Silva, 2005; Pineda, 2005; Hobson and Bishop, 2016).

Recently, Hobson and Bishop (2016) studied the connection of movement perception and alpha band with several baseline references. They noticed that the static image within the stimulus as a baseline produced the strongest contrast in the alpha power over the central electrodes when compared to movement perception. Our paradigm is an upgrade to their experiment with a continuous naturalistic stimulus, due to the nearly still positions of the dancer in our stimulus within the dynamic dance choreography. Based on our results of decreased alpha synchrony during High Acceleration, the findings of Hobson and Bishop can be extended to naturalistic whole-body movement.

During Dance & Music, the desynchronization on the alpha band during fast movement occurred over several electrode pairs including pre-frontal, fronto-central, central and parieto-occipital electrodes. Anterior desynchronization on the alpha band is associated with decrease in the mu wave, which is traditionally associated to the perception and conduction of movement (Pineda, 2005 for a review but see also Caramazza et al., 2014 for contrasting views). Posterior alpha is, instead, associated to the attentional processes in timing and inhibition (Klimesch, 2012 for a review). Thus, both alpha and mu waves seem to be modified during multimodal perception of human movement.

During Stick Figure, the changes on the alpha band are diminished during fast movement when compared to the slow movement, and occur mainly between the fronto-central and parieto-occipital electrodes referring to changes in the visual observation and attention (Hobson and Bishop, 2016). During Dance, the differences in the alpha synchrony occur over the prefrontal, fronto-central and central electrodes which could be related to not only motor-sensory but also cognitive processes. Interestingly, all the other alpha synchrony

decreases during fast movement of the unimodal dancer but the synchrony over left fronto-central and central electrode pairs can increase during fast movement. However, this local increase in synchrony diminishes during multimodal presentation of dance. Further research needs to be done to investigate the replicability of this result during unimodal human movement.

Dancers and theta synchrony in cognitive and multisensory processing

Dancers had increased interhemispheric theta synchrony over the fronto-central electrodes during Dance & Music. The enhanced synchrony may occur due to several individual, but simultaneous, brain processes related to cognition and emotion, or due to a combination of them. In line with our hypothesis, the increased theta synchrony may reflect the cognitive and affective qualities which develop during dance training. Dancers might create mental representations for music and movement during dance training, similarly to musicians (Bangert and Altenmuller, 2003), or even develop a specialized network which activates in perception of dance and music (Bangert et al., 2006). Anatomically, the fronto-central electrodes are located over the premotor areas. However, because of the electrically anisotropic nature of the skull and the cerebrospinal fluid, the actual origin of the EEG signal is more difficult to define (Nunez and Srinivasan, 2006).

Theta synchrony is suggested to be induced into the cortex via the hippocampal-cortical pathway (Ekstrom et al., 2005; Klimesch, 1996). In literature, increased theta synchrony has been associated with cognitive processes such as memory (Klimesch et al., 1997; 2001), multimodal interaction and attention (Wang et al., 2016), spatial awareness both with and without visual and self-motion cues (Ekstrom et al., 2005; Kahana et al., 1999; Landau et al., 2015; Vass et al., 2016) as well as with sensory-motor interaction (Zarka et al.,

2014; Bland and Oddie, 2001 for a review), predictive timing of movement (Arnal and Giraud Mamessier, 2012 for a review) and emotional processing (Balconi and Lucchiari, 2006; Knyazev et al., 2009; Krause et al., 2000). Interestingly, theta synchrony did not differ between groups during Dance or Stick Figure. Thus, professional dancers have increased phase synchrony related to processes which are involved in the observation of multimodal human movement. During dance education, observing and producing multimodal biological movements form the real environment in which dancers spend their days over several years.

Memory processes related to the spatial awareness and to the form of the movement can be assumed to be similar in both Dance and Dance & Music stimuli. Also, timing of the movement to the music is similar during Dance & Music and Stick Figure. Henley (2015) showed that dancers better perceive changes in space and time, but not in shape, during a manipulation task of dance movement when compared to laymen. Being a natural condition, multimodal stimulus might increase the processes related to the spatial awareness when compared to unimodal dance movement. Importantly, during Stick Figure there was no spatial reference but the figure moved on a unicolor black background. On the other hand, observing the timing of the movement to the music might be more natural for dancers when watching the real dancer than when watching the stick figure, enhancing the cortical processes of temporal movement prediction reflected by the theta synchronization.

Many participants reported being familiar to the music presented in our study. In contrast, nobody was familiar with the dance choreography which is not only generally less known but was also modified by the dancer for this experiment. However, dancers are more likely familiar with observing dance movement *per se*. Zarka and colleagues (2014) showed how theta phase synchrony was increased when watching normal walking when compared to upside-down and uncoordinated walking. Familiarity to normal walking might be the reason for this increase in theta synchrony, which could help explain the increased theta synchrony

in dancers in our study. However, in the research of Zarka and colleagues, theta phase synchrony was increased on the centro-parietal electrodes, whereas in our research the increase was on the fronto-central electrodes.

Due to the general familiarity, the dancers participating in our study might have paid more attention to the visual dance stimulus of observing dance whereas the musicians and laymen may have chosen to primarily focus on the more familiar auditory stimulus. Indeed, Wang and colleagues (2006) reported how attention to the visual stimulus, but not to the auditory stimulus, during an audio-visual presentation increases the fronto-parietal theta power. Also, the sensory-motor interaction could be enhanced in dancers when compared to musicians and laymen increasing the theta synchrony. Several fMRI studies in familiarity with movement show how dancers' brains process learned movement repertoires differently compared to either laymen and other movement specialists (Calvo-Merino et al., 2005), or to their own brain activity before learning the choreography (Cross et al., 2006). These premotor brain regions could also contribute to the changes in the cortical synchrony over the fronto-central electrodes observed in our study. Importantly, we used a wide pool of dancers and nobody was particularly familiar to the peculiar movement sequences presented in our study.

Mirror neuron system, movement and embodied emotions

Not only portrayed emotions but also induced emotions can be successfully recognized from dance movement (Camurri et al., 2003; Van Dyck et al., 2014). In addition, music has been shown to evoke strong emotions, and even chills, among musicians and laymen in several experiments (Blood and Zatorre, 2001; Brattico et al., 2011; Salimpoor et al., 2011; Koelsch, 2014 for a review). *Carmen* is an artwork with strong emotions and for our study we selected the most emotionally intense scenes.

Van Dyck and colleagues (2013) showed that the movements of participants who danced after being induced to feel emotional states of happiness were faster, more accelerated, more expanded and more impulsive than after sad emotion induction. Their result could be interpreted to indicate that the feelings of strong arousal evoke more accelerated movement, joyful happiness being positive valence but also a high-arousal emotion, sadness belonging to the negative valence and low arousal class (Mehrabian and Russell, 1974). Fast movement in our study did not include only happy movement but also movement interpreting rage and anger, which classify in negative valence but high arousal class. In contrast, low acceleration movement in our study was not only the interpretation of sadness but also tenderness (positive valence, low arousal).

Krause and colleagues (2000) suggested that the arousal level of the emotional stimulus is an important factor in the increased spectral power of the theta band over the anterior electrodes. In their experiment, aggressive, but not sad, film content increased synchronization on the band of 4-6 Hz when compared to neutral film content. In the studies of emotional face expression, both implicit and explicit recognition of emotion have been shown to modify theta power over the frontal and central electrodes (Balconi and Lucchiari, 2006; Knyazev et al., 2009). Balconi and Lucchiari (2006) suggested that the increase in the anterior theta power is related to a network of attention in maintaining a state of alertness when salient emotional stimuli are encountered.

In our study, the enhanced theta synchrony of dancers during audio-visual dance may reflect the processes involved in recognizing emotions from the whole-body movement. Interestingly, these processes would increase the cortical synchronization over the fronto-central electrodes on the theta band but not the desynchronization on the alpha band, which has earlier been associated with the social cognition due to mu desynchronization evoked by the activation of the mirror neuron system (Oberman et al., 2007). Recently, it has been

argued critically that mu suppression over the central electrodes should not be taken as a straightforward indicator for the activation of the human mirror neuron system (Hobson and Bishop, 2016), nor linking mirror neurons to empathy (Lamm and Majdandzic, 2015 for a review). Despite considering the emotional aspect in the alpha desynchronization during the movement of strong arousal, in our study the alpha synchrony was decreased most likely due to the accelerated dance movement.

In our study, the emotional dance performance increased theta synchrony in dance experts, and the alpha desynchrony correlated with movement quantity. These results suggest that emotional content of human movement might not be understood via the mirror neuron system but rather via the same pathways as other non-corporal emotional stimuli. Changes in theta power have been linked to the hippocampal-cortical pathway (Ekstrom et al., 2005; Klimesch, 1996), hippocampus being crucial in memory related processes (Bird and Burgess, 2008 for a review). Observed movement might evoke processes of autobiographical memory and of emotions related to these memories (Phelps, 2004 for a review). This approach of intertwined autobiographical memories and human movement in understanding embodied emotions would challenge the prevailing, though recently criticized, theory of understanding emotions from human movement via activation of the mirror neuron system due to instant mental imitation of the observed movement (Caramazza et al., 2014; Lamm and Majdandzic, 2015 for reviews). Alternatively, the processes of episodic memory and mental movement imitation could both contribute to the emotional understanding of human movement.

Methodological consideration

Phase synchrony is a measure independent of amplitude power. However, some correlation between phase synchrony and amplitude power has been found, at least on the beta band

(Nikouline et al., 2001). In preliminary research conducted as an MA thesis in the University of Jyväskylä (Luopajarvi, 2012), we did not find differences in amplitude power between groups on any of the frequency bands, not even when alpha and beta bands were divided into sub-bands. Thus, in our study we chose to focus only on the phase synchrony.

Since we set such a high threshold for the interpretation of the results to be statistically significant, our results might include some false negatives. Thus, further research is necessary to study not only the phase synchrony within a frequency band, but also the changes in the spectral power of the frequency bands as well as cross-frequency coupling during an emotional and complex continuous whole-body movement. Most importantly, our study shows that continuous dance is suitable for studying cortical plasticity induced by professional dance expertise as well as for analysing cortical processes related to movement quantity. In addition, dance expertise develops the brain processes not associated with the ones involved in the observation of the movement quantity.

Conclusion

Our results suggest that the perception of movement decreases alpha phase synchrony over various cortical regions. This desynchronization is stronger during the presentation of a multimodal human stimulus than those of a stick figure or a unimodal human dancer. Interestingly, the professional dance training seems not to shape these processes related to movement quantity but modifies more complex processes reflected by the increased theta phase synchrony over the fronto-central electrodes. When compared to musicians and laymen, dancers may have more refined cortical processes possibly related to attention in multimodal processing, spatial awareness, prediction of the timing of the movement and understanding of embodied emotions. Further research is required to understand, which of

these processes are modified and through what brain mechanisms the dance training improves them. However, based on our results, we propose a possibility that the brain mechanisms in understanding emotions from human movement are similar to the ones evoked during other emotional stimuli, such as facial expressions (Knyazev et al., 2009) or emotional film content (Krause et al., 2000). Changes in theta power have been linked to the hippocampal-cortical pathway (Ekstrom et al., 2005; Klimesch, 1996), suggesting the importance of episodic memory in emotional processing (Phelps, 2004 for a review). Since the relevance of the mirror neuron system in empathy has recently been criticized (Caramazza et al., 2014; Hobson and Bishop, 2016; Lamm and Majdandzic, 2015), the embodied memories might be a plausible direction for the future studies of embodied social cognition. Also, our results encourage the research in dance/movement therapy to create a brain-based theory for the behavioural improvement this therapy method is already shown to have in autism (Koch et al., 2015; Koehne et al., 2016) and depression (Jeong et al., 2005; Koch et al., 2007), both conditions including atypical emotional processing. In addition, during the boom of the ubiquitous virtual interaction, our results remind us that the brain dynamics are strongest when observing a human being in a naturalistic multimodal context.

Author Contributions

H.P., P.T. and M.T. conceived and conducted the experiment, H.P. analysed the results. H.P., P.T. and M.T. wrote the main manuscript text and H.P. prepared figures 1-3 and tables 1-3.

All authors reviewed the manuscript.

Acknowledgements

This work was supported by Kone Foundation, Signe and Ane Gyllenberg Foundation, Academy of Finland, Finnish Cultural Foundation and The Art and Science Association of Jyväskylä, Finland. We would like to thank Miika Leminen, Tommi Makkonen, Niia Virtanen and Johanna Tuomisto for their assistance during the EEG recordings and data processing, Mira Kautto for modifying and performing the dance choreography, Jari Lipsanen for his valuable advice in the statistical analysis, Federico Berges Arteaga for image production and Steve Lamattina for proofreading.

Conflict of interest

The authors declare no competing financial interests.

Data Accessibility

Since the participants were not informed about the possibility to share data with researchers outside the research team, for ethical reasons, we are unable to make data publicly available.

Abbreviations

FDR	false discovery rate
FIR	finite impulse response
fMRI	functional magnetic imaging
EEG	electroencephalography
ERP	event-related potential

GG	Greenhouse-Geisser
ICA	independent component analysis
PSV	phase synchrony value

References

- Arnal, L.H., and Giraud Mamessier, A-L. (2012). Cortical oscillations and sensory predictions. *Trends Cogn. Sci.* *16*(7), 390–398.
- Balconi, M., and Lucchiari, C. (2006). EEG correlates (event-related desynchronization) of emotional face elaboration: A temporal analysis. *Neurosci. Lett.* *392*, 118–123.
- Bangert, M., and Altenmüller, E.O. (2003). Mapping perception to action in piano practice: a longitudinal DC-EEG study. *BMC Neuroscience*, *4*, 26.
- Bangert, M., Peschel, T., Schlaug, G., Rotte, M., Drescher, D., Hinrichs, H., Heinze, H.J., and Altenmüller, E. (2006). Shared networks for auditory and motor processing in professional pianists: Evidence from fMRI conjunction. *NeuroImage*, *30*(3), 917–926.
- Bhattacharya, J., and Petsche, H. (2000). Musicians and the gamma band: A secret affair? *Neuroreport* *12*, 371–374.
- Bird, C.M, Burgess, N. (2008). The hippocampus and memory: Insights from spatial processing. *Nat. Rev. Neurosci.* *9*(3), 182–194.
- Bland, B.H., and Oddie, S.D. (2001). Theta band oscillation and synchrony in the hippocampal formation and associated structures: The case for its role in sensorimotor integration. *Behav. Brain Res.* *127*, 119–136.

Blood, A.J., and Zatorre, R.J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proc. Natl. Acad. Sci. U.S.A.* *98*, 11818–11823.

Brattico, E., Alluri, V., Bogert, B., Jacobsen, T., Vartiainen, N., Nieminen, S., and Tervaniemi, M. (2011). A functional MRI study of happy and sad emotions in music with and without lyrics. *Front. Psychol.* *2*, 308.

Burger, B., and Toiviainen, P. (2013). MoCap Toolbox – A Matlab toolbox for computational analysis of movement data. In *Proceedings of the 10th Sound and Music Computing Conference (SMC)*, R. Bresin, ed. (Stockholm, Sweden: KTH Royal Institute of Technology).

Burunat, I., Alluri, V., Toiviainen, P., Numminen, J., and Brattico, E. (2014). Dynamics of brain activity underlying working memory for music in a naturalistic condition. *Cortex* *57*, 254–269.

Calvo-Merino, B., Glaser, D.E., Grézes, J., Passingham, R.E., and Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cereb. Cortex* *15*, 1243–1249.

Camurri, A., Lagerlöf, I., and Volpe, G. (2003). Recognizing emotion from dance movement: Comparison of spectator recognition and automated techniques. *Int. J. Hum-Comput. St.* *59*, 213–225.

Canolty, R.T., and Knight, R.T. (2010). The functional role of cross-frequency coupling. *Trends Cogn. Sci.* *14*(11), 507–515.

Caramazza, A., Anzellotti, S., Strnad, L., and Lingnau, A. (2014). Embodied Cognition and Mirror Neurons: A Critical Assessment. *Annu. Rev. Neurosci.* *37*, 1–15.

Cevallos, C., Zarka, D., Hoellinger, T., Leroy, A., Dan, B., and Cheron, G. (2015). Oscillations in the human brain during walking execution, imagination and observation. *Neuropsychologia* 79, 223.

Chen, J.L., Penhune, V.B., and Zatorre, R.J. (2009). The role of auditory and premotor cortex in sensorimotor transformations. *Ann. N.Y. Acad. Sci.* 1169, 15–34.

Cross, E.S., Hamilton, A.F., and Grafton, S.T. (2006). Building a motor simulation de novo: Observation of dance by dancers. *Neuroimage* 31(3), 1257–1267.

Delorme, A., and Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics. *J. Neurosci. Meth.* 134(1), 9–21.

Ekstrom, A.D., Caplan, J.B., Ho, E., Shattuck, K., Fried, I., and Kahana, M.J. (2005). Human hippocampal theta activity during virtual navigation. *Hippocampus* 15, 881–889.

Ewen, J.B., Lakshmanan, B.M., Hallett, M., Mostofsky, S.H., Crone, N.E., and Korzeniewska, A. (2015). Dynamics of functional and effective connectivity within human cortical motor control networks. *Clin. Neurophysiol.* 126(5), 987.

Hänggi, J., Koeneke, S., Bezzola, L., and Jäncke, L. (2010). Structural neuroplasticity in the sensorimotor network of professional female ballet dancers. *Hum. Brain Mapp.* 31, 1196–1206.

Hanke, M., Baumgartner, F.J., Ibe, P., Kaule, F.R., Pollmann, S., Speck, O., Zinke, W., and Stadler, J. (2014). A high-resolution 7-Tesla fMRI dataset from complex natural stimulation with an audio movie. *Sci. Data* 1, 140003.

Henley, M.K. (2015). Comparison of shape, space, and time judgments in expert dancers and novices: Evidence that production enhances perception. *J. Dance Med. Sci.* 19(3), 103–109.

Herholz, S.C., and Zatorre, R.J. (2012). Musical training as a framework for brain plasticity: Behavior, function, and structure. *Neuron* 76, 486–502.

Hobson, H.M., Bishop, D.V.M. (2016). Mu suppression—A good measure of the human mirror neuron system? *Cortex* 82, 290–310.

Hong, B., Acharya, S., Ku, Y., Gao, S., and Thakor, N.V. (2006). Measurement of dynamic coupling of independent EEG components from cognitive tasks. *Int. J. Bioelectromagn.* 8(1), VII/1–VII/7.

Jäncke, L. (2012). The dynamic audio-motor system in pianists. *Ann. N. Y. Acad. Sci.*, 1252, 246–252.

Jeong, Y.J., Hong, S.C., Lee, M.S., Park, M.C., Kim, Y.K., and Suh, C.M. (2005). Dance movement therapy improves emotional responses and modulates neurohormones in adolescents with mild depression. *Int. J. Neurosci.* 115(12), 1711–20.

Kahana, M.J., Sekuler, R., Caplan, J.B., Kirschen, M.P., and Madsen, J.R. (1999). Human theta oscillations exhibit task dependence during virtual maze navigation. *Nature* 399, 781–784.

Karpati, F.J., Giacosa, C., Foster, N.E.V., Penhune, V.B., and Hyde, K.L. (2015). Dance and the brain: A review. *Ann. N.Y. Acad. Sci.* 1337, 140–146.

Kahana, M.J. (2006). The Cognitive Correlates of Human Brain Oscillations. *J. Neurosci.* 26(6), 1669–1672.

Kauttonen, J., Hlushchuk, Y., and Tikka, P. (2015). Optimizing methods for linking cinematic features to fMRI data. *Neuroimage* 110, 136–48.

Klimesch, W. (1996). Memory processes described as brain oscillations in the EEG-alpha and theta bands. *Psychology* 6(6).

Klimesch, W., Doppelmayr, M., Schimke, H., and Ripper, B. (1997). Theta synchronization and alpha desynchronization in a memory task. *Psychophysiology* 34, 169–176.

Klimesch, W., Doppelmayr, M., Yonelinas, A., Kroll, N.E., Lazzara, M., Rohm, D., and Gruber, W. (2001). Theta synchronization during episodic retrieval: Neural correlates of conscious awareness. *Brain Res Cogn Brain Res* 12, 33–38.

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn Sci* 16(12), 606–617.

Knyazev, G.G., Slobodskoj-Plusnin, J.Y., and Bocharov, A.V. (2009). Event-related delta and theta synchronization during explicit and implicit emotion processing. *Neuroscience* 164, 1588–1600.

Koch, S.C., Morlinghaus, K., and Fuchs, T. (2007). The joy dance: Specific effects of a single dance intervention on psychiatric patients with depression. *Art. Psychother.* 34, 340–349.

Koch, S.C., Mehl, L., Sobanski, E., Sieber, M., and Fuchs, T. (2015). Fixing the mirrors: A feasibility study of the effects of dance movement therapy on young adults with autism spectrum disorder. *Autism* 19(3), 338–50.

Koehne, S., Behrends, A., Fairhurst, M.T., and Dziobek, I. (2016). Fostering social cognition through an imitation- and synchronization-based dance/movement intervention in adults with autism spectrum disorder: A controlled proof-of-concept study. *Psychother. Psychosom.* 85(1), 27–35.

Koelsch, S. (2014). Brain correlates of music-evoked emotions. *Nat. Rev. Neurosci.* *15*, 170–180.

Krause, C.M., Viemero, V., Rosenqvist, A., Sillanmaki, L., and Astrom, T. (2000). Relative electroencephalographic desynchronization and synchronization in humans to emotional film content: an analysis of the 4–6, 6–8, 8–10 and 10–12 Hz frequency bands. *Neurosci. Lett.* *286*, 9–12.

Laban, R. (1950). *The mastery of movement*, 4th revised version (Plymouth: Northcote House).

Lamm, C., and Majdandzic, J. (2015). The role of shared neural activations, mirror neurons, and morality in empathy – A critical comment. *Neurosci. Res.* *90*, 15–24.

Landau, A.N., Schreyer, H.M., van Pelt, S., and Fries, P. (2015). Distributed attention is implemented through theta-rhythmic gamma modulation. *Curr. Biol.* *25*, 2332–2337.

Li, J., Luo, C., Peng, Y., Xie, Q., Gong, J., Dong, L., Lai, Y., Li, H., and Yao, D. (2014). Probabilistic diffusion tractography reveals improvement of structural network in musicians. *PLoS One* *9*(8), e105508.

Li, G., He, H., Huang, M., Zhang, X., Lu, J., Lai, Y., Luo, C., and Yao, D. (2015). Identifying enhanced cortico-basal ganglia loops associated with prolonged dance training. *Sci. Rep.* *5*, 10271.

Luck, G., and Sloboda, J. (2008). Exploring the spatio-temporal properties of simple conducting gestures using a synchronization task. *Music Percept.* *25*(3), 225–239.

Luck, G., Toiviainen, P., and Thompson, M. (2010). Perception of expression in conductors' gestures: A continuous response study. *Music Percept.* *28*(1), 47–57.

Luopajarvi, R. (2012). Tanssi kuin kukaan ei katsoisi – Nuorten musiikillinen tunneilmaisu liikkeen avulla. MA thesis, University of Jyväskylä, viewed 15 February 2017, <<https://jyx.jyu.fi/dspace/bitstream/handle/123456789/38534/URN%3ANBN%3Afi%3Aaju-201209122391.pdf?sequence=1>>.

Mathewson, K.E., Lleras, A., Beck, D.M., Fabiani, M., Ro, T., and Gratton, G. (2011). Pulsed out of awareness: EEG alpha oscillations represent a pulsed inhibition of ongoing cortical processing. *Front. Psychol.* 2, 99.

Mehrabian, A., and Russell, J.A. (1974). *An approach to environmental psychology* (Cambridge, Mass.: MIT Press).

Nikouline, V.V., Linkenkaer-Hansen, K., Huttunen, J., and Ilmoniemi, R.J. (2001). Interhemispheric phase synchrony and amplitude correlation of spontaneous beta oscillations in human subjects: a magnetoencephalographic study. *Neuroreport* 12(11), 2487-91.

Nummenmaa, L., Glerean, E., Viinikainen, M., Jääskeläinen, I.P., Hari, R., and Sams, M. (2012). Emotions promote social interaction by synchronizing brain activity across individuals. *Proc. Natl. Acad. Sci. U.S.A.* 109(24), 9599–9604.

Nummenmaa, L., Smirnov, D., Lahnakoski, J.M., Glerean, E., Jääskeläinen, I.P., Sams, M., and Hari, R. (2014). Mental Action Simulation Synchronizes Action–Observation Circuits across Individuals. *J. Neurosci.* 34(3), 748–757.

Nunez, P.L., Srinivasan, R. (2006). *Electric fields of the brain: The neurophysics of EEG*. Oxford University Press.

Oberman, L.M., Pineda, J.A., and Ramachandran, V.S. (2007). The human mirror neuron system: A link between action observation and social skills. *Soc. Cogn. Affect Neurosci.* 2, 62–66.

Orgs, G., Dombrowski, J.H., Heil, M., and Jansen-Osmann, P. (2008). Expertise in dance modulates alpha/beta event-related desynchronization during action observation. *Eur. J. Neurosci.* 27, 3380–3384.

Pavlidou, A., Schnitzler, A., and Lange, J. (2014). Beta oscillations and their functional role in movement perception. *Transl. Neurosci.* 5(4), 286–292.

Phelps, E.A. (2004). Human emotion and memory: Interactions of the amygdala and the hippocampal complex. *Curr. Opin. Neurobiol.* 12(2), 198–202.

Pilgramm, S., Lorey, B., Stark, R., Munzert, J., Vaitl, D., and Zentgraf, K. (2010). Differential activation of the lateral premotor cortex during action observation. *B.M.C. Neurosci.* 11, 89.

Pineda JA. (2005). The functional significance of mu rhythms: translating "seeing" and "hearing" into "doing". *Brain Res Brain Res Rev.* 50(1):57-68.

Rizzolatti, G., Fadiga, L., Fogassi, L., and Gallese, V. (1996). Premotor cortex and the recognition of motor actions. *Brain Res. Cogn. Brain Res.* 3, 131–141.

Rizzolatti, G., Fogassi, L., and Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2, 661–70.

Ross, P.D., Polson, L., and Grosbras, M.H. (2012). Developmental changes in emotion recognition from full-light and point-light displays of body movement. *PLoS One* 7, e44815.

Salimpoor, V.N., Benovoy, M., Larcher, K., Dagher, A., and Zatorre, R.J. (2011). Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. *Nat. Neurosci.* 14(2), 257–262.

Samaha, J., Bauer, P., Cimaroli, S., and Postle, B.R. (2015). Top-down control of the phase of alpha-band oscillations as a mechanism for temporal prediction. *Proc. Natl. Acad. Sci. U.S.A.* *112*(27), 8439–8444.

Tomassini, A., Spinelli, D., Jacono, M., Sandini, G., and Morrone, M.C. (2015). Rhythmic oscillations of visual contrast sensitivity synchronized with action. *J. Neurosci.* *35*(18), 7019–7029.

van Driel, J., Knapen, T., van Es, D.M., Cohen, M.X. (2014). Interregional alpha-band synchrony supports temporal cross-modal integration. *Neuroimage* *101*, 404–415.

Van Dyck, E., Maes, P., Hargreaves, J., Lesaffre, M., and Leman, M. (2013). Expressing induced emotions through free dance movement. *J. Nonverbal Behav.* *37*, 175.

Van Dyck, E., Vansteenkiste, P., Lenoir, M., Lesaffre, M., and Leman, M. (2014). Recognizing induced emotions of happiness and sadness from dance movement. *PLoS One* *9*(2), e89773.

Vass, L.K., Copara, M.S., Seyal, M., Shahlaie, K., Tomaszewski Farias, S., Shen, P.Y., and Ekstrom, A.D. (2016). Oscillations go the distance: Low frequency human hippocampal oscillations code spatial distance in the absence of sensory cues during teleportation. *Neuron* *89*, 1180–1186.

Wang, Y., Hong, B., Gao, X., and Gao, S. (2006). Phase synchrony measurement in motor cortex for classifying single-trial EEG during motor imagery. *Proceedings of the 28th IEEE, EMBS Annual International Conference, New York City, USA, Aug 30-Sept 3.*

Wang, W., Viswanathan, S., Lee, T., and Grafton, S.T. (2016). Coupling between theta oscillations and cognitive control network during cross-modal visual and auditory attention: Supramodal vs modality-specific mechanisms. *PLoS One* *11*(7), e0158465.

Wilbers, L., Deuker, L., Fell, J., and Axmacher, N. (2012). Are autobiographical memories inherently social? Evidence from an fMRI study. *PLoS One* 7(9), e45089.

Wilkins, R.W., Hodges, D.A., Laurienti, P.J., Steen, M., and Burdette, J.H. (2014). Network science and the effects of music preference on functional brain connectivity: From Beethoven to Eminem. *Sci. Rep.* 4, 6130.

Zarka, D., Cevallos, C., Petieau, M., Hoellinger, T., Dan, B., and Cheron, G. (2014). Neural rhythmic symphony of human walking observation: Upside-down and uncoordinated condition on cortical theta, alpha, beta and gamma oscillations. *Front. Syst. Neurosci.* 8, 169.

Table and figure legends

Table 1 Detailed background information of the participants. To protect the anonymity of the participants, in some cases the specific information of the institute is replaced with XXX.

Table 2 Electrode pairs with significant synchronization differences for the main factor Group (dancers, musicians, laymen) during the Dance & Music stimulus in conditions High Acceleration and Low Acceleration over the frequency band theta (4-8 Hz). Significant differences are written in **bold**. pGG stands for Greenhouse-Geisser adjusted p value, pFDR for the p value with False Discovery Rate correction, and PSV for the phase synchrony value.

Table 3 Electrode pairs with significant synchronization differences for the main factor Condition (High Acceleration, Low Acceleration) during the Dance, Dance & Music and Stick Figure stimuli in groups dancers, musicians and laymen over the frequency band alpha

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(8-13 Hz). pGG stands for Greenhouse-Geisser adjusted p value, pFDR for the p value with False Discovery Rate correction, and PSV for the phase synchrony value.

Figure 1 A still image from the choreography presented by a real dancer (on left) and a stick figure (on right).

Figure 2 Significant differences for the main factor Group (dancers, musicians and laymen) during Dance & Music stimulus on the theta band (4-8 Hz). Over the electrode pairs FC3 – FCz and FC3 – FC4 the synchronization is significantly stronger in dancers when compared to laymen (grey line). Over the electrode pairs FC5 – FCz and FC5 – FC4 the synchronization is significantly stronger in dancers when compared to musicians and laymen (black line).

Figure 3 Significant differences for the main factor Condition (High Acceleration, Low Acceleration) during Dance (on left), Dance & Music (in the middle) and Stick Figure (on right) stimuli on the alpha band (8-13 Hz). The black lines connect the electrode pairs over which the synchronization is significantly stronger during Low Acceleration when compared to High Acceleration.

Dancers								
Gender	Age	Student/professional	Studies started	Graduated	Education	Style	Age when started to dance	Handedness
M	34	Professional		2009	Theater Academy, University of Arts, Helsinki	Contemporary dance	N/A	R
M	35	Professional		2005	Theater Academy, University of Arts, Helsinki	Contemporary dance	ballet: 7 years	L
F	25	Professional		2012	XXX University of Applied Sciences	Contemporary dance	ballet: 4 years	R
F	30	Professional		2008	Theater Academy, University of Arts, Helsinki	Contemporary dance	ballet: 7 years	R
F	31	Professional		2011	Arts Academy, XXX University of Applied Sciences	Contemporary dance	8	R
F	40	Professional		1998	Theater Academy, University of Arts, Helsinki	Contemporary dance	3	R
F	25	Student	2012		Theater Academy, University of Arts, Helsinki	Contemporary dance	4	R
F	28	Professional		2011	XXX University of Applied Sciences	Contemporary dance	17	R
F	24	Professional		2012	Theater Academy, University of Arts, Helsinki	Contemporary dance	7	R
F	30	Professional		2011	Theater Academy, University of Arts, Helsinki	Contemporary dance	16	R
F	32	Professional		2013	Theater Academy, University of Arts, Helsinki	Contemporary dance	13	L
F	28	Professional		2010	Arts Academy, XXX University of Applied Sciences	Circus	ballet: 7 years	R

M	30	Professional		2010	Theater Academy, University of Arts, Helsinki	Contemporary dance	15	R
M	27	Self-taught				Stree dance	19	R
M	23	Self-taught				Popping	17	R
F	29	Student	2013		Tanssivintti, Alexander Theater, Helsinki	Contemporary dance	11	R
F	30	Professional	2007		BA (Hons), London	Contemporary dance	12	R
M	25	Self-taught				Locking	16	R
Musicians								
Gender	Age	Student/professional	Studies started	Graduated	Education	Instrument	Age when started to play	Handedness
M	27	Student	2008		Sibelius Academy, University of Arts, Helsinki	Choir leader	piano: 7 years	R
M	20	Student	2013		Sibelius Academy, University of Arts, Helsinki	Jazz piano	10	R
M	26	Student	2008		Sibelius Academy, University of Arts, Helsinki	Music education	guitar, piano: 8 years	R
F	24	Student	2008		Sibelius Academy, University of Arts, Helsinki	Recorder	6	R
F	22	Student	2013		Sibelius Academy, University of Arts, Helsinki	Electric base guitar	11	R
F	26	Student	2011		Sibelius Academy, University of Arts, Helsinki	Pop & jazz singing	14	R
F	27	Student	2012		Sibelius Academy, University of Arts, Helsinki	Pop & jazz singing	piano: 7 years	R
F	31	Professional		2012	Sibelius Academy, University of Arts,	Classical	piano: 4	R

					Helsinki	singing	years	
M	28	Student	2008		Sibelius Academy, University of Arts, Helsinki	Recorder	singing: 8 years	R
F	24	Student	2010		Sibelius Academy, University of Arts, Helsinki	N/A	N/A	R
F	29	Student	2008		Sibelius Academy, University of Arts, Helsinki	Music education	violin: 6 years	R
F	24	Student	2011		Sibelius Academy, University of Arts, Helsinki	Viola	5	R
F	N/A	Student	2010		Sibelius Academy, University of Arts, Helsinki	Oboe	piano: 4 years	R
F	21	Student	2013		Sibelius Academy, University of Arts, Helsinki	N/A	N/A	R
F	23	Student	2013		Sibelius Academy, University of Arts, Helsinki	Saxophone	10	R
F	23	Student	2009		Sibelius Academy, University of Arts, Helsinki	Music education	piano: 4 years	R
F	23	Student	2012		Sibelius Academy, University of Arts, Helsinki	Piano	5	L
F	26	Student	2007		Sibelius Academy, University of Arts, Helsinki	Music education	violin: 6 years	R
M	25	Student	2011		Sibelius Academy, University of Arts, Helsinki	N/A	N/A	L
Laymen								
Gender	Age	Student/prof essional	Education	Handedness				
F	26	Professional	Master's degree	R				

F	20	Student	University student	R
M	26	Student	University student	R
M	33	Professional	Bachelor's degree	R
M	31	Professional	Bachelor's degree	L
F	25	Student	Bachelor's degree	R
M	20	Student	University student	R
F	26	Student	University student	R
F	23	Student	University student	R
F	22	Student	University student	R
F	22	Student	University student	R
F	20	Student	University student	R
F	24	Student	University student	R
F	22	N/A	N/A	R
F	28	Student	University student	R
F	26	Student	University student	R
M	30	Student	University student	R
F	26	Student	University student	L

4 – 8 Hz Electrode pair	F(2,51)	pGG	Multiple comparison (Bonferroni)	pFDR	Q	Mean PSV Dancers (standard deviation)	Mean PSV Musicians (standard deviation)	Mean PSV Laymen (standard deviation)
FC3 – FC4	5.67	0.0060	Dancers > Musicians p=0.0044 Dancers > Laymen p=0.24 Laymen > Musicians p=0.37	0.035	0.035	0.44 (0.034)	0.41 (0.016)	0.42 (0.015)
FC4 – FC5	10.28	0.00018	Dancers > Musicians p=0.00032	0.0041	0.0041	0.41 (0.025)	0.38 (0.0083)	0.39 (0.011)

			Dancers > Laymen p=0.0023 Laymen > Musicians p=1.0					
FCz – FC3	7.65	0.0012	Dancers > Musicians p=0.00087 Dancers > Laymen p=0.33 Laymen > Musicians p=0.082	0.0096	0.0096	0.47 (0.027)	0.44 (0.019)	0.46 (0.025)
FCz – FC5	8.26	0.00078	Dancers > Musicians p=0.0020 Dancers > Laymen p=0.0039 Laymen > Musicians p=1.0	0.0090	0.0090	0.41 (0.021)	0.39 (0.013)	0.39 (0.012)

Table 2 Electrode pairs with significant synchronization differences for the main factor Group (dancers, musicians, laymen) during the dance & music stimulus in conditions High Acceleration and Low Acceleration over the frequency band theta (4-8 Hz). Significant differences are written in **bold**. pGG stands for Greenhouse-Geisser adjusted p value, pFDR for the p value with False Discovery Rate correction, and PSV for the phase synchrony value.

Dance							
8 – 13 Hz Electrode pair	F(1,51)	pGG	Multiple comparison (Bonferroni)	pFDR	Q	Mean PSV High Acceleration (standard deviation)	Mean PSV Low Acceleration (standard deviation)
FC6 – FC4	13.32	0.00062	Low > High Acceleration p=0.00062	0.0064	0.0064	0.468 (0.0697)	0.480 (0.0695)
FC6 – FCz	6.59	0.013	Low > High Acceleration p=0.013	0.041	0.041	0.403 (0.0615)	0.411 (0.0577)

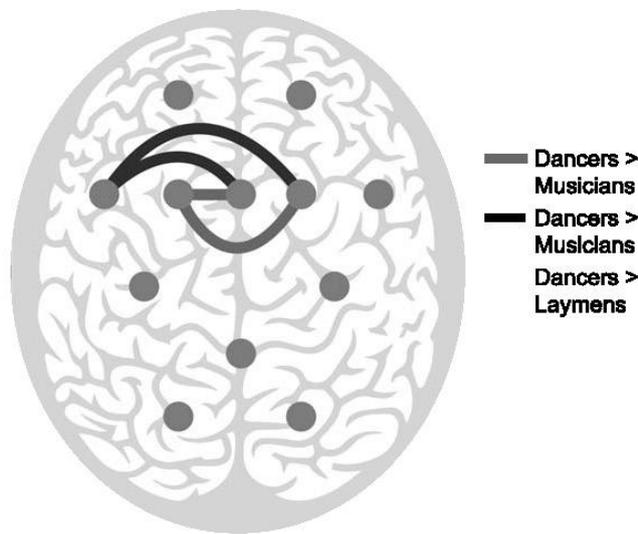
FC4 – FCz	18.32	0.000082	Low > High Acceleration p=0.000082	0.0013	0.0013	0.457 (0.0645)	0.470 (0.0604)
FC4 – FC3	10.15	0.0025	Low > High Acceleration p=0.0025	0.0019	0.0019	0.421 (0.0556)	0.429 (0.0532)
FC3 – C3	7.28	0.0094	High > Low Acceleration p=0.0094	0.037	0.037	0.428 (0.0562)	0.422 (0.0495)
FC3 – Fp1	6.05	0.017	Low > High Acceleration p=0.017	0.049	0.049	0.432 (0.0605)	0.440 (0.0549)
FC3 – Fp2	6.74	0.012	Low > High Acceleration p=0.012	0.043	0.041	0.411 (0.0622)	0.418 (0.0553)
FC5 – C3	9.03	0.0041	High > Low Acceleration p=0.0041	0.026	0.026	0.468 (0.0707)	0.461 (0.0670)
FC5 – Fp1	8.45	0.0054	Low > High Acceleration p=0.0054	0.028	0.028	0.419 (0.0627)	0.426 (0.0627)
FC5 – Fp2	7.31	0.0093	Low > High Acceleration p=0.0093	0.041	0.037	0.400 (0.0621)	0.405 (0.0596)
Fp1 – Fp2	19.47	0.000053	Low > High Acceleration p=0.000053	0.0017	0.0013	0.476 (0.0783)	0.490 (0.0792)
Dance & Music							
8 – 13 Hz Electrode pair	F(1,51)	pGG	Multiple comparison (Bonferroni)	pFDR	Q	Mean PSV High Acceleration (standard deviation)	Mean PSV Low Acceleration (standard deviation)
CPz – C3	5.10	0.028	Low > High Acceleration p=0.028	0.0072	0.0072	0.398 (0.0273)	0.404 (0.0267)
CPz – PO1	7.47	0.0086	Low > High Acceleration p=0.0086	0.0033	0.0033	0.401 (0.0244)	0.409 (0.0282)
C4 – FC4	6.88	0.011	Low > High	0.0038	0.0038	0.420	0.427

			Acceleration p=0.011			(0.0309)	(0.0309)
C4 - FCz	11.78	0.0012	Low > High Acceleration p=0.0012	0.00075	0.00075	0.394 (0.0205)	0.401 (0.0218)
C4 – FC3	6.01	0.018	Low > High Acceleration p=0.018	0.0049	0.0049	0.386 (0.0198)	0.390 (0.0228)
C4 – Fp2	4.61	0.036	Low > High Acceleration p=0.036	0.0087	0.0087	0.383 (0.0198)	0.387 (0.0216)
FC6 – FC4	13.63	0.00054	Low > High Acceleration p=0.00054	0.00047	0.00047	0.463 (0.0408)	0.474 (0.0409)
FC6 - FCz	12.93	0.00073	Low > High Acceleration p=0.00073	0.00050	0.00050	0.398 (0.0197)	0.407 (0.0263)
FC6 – FC3	10.20	0.0024	Low > High Acceleration p=0.0024	0.0013	0.0012	0.388 (0.0247)	0.396 (0.0283)
FC6 – Fp1	13.81	0.00050	Low > High Acceleration p=0.00050	0.00050	0.00047	0.399 (0.0270)	0.408 (0.0341)
FC6 – Fp2	10.72	0.0019	Low > High Acceleration p=0.0019	0.0011	0.0011	0.410 (0.0346)	0.416 (0.0373)
FC6 – PO1	8.12	0.0063	Low > High Acceleration p=0.0063	0.0027	0.0027	0.389 (0.0119)	0.393 (0.0139)
FC4 – FCz	22.06	0.000020	Low > High Acceleration p=0.000020	0.00014	0.00012	0.448 (0.0267)	0.464 (0.0349)
FC4 – FC3	19.63	0.000050	Low > High Acceleration p=0.000050	0.00015	0.00012	0.412 (0.0302)	0.425 (0.0338)
FC4 – Fp1	13.10	0.00068	Low > High Acceleration p=0.00068	0.00052	0.00050	0.407 (0.0313)	0.416 (0.0362)

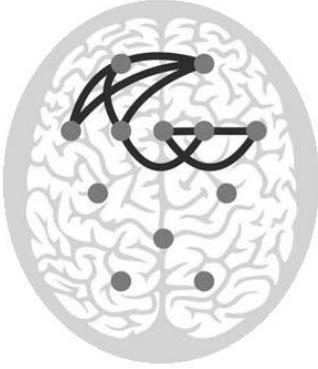
FC4 – Fp2	7.62	0.0080	Low > High Acceleration p=0.0080	0.0032	0.0032	0.417 (0.0430)	0.424 (0.0444)
FC4 – PO1	16.52	0.00017	Low > High Acceleration p=0.00017	0.00029	0.00029	0.389 (0.0142)	0.395 (0.0178)
FCz – PO1	6.13	0.017	Low > High Acceleration p=0.017	0.0048	0.0048	0.384 (0.0149)	0.389 (0.0174)
FC3 – Fp1	14.82	0.00033	Low > High Acceleration p=0.00033	0.00038	0.00038	0.424 (0.0372)	0.434 (0.0392)
FC3 – Fp2	6.27	0.016	Low > High Acceleration p=0.016	0.0049	0.0048	0.404 (0.0306)	0.412 (0.0314)
FC3 – PO1	4.76	0.034	Low > High Acceleration p=0.034	0.0083	0.0083	0.383 (0.0144)	0.387 (0.0143)
FC3 – PO2	9.35	0.0035	Low > High Acceleration p=0.0035	0.0016	0.0016	0.392 (0.0188)	0.397 (0.0205)
FC5 – Fp1	19.60	0.000050	Low > High Acceleration p=0.000050	0.00012	0.00012	0.413 (0.0300)	0.425 (0.0367)
FC5 – Fp2	7.08	0.010	Low > High Acceleration p=0.010	0.0036	0.0036	0.392 (0.0224)	0.399 (0.0254)
FC5 – PO2	7.15	0.010	Low > High Acceleration p=0.010	0.0036	0.0036	0.390 (0.0190)	0.396 (0.0185)
C3 – Fp1	4.48	0.039	Low > High Acceleration p=0.039	0.0090	0.0090	0.389 (0.0205)	0.395 (0.0257)
Fp1 – Fp2	15.64	0.00024	Low > High Acceleration p=0.00024	0.00033	0.00033	0.463 (0.0620)	0.479 (0.0671)
Fp1 – PO2	6.13	0.017	Low > High Acceleration	0.0050	0.0048	0.393 (0.0227)	0.398 (0.0221)

			p=0.017				
Fp2 – PO1	5.92	0.019	Low > High Acceleration p=0.019	0.0049	0.0049	0.391 (0.0173)	0.396 (0.0207)
Fp2 – PO2	10.16	0.0025	Low > High Acceleration p=0.0025	0.00012	0.00012	0.386 (0.0186)	0.391 (0.0190)
PO1 – PO2	4.22	0.045	Low > High Acceleration p=0.045	0.0100	0.0100	0.427 (0.0265)	0.433 (0.0280)
Stick figure							
8 – 13 Hz Electrode pair	F(1,51)	pGG	Multiple comparison (Bonferroni)	pFDR	Q	Mean PSV High Acceleration (standard deviation)	Mean PSV Low Acceleration (standard deviation)
FC6 – Fp1	5.81	0.020	Low > High Acceleration p=0.020	0.049	0.049	0.397 (0.0257)	0.402 (0.0269)
FC4 – FCz	8.37	0.0056	Low > High Acceleration p=0.0056	0.016	0.016	0.455 (0.0300)	0.463 (0.0338)
FC4 – Fp1	8.95	0.0043	Low > High Acceleration p=0.0043	0.015	0.015	0.408 (0.0263)	0.415 (0.0300)
FC4 – PO1	10.28	0.0023	Low > High Acceleration p=0.0023	0.014	0.014	0.392 (0.0158)	0.397 (0.0181)
FCz – PO1	9.57	0.0032	Low > High Acceleration p=0.0032	0.014	0.014	0.386 (0.0183)	0.392 (0.0207)
FC3 – PO2	0.30	0.00017	Low > High Acceleration p=0.00017	0.0015	0.0015	0.387 (0.0154)	0.388 (0.0163)
Fp1 – Fp2	23.17	0.000014	Low > High Acceleration p=0.000014	0.00024	0.00024	0.474 (0.0609)	0.485 (0.0602)

Table 3 Electrode pairs with significant synchronization differences for the main factor Condition (High Acceleration, Low Acceleration) during the dance, dance & music and stick figure stimuli in groups dancers, musicians and laymen over the frequency band alpha (8-13 Hz). pGG stands for Greenhouse-Geisser adjusted p value, pFDR for the p value with False Discovery Rate correction, and PSV for the phase synchrony value.



Dance



— Low Acceleration >
High Acceleration

Dance & Music



— Low Acceleration >
High Acceleration

Stick Figure



— Low Acceleration >
High Acceleration