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DANCE ON CORTEX

ERPS AND PHASE SYNCHRONY IN DANCERS AND MUSICIANS DURING A CONTEMPORARY DANCE PIECE

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ABSTRACT

Music and dance have been important parts of the human experience for millennia. They have enabled interaction which has given rise to resilient communities and rich cultures. Neuroscience has studied music for decades. It has been found to activate both the cortical and deeper brain areas in a unique way. Neuroscience of dance, instead, is a young but quickly growing field. Studies of professional dancers and musicians have highlighted the importance of multimodal interaction and motor-related brain regions in cerebral processing of dance and music.

Current direction of neuroscience is to study the brain in its natural environment. Therefore, simplified stimuli made for the laboratory conditions have been replaced by the stimuli of the real world, such as arts and social interaction. Despite these continuous stimuli have already been successfully studied with functional magnetic resonance imaging (fMRI), methods to study cortical electroencephalography (EEG) under such stimuli are lacking. The purpose of my doctoral research is to develop and use two methods for studying the brain with EEG during the perception of dance and music. One of these methods is based on the event-related potentials (ERPs) to investigate the influence of fast changes of musical features in the brain in a short timescale. The other method utilizes changes in phase synchrony between two electrode channels when investigating cortical dynamics during observation of dance and music over a longer timescale. In my doctoral research, the developed methods are applied in studying differences in cortical dynamics of professional dancers, musicians and laymen.

By both methods, differences in brain activity were found between the groups of experts and laymen when watching dance or listening to music. In addition, these methods detected changes in lower lever brain processes related to uni- and multimodal processing and acceleration of dance movement. By the ERP method, dancers were shown to have an enhanced auditory P50 response when compared to musicians and laymen which refers to dancers' modulated processing of musical features in an early preattentive level. The method of phase synchrony revealed enhanced theta (4-8 Hz) synchrony in dancers when compared to two other groups when watching audio-visual dance. During music, dancers had enhanced theta and gamma (30-48 Hz) synchrony when compared to conditions without music. Both theta and gamma are associated with higher order processing related to multimodal integration, memory and emotions. In contrast, musicians had decreased alpha (8-13 Hz) and beta (13-30 Hz) synchrony when listening to music. These frequency bands are associated with movement preparation and execution. In addition, laymen were the only group which showed systematic changes in synchrony during dance when compared to the conditions without dance. These changes occurred on theta, alpha, beta and gamma bands.

The processing of early changes within uni- and multimodal stimuli, and the accelerated movement of the body did not differ between dancers, musicians and laymen. In all groups, the auditory ERP responses were generally suppressed and sped up during multimodal presentation of music when compared to the unimodal stimulus. Also, the alpha synchrony was decreased in all groups during the parts of the choreography with accelerated large dance movement when compared to parts with nearly still presence. These changes were the strongest during the audio-visual stimulus with a real dancer. Also, during audio-visual dancing stick figure and silent dance some cortical regions showed decreased alpha synchrony for fast dance movement. Decreased alfa-synchrony is associated to motor processing and higher state of alertness in general.

These results show that the methods developed in my doctoral research are suitable in analysing continuous EEG of naturalistic artistic stimuli, and in detecting changes in cortical processing of dancers and musicians during such stimuli. The results of the study suggest that dancers have modulated cortical processing related to multimodal interaction, memory and/or emotions whereas musicians have a special motor-related processing when listening to music. The methods developed in my doctoral research can be used when watching a live performance to study further dance and musical expertise. These methods can be directly applied during music production and light dancing.

Several neurological and psychiatric disorders are associated with abnormalities in oscillatory activity, especially in cross-frequency coupling. Therefore, development of the phase synchrony method to that direction is essential. Together this array of methods could be applied in estimating the efficiency and developing further expressive therapies, such as dance-movement therapy, and in alleviating symptoms as a part of holistic treatment plan for conditions such as Parkinson’s disease, dementia, autism, and pain and mood disorders.

TIIVISTELMÄ

Musiikki ja tanssi ovat tuottaneet kallisarvoisia kokemuksia ihmisille jo vuosituhansien ajan. Niiden kautta syntyneen vuorovaikutuksen avulla on muodostunut elinvoimaisia yhteisöjä ja rikkaita kulttuureja. Musiikkia on tutkittu neurotieteen näkökulmasta jo vuosikymmeniä. Sen on osoitettu aktivoivan sekä aivokuoren alueita että syvempiä aivojen rakenteita ainutlaatuisella tavalla. Tanssin neurotiede sen sijaan on nuori, mutta nopeasti kasvava tieteenala. Ammattitanssijoilla ja -muusikoilla tehdyt tutkimukset osoittavat eri aistien vuorovaikutteisen informaation ja liikkeen aivoalueiden tärkeyden tanssin ja musiikin herättämissä aivoprosesseissa.

Tällä hetkellä neurotiede suuntautuu tutkimaan aivoja niiden luonnollisessa ympäristössä. Sen vuoksi laboratorio-olosuhteisiin suunnitellut yksinkertaiset ärsykkeet on korvattu todellisen maailman ärsykkeillä, kuten taiteella ja sosiaalisella vuorovaikutuksella. Vaikka tällaisia jatkuvia ärsykkeitä on jo menestyksellisesti tutkittu funktionaalisella aivokuvantamisella (fMRI), menetelmät näiden ärsykkeiden tutkimiseen aivosähkökäyrällä (EEG) puuttuvat. Väitöskirjatyöni tarkoituksena on kehittää kaksi menetelmää ja käyttää niitä aivojen tutkimiseen EEG-tekniikalla tanssin katselun ja musiikin kuuntelun aikana. Toinen menetelmä perustuu tapahtumasidonnaisiin aivovasteisiin (ERP) tutkittaessa musiikkipiirteiden nopeiden muutosten vaikutusta aivoissa lyhyellä aikajänteellä. Toinen menetelmä taas perustuu kahden elektrodikanavan välille syntyvään vaihesynkroniaan tutkittaessa aivokuoren toiminnan muutoksia tanssi- ja musiikkihavainnon aikana pidemmällä aikajänteellä. Väitöskirjatyössäni kehitettyjä menetelmiä käytetään ammattitanssijoiden, -muusikoiden ja kontrolliryhmän aivokuoren toiminnan erojen tutkimiseen.

Sekä ERP- että vaihesynkroniamenetelmän avulla havaittiin eroja ammattilaisryhmien ja kontrolliryhmän välillä tanssin katselun ja musiikkin kuuntelun aikana. Lisäksi näillä menetelmillä havaittiin muutoksia matalamman tason aivoprosesseissa, jotka liittyivät yksi- ja moniaistillisen ärsykkeen käsittelyyn sekä kehon liikkeen kiihtyvyyden muutoksiin. ERP-menetelmän avulla tanssijoilla voitiin osoittaa olevan suurempi P50-kuulovaste verrattuna muusikoihin ja kontrolliryhmään, mikä viittaa musiikkipiirteiden kehittyneeseen käsittelyyn aikaisella esi-tietoisella tasolla. Vaihesynkronia-menetelmän avulla tanssijoilla havaittiin voimistunut theta-synkronia (4-8 Hz) verrattuna kahteen muuhun ryhmään audiovisuaalista tanssia katsottaessa. Tanssijoilla todettiin musiikin kuuntelun aikana voimistunut theta- ja gamma-synkronia (30-48 Hz) verrattuna ärsykkeisiin ilman musiikkia. Sekä theta- että gamma-synkronia liitetään korkeamman tason aivoprosesseihin, kuten moniaistillisen ärsykkeen yhdistämiseen, muistiin ja tunteisiin. Muusikoilla sen sijaan oli heikentynyt alfa- (8-13 Hz) ja beta-synkronia (13-30 Hz) musiikin kuuntelun aikana. Nämä taajuuskaistojen

synkronian heikkenemiset yhdistetään liikkeeseen valmistautumiseen ja sen suorittamiseen. Kontrolliryhmä oli ainoa ryhmä, jolla löytyi systemaattisia synkronian muutoksia tanssin katsomisen aikana verrattuna ärsykkeisiin ilman tanssia. Nämä muutokset esiintyivät theta, alfa, beta ja gamma-kaistoilla.

Tanssiin ja musiikkiin liittyvän nopeasti muuttuvan yksi- ja moniaistillisen ärsykkeen ja kehon kiihtyvän liikkeen käsittelyssä ei havaittu eroja tanssijoiden, muusikoiden ja kontrolliryhmän välillä. Kaikissa ryhmissä ERP-kuulovasteet heikkenivät ja ilmaantuivat nopeammin moniaistillisesti esitetyn musiikin aikana, kun sitä verrattiin vain ääniärsykkeenä esitettyyn musiikkiin. Alfa-synkronia laski kaikissa ryhmissä koreografian kiihtyvää suurta liikettä sisältävien osioiden aikana, kun sitä verrattiin lähes paikallaanolevan läsnäolon osioihin. Nämä muutokset olivat voimakkaimpia tanssijan esittämän audiovisuaalisen ärsykkeen aikana. Samantyyppisiä muutoksia havaittiin myös äänettömän tanssin ja audio-visuaalisen tikku-ukon ärsykkeiden aikana. Heikentynyt alfa-synkronia viittaa liikkeen käsittelyyn sekä yleisen vireystason nousuun.

Nämä tulokset osoittavat, että väitöskirjatyössäni kehitetyt menetelmät soveltuvat luonnollisen taiteellisen ärsykkeen synnyttämän jatkuvan EEG-aineiston analysointiin sekä aivokuoren toiminnan muutoksien havainnointiin ja tutkimiseen tanssijoilla ja muusikoilla kyseisen ärsykkeen aikana. Tutkimuksen tulokset viittaavat siihen, että tanssijoiden aivokuoren, erityisesti moniaistilliseen tanssin katseluun, muistiin ja/tai tunteisiin liittyvät toiminnat eroavat tanssijoilla muusikoista ja maallikoista. Muusikoilla sen sijaan musiikin kuuntelu herättää erityisiä liikkeeseen liittyviä aivokuoren prosesseja. Tässä tutkimuksessa kehitettyjä menetelmiä voidaan käyttää live-esityksen katselun aikana tanssijoiden ja muusikoiden aivokuoren eroavaisuuksien syvempään ymmärtämiseen. Näitä menetelmiä voi suoraan soveltaa musiikin soittamisen ja kevyen tanssimisen aikana.

Aivojen oskillaation epätavalliset muutokset liittyvät moniin neurologisiin ja psykiatrisiin häiriöihin. Nämä muutokset esiintyvät erityisesti eri tajuuskaistojen välisessä synkroniassa. Sen takia on olennaista kehittää vaihesynkronia-menetelmää taajuuskaistojen välisen synkronian suuntaan. Tätä uutta metodologista kokonaisuutta voitaisiin soveltaa terapian vaikuttavuuden arvioinnissa ja ilmaisullisten terapioiden, kuten tanssi- ja liiketerapian, kehittämisessä pidemmälle esimerkiksi Parkinsonin taudin, muistisairauksien, autismin, ja kipu- ja mielialahäiriöiden oireiden lievittämiseksi ja jopa parantamiseksi osana kokonaisvaltaista hoito-ohjelmaa.

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Hanna Poikonen

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This dissertation is based on the following publications:

I Poikonen, H., Alluri, V., Brattico, E., Lartillot, O., Tervaniemi, M. & Huotilainen, M. Event-related brain responses while listening to entire pieces of music. Neuroscience 312, 58-73 (2016).

II Poikonen, H., Toiviainen, P. & Tervaniemi, M. Early auditory processing in musicians and dancers during a contemporary dance piece. Scientific Reports 6, 33056 (2016).

III Poikonen, H., Toiviainen, P. & Tervaniemi, M. Dance on cortex: Enhanced theta synchrony in experts when watching a dance piece. European Journal of Neuroscience 47(5), 433-445 (2018).

IV Poikonen, H., Toiviainen, P. & Tervaniemi, M. Naturalistic music and dance: Cortical phase synchrony in musicians and dancers. PLoS One 13(4), e0196065 (2018).

The publications are referred to in the text by their roman numerals.

ABBREVIATIONS

ANOVA	analysis of variance
EEG	electroencephalography
EPSP	excitatory postsynaptic potential
ERD	event-related desynchrony
ERP	event-related potential
FDR	false discovery rate
FIR	finite impulse response
fMRI	functional magnetic resonance imaging
fNIRS	functional near-infrared spectroscopy
GG	Greenhouse-Geisser
HG	Heschl's gyrus
ICA	independent component analysis
IPSP	inhibitory postsynaptic potential
ISI	inter-stimulus interval
MEG	magnetoencephalography
MNS	mirror neuron system
MoRI	magnitude of the rapid increase
MTG	middle temporal gyrus
N100	negative evoked potential around 100 ms after a stimulus
P50	positive evoked potential around 50 ms after a stimulus
P200	positive evoked potential around 200 ms after a stimulus
PLFP	preceding low-feature phase
PMC	premotor cortex
PSV	phase synchrony value
RMS	root mean square
STG	superior temporal gyrus
SMA	supplementary motor area

1 INTRODUCTION

The purpose of my doctoral research is to develop and use two methods for studying the brain with EEG during the perception of dance and music. One of these methods is based on the event-related potentials (ERPs) to investigate the influence of fast changes of musical features in the brain in a short timescale. The other method utilizes changes in phase synchrony between two electrode channels when investigating cortical dynamics during observation of dance and music over a longer timescale. In my doctoral research, the developed methods are applied in studying differences in cortical dynamics of professional dancers, musicians and laymen.

1.1 TEST SETTINGS IN EXPERIMENTAL PSYCHOLOGY FROM PAST TO NOW

In the dawn of the experimental psychology, the test settings were as simple as playing a sine wave sound or showing a flash of light to a human participant. The cortical reactions were studied with preliminary electroencephalography (EEG), which meant in practise attaching a few electrodes on scalp. Depending on the state of alertness of the participant, the signal of the electrodes varied in amplitude and frequency. After showing a sequence of a simple unitary stimulus and averaging these epochs, event-related components (ERPs) were revealed. These components were reasoned to be the reflection of the sensory processes of the brain and they were surprisingly similar, though occurring on different parts of the head, no matter if the stimulus was visual or auditory.

A long way has been walked to reach the complex experimental procedures of today. With the expanding human knowledge and processing power of the computers as well as the rapid development of the brain imaging technology, such a development has been possible. The riddles of the brain have ever more detailed answers, though much of the brain processes in health and disease, cognition and affection, collaboration and isolation, remain beyond understanding. The simple experiments of the past have enabled the advances in the research of the higher brain functions, such as memory, imagination and empathy. Artistic stimuli and expertise play key roles in understanding the exclusivities of the human brain - the ability to reason, create and smoothly surf back and forth between past, present and future.

1.2 ABOUT NEUROSCIENCES OF MUSIC

Neurosciences of music have a tradition of a few decades and the results have been successfully applied not only in the versatile fields of sound art and music education but also in hospitals, schools and therapy settings. In addition to auditory processes, music excites the brain in a unique manner related to cognition, affection and movement. Professional musicians are an excellent group to study when aiming to understand the influence the decade-long immersion to music on an everyday level has on the brain.

1.2.1 FROM AUDITION TO COGNITION AND AFFECTION

Music is shown to activate auditory cortex differently than speech, environmental, sinusoidal and other non-musical sounds (Alho et al., 1996; Belin et al., 2000; Meyer et al., 2006a, 2006b; Tervaniemi et al., 2009). Alluri and colleagues (2012) showed that the brain regions, which activated corresponding to the musical features encapsulating timbre and loudness of a musical piece, locate in the auditory regions on the left and right temporal cortex. These regions are superior temporal gyrus (STG) and middle temporal gyrus (MTG) on the former and STG and Heschl's gyrus (HG) on the latter.

Last decades of the past century were dedicated to the musical cognition to understand the cortical connections of music and cognition. On the ongoing century, the focus of research has shifted to music and its emotional content which occur deeper in the brain, in the subcortical structures. Meyer and colleagues (2006a,b) investigated the perception of musical timbre by choosing as stimuli instrument sounds and comparing them to the sine wave sounds. In addition to the enhanced N100/P200 responses[1], they revealed how instruments with varying timbre activated also brain regions associated with emotional and auditory imagery functions. Grewe and colleagues (2005; 2007) studied the strong emotional experience of chills evoked by music noting that the peak emotion of chills is a result of attentive, experienced and conscious musical enjoyment. Furthermore, results by Schaefer and colleagues (2011) suggest that recollecting an event with emotional content involves multiple neural retrieval subprocesses.

Vuust and colleagues (2010) reason in their review how predictions play the key role in music-evoked emotion. Creating a musical structure and violating the expectations in it in both immediate and large-scale context produce not only the one-dimensional feeling of surprise but indeed a large variety of emotions. The hedonic evaluation of responses such as chills and swing is mediated through reward system, and is as such related to the underlying principles of musical expectancy.

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[1] N100 and P200 are event-related responses (ERPs) occurring within approximately 200 milliseconds after an important stimulus event. For further information, see Chapter 3.2.2 Event-related potentials: Early components on page 29.

What distinguishes it from other emotional stimuli, is the ability of music to stimulate the hippocampal structures (Salimpoor et al., 2011; Koelsch, 2014 for a review). Emotional stimuli including music stimulates other limbic structures such as amygdala, insula and orbitofrontal cortex. However, in striking contrast to monetary, food-related and erotic rewards, which do not activate the hippocampus, several studies on music-evoked emotions have reported activity changes within the hippocampal formation. This indicates that music-evoked emotions are not related to reward alone. In general, hippocampal activity has been associated with learning, memory and navigation is space (Ekstrom et al., 2005). Enhanced synchrony on the cortical theta band[2] (4-8 Hz) is associated to the activity in the cortico-hippocampal loop. Indeed, the unique character of music to create emotions through expectations, which are always connected to the musical memories either in immediate or autobiographical past, might have its origins in the activation of hippocampus.

1.2.2 MOTOR CONTROL

In addition to several auditory brain regions, music is shown to activate motor related areas. The kind of motion control required to conduct refined movement sequences of complex action, such as playing an instrument, has fascinated brain researchers for decades. Neural mechanisms of timing are not controlled by a single brain region but by a network of regions that control specific parameters of movement. The cerebellum computes predictive models of movement and controls the motor timing at short time scales, in milliseconds (Lewis & Miall, 2003; Buhusi & Meck, 2005). It is in charge of feedforward control and online error correction based on feedback. It is shown to play a role in acquisition and integration of sensory information and be in charge of fine-grained correction and precise control of movement trajectories (Balasubramanian et al., 2004; Shimansky et al. 2004; Loehr & Palmer, 2006). Basal ganglia, premotor cortex and supplementary motor area, instead, are shown to be in charge of high-level control of sequence execution (Lewis & Miall, 2003; Buhusi & Meck, 2005). They control the longer time intervals of movement of one second and above. Timing in terms of perception and reproduction of more complex musical rhythms are shown to be processed on prefrontal cortex, dorsal premotor cortex (PMC) and lateral cerebellar hemispheres (Bengtsson et al., 2004; Lewis et al., 2004; Chen et al., 2008). Versatile motor control is required in sequenced movement such as finger sequences for key presses and coordination of subcomponents of complex multi-joint movements. Several brain regions are associated to the production and learning of movement sequences. Basal ganglia, for example, is associated

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[2] Theta band is brain oscillation occurring on the frequencies from 4 to 8 Hz. Other frequencies studied in this dissertation are alpha (8-13 Hz), beta (13-30 Hz), and gamma (30-48 Hz). For further information, see Chapter 3.2.3 Frequency bands on page 30.

with well-learned sequences (Doyon et al., 2003) whereas supplementary motor area (SMA) and pre SMA in organizing and chunking of more complex movement sequences (Sakai et al., 2004; Kennerley et al, 2004). Sequence learning and integration of individual movements into unified sequences has been linked to the cerebellum (Penhune & Dyon, 2005; Thach, 1998). The premotor cortex, instead, is suggested to be in charge of the production of complex sequences and motor prediction (Janata & Grafton, 2003; Schubotz & von Cramon, 2003).

Parietal, sensorimotor and premotor cortices are shown to activate when the control of movements requires integration of spatial, sensory and motor information (Johnson et al., 1996; Rizzolatti et al., 1998). The separate neural systems may underlie the ability to learn and produce the spatial and sequential components of a complex task (Hikosaka et al., 2002; Parsons et al., 2005).

The perception and production of rhythm, beat and groove have been studied by several methods. The behavioural studies demonstrate that rhythm and pitch can be perceived separately that but that they also interact when creating a musical perception (Krumhansl, 2000; Jones et al., 2002). The analysis of rhythm may depend to a large extent on interactions between the auditory and motor systems (Bengtsson et al., 2004; Lewis et al., 2004; Janata & Grafton, 2003). However, even in studies where subjects only listen to rhythms, the basal ganglia, cerebellum, PMC and SMA are often shown to be actively involved (Grahn & Brett, 2007). The mental representations of rhythm have been studied by manipulated auditory feedback. Delays and distortions in the auditory feedback alter significantly the motor performance (Pfordresher & Palmer, 2006). Circuitry linking auditory systems to motor systems may be a neural substrate of this cognitive representation.

Whereas the ventral stream from the primary auditory area is related to time-independent object processing, the dorsal stream projecting to the parietal targets is in charge of spatial processing and tracking of time-varying events. The dorsal stream participates to the auditory-motor transformations analogously to the visual dorsal stream (Rauschecker, 2011).

Music and motion seem to be tightly intertwined - also in the brain. No wonder music creates an urge to move, from a gentle swing of the torso to the energetic dance of the whole body. In music production, each brain region has its own contribution to create fast and harmonious movement sequences.

1.2.3 MUSICAL EXPERTISE

Musicians can produce actions more quickly than the central nervous system can perceive sounds or other external sources of feedback which propagate through senses (Keele, 1968; Schmidt, 1975). Performers' auditory and motor memory for music unify, allowing auditory retrieval to engage the motor commands to produce the required movements. Anticipation of the intended sounds selects and initiates correct actions. This kind of anticipation may help in explaining why musicians can so easily adapt and generalize their movements to different contexts.

Musicians show structural differences in the brain relative to non-musicians (Gaser & Schlaug, 2003; Schneider et al. 2002; de Manzano & Ullén, 2018), with larger gray matter volume in areas that are important for playing an instrument. These areas include motor, auditory and visuospatial regions (Gaser & Schlaug, 2003; Zatorre et al., 2007 for a review; de Manzano & Ullén, 2018). Bermudez and colleagues (2009) found correlations in the cortical thickness of musicians' frontotemporal network. The functional evidence highlights the importance if this network in the performance of musical tasks. The auditory–motor pathways in general are shown to be anatomically modulated in musicians (Halwani et al., 2011).

Han and colleagues (2009) suggested that higher gray matter density in the left primary sensorimotor cortex, right cerebellum, and higher white matter integrity in the internal capsule of pianists could reflect the movement-related increases during music practice in adolescence. They obtained the results by comparing pianists with a mean starting age of 12 to non-musicians. Hyde and colleagues (2009), instead, found a correlation in the structural brain changes after only 15 months of musical training in early childhood, and improvements in musically relevant motor and auditory skills. Steele and colleagues (2013) studied early- and late-trained musicians and found that the early-trained group had greater connectivity in corpus callosum. The fractional anisotrophy of this region was related to age of onset of training and sensorimotor synchronization performance. The sensitive period before the age of 7 years seemed to result changes in white-matter connectivity which help in building experience upon. Both functional and structural connectivity of corpus callosum is shown to have instrument specific use-dependent plasticity (piano and string players; Vollmann et al. 2014). Fauvel and colleagues (2014) noticed differences in the resting state fMRI between musicians and nonmusicians and they interpreted the results as a consequence of repeated collaborative use in general networks supporting memory, perceptual-motor and emotional features of musical practice.

Musical aptitude is shown to correlate with the volume of the primary auditory cortex and with neurophysiological responses to sinusoidal tones in this area (Schneider et al., 2002). The fMRI research has revealed how musicians have modulated sound processing in auditory and premotor areas (e.g. Schlaug, 2015 for a review). Functional coupling between the auditory and premotor cortex is not static but varies during playing music (Jäncke, 2012). Moreover, musicians show enhanced electrophysiological responses in the auditory cortex to contour and interval information in melodies (Fujioka et al., 2004), and in the auditory brainstem (Lee et al., 2009) when listening to musical intervals. Brain responses have revealed that musicians have stronger responses to the sound of their own instrument compared to the sinusoidal sound or the sounds of other instruments (Meyer et al., 2006a,b;

Pantev et al., 1998, 2001). Cortical processing of music differs in musicians starting from the preattentive ERP components (Tervaniemi, 2009 for a review). Bhattacharya and colleagues (2001) showed that the gamma-band synchrony increases over distributed cortical areas with musical practice. This increase found in professional musicians when compared to laymen refers to more advanced musical memory when dynamically binding together several features of the intrinsic complexity of music. In addition, professional training in music refines emotional arousal, which was studied in a whole musical piece by Mikutta and colleagues (2014). In the EEG analysis, a mid-frontal theta activity was observed in professional musicians but not in amateurs. During high arousal, professional musicians exhibited an increase of posterior alpha, central delta, and beta rhythm. Strait and colleagues (2009) brought up the subcortical role in the auditory processing of emotional states as a result of their experiment, in which musical training was shown to enhance the perception of vocally expressed emotions measured by brainstem potentials.

Behavioral studies have shown superior processing of well-formed musical structures, such as rhythm, in musicians when compared to nonmusicians and to random musical structure (Kalakoski, 2007; Meinz & Salthouse, 1998). Premotor cortices show modulated responses to metrically organized rhythm patterns even in nonmusicians (Chen et al., 2008), indicating that auditor coupling may be a basic feature of neural organization, although training is suggested to enhance it (Grahn and Rowe, 2009). Indeed, auditory and premotor cortices are coactivated when pianists play music without auditory feedback or listen to music without playing (Bangert et al., 2006; Baumann et al., 2007). Similarly, magnetoencephalography (MEG) shows motor cortical responses in musicians to sound only (Haueisen and Knösche, 2001), whereas increased motor cortical excitability, elicited via transcranial magnetic stimulation, was observed when pianists listened to a well-rehearsed piano melody as opposed to a flute melody (D'Ausilio et al., 2006).

There are several studies investigating the transfer effects of musicianship to the fields such as speech, sound discrimination and mathematics. Although advances of speech and sound discrimination are shown in musicians (Kuhnis et al., 2013; Elmer et al., 2013; Strait et al., 2009), other transfer effects may be explained with other factors such as genetics. Ullén and colleagues (2015) committed a large twin study and noticed that voluntary musical practise and musical perceptual ability were essentially caused by genetic pleiotropy. In addition, differences in intelligence quotient and personality traits of openness to experience and musical perceptual ability as well as the psychological flow experienced during musical activities, which are all important to dedicated musical practise, were correlated with genes. However, in another twin study, de Manzano and Ullén (2018) concluded that changes in the cortical thickness and white matter were caused by musical training.

Mastering an instrument is a comprehensive task combining both genetic and rehearsed abilities. Extraordinary communication of auditory and motor areas in the brain is needed to produce precise and quick movement sequences. Outstanding memory and situational awareness carry the musician into a capturing performance. On top of all, musicianship requires finely tuned emotional sensitivity to be able to transmit the delicate emotional messages encoded into the flow of music.

1.3 ABOUT NEUROSCIENCES OF DANCE

Neuroscience of dance is the natural next step after the discoveries in the interaction of motor system and auditory areas related to music. In addition to music and movement, embodied communication, touch and self-awareness are inseparable elements of dance. These elements are crucial for the wellbeing of both an individual and a community. Therefore, explorations of dance and the brain go beyond audio-motor interaction reaching out to the core structures of humanity. Professional dancers are in the forefront of interest and information when approaching this yet rather unknown branch of neuroscience.

1.3.1 MULTISENSORY PROCESSING OF FINE-TUNED AND COMPLEX MOVEMENT

Both watching and performing dance are multisensory processes combining movement, audition, vision, touch and proprioception. Due to technical challenges caused by movement artefacts, recording brain activity while dancing is still not vastly conducted. Thus, in the context of neuroscience of dance, discussion of mirror neuron system (MNS), also known as action observation network, is unavoidable since many studies are based on the observation of dance. Recently, criticism has been presented against MNS theory (Caramazza et al., 2014; Hobson and Bishop, 2016; Lamm and Majdandzic, 2015). However, a proper alternative has not been proposed. Mirror neurons were discovered by Rizzolatti and colleagues (2001 for a review) when they were measuring single-cell electrodes from a primate. They noticed that the same neurons activated both when the primate conducted an action and when it watched the researcher to do the same action. Thus, MNS is thought to support the observation and simulation of other's actions. In humans, premotor and parietal cortices may be involved in action simulation along with the supplementary motor area, superior temporal sulcus and primary motor cortex (Cross et al., 2006; Kruger et al., 2014).

Cross and colleagues (2006) studied with fMRI the simultaneous observation and imagination of familiar and novel dance steps in expert dancers. Brain activity associated with observing and imagining movements was found in the action observation and simulation networks, such as premotor cortex and inferior parietal lobule. This activity was related to the experience participants had with the dance steps and to the subjective rating of their ability to perform the steps. In a sequential fMRI study, Cross and colleagues (2009) scanned nondancers before and after 5 days of training in observation and performance of a dance video game. Training-induced brain activity was found in the action observation and simulation networks, including the premotor cortex and inferior parietal lobule.

Jola and colleagues (2013), instead, were interested in the spectators' experience. In the fMRI scanner, they presented the uni- and multisensory versions of an unfamiliar dance to novice dance spectators. Activity in the superior temporal gyrus correlated between subjects for audio-visual integration. In other studies (Jola et al., 2012; Jola & Grosbras, 2013), they investigated experienced dance spectators and novice spectators when watching live and taped dance performance. They noticed enhancement in corticospinal excitability induced by transcranial magnetic stimulation and measured by motor-evoked potentials both in live versus taped dance and in experienced versus novice than spectators. Brown and colleagues (2006) studied real tango steps during positron emission tomography imaging and they noticed that cerebellum was related to the entrainment of dance steps to music. Putamen instead was in charge of metric motion and superior parietal lobule of spatial guidance of leg movements.

Further studies immersed into the challenging task of measuring brain responses of actual dancing. Tachibana and colleagues (2011) and Ono and colleagues (2014) approached the task by functional near-infrared spectroscopy (fNIRS) imaging. FNIRS measures brain activity in terms of oxyhaemoglobin dynamics similarly to fMRI but has a higher temporal resolution and less motion sensitivity. Tachibana and colleagues studied dancers when they performed a dance video game. Task-related brain activation was found in the superior temporal gyrus and superior parietal lobule and increased as a function of task difficulty. Sequentially, Ono and colleagues showed by using the same video game that frontotemporal oxyhaemoglobin dynamics predicts performance accuracy in the dance game. Cruz-Garza and colleagues (2014), instead, studied dance with EEG and machine learning. The movements could be classified based on the expressiveness in thought or in performed action. They reported selectively increased activity in the premotor, motor and parietal regions during the tasks enabling successful classification despite the motion artefacts.

As reviewed above, the brain in dance has been approached with versatile imaging methods, dance styles and test settings. However, a coherent theoretical background is strikingly lacking. As comparison, theory and notation of Western classical music gave a firm basis for the neurosciences of music in its early stages. In neurosciences of dance, the theory of Rudolf Laban would bring a fundamental structure to this young and scattered field (Maletic, 1987). For example, labanotation is an equivalent notation for movement as music notation is for music. Sharing a common dance theory would help in developing the field into a coherent direction. With a fundamental structure and precise preliminary research, the neurosciences of dance could be elevated to the same internationally praised heights where neurosciences of music have climbed over the decades.

1.3.2 DANCE EXPERTISE

Career as a professional dancer requires several unique characters, starting from the refined control of the whole body in stillness and in movement, all the way to the collaboration in embodied and verbal levels. In addition, the interaction with sound and space is constant. Dance expertise requires a versatile set of complex skills related to multimodal processing, spatial awareness, embodied interaction, movement timing and execution as well as mnemonic and emotional processing. Expertise in dance is shown to modify the brain functions vastly, especially in the premotor regions (Orlandi et al., 2017; Karpati et al. 2015, for a review), and modulate interpersonal entrainment in movement (Sofianidis et al., 2014; Washburn et al., 2014).

Dance expertise has been linked to structural differences in the brain. The brain structure of professional dancers and musicians has been investigated in comparative studies, structural MRI showing that the gray matter in both groups of experts is thicker on superior temporal regions when compared to laymen (Karpati et al., 2017). In addition, Karpati and colleagues suggested that the gray matter structure in the STG is correlated with performance on dance imitation, rhythm synchronization and melody discrimination tasks. On the other hand, the structure of the white matter seems to be different in dancers, musicians and laymen. Giacosa and colleagues (2016) suggested that dancers have increased diffusivity and reduced fibre coherence in corpus callosum, corticospinal tract and superior longitudinal fasciculus whereas musicians showed reduced diffusivity and greater coherence of fibres in similar regions. Further, the diffusivity measures were related to performance on dance and music tasks that differentiated the groups. Also, the functional integration in the cortical basal ganglia loops, that govern motor control and integration, is suggested to be enhanced in dancers when compared to laymen (Li et al. 2015).

Calvo-Merino and colleagues (2005) studied ballet dancers and capoeira practitioners in the fMRI scanner. They noticed that several motor related areas are specified to observe the movement the practitioner was trained for. Bilateral premotor cortex, intraparietal sulcus, right superior parietal lobe and left posterior superior temporal sulcus had a higher activation in dancers when watching ballet movements when compared to capoeira movements. In addition, Pilgrimm and colleagues (2010) studied ballroom dancers and nondancers, and noticed that dancers had a greater activation in the premotor cortex when observing ballroom dance videos.

In an EEG study, event-related desynchrony (ERD) was noticed to increase in dancers when watching dance in comparison to nondance movements (Orgs et al. 2008). The increase in ERD was observed in power of alpha and beta frequency bands and is thought to represent inhibition of sensorimotor cortex activity by the action observation system. In another EEG study utilizing the event-related paradigm, event-related potentials (ERPs) differed based on dance experience when professional tango dancers, beginner tango dancers and non-dancers watched tango steps which were committed either correctly or incorrectly (Amoruso et al., 2014). Anticipatory activity generated by frontal, parietal and occipital brain regions showed difference between groups and predicted later activity in motor and temporal regions.

These are the preliminary studies made to understand the structural and functional brain processes which are unique to the professional dancers. Based on such conversation openers, more complex paradigms can be designed to understand the dance expertise not only in perception, sound and movement, but also in cognition, affection and imagination. Furthermore, presence, embodied awareness and collaboration, which all are as self-evident components of dance to a professional dancer as music and movement, can be investigated.

2 AIMS OF THE STUDY

Aims of the whole work described in this Doctoral dissertation

The research presented in this dissertation had two aims. *First*, to develop methods to analyse continuous EEG data of artistic multimodal stimuli of dance and music. Previously, there has been no method to analyse continuous music with ERPs nor continuous dance with any EEG method. *Second*, to apply these methods in comparing the brain functions of professional dancers, professional musicians and people without background in dance or music when watching a contemporary dance piece. These results help in understanding the brain processes related to dedicated dance and music practises. Both the methods and the gained knowledge of expertise could later be applied in dance and music based therapy interventions in treating and alleviating the symptoms of a wide range of health conditions, such as autism, dementia, Parkinson's disease, stroke, brain lesions, and pain and mood disorders.

The specific aims of each study

Study I: In the first study, we develop a method for EEG based on fast changes in musical features to analyse real musical pieces across the musical genres. We look for rationale behind the magnitude and latency of the ERPs with the magnitude of the rapid increase (MoRI) in the musical feature and the length of the preceding low-feature phase (PLFP), which is comparable to the inter-stimulus interval (ISI) of traditions ERP research.

Study II: In the second study, we aim to prove the functionality of the method developed in Study I by replicating the analysis to different musical pieces and different participants. By using this method, we investigate the influence of expertise in dance and music in the processing of fast changes in musical features during continuous music. Since professional background in music is shown to facilitate the brain processes for individual sounds compared to laymen, we hypothesize that these kinds of changes would also be detected during continuous music listening. Further, the comparison of dancers and musicians may help in defining whether these changes are influenced by personal history in intense listening of music or in active music-making. In addition, we compare the event-related auditory processing during uni- and multimodal stimuli (Music and Dance & Music, respectively).

Study III: The third study focuses on developing a method for EEG, based on movement acceleration, to analyse continuous dance. We investigate the influence of expertise in dance and music in the processing of continuous dance and music in different frequency bands. We consider that dance training could shape perception in unimodal and multimodal conditions. We are interested whether this kind specification would be measurable with the phase synchrony of EEG. We also contrast fast and slow parts of the choreography, and hypothesize alpha synchrony to decrease over the central and posterior electrodes during large dance movement when compared to nearly still presence. We also compare cortical phase synchrony during energetic dance and nearly still presence in uni- and multimodal setting. Such a comparison is made with both a real dancer and a dancing stick figure to understand the relevance of the human body in visual perception.

Study IV: In the fourth study, we compare cortical phase synchrony in different frequency bands during uni- and multimodal dance and music stimuli. We contrast energetic dance and nearly still presence (High Acceleration and Low Acceleration, respectively) separately for dancers, musicians and laymen. We expect dancers to have significant changes in theta band during dance performance. We are curious whether these changes in dancers would be evoked by music, dance, or both. Also, we anticipate music (but not dance) to evoke changes in cortical synchrony in musicians.

3 METHODS

3.1 SUBJECTS AND PROCEDURE

3.1.1 PARTICIPANTS

Study I

Sixteen right-handed native Finnish speakers took part in the experiment; 10 females and 6 males, age ranged from 20 to 46 years (27.1 on average). No participants reported hearing loss or history of neurological illnesses. All participants were musical laymen with no professional musical education. However, many participants reported a background in different music-related interests such as learning to play an instrument, producing music with a computer, dancing or singing. Age and the non-professional musical background of each participant are reported in the Table A1. The experimental protocol was conducted in accordance with the Declaration of Helsinki and approved by the ethics committee of the Faculty of the Behavioural Sciences at the University of Helsinki.

Studies II, III and IV

In studies II, III and IV the same pool of participants was used and the data of these three studies were collected during the same sessions. However, because of the special requirements of the data analysis, slightly different groups entered the data analysis of Study II in comparison to Studies III and IV, which had identical grouping.

20 professional musicians, 20 professional dancers and 20 people without a professional background in either music or dance participated in the experiment. 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 A2. 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. 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. All subjects gave written informed consent. 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.

Study II
Two participants from each group were left out from the data analysis since their EEG data lacked several electrodes around the brain area of our interest. Thus, in the groups of musicians and dancers there were 13 female and 5 male participants and in the control group 12 female and 6 male participants. The age of the participants ranged from 21 to 31 years (25.4 on average) among musicians, from 23 to 40 years (29.1 on average) among dancers and from 20 to 37 years (25.3 on average) among laymen.

Study III and Study IV
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, a musician and a participant in the control group. Therefore, their data could not be used in the data analysis. In addition, a musician and a participant in the control group had too many either missing or noisy EEG channels and we excluded them from the analysis.

Thus, in the groups of musicians and laymen there were 13 female and 5 male participants and in dancers 12 female and 6 male participants. The age of the participants ranged from 21 to 31 years (25.6 on average) among musicians, from 23 to 40 years (29.2 on average) among dancers and from 20 to 37 years (25.0 on average) among laymen.

3.1.2 PROCEDURE

Study I
The stimuli were presented to the participants with Presentation 14.0 program in a random order via headphones with and an intensity of 50 decibels above the individually determined hearing threshold. The participants were advised to listen to the music while sitting as still as possible with eyes open. The playback of each piece of music was launched by the researcher after a short conversation with the participants via microphone.

Study II, III and IV
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 and watch the dance video as still as possible. The playback of each trial was launched by the researcher. 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.

3.2 ELECTROENCEPHALOGRAPHY (EEG)

EEG is a widely-used method in both clinical and research use in recording brain activity. The advantages of EEG are non-invasiveness, relatively low price of the EEG device and of building an EEG laboratory, and excellent millisecond-scale temporal resolution. However, due to the electrical properties of cerebrospinal fluid and skull, the analysis of the origin of the signal is not straightforward. The spatial scale can be improved with covering the head densely with EEG electrodes and using advanced computational methods in solving the inverse problem when estimating the origin of the electromagnetic signal from the brain tissue.

3.2.1 THE ORIGIN OF THE EEG SIGNAL

There are two types of synapses, electric and chemical. Most the synapses are chemical, in which neurotransmitters transmit the signal chemically from a presynaptic neuron to a postsynaptic neuron. Transmembrane potential of a postsynaptic neuron changes due to neurotransmitters. The potential gained is called a postsynaptic potential (Tortora and Derrickson, 2006). A neurotransmitter can affect the postsynaptic cell either by depolarizing or hyperpolarizing the part of the membrane into which the neurotransmitter is drifted. Depolarization causes excitatory postsynaptic potential (EPSP) which increases the intracellular voltage, which enables the action potential to arise with lower stimulus. Hyperpolarisation, instead, occurs when inhibitory postsynaptic potential (IPSP) is formed. Then, the action potential is more unlikely to initiate (Tortora and Derrickson, 2006).

Current sinks and sources in the brain tissue formed by EPSPs and IPSPs are the most important source of electromagnetic changes in the brain. These changes can be detected externally with EEG and MEG. EPSPs produce a local membrane current sink into the extracellular area of the synapse (Figure 1). Also, corresponding magnitude of distributed passive sources are produced to preserve current conservation. Vice versa, IPSPs cause a local membrane current source. More distant distributed passive sinks also must occur to preserve current conservation (Nunez and Srinivasan, 2006).

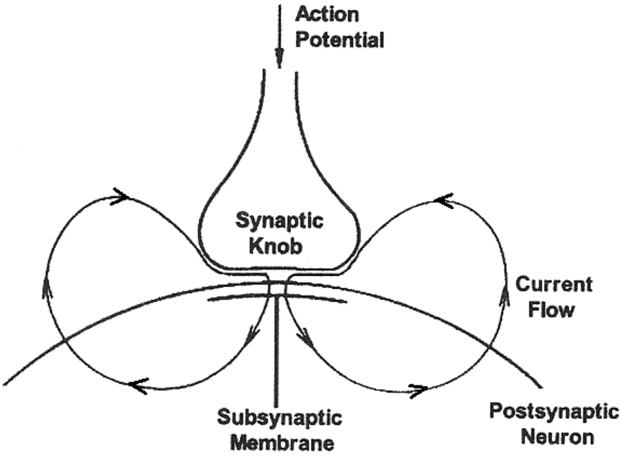

Figure 1 Membrane current due to local excitatory synaptic action. An action potential propagates from the presynaptic neuron into the synaptic knob in which a neurotransmitter is released. The neurotransmitter affects the membrane of the postsynaptic neuron and more positive ions flow into the postsynaptic neuron. A current sink is formed into the extracellular region of the synapse due to the local shortfall of positive ions. More distant distributed current sources balance the ion inflow to preserve current conservation (Figure modified from Nunez and Srinivasan, 2006).

A combination of active/passive source and passive/active sink forms a dipole source in which the source head emits flow of an ionic substance and sink head accepts the flow. If the current source and sink heads alter in a high frequency, the currents couple and induce a magnetic field. In general, the brain activity occurs in such low frequencies that there is no need to study the coupling between electric and magnetic fields allowing the fields to be studied separately (Nunez and Srinivasan, 2006). Still, electric and magnetic activity of the brain measured with EEG and MEG, respectively, have different origins. EEG detects the radial electrical changes on the cortex whereas MEG detects the tangential electric currents which elicit a magnetic field outside of the brain.

A dipole is an extremely simplified model of the formation of brain activity, even in a microscopic level. A bit more informative way to express the local brain function is to use field variables (also called synaptic action fields). Simply put, synaptic action fields are defined as the numbers of active excitatory and inhibitory synapses per unit volume of tissue at any given time, independent of their possible participation in cell assemblies (Nunez and Srinivasan, 2006). Synaptic action fields generate electric and magnetic fields in the brain. As known, a bunch of neurons of a unified area tends to function in synchrony even though there is no initial firing signal present. In addition to synchronized activation of neurons, the propagation of the brain activation depends on cell assemblies. Cell assemblies connect different parts of the brain together and enable the brain to process a lot of information simultaneously in different locations on the cortex and to transmit processed information rapidly to other locations on the cortex. It is estimated that the typical path length between any two cortical neurons is only two or three synapses. Cognitive function of the brain, for example, is based on dense neural network which enables several parts of the cortex to co-operate and to work for the same procedure (Nunez and Srinivasan, 2006).

3.2.2 EVENT-RELATED POTENTIALS: EARLY COMPONENTS

Event-related potentials (ERPs) measured invasively on the cortical surface or noninvasively on the scalp indicate the summated dipole fields of extracellular currents. These dipole fields are generated by cortical pyramidal cell populations that have become synchronously active because of an external sensory event or an internal motor or cognitive event. The subsecond temporal time scale of ERP detects the rapid changes in cognitive dynamics. When interpreting ERPs, it is crucial to consider the latency and amplitude of the positive and negative components. These components span over brief periods of time before or after a measurable event and have their origin in sensory, motor and higher cognitive processes (Bressler and Ding, 2006). The EPR components do not only reflect the basic sensory processes evoked by the stimulus but some of the components are evoked by the psychological demands of the situation (Rugg and Coles, 2002).

The early post-stimulus components, P50, N100 and P200, are exogenous indicating the response to the physical properties of the sensory stimulus. Since these early sensory components are considered obligatory and normally present with or without attention, awake or asleep, and aroused or relaxed, they have clinical value as a test of the integrity of the subcortical sensory pathways. N100 is a broadly negative wave over the fronto-central scalp that begins at 60-80 milliseconds and can last until 160 milliseconds after the onset of a sound. Even though the sensory N100 component largely reflects the acoustic energy on stimulus onset, the longer duration of the stimulus may increase the amplitude of N100. Also, an extension in the silent period preceding the stimulus onset, ISI, increases the N100 amplitude (Woods, 1995).

Generally, the N100 is thought to represent the initial extraction of the information from sensory analysis of the stimulus (Näätänen and Picton, 1987 for a review), or the excitation relating to the allocation of a channel for information processing out of the auditory cortex (Hansen and Hillyard, 1980). The N100-P200 complex is referred to as the vertex potential because of its largest amplitude on the upper surface of the brain (Hillyard and Kutas, 1983). Sensory gaiting, reflecting healthy inhibitory functions to filter out irrelevant sensory information, is shown to suppress P50, N100 and P200 responses in a paired-sound paradigm (Fuerst et al., 2007; Rentzsch et al., 2008).

A basic form of spatial analysis, topographic mapping, may be performed when the electrodes on the scalp form a dense grid. Topographic distribution is one of the most important features of ERP which complements other features such as amplitude, latency, polarity and frequency content. Topographic mapping is sometimes useful when clarifying the location of some ERP components which are otherwise difficult to disambiguate. When more complex spatial analysis of ERP is required, spatial spectral analysis, spatiotemporal Principal Component Analysis and inverse transformation can be used to estimate the cortical sources (Bressler and Ding, 2006).

Alluri and colleagues (2012) suggested that timbre-related acoustic components of continuous music correlate positively with activations in large areas of the temporal lobe. Since we wanted to study fast neural responses on auditory areas in the temporal cortices, we chose to focus on the timbral features of brightness, spectral flux, and zerocrossing rate. In addition, the feature root mean square (RMS) related to loudness was studied. The ERP method is shown to be adequate in the studies of musical timbre (Pantev et al., 2001; Caclin et al., 2008). Also, Meyer and colleagues (2006a,b) proposed that the N100 and P200 responses are enhanced to instrumental tones when compared to sine wave tones.

3.2.3 FREQUENCY BANDS

The brain oscillations are traditionally divided to five frequency bands: delta (0.5-4 Hz), theta (4-8 Hz), alpha (8-13 Hz), beta (13-30 Hz) and gamma (> 30 Hz). Alpha and beta band have been associated with motor processes (Hobson and Bishop, 2016; Pineda, 2005; Pavlidou et al., 2014). Anterior desynchronization on the alpha band is associated with decrease in the mu wave, which is traditionally connected to the perception and conduction of movement (Pineda, 2005 for a review but see also Caramazza et al., 2014). Posterior alpha instead is associated to the attentional processes in timing and inhibition (Klimesch, 2012 for a review). Theta band, and its coupling to gamma band, are suggested to be crucial in several cognitive and affective functions (Krause et al., 2000; Kahana, 2006; Canolty and Knight, 2010). 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). 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). 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).

3.2.3.1 Phase synchrony

ERPs may take a form of continuous periodic response when sensory stimuli are presented rapidly and repetitively. The phenomenon is called steady-state response and these evoked potentials have the same repetition frequency as the stimulus. The frequency, on which the steady-state response has the maximal value, is suggested to represent the natural resonant frequencies of oscillating neuronal populations in the sensory cortices. On visual cortex, evoked and induced oscillations in the gamma frequency range have been proposed to be responsible for visual binding, Gestalt perception, and attention and memory representations (Herrmann, 2001). The oscillation has also proven useful in the assessment of cognitive function (Silberstein et al., 1995).

Steady-state response is a special case presenting the ability of neurons to function in synchrony. Generally, synchronization is the fundamental way of neurons to communicate within and between brain regions. Neurons can be coupled on the same frequency or over different frequency bands (cross-frequency coupling; Canolty and Knight, 2010). Different states of consciousness have characteristic synchronization frequencies, delta in deep sleep, alpha in a relaxed awake state and higher frequencies in concentration and higher brain functions, as simplified examples. Interpreting facial expressions of a friend or walking on a busy street while talking on the phone are specific examples of complex everyday tasks. When performing such a demanding task, lower frequencies, such as theta, sync higher frequencies, such as various frequencies in gamma, to form a wide, coherent and dynamic network (Voytek and Knight, 2015).

3.2.3.2 Phase synchrony value

From the point of view of signal processing, the brain is a nonstationary and noisy system. There are several methods to evaluate the neuronal synchronization based on the amplitude and/or the phase of the synchrony. Amplitude-based power measures reveal synchrony locally whereas calculations of the phase synchrony discover synchronies also over distant brain regions. Since our interest was to study the synchronous neural assemblies across the brain, we chose the phase synchrony approach. We wanted to use a simple method which had already been shown successful in studying a continuous artistic stimulus, and therefore, we chose the method of phase synchrony value (PSV; Tass et al., 1998; Bhattacharya and Petsche, 2000). A disadvantage of the PSV method is that it doesn’t eliminate the zero-lagged interactions possibly leading to a problem of volume conduction.

Phase-locking index and weighted phase locking-index are less sensitive to volume conduction. However, to the extent of our knowledge, these methods have not yet been used in analysing naturalistic artistic stimuli.

The PSV is calculated based on the Hilbert transform of the band-pass filtered EEG signal. The synchronization indices are estimated based on the Shannon entropy of the inter-electrode phase difference distribution. Let $\varphi_i(t)$ and $\varphi_j(t)$ denote the instantaneous phases of the signal measures from sensors i and j. To obtain the synchronization index, we calculate the phase difference distribution of $\varphi_i(t) - \varphi_j(t) \in [0,2\pi]$ using N bins, denoted by $(p_k), k = 1,\dots,N$. The phase synchronization index is obtained as $\rho_{ij} = (S - S_{max})/S_{max}$, where $S = -\sum_{k=1}^{N} p_k \ln p_k$, and $S_{max} = \ln N$. In our analyses, we used N=50.

3.2.4 EEG STIMULI

Study I

Three pieces of music from different genres were used as stimuli: a modern tango (*Adios Nonino* by Astor Piazzolla, stimulus length 8 minutes 30 seconds from which the last 30 seconds were not included into the analysis due to the audience applauses), an acoustic lullaby (*Bless* by Kira Kira, stimulus length 5 minutes 43 seconds) and a deep techno track (*My Black Sheep* by Len Faki and remixed by Radio Slave, stimulus length 5 minutes 20 seconds). *Adios Nonino* was chosen due to its large variation among several musical features related to loudness, timbre, tonality and rhythm and to allow comparison to the work of Alluri and colleagues (2012; 2013). The acoustic lullaby had English lyrics pronounced in an unclear way which made the singing sound more like humming. The techno piece consisted of rhythmical sound spread over a wide frequency spectrum with a predominant regular beat but without a melody. It was chosen due to the strong, even rhythmical structure and the lack of harmony in contrast to the acoustic lullaby with lingering melody. The musical structure of *Adios Nonino* is versatile whereas *Bless* and *My Black Sheep Radio Slave* had more constant structure with repetitive musical patterns.

Study II, III and IV

Audiovisual excerpts of *Carmen* composed by Bizet-Shchedrin were used as stimuli. 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.

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 2, 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.

Figure 2 A still image from the choreography presented by a real dancer (on left) and a stick figure (on right).

3.2.5 EEG ACQUISITION

Study I
The EEG data were recorded with 10-20 system (Jasper, 1958) with BioSemi bioactive electrode caps with 64 EEG channels and 5 external electrodes placed at the tip of the nose, left and right mastoids and around the right eye both horizontally and vertically. The offsets of the active electrodes were kept below 25 mV in the beginning of the measurement and the data were collected with a sampling rate of 2048 Hz. The beginning and the end of each musical piece was marked with a trigger into the EEG data.

Study II, III and IV
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.

3.2.6 EEG DATA ANALYSIS

Carterette and Kendall (1999) describe the perceptual process as something that operates on the principle of contrast or change. When listening to music, the sensory mechanisms look for changes in order to make sense about the auditory information. In addition, Kluender and colleagues (2003) suggest that the perceptual systems of all sensory modalities respond mainly to changes. Looking for strong contrast, being it in musical features or in movement acceleration, was the fundamental guideline when designing the data-analysis of all four studies.

3.2.6.1 MIRToolbox

Study I and II

For Studies I and II, we used MIRtoolbox (version 1.3.1; Lartillot and Toiviainen, 2007) to computationally extract the musical features. Since our interest was to study the early auditory processing evoked by fast changes in music, we chose to analyse the following low-level features: Brightness, RMS amplitude, zero-crossing rate and spectral flux. Low-level features are those that are perceived in a bottom-up fashion without a need for domain-specific knowledge. For instance, loudness, pitch and timbre processing automatically recruit sensory mechanisms, and are performed rapidly in very short-time spans. On the other hand, rhythm and melody contour encapsulate context-dependent aspects of music and recruit perceptual processes that are top-down in nature, and require a longer time-span. Each one of four features chosen captures a different perceptual element in music. Excluding RMS, these musical features are the same as found to activate the auditory areas in the temporal cortices in the study by Alluri and colleagues (2012).

Brightness was computed as the amount of spectral energy above a threshold value fixed by default in MIRtoolbox at 1500 Hz for each analysis window (Lartillot and Toiviainen, 2007). Brightness is influenced by both the pitch of the sound and the characteristic spectrum of the instrument with which the sound is created. RMS is related to the dynamics of the song and defined as the root average of the square of the amplitude (Lartillot and Toiviainen, 2007). Louder sounds have high RMS values whereas quieter ones have low RMS values. The zero-crossing rate, known to be an indicator of noisiness, is estimated by counting the number of times the audio waveform crosses the temporal axis (Lartillot and Toiviainen, 2007). Higher zero-crossing rate indicates that there is more noise (less harmonic sounds) in the audio frame under consideration. Spectral flux represents the Euclidian distance between the spectral distributions of successive frames (Lartillot and

Toiviainen, 2007). If there is a large amount of variation in spectral distribution between two successive frames, the flux has high values. Spectral flux curves exhibit peaks at transition between successive notes or chords. These musical features were obtained by employing short-time analysis using a 25-millisecond window with a 50% overlap (Tzanetakis and Cook, 2002). Overlapping of windows is recommended in the analysis of musical features to detect fast changes in the features and their possible inactive periods with a precise time resolution.

We designed an algorithm, implemented in MATLAB, for the search of time points with rapid increase of a musical feature. The algorithm was tuned using specific parameter values adapted to each musical feature in each song of Studies I and II. In our studies, the time period with low feature values preceding the rapid increase in the value of the musical feature corresponds to the ISI) of the previous literature. However, in our studies, the intervals are not between individual stimuli anymore nor are the intervals completely silent, and thus this ISI-type of period is called the Preceding Low-Feature Phase (PLFP) in Studies I and II.

The length of the PLFP was modified and the rapid increase was required to exceed a value called magnitude of the rapid increase (MoRI). The mean values of all the segments of each one of the 20 sound excerpts and each musical feature were calculated and the magnitude of the change from the lower threshold value Vn- to the higher threshold value Vn+ was defined based on the mean value (MVn) in each sound excerpt for each musical feature. The largest changes in the musical features were when the Vn- remained under -20 % of MVn and Vn+ increased above +20 % of MVn. The smallest changes in the musical features were when the Vn- remained under -15 % of MVn and Vn+ increased above +15 % of MVn. Valid triggers were preceded by a PLFP whose magnitude did not exceed the lower threshold Vn-. The length of PLFP with values below Vn- was 625 milliseconds minimum and 1 second maximum. In all cases, valid triggers had an increase phase that lasted less than 75 milliseconds during which the feature value increased from Vn- to Vn+.

3.2.6.2 MoCapToolbox

Study III and IV

For Studies III and IV, we used MoCap Toolbox (version 1.1; Burger and Toiviainen, 2013) to computationally extract the movement qualities. 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; Luopajärvi, 2012).

Changes in the cortical synchrony are generally found within a couple of seconds after observing the initiation of movement. We were interested in rhythmical movement with continuous and overlapping flow of newly initiated movements. 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. 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. Movements during Low Acceleration can be described as very subtle dancing with strong embodied presence. Despite the absence of vast dance movement, these parts of the choreography reflect internal dance, and are crucial for the aesthetic aspects and for interpretation of the emotions relevant for the storyline.

3.2.6.3 EEGLAB

Preprocessing

Study I

The EEG data of all the participants were first preprocessed with EEGLAB (version 9.0.2.2b; Delorme and Makeig, 2004). The external electrode of the nose was set as a reference. The data were down-sampled to 256 Hz, high-pass filtered with 1 Hz and low-pass filtered with 30 Hz with finite impulse response (FIR) filtering based on the firls (least square fitting of FIR coefficients) MATLAB function. Visually detected EEG channels with a noisy signal were removed from the analysis.

Study II

The EEG data of all the participants were first preprocessed with EEGLAB (version 9.0.2.2b). 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 30 Hz.

Study III and IV

The EEG data of all the participants were first preprocessed with EEGLAB (version 12.0.2.5b). 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. 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 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.

ERP and Synchrony

Study I and II: ERP analysis

The triggers related to the musical features extracted with MIRtoolbox were added to the preprocessed EEG data. In continuous speech, the best ERP-related results are gained when the triggers are set into the beginning of the word (Teder et al., 1993; Sambeth et al., 2008). Long inter-stimulus interval is shown to increase the amplitude of the N100 component (Polich et al 1987). Additionally, strong stimulus intensity has been shown to enhance ERP responses (Picton et al., 1977; Polich et al., 1996). Previous knowledge from the individual sound processing was utilized in our study of continuous music, in which the individual sounds are connected to each other in an overlapping and dynamic manner.

In Study I, eight triggers per each feature per each song were set in 10 cases out of the 12 combinations of the song and the musical feature. However, in two cases (for RMS of *Bless* and for brightness of *My Black Sheep Radio Slave*), only 7 triggers were set because in these cases only seven time points during the song matched with the computationally set limits of the musical feature. For each musical feature, the triggers were set in the manner described in detail in Table A3. In Study II, approximately 10 triggers per each feature were set.

After adding the triggers into the preprocessed data, the data were treated with Independent Component Analysis (ICA) decomposition with the runica algorithm of EEGLAB (Delorme and Makeig, 2004) trained with default settings (decomposition of input data using the logistic infomax ICA algorithm of Bell and Sejnowski (1995) with the natural gradient feature of Amari and colleagues (2000) to detect and remove artefacts related to eye movements and blinks as well as the heartbeat. ICA decomposition gives as many spatial signal source components as there are channels in the EEG data. Thus, in Study I, there were 68 components excluding the data of four participants for whom one noisy channel each had been removed in preprocessing. 67 ICA components were decomposed. Typically, 2 to 5 ICA components related to the eye and heartbeat artefacts were removed. The noisy EEG data channels of the abovementioned four participants were interpolated. Thus, in Study II the amount of ICA components was 128 in 22 participants. In the remaining 32 participants, several noisy channels each were removed in preprocessing and therefore less than 128 ICA components were decomposed in them. Noisy EEG data channels of these 32 participants were interpolated. The average number of interpolated channels among these 32 participants was 3.1 channels, the actual number of interpolated channels varying from one per person up to 8 per person. The continuous EEG data were separated into epochs according to the triggers. In Study I, the epochs started 3000 milliseconds before the trigger and ended 2000 milliseconds after the trigger. In Study II, the epochs started 500 milliseconds before the trigger and ended 1000 milliseconds after the trigger. In both studies, the baseline was defined according to the 500-millisecond time period before the trigger. To double check the removal of the eye artefacts, the epochs with amplitudes above ± 100 microvolts were rejected. In addition, in Study I, all the epochs were visually inspected and no artefacts were detected in the data.

Study III and IV: Synchrony analysis

We calculated the PSVs (presented in detail in the chapter 3.2.3.2 Phase synchrony value) of the EEG data to the same 5-second segments as were defined before as High Acceleration and Low Acceleration. A similar method has also been used in EEG data analysis with continuous music stimuli (Bhattacharya and Petsche, 2000). The data were analysed within a time-window of 5 seconds and then these PSVs for each 5-second trial were averaged so that there was a PSV value for each participant in each condition.

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 gap) so that each electrode was compared pairwise to all the other ones resulting in 66 electrode pairs of comparison. This subset of electrodes was chosen to reduce the load in the statistical analyses. Type 1 error increases rapidly when increasing the set of electrodes under 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.

3.3 STATISTICAL ANALYSES

Study I

The statistical analyses of the ERP data were conducted with MATLAB version R2013a utilizing the Statistics Toolbox. T-tests were calculated over the Cz electrode for each musical feature of each musical piece. The peak value of each participant was defined in the following manner. N100: A minimum value within a time window from 80 milliseconds to 150 milliseconds. P200: A maximum value within 150 and 350 milliseconds. The repeated measures ANOVA for the factors Piece (*Adios Nonino* by Astor Piazzolla, *Bless* by Kira Kira and *My Black Sheep Radio Slave* by Len Faki) and Musical feature (brightness, zero-crossing rate, spectral flux and RMS) was calculated for the same peaks over the electrode Cz as used in the t-tests.

Study II

The statistical analyses were conducted with MATLAB version R2015b. In the statistical analysis, 16 electrodes (B1, B21, B22, B32, C1, C2, C11, C22, C23, C24, D1, D2, D13, D14, D15 and D18 of the 128-channel BioSemi EEG gap) were averaged as one signal. Cz was not included among the averaged channels because it was not recorded from five participants due to a broken electrode. Each participant had 8-10 trials for each musical feature in each sensory modality. The repeated measures ANOVA (between-subject factor: Group (musicians, dancers, control group); within-subject factors: Modality (auditory, audio-visual stimulus) and Musical feature (brightness, spectral flux, RMS, zero-crossing rate)) was calculated for both amplitude and latency of the P50, N100 and P200 responses. The following time windows were chosen. P50: From 30 to 90 milliseconds; N100: From 50 to 150 milliseconds; P200: From 100 to 280 milliseconds.

Study III

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 by pGG 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, these results are referred by p indicating the p values of the multiple comparisons. 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 pGG 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 pGG and the pFDR 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. 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.

Study IV

The statistical analyses were conducted with MATLAB version R2016a. In the statistical analysis, repeated measures ANOVA (between subject factor Dance: No Dance (rest and unimodal music), Low Acceleration and High Acceleration; within subject factor Music: Music Off (rest and unimodal dance of Low Acceleration and High Acceleration) and Music On) was conducted separately for each electrode pair (66 electrode pairs), each frequency band (theta, alpha, beta and gamma) and each group (dancers, musicians and laymen). The main effects for the factor Dance and Music, and the Dance*Music interaction were calculated with the GG adjustment. The multiple comparisons of Dance and Music were calculated with the critical value of Bonferroni. FDR was calculated for each set of 66 electrode pairs from their pGG values to control the expected proportion of false positives. In the results section of this dissertation and in the paper of Study IV, we report only the statistically significant results in which both the pGG and the pFDR are <.05.

4 RESULTS

4.1 AUDITORY EVENT-RELATED POTENTIALS DURING CONTINUOUS DANCE AND MUSIC (STUDIES I AND II)

Study I

The temporal evolution for the values of the feature brightness of Astor Piazzolla's piece *Adios Nonino* and the corresponding brain responses over the same time window are shown in the Figure 3. For Figures 3 and 4, three frontal electrodes (F1, Fz, F2), central electrodes (C1, Cz, C2), parietal electrodes (P1, Pz, P2) and occipital electrodes (O1, Oz, O2) were pooled together to reduce noise in the plotted curves. Evolution of the musical feature spectral flux and its brain responses can be seen for Kira Kira's piece *Bless* in Figure 4.

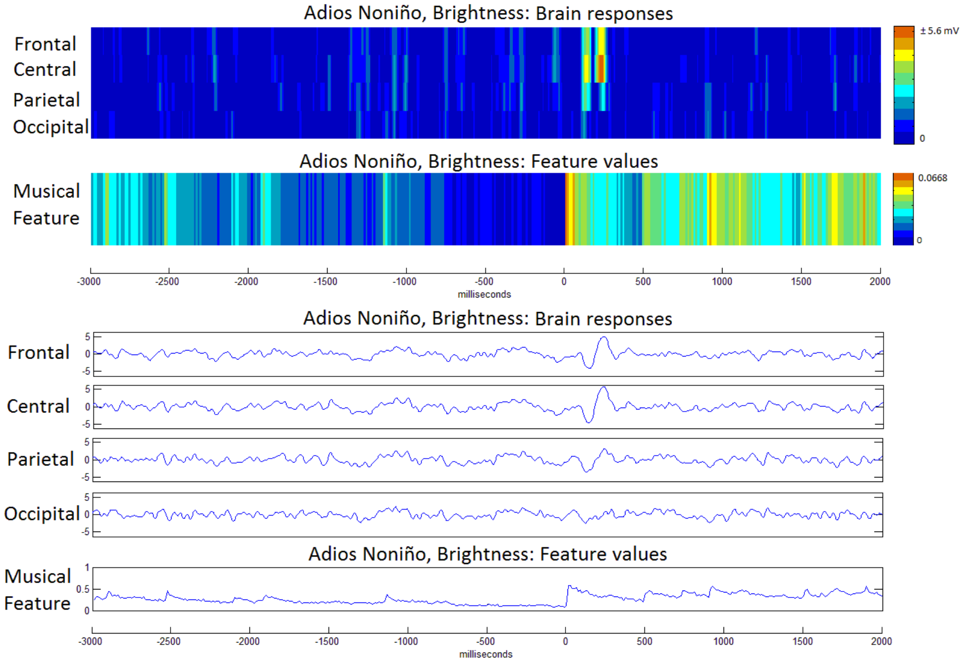

Figure 3 BRAIN RESPONSE TO THE TRIGGERS RELATED TO INCREASE OF BRIGHTNESS IN *ADIOS NONINO* BY ASTOR PIAZZOLLA. The absolute values of the amplitudes of the EEG epochs are presented in the graph above over the frontal (F1, Fz and F2, which are averaged into one signal), central (C1, Cz and C2, which are averaged into one signal), parietal (P1, Pz and P2, which are averaged into one signal) and occipital (O1, Oz and O2, which are averaged into one signal) areas with the EEG epochs from -3 seconds to +2 seconds from the stimulus onset, and the temporal evolution of the musical feature brightness for the same 5-second time window. The stimulus onset is defined by the end of the Preceding Low-Feature Phase (PLFP) period. The brain responses of the EEG epochs are presented in the graph below with the same pooling of electrodes as in the graph above. The feature values present the values of the feature brightness from -3 seconds to +2 seconds from the end of the PLFP period. The brightness curves for the different triggers are averaged into one single curve over the time period from -3 to +2 seconds of the time points of the triggers.

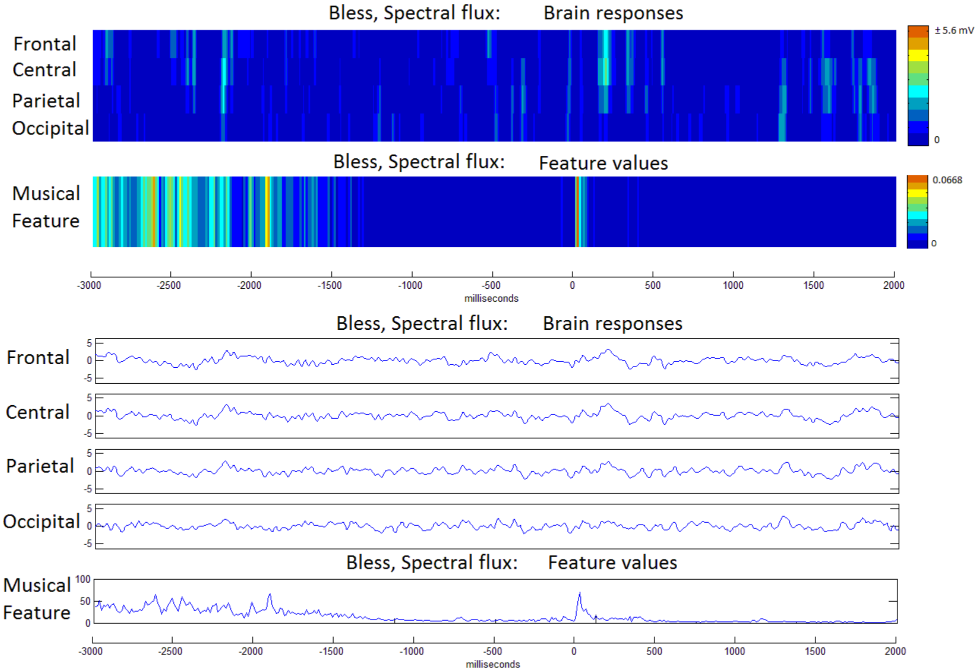

Figure 4 BRAIN RESPONSE TO THE TRIGGERS RELATED TO INCREASE OF SPECTRAL FLUX IN *BLESS* BY KIRA KIRA. The absolute values of the amplitudes of the EEG epochs are presented in the graph above over the frontal (F1, Fz and F2, which are averaged into one signal), central (C1, Cz and C2, which are averaged into one signal), parietal (P1, Pz and P2, which are averaged into one signal) and occipital (O1, Oz and O2, which are averaged into one signal) areas with the EEG epochs from -3 seconds to +2 seconds from the stimulus onset, and the temporal evolution of the musical feature spectral flux for the same 5-second time window. The stimulus onset is defined by the end of the Preceding Low-Feature Phase (PLFP) period. The brain responses of the EEG epochs are presented in the graph below with the same pooling of electrodes as in the graph above. The feature values present the values of the feature spectral flux from -3 seconds to +2 seconds from the end of the PLFP period. The curves of spectral flux for the different triggers are averaged into one single curve over the time period from -3 to +2 seconds of the time points of the triggers.

The graphs reveal the dependence of the change in the voltage measured with ERP signal on the change in the musical feature value. The high value in the musical feature is not alone sufficient to elicit an ERP component but the high feature value needs to be preceded by a relatively long time period with low feature values. The distribution of the increased electrical activity over the cortex can be observed on the graphs of frontal, central, parietal and occipital brain regions. Alluri and colleagues (2012) revealed with fMRI that the low-level musical features, as the ones used in our study, increase activation mainly on the auditory regions located on temporal cortices. In our study, the ERP components indeed are the largest on the central region, which is associated with increased activity originating from the core auditory areas of temporal cortices. Thus, our results suggest that the rapid changes in the low-level musical features evoke neural responses in the temporal auditory areas.

Figure 5 reveals in detail the brain responses on the central area for all musical features of brightness, zero-crossing rate, spectral flux and RMS of all musical pieces of Astor Piazzolla: *Adios Nonino*, Kira Kira: *Bless* and Len Faki: *My Black Sheep Radio Slave* over the electrode Cz. The conventional ERP responses are shown for several features of several musical pieces. The clearest sensory N100 and P200 components were elicited for the brightness feature of Astor Piazzolla: *Adios Nonino* which is illustrated over a longer time window in the Figure 3. The results of the t-tests comparing the N100 amplitudes of the Cz electrode in response to each feature and each musical piece against the zero baseline are listed in Table A4 and for the P200 amplitudes in Table A5.

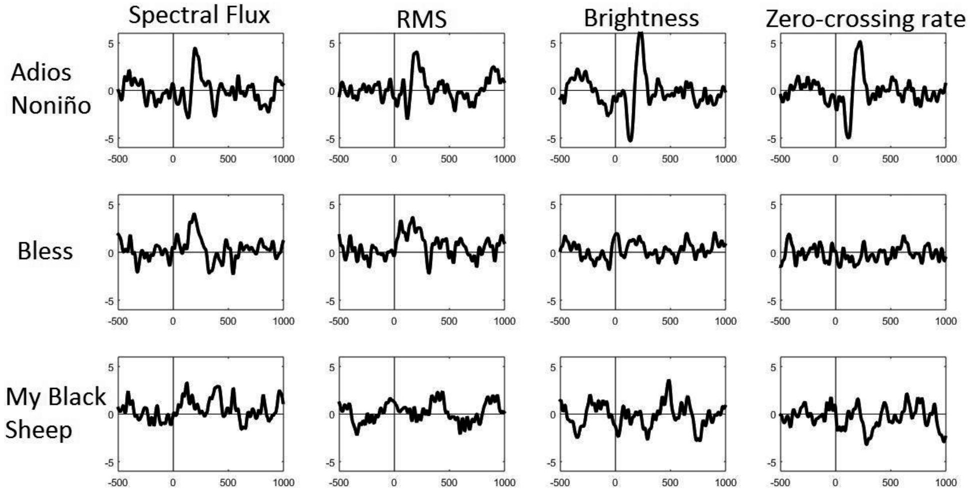

Figure 5 Recapitulation of ERP responses for features spectral flux, RMS, brightness and zero-crossing rate of pieces Astor Piazzolla: *Adios Nonino*, Kira Kira: *Bless* and Len Faki: *My Black Sheep Radio Slave*. The ERP responses are the values measured over the electrode Cz.

At N100 amplitude, the following sound features elicited responses which significantly differed from zero baseline: Spectral flux t(15)=-6.40, p<.0001; RMS t(15)=-2.97, p=.0095; brightness t(15)=-6.40, p<.0001 and zero-crossing rate t(15)=-7.35, p<.0001) of *Adios Nonino*, zero-crossing rate t(15)=-2.76, p=.015 of *Bless* and brightness t(15)=-3.06, p=.0079 and zero-crossing rate t(15)=-2.53, p=.023 of *My Black Sheep Radio Slave*. For all pieces and all musical features of the P200 component, the elicited responses differed significantly from zero baseline, as can be seen in detail in Table A5. In Figures 6-8, scalp maps for selected statistically significant ERP components are presented. In these figures, the ERP components are the strongest in the central region, which suggest the signal summation of the left and right temporal cortices originating from the auditory areas.

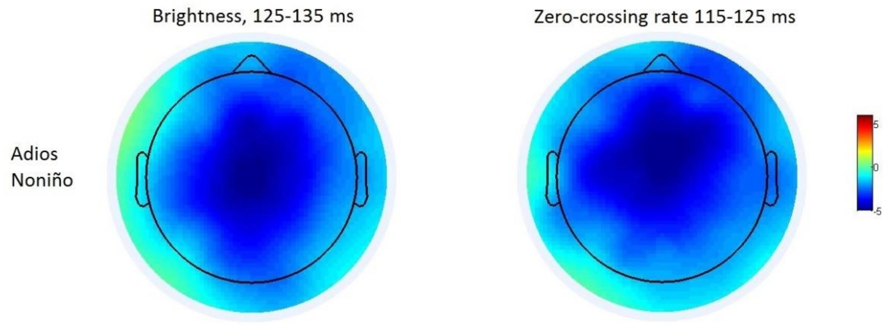

Figure 6 Scalp maps for selected ERP components of the pieces and the musical features, for which the ERP components differ significantly from the zero baseline. The latencies of N100 component for *Adios Nonino* are: Brightness 131 ms and zero-crossing rate 122ms.

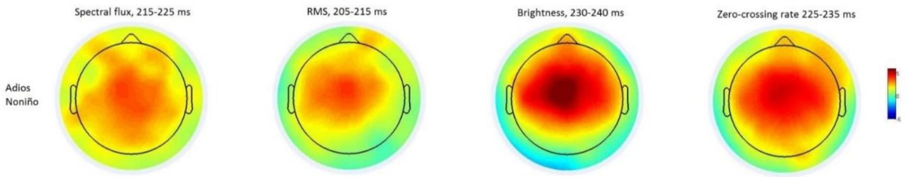

Figure 7 Scalp maps for selected ERP components of the pieces and the musical features, for which the ERP components differ significantly from the zero baseline. The latencies of P200 component for *Adios Nonino* are: Specral flux 221 ms, RMS 210 ms, brightness 234 ms and zero-crossing rate 232 ms.

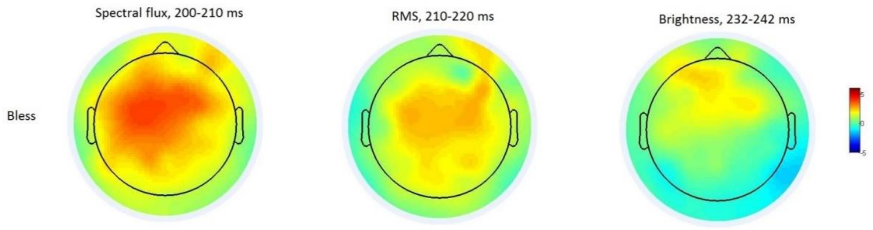

Figure 8 Scalp maps for selected ERP components of the pieces and the musical features, for which the ERP components differ significantly from the zero baseline. The latencies of P200 component for *Bless* are: Spectral flux 203 ms, RMS 215 ms and brightness 237 ms.

The electrode location factors (Laterality and Anterior-posterior distribution) did not interact with any of the factors of interest (Piece and Musical feature).

Therefore, we report here only the results from the repeated measures ANOVA for the factors Piece (*Adios Nonino* by Astor Piazzolla, *Bless* by Kira Kira and *My Black Sheep Radio Slave* by Len Faki) and Musical feature (brightness, zero-crossing rate, spectral flux and RMS) over the electrode Cz.

For N100 component, the main effect of Piece was significant: F(2,180)=22.04, p<.0001, resulting from larger N100 amplitudes for *Adios Nonino* by Astor Piazzolla (-4.17 μV) compared with *My Black Sheep Radio Slave* by Len Faki (-1.09 μV) and *Bless* by Kira Kira (-0.78 μV). We also found a significant main effect of Musical feature: F(3,180)=6.17, p=.0005, deriving from larger N100 responses to the musical features of zero-crossing rate (-3.19 μV) and brightness (-2.81 μV) compared to spectral flux (-1.11 μV) and RMS (-0.96 μV). For brightness and RMS the largest N100 was elicited in *Adios Nonino* and smallest in *Bless*. For zero-crossing rate and spectral flux the largest N100 was elicited with *Adios Nonino* and smallest in *My Black Sheep Radio Slave*.

For the amplitudes of the P200 component, the repeated measures ANOVA revealed a significant main effect of Piece: F(2,180)=11.51, p<.0001, deriving from larger P200 amplitudes for *Adios Nonino* (5.27 μV) compared with *Bless* (4.19 μV) and *My Black Sheep Radio Slave* (3.03V). For Feature, the main effect was not significant: F(3,180)=1.24, p=0.30. For RMS and spectral flux, the P200 was largest in *Bless* and smallest in *My Black Sheep Radio Slave*, and for brightness and zero-crossing rate the P200 was largest in *Adios Nonino* and smallest in *My Black Sheep Radio Slave*.

Study II

The musical features under interest evoked auditory brain responses resembling those recorded in traditional ERP paradigms. Figure 9 shows the grand-average ERPs in the auditory and audio-visual conditions of the musical feature brightness for musicians, dancers and laymen. Figure 10 shows the recapitulation of the grand-average ERPs in the auditory and audio-visual conditions of brightness, RMS, zero-crossing rate and spectral flux for musicians, dancers and laymen. Scalp maps of the P50, N100 and P200 responses in the auditory and audio-visual condition of brightness for musicians, dancers and laymen are presented in Figure 11. Statistical evaluation of the data indicated that most but not all the P50 and N100 responses differed from the zero baseline while all the P200 responses did (see Table A6 for the t-tests of P50 response and Table A7 of N100 response).

In the repeated measures ANOVA, Group (musicians, dancers, control group) was set as the between-subject factor and Modality (auditory, audio-visual stimulus) and Musical feature (brightness, spectral flux, RMS, zero-crossing rate) were set as the within-subject factors.

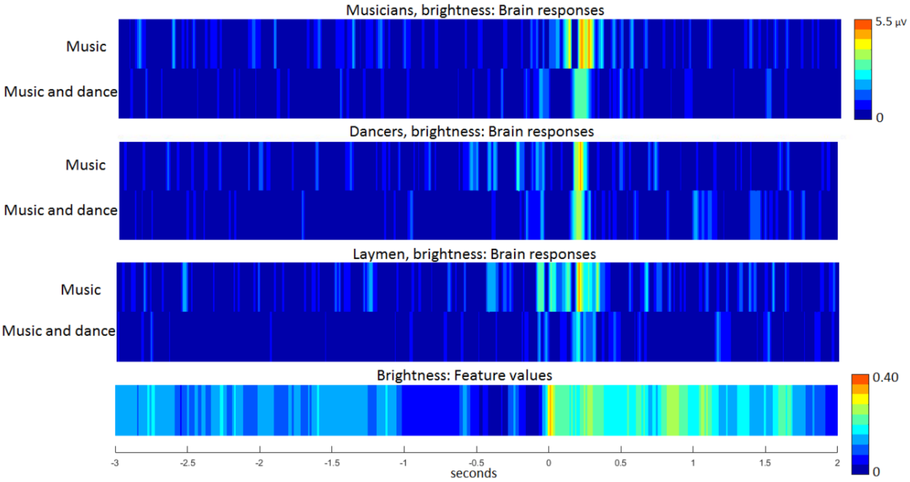

Figure 9 Brain responses of rapid increase in the musical feature brightness in musicians, dancers and laymen during auditory (music) and audio-visual (music and dance) condition. The absolute values of the amplitudes of the EEG epochs are presented over the 16 electrodes in the fronto-central region with the EEG epochs from -3 seconds to +2 seconds from the stimulus onset, and the temporal evolution of the musical feature brightness for the same 5-second time window. The stimulus onset is defined by the end of the Preceding Low-Feature Phase (PLFP) period.

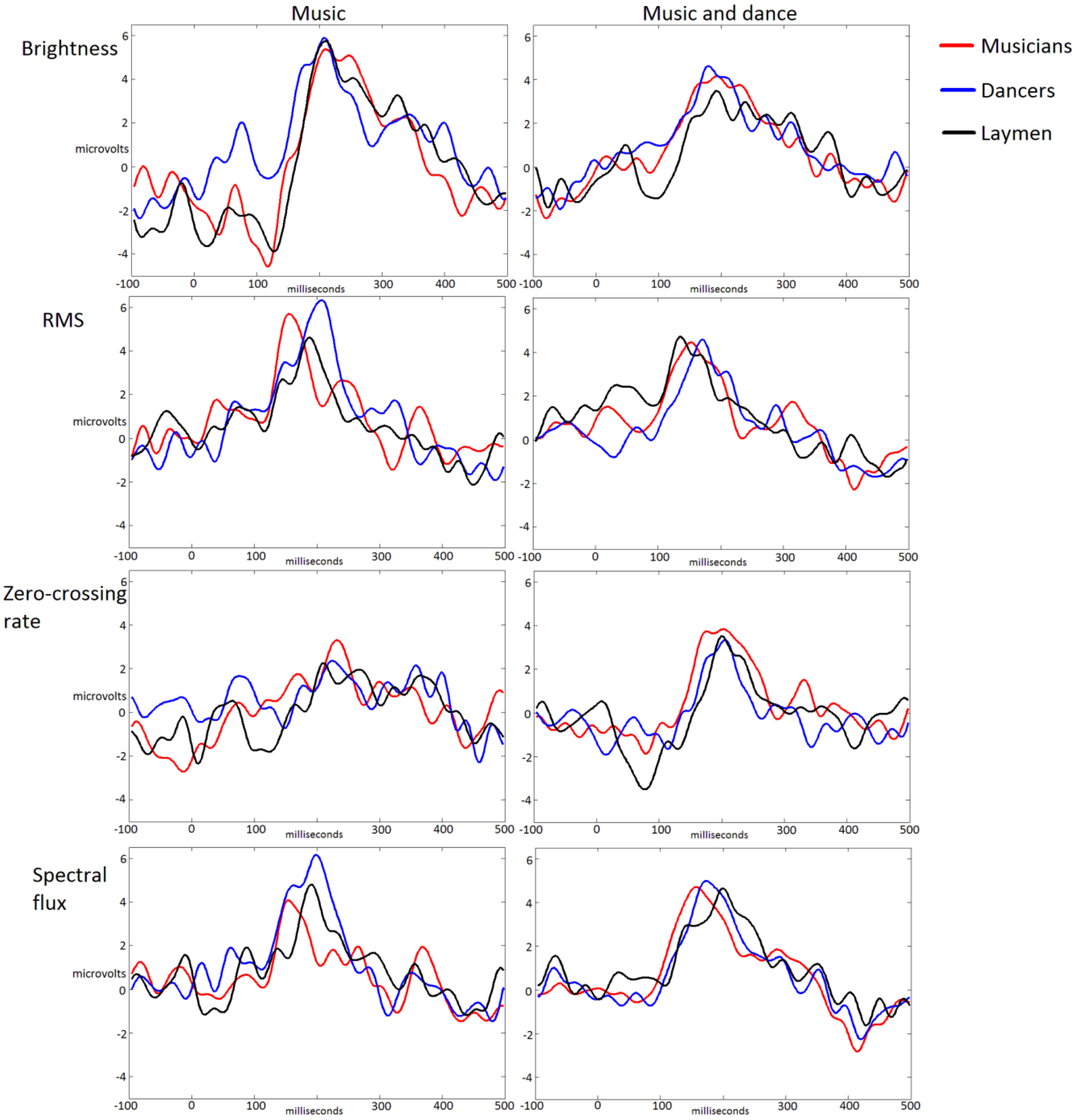

Figure 10 ERPs of the mean value over the averaged signal of 16 electrodes for the rapid changes in the musical features brightness, RMS, zero-crossing rate and spectral flux during the presentation of the auditory stimulus only (music; graphs in the column on the left) and during the stimulus of audiovisual entity (music and dance; graphs in the column on right). In each graph three groups of participants are compared: Musicians, dancers and control group. For brightness, RMS, zero-crossing rate and spectral flux the number of extracted epochs for each test subject were 9, 8, 8 and 10, respectively, excluding a minimal number of epochs rejected due to noisy data.

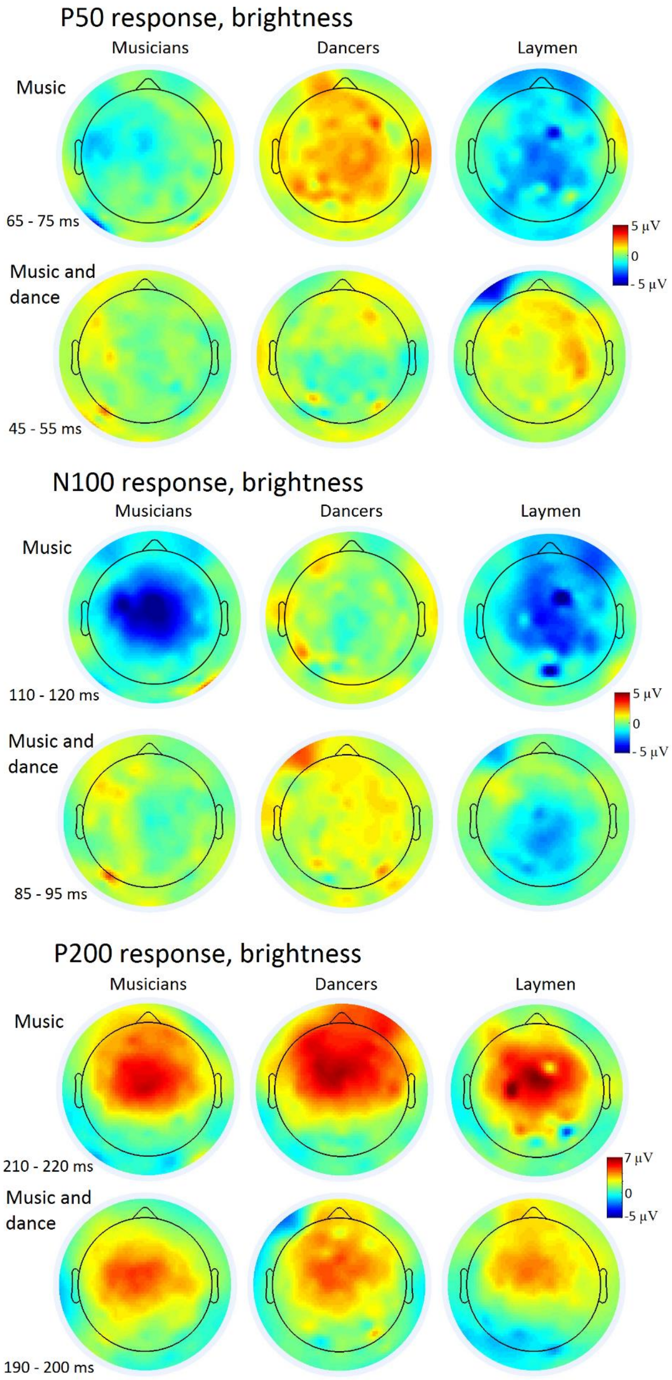

Figure 11 Scalp maps for the P50 (above), N100 (middle) and P200 responses (below) of brightness for musicians, dancers and laymen in auditory (music) and audio-visual (music and dance) condition.

P50 response

For the P50 response, neither the amplitude nor the latency showed a significant main effect for the factor Group. For the P50 latency, Modality showed a significant main effect with the GG adjustment, F(1,51)=8.41, pGG=.0055 resulting from the latencies of auditory (mean latency 62.5 ms) and audio-visual stimulus (57.1 ms). For P50 amplitude, Musical feature showed a significant main effect, F(3,153)=8.11, p=.00020 (mean amplitude of brightness 1.79 µV, RMS 3.58 µV, spectral flux 2.04 µV, zero-crossing rate 1.57 µV). For P50 amplitude the Group*Musical feature interaction F(6,153)=2.67, pGG=.026 was caused by the difference between dancers (2.97 µV) and laymen (1.11 µV), p=.014, and between dancers and musicians (1.28 µV), p=0.030, in the feature brightness revealed by multiple comparison of Group for the musical feature brightness with the critical value of Bonferroni. In addition, P50 amplitude had a significant Musical feature*Modality interaction F(3,153)=3.57, pGG=.037 rising from the difference of the auditory (1.27 µV) and the audio-visual (2.31 µV) stimulus of brightness, p=.047 and of zero-crossing rate, p=.0044, with the amplitudes of 2.71 µV and 0.42 µV, respectively, revealed by multiple comparison of Modality with the critical value of Bonferroni. The amplitudes that did not differ significantly, for the auditory stimulus RMS 3.81 µV and spectral flux 2.31 µV, and for the audio-visual stimulus RMS 3.35 µV and spectral flux 1.77 µV.

N100 response

For the N100 latency the main effects for the factor Modality (F(2,51)=11.35, pGG=.0014, auditory (98.4 ms) and audio-visual stimulus (86.3 ms)) and for the factor Musical feature (F(3,153)=5.69, pGG=.0025, the mean latency of brightness 97.5 ms, RMS 85.7 ms, spectral flux 88.1 ms, zero-crossing rate 98.1 ms) were significant. For N100 amplitude, the interaction Group*Musical feature was significant, F(6,153)=2.31, pGG=.046, rising from the difference between dancers (-2.04 µV) and laymen (-4.69 µV) for the musical feature brightness, p=.023, revealed by multiple comparison of Group for the musical feature brightness with the critical value of Bonferroni. With the mean amplitude of -4.43 µV, musicians did not differ significantly from the other groups. Also, for the N100 amplitude, the main effects of Modality (F(1,51)=5.85, pGG=.019, auditory (-3.17 µV) and audio-visual (-2.41 µV) stimulus) and Musical feature (F(3,153)=14.88, pGG=.00000014, brightness mean -3.72 µV, RMS -1.60 µV, spectral flux -1.96 µV, zero-crossing rate -3.87 µV) were significant as well as the interaction of Musical feature*Modality, F(3,153)=8.44, pGG=.00015 caused by the difference of the auditory (-5.15 µV) and the audio-visual (-2.29 µV) stimulus of brightness, p=.000036, revealed by multiple comparison of Modality with the critical value of Bonferroni. The amplitudes that did not differ significantly, were for the auditory stimulus RMS -1.90 µV, spectral flux -2.13 µV and zero-crossing rate -3.50 µV, and for the audio-visual stimulus RMS -1.30 µV, spectral flux -1.80 µV and zero-crossing rate -4.25 µV.

P200 response

For the P200 response, neither the amplitudes nor the latencies differed significantly between the groups. For P200 latency, the main effect of Musical feature (F(3,153)=13.80, pGG=.0000012, the mean latency of brightness 207.7 ms, RMS 177.5 ms, spectral flux 185.1 ms, zero-crossing rate 206.6 ms) and Modality (F(1,51)=6.04, pGG=.017, auditory (200.2 ms) and audio-visual stimulus (188.3)) were significant. For P200 amplitude, the main effect of Musical feature (F(3,153)=5.65, pGG=.0059, the mean latency of brightness 7.33 µV, RMS 7.08 µV, spectral flux 6.80 µV, zero-crossing rate 5.56 µV) and Modality (F(1,51)=5.63, pGG=.021, auditory (7.08 µV) and audio-visual stimulus (6.30 µV)) were significant as well as the Musical feature*Modality interaction (F(3,153)=4.79, pGG=.0056 rising from the difference of the auditory (8.16 µV) and the audio-visual (6.51 µV) stimulus of brightness, p=.0064 and of RMS, p=.0066, with the amplitudes of 7.90 µV and 6.26 µV, respectively, revealed by multiple comparison of Modality with the critical value of Bonferroni. The remaining P200 amplitudes, which did not differ significantly between the modalities, were for the auditory stimulus spectral flux 6.87 µV and zero-crossing rate 5.40 µV, and for the audio-visual stimulus spectral flux 6.72 µV and zero-crossing rate 5.71 µV.

4.2 CORTICAL PHASE SYNCHRONY DURING CONTINUOUS DANCE AND MUSIC (STUDIES III AND IV)

Study III

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, pGG=.0060, Dancers > Musicians p=0.0044), FC4-FC5 (F(2,51)=10.28, pGG=.00018, Dancers > Musicians p=0.00032), FCz-FC3 (F(2,51)=7.65, pGG=.0012, Dancers > Musicians p=0.00078) and FCz-FC5 (F(2,51)=8.26, pGG=.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 electrode locations of these group differences are illustrated in Figure 12. The statistically significant results according to both pGG and pFDR are presented in Table A8 for the main factor Group. On theta band, there were no further group differences during the stimuli of rest, Music, Dance or Stick Figure.

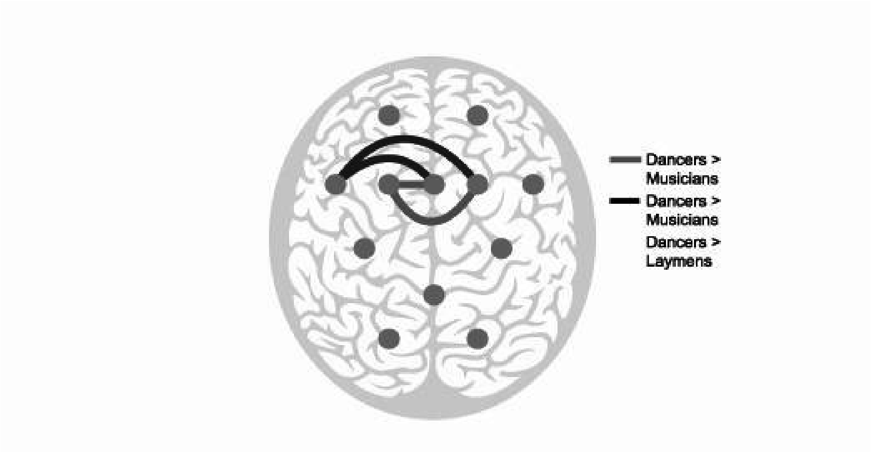

Figure 12 Scalp Significant differences for the main factor Group (dancers, musicians and laymen) during Dance & Music stimulus on the theta band (4-8 Hz). Over the electrode pairs FC3 – FCz and FC3 – FC4 the synchronization is significantly stronger in dancers when compared to laymen (gray line). Over the electrode pairs FC5 – FCz and FC5 – FC4 the synchronization is significantly stronger in dancers when compared to musicians and laymen (black line).

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 with the p value smaller than .05, 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 with p value smaller than .05 indicated *High Acceleration > Low Acceleration*.

During the Dance & Music stimulus the main factor Condition with the p value smaller than .05, the following electrode pairs CPz – C3, CPz – PO1, C4 – FC4, C4 – FCz, C4 – FC3, C4 – Fp2, FC6 – FC4, 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 with the p value smaller than .05, 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 illustrated in Figure 13 and presented in detail in Table A9.

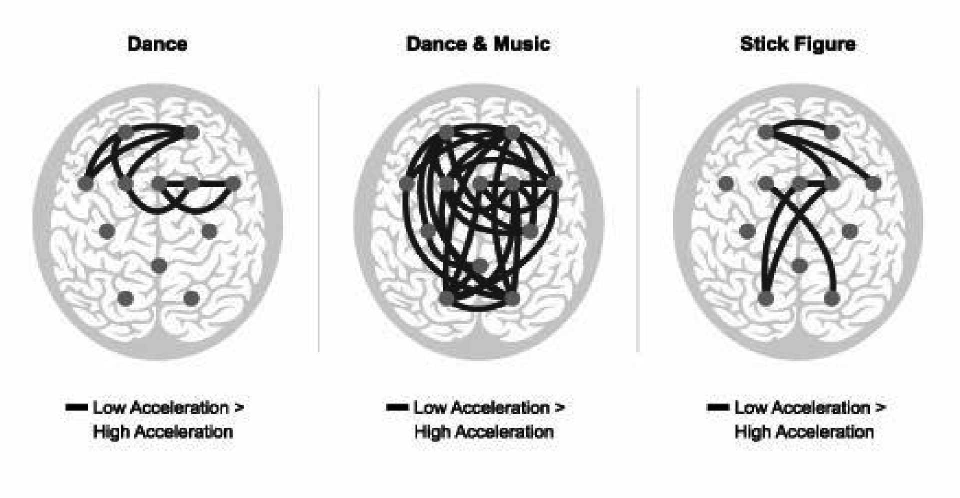

Figure 13 Significant differences for the main factor Condition (High Acceleration, Low Acceleration) during Dance (on left), Dance & Music (in the middle) and Stick Figure (on right) stimuli on the alpha band (8-13 Hz). The black lines connect the electrode pairs over which the synchronization is significantly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

Study IV

All the significant effects of dancers are presented in detail in Table A10. They had a significant main factor Music in the theta, beta and gamma bands. There was no significant main factor Dance nor Dance*Music interactions found in dancers. In addition, dancers had no significant main factor Music in the alpha band.

All the significant effects of musicians are presented in detail in Table A11. They had a significant main factor Music in the alpha and beta bands. There was no significant main factor Dance nor Dance*Music interactions found in musicians. In addition, musicians had no significant main factor Music in the theta nor gamma band.

All the significant effects of laymen are presented in detail in Table A12. They had a significant main factor Music in the theta and gamma bands and significant main factor Dance in the alpha band. Dance*Music interaction was significant in laymen in the theta, alpha, beta and gamma bands. Laymen had no significant main factor Music in the alpha nor beta bands and no significant main factor Dance in the theta, beta nor gamma bands.

These results will be further specified below, within each frequency band and for all groups of participants, comparing experimental situations in which music/dance was on/off. When the dance was on, it was divided to the segments according to the acceleration of the movement: Low Acceleration (nearly still presence or a tender movement of an individual body part) and High Acceleration (vast energetic dance movement). In all the results, they are considered as statistically significant only if pGG < .05 and pFDR < .05.

Theta phase synchrony, 4-8 Hz

In dancers, on theta band, the phase synchrony was significantly stronger in Music On when compared to Music Off over the following electrode pairs CPz – FCz, CPz – Fp1, C4 – PO1, FC6 – FC5, FC6 – PO2, FC4 – FC3, FC4 – FC5, FC4 – Fp1, FCz – FC3, FCz – FC5, FCz – Fp1, FC3 – FC5, FC5 – C3, FC5 – Fp1, FC5 – PO2 and C3 – PO2 (Figure 14).

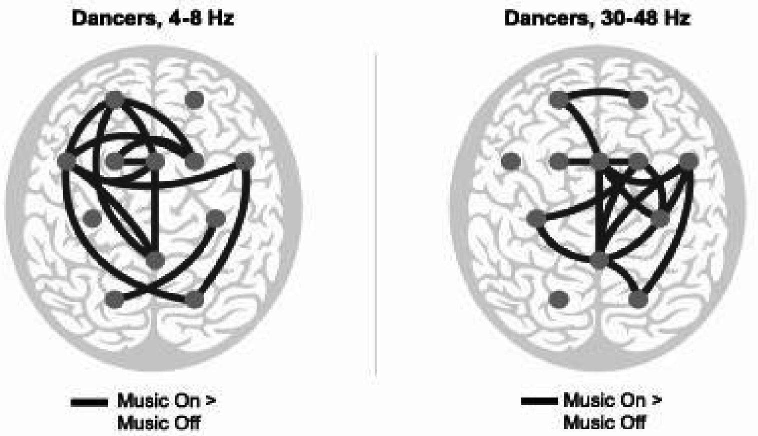

Figure 14 Significant differences for the main factor Music (Music On, Music Off) for dancers on theta (4-8 Hz; left) and gamma band (30-48 Hz; right). The black lines connect the electrode pairs over which the synchronization is significantly stronger during Music On when compared to Music Off. Each gray dot illustrates the location of an EEG electrode on the scalp.

In laymen, on theta band, the phase synchrony was significantly stronger in Music On when compared to Music Off over the electrode pair FC6 – Fp1. Dance*Music interaction was significant in laymen on theta band over the electrode pairs FC5 – Fp1, C4 – PO1, FC6 – PO1 and FC5 – Fp2 (Figure 15). In

Music Off condition over FC5 – Fp1 the synchrony was significantly stronger during both Low and High Acceleration when compared to Dance Off and over C4 – PO1, FC6 – PO1 and FC5 – Fp2 synchrony was significantly stronger only during Low Acceleration when compared to Dance Off while in Music On condition there were no statistically significant differences.

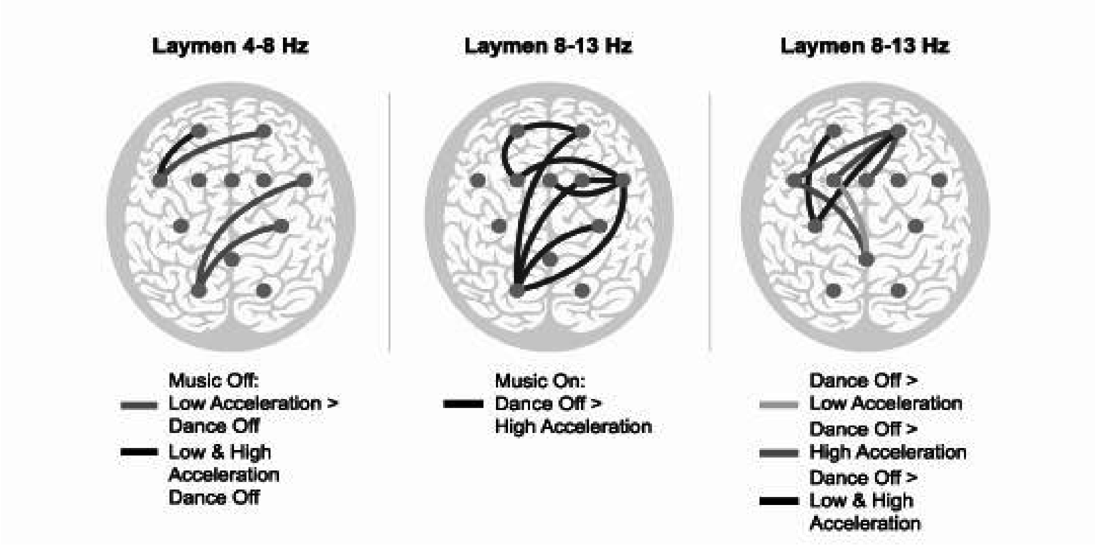

Figure 15 Significant differences for the Dance*Music interaction (Dance Off, Low Acceleration, High Acceleration; Music Off, Music Off) and main factor Music (Music On, Music Off) for laymen on theta (4-8 Hz; on left) and alpha band (8-13 Hz; in the middle Dance*Music interaction during Music On; on right main factor Music). The colour coding of the lines which connect the electrode pairs with significant differences is explained next to each image. Each gray dot illustrates the location of an EEG electrode on the scalp.

Alpha phase synchrony, 8-13 Hz

In musicians, on alpha band, the phase synchrony was significantly stronger in Music Off when compared to Music On over the electrode pair FC3 – C3.

On alpha band, laymen had a significant main effect of Dance over several electrode pairs. Dance Off evoked a stronger synchrony in comparison to High Acceleration over the electrode pairs CPz – FC5, FCz – Fp2, FC3 – Fp2 and FC5 – Fp2 (Figure 4.15). Over the electrode pair CPz – FC3 the synchrony during Dance Off was significantly stronger than during Low Acceleration, and over the pairs C3 – Fp1 and C3 – Fp2 Dance Off was significantly stronger than both Low and High Acceleration. In addition, laymen had a significant Dance*Music interaction on the alpha band over the following electrode pairs C4 – PO1, FC6 – FC4, FC6 – FCz, FC6 – FC3, FC6 – PO1, FC4 – PO1, FC3 – Fp1, Fp1 – Fp2 and Fp2 – PO1 (Figure 4.15). Over all these pairs, in Music On condition the synchrony during Dance Off was significantly stronger when compared to High Acceleration.

Beta phase synchrony, 13-30 Hz
In dancers, on beta band, only the electrode pair FC4 – Fp1 produced a significant main factor Music (Music On > Music Off).
In musicians, on beta band, the phase synchrony was significantly stronger in Music Off when compared to Music On over the following electrode pairs CPz – PO1, FC4 – FC3, FCz – C3, FC3 – FC5, FC3 – C3, FC5 – C3 and PO1 – PO2 (Figure 16).

In laymen, over the pair C4 – FC5, the Dance*Music interaction was significant on beta band, in which the synchrony was stronger during Dance Off when compared to both Low and High Acceleration in Music On condition.

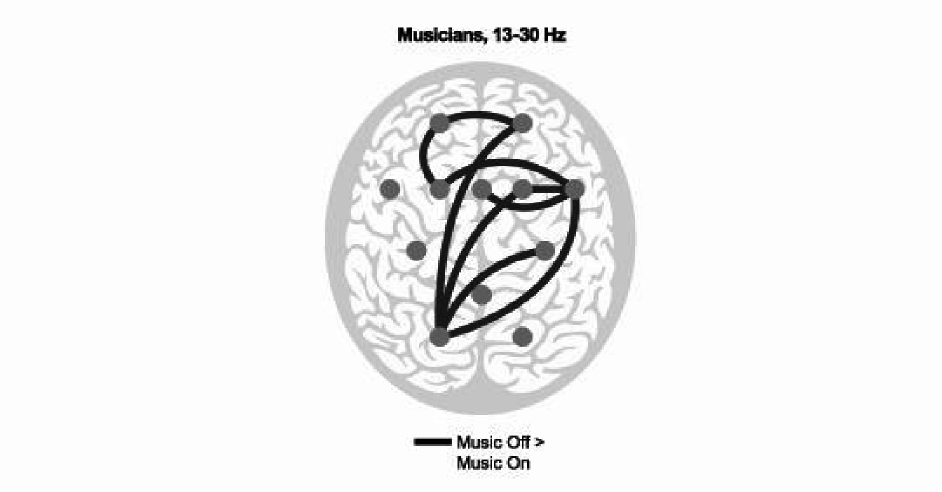

Figure 16 Significant differences for the main factor Music (Music On, Music Off) for musicians on beta band (13-30 Hz). The black lines connect the electrode pairs over which the synchronization is significantly stronger during Music On when compared to Music Off. Each gray dot illustrates the location of an EEG electrode on the scalp.

Gamma phase synchrony, 30-48 Hz
In dancers, on gamma band, the synchrony was significantly stronger in Music On when compared to Music Off over the following electrode pairs CPz – C4, CPz – FC6, CPz – FC4, CPz – FCz, CPz – C3, CPz – PO2, C4 – FC6, C4 – FC4, C4 – FCz, FC6 – FCz, FC6 – PO2, FC4 – FCz, FCz – FC3, FCz – C3, FCz – Fp1 and Fp1 – Fp2 (Figure 14).

In laymen, on the gamma band, the phase synchrony was significantly stronger in Music On when compared to Music Off over the electrode pairs C4 – Fp1 and C3 – Fp2. Dance*Music interaction was significant in laymen on gamma band over the pair C4 – FC3, in which the synchrony was significantly stronger during Low Acceleration when compared to Dance Off in Music Off condition.

5 DISCUSSION

This Doctoral dissertation was aimed at investigating early ERPs and cortical synchrony of professional dancers, musicians and laymen during the perception of continuous music and dance. Since methods in EEG to study naturalistic music and dance are lacking, two methods were developed to analyse continuous EEG data of artistic stimuli. These methods were used in studying cortical differences between dancers, musicians and laymen when watching the dance piece *Carmen*.

In Study I, we investigated people with diverse musical backgrounds by music from different genres (tango nuevo, deep techno, acoustic lullaby). In Study II, we focused on uni- and multimodal presentation of music from the contemporary dance piece *Carmen* studying the difference related to the professional experience in music and dance. In Study I and II, the ERP method showed its validity with different stimuli and in different groups of participants. Curiously, in Study II, we found an early P50 component, which was absent in Study I, and emerged only in dancers. Thus, expertise in dance seems to shape musical processing already in the preattentive level.

In Study III, dancers had enhanced theta synchrony when watching audio-visual dance when compared to musicians and laymen. Theta synchrony is associated with spatial, multimodal and emotional processing (Ekstrom et al., 2005; Balconi and Lucchiari, 2006; Knyazev et al., 2009; Wang et al., 2016; Bland and Oddie, 2001 for a review). Study IV suggests enhanced theta and gamma phase synchrony in dancers when listening to music but decreased alpha and beta synchrony in musicians. Cortical gamma synchrony is related to higher-order processing whereas alpha and beta to movement observation and production (Bhattacharya et al., 2001; Pineda, 2005; Kucewicz et al., 2014; Pavlidou et al., 2014; Hobson and Bishop, 2016). The results of Studies III and IV leave us with questions about the significance of cross-frequency coupling, such as theta-gamma phase amplitude coupling, in experts when observing their own artform (Canolty and Knight, 2010 for a review).

5.1 AUDITORY ERPS EVOKED BY CONTINUOUS ARTISTIC STIMULI

The results of Study I show a relationship between the magnitude of the ERP components and the magnitude of the rapid change in the feature value as well as the length of the preceding time with low-feature values. Teder and colleagues (1993) highlighted the relevance of the length of the ISI in the elicitation and magnitude of N100 component for continuous natural speech.

Based on the results of Study I, the length of the PLFP preceding the time point of interest plays a role in the elicitation of N100 also in continuous music. The prolonged PLFP seems to increase the amplitude of N100. In addition, stimulus intensity has been shown to influence the N100 amplitude such that a stimulus with stronger intensity elicits a larger N100 (Picton et al., 1977). Similarly, in Study I the N100 and P200 amplitudes seem to correlate positively with the increase of the magnitude of the rapid change in the musical feature of interest. Therefore, the earlier results which coupled the intensity of the sound and the length of the ISI with the magnitude of the ERP components seem to be valid also in the context of the dynamics of the musical features. In other words, the ERP components are elicited not only by simple sound streams with precisely defined silent ISIs but also by dynamic continuous natural stimuli such as a musical piece.

Alluri and colleagues (2012) showed that the brain regions activated corresponding to the musical features encapsulating brightness, RMS, spectral flux and zero-crossing rate of the same musical piece as the one used in Study I (*Adios Nonino*) locate in the auditory regions on the right and left temporal cortex, namely STG and MTG on the left hemisphere and STG and HG on the right hemisphere. Due to summation of the electric dipoles in the brain tissue, the EEG signal originating from these regions is the strongest on the frontal and central middle line. Therefore, it is very likely that the ERP components measured in our study are generated in the same brain regions as revealed in the study of Alluri and colleagues (2012) and that these auditory-related regions are sensitive in detecting rapid changes in these musical features.

Study II expands the paradigm of Study I to multimodal processing. Simultaneous presentation of a dance choreography with music makes this paradigm unique in ERP research. In the field of multimodal processing, paradigm of Study II is an upgrade to the earlier studies of ecologically valid audio-visual stimuli (Stekelenburg and Vroomen, 2007; Vroomen and Stekelenburg, 2009). The results of Study II help in understanding how individual characters of a complex sound scene are processed in the brain. The auditory N100 and P200 responses were suppressed and sped up in dancers, musicians and laymen during the audio-visual stimulus of a dance choreography compared to the unimodal presentation of the music of the choreography. Previously, Stekelenburg and Vroomen (2007) showed how the auditory N100 and P200 responses were suppressed and sped up only if the visual stimulus was synchronized with the auditory event and reliably predicted the sound. As stimuli, they used natural human actions such as the pronunciation of a letter or a hand clap. In their study, N100 amplitude decreased when the visual cue reliably predicted the onset of the sound reducing the temporal uncertainty. In contrast, the P200 amplitude decreased when the content of the visual cue and the sound were coherent, such as the pronunciation of the same letter in voice and in the video. Therefore, N100 likely reflects the multisensory integration related to coherent timing of all the unimodal elements whereas P200 is rather related to the associative and semantic coherence of them (Stekelenburg and Vroomen, 2007). Thus, suggested by the results of the earlier studies (Stekelenburg and Vroomen, 2007; Vroomen and Stekelenburg, 2009; Guo and Koelsch, 2016), dance movement has elements which reliably predict, both temporally and associatively, fast changes in the musical features reducing the surprise of the sudden change in music. Importantly, neither dancers nor musicians were shown to be more sensitive than laymen to these movement cues suggesting that processes underlying multisensory integration are not modified by the training of music and movement.

In the studies of Stekelenburg and Vroomen (Stekelenburg and Vroomen, 2007; Vroomen and Stekelenburg, 2009) the audio-visual interaction might have facilitated the auditory processing (van Wassenhove et al., 2005) by amplifying the signal intensity in the unimodal sensory cortices (Calvert et al., 1999). Optionally, the visual cue could evoke sensory gating on the auditory cortex (Oray et al., 2002) by reducing the novelty and surprise of the sound. The sensory gaiting is shown to suppress P50, N100 and P200 responses in a paired-sound paradigm (Fuerst et al., 2007; Rentzsch et al., 2008). Professional musicians have a reduced paired-sound P50 suppression (Kizkin et al., 2006), yet their N100 is reduced in a manner comparable to that of controls.

The results of Studies I and II suggest that continuous artistic stimuli are, at least partly, processed similarly on the auditory cortex as short simplified uni- and multimodal sounds. In addition, unimodal in comparison to multimodal processing of music does not differ between dancers, musicians and laymen.

5.2 AUDITORY ERPS IN EXPERTISE

The results of Study II suggest that preattentive processing of changes in timbral brightness of continuous music is modulated in dancers compared to musicians and laymen. As already known, expertise in music can dramatically modulate the auditory processing in the brain (for reviews, see Herholz and Zatorre, 2012; Pantev and Herholz, 2011; Tervaniemi, 2009). In our study, the ERPs of musicians did not differ from those of laymen. This result, which is opposite to the clear majority of ERP studies of musicians, may be explained by the methodological differences. In our study, we used remarkably fewer ERP epochs than is used in conventional ERP studies (100 averaged epochs in contrast to our 10). Also, previous studies used shorter music stimuli in contrast to our continuous natural music. Many previous studies investigated the expertise in detecting violations in harmony or consonance, and in listening to different instruments. These approaches are rather different to our study, in which real musical piece without manipulation was used. However, continuous music was enough to evoke changes in dancers: P50 to brightness was larger in dancers than in musicians and laymen. N100 to brightness in laymen was larger than in dancers, which might be a counter effect of the strong P50 of dancers. In the P200 response the group differences are already diminished.

The processes involved in movement-related imagination could be more active in dancers during their listening to music (Olshansky et al., 2015; Bar and DeSouza, 2016), possibly increasing the sensitivity to the fast changes in brightness. Optionally, intense and versatile physical training with music could improve cerebral processes which enhance the early reaction to these changes. Fine temporal changes in music are essential for dancers to create precise rhythmical movement which could, after years of exposure, lead to sensitization in the early auditory processes without concomitant sensitization of the longer-latency responses. All large changes of the musical features in the millisecond-scale occur with respect to the temporal structure of music. In addition, pitch, which is an important but not the only factor for brightness, and temporal structure are suggested to be largely integrated in auditory-motor transformations (Brown et al., 2013).

Functional integration in the cortico-basal ganglia loops that govern motor control and integration is suggested to be enhanced in dancers compared to laymen (Li et al., 2015). Basal ganglia project not only to the motor cortex but are highly interconnected with widespread areas on the cerebral cortex. Thus, they also play an important role in non-motor cognitive and sensory functions and in a wide range of learning challenges (Middleton and Strick, 2000, for a review). In vision, cortico-basal ganglia loop participates in action selection in response for a visual stimulus (Seger, 2008, for a review). The auditory cortico-basal ganglia network is less studied but there is evidence for a similar network as in visual domain (e.g. Geiser et al., 2012). Cortico-basal ganglia loop is crucial in the voluntary attentive movements whereas basal ganglia-brainstem loop is involved in the involuntary movements, such as breathing, swallowing and maintaining the body posture. In Parkinson’s and Huntington’s diseases the function of both cortico-basal ganglia loop and basal ganglia-brainstem loop is suggested to be violated (Takakusaki et al., 2004 for a review). The whole-body movement training of professional dancers seems to modify the cortico-basal ganglia network (Li et al., 2015). When compared to laymen, musicians show modulation on the cortical areas related to sound and movement, especially on the dominant hand of the instrument, and increased connectivity strength in motor-related regions (Elbert et al., 1995; Li et al., 2014; Luo et al., 2012; Zhang et al., 2015). However, it might be the improved cortico-basal ganglia loop of dancers which plays a key role in the enhancement of the preattentive auditory processing of dancers. Similarly to sportsmen, whose motor-related brain areas are sensitized to sports sounds (Woods et al., 2014), auditory-motor processes of dancers may be sensitized to musical cues such as rapid changes in brightness. Furthermore, continuous music, which is generally used in dance training, might be a unique stimulus in enhancing top-down controlling of the basal ganglia to the auditory cortex in dancers.

5.3 PHASE SYNCHRONY DURING MUSIC IN DANCERS AND MUSICIANS

In our studies, music did not reveal changes only in the ERPs but also in the phase synchrony of professional dancers. In dance training, music has a crucial role. It forms a setting, in which dancers produce movements that are in coherence (or intentionally in contrast) with the prevailing sound. The coherence (or opposition) is created in terms of rhythm, sentiment and movement style. When freely listening, a dancer might be rather focused on the gist or the general pulse of the music than to the sequence of an individual instrument, melody contour or a rhythmical pattern. In Study IV, dancers had enhanced theta and gamma synchrony over several pairs from prefrontal to parieto-occipital electrodes during Music On when compared to Music Off which could refer to the activation of higher-level brain processes (Krause et al., 2000; Kahana, 2006; Canolty and Knight, 2010).

Müller and colleagues (2013) studied cortical synchrony during collaborative musical improvisation and suggested a preponderance of delta and theta frequencies in inter-brain synchronization. They showed that inter-brain coupling generally emerges on lower frequencies but faster frequencies may sometimes be required to support highly coordinative actions. Importantly, inter-brain theta synchrony increased also when a musician was only observing his partner improvising. Dancers are shown to entrain better with short dance movement sequences of an actor than laymen (Washburn et al., 2014). Therefore, a comparative study with EEG of dancers and musicians in collaborative improvisation would be a reasonable next step. Reasults of such a study might help in understanding the mechanisms behind the enhanced synchrony over the frequency bands of our study.

In Study IV, only musicians had a systematic decrease in alpha and beta synchrony when listening to music. A musician may be mentally playing the tones with his instrument, especially if the musical piece is familiar or played by an instrument specialized by him (Bangert et al., 2006; Keller 2012 for a review). Desynchronization over the fronto-central and central electrodes in the alpha band, as found in our study, is linked to the activation of the MNS, and, therefore, a probable indicator for motor processing (Rizzolatti and Craighero, 2004 for a review). In the beta band, which is also associated to motor processing, musicians had several electrode pairs in fronto-central, central, centro-parietal and parieto-occipital electrodes with a decreased synchrony in Music On when compared to Music Off.

Musicians are trained to be rhythmically precise to create temporally coherent sound sequences. In general, both beat perception and preparation for a movement of body parts, such as fingers, have been shown to evoke changes on the alpha and beta bands (e.g. Fujioka et al., 2009; Krause et al. 2010; Schnitzler and Gross, 2005 for a review). Further, functional interaction at alpha and beta frequency is linked to motor control. In self-paced motor tasks, beta oscillation is shown to decrease preceding movements by one or more seconds (Hari and Salmelin, 1997; Pfurtscheller and Lopes da Silva, 1999). Fujioka and colleagues (2009) proposed that beta band activity in auditory cortex may help to signal timing cues to facilitate motor preparatory processes for sound synchronization and stated that it is highly likely that oscillatory activities are spread spatially across brain areas and are not limited to the auditory cortical sources.

Fujioka and colleagues (2009) reasoned that the gamma activity may reflect an endogenous process related to musical beat encoding and the anticipation of the stimulus timing. Largely exogenous processes related to auditory-motor communication may be the origin of beta synchrony and could explain why the power peak was absent in beat omission on the beta band. Anticipation of the rhythm is crucial for a dancer to move in harmony with music whereas precise auditory-motor processing is indispensable for a musician to maintain the flow of sounds with his instrument. These different manners of free music listening in dancers and musicians may play the key role in the results of Study IV.

5.4 PHASE SYNCHRONY DURING DANCE IN DANCERS AND LAYMEN

In addition to music listening, theta synchrony was enhanced in dancers when watching audio-visual dance. In Study III, theta phase synchrony in the fronto-central electrodes was increased in dancers during Dance & Music stimulus when compared to musicians and laymen. Increased interhemispheric theta synchrony over the fronto-central electrodes in dancers during Dance & Music stimulus may occur due to several individual, but simultaneous, brain processes, or due to a combination of them. Theta synchrony is suggested to be induced to the cortex via the hippocampal-cortical pathway (Ekstrom et al., 2005; Klimesch, 1996). Interestingly, theta synchrony did not differ between groups during the stimuli of Dance or Stick Figure. Thus, professional dance education may have a connection to the cortical processes which are involved in the observation of multimodal human movement. During dance education, both observing and producing multimodal human movements form the real environment in which dancers spend their days over several years.

Many participants in each group reported being familiar to the music presented in our study. In contrast, none of them was familiar with the dance choreography which is not only generally less known but was also modified by the dancer for our experiment. However, dancers are more likely familiar with observing dance movement per se. 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. Wang and colleagues (2006) reported that 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 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.

In Study III, we found differences related to the movement quantity on the alpha band. There was a clear decrease in the alpha synchrony over several electrode pairs across the brain during High Acceleration when compared to Low Acceleration. 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 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).

5.5 MIRROR NEURON SYSTEM, MOVEMENT AND EMPATHY

When interpreting the results of Studies III and IV, discussion about the MNS in movement and embodied emotions is relevant (Hobson and Bishop, 2016; Lamm and Majdandzic, 2015 for a review). Not only portrayed emotions but also induced emotions can be successfully recognized from dance movement (Camurri et al., 2003; Van Dyck et al., 2014). 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. 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 MNS (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, the differences in synchrony between High and Low Acceleration on the alpha band in Study III are more likely related to the lower-level sensory-motor, and attentional processes. These differences in synchorny may be evoked due to the amount of movement perceived. Hobson and Bishop (2016) studied the connection of movement perception and alpha band with several baseline references and 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 test setting is an upgrade to their experiment with a continuous naturalistic stimulus, due to the nearly still positions of the dancer within the dynamic dance choreography.

During Dance & Music in Study III, the desynchronization on the alpha band during fast movement occurred over several electrode pairs including pre-frontal, fronto-central, central and parieto-occipital electrodes. Both alpha and mu waves seem to be modified during multimodal perception of human movement (Pineda, 2005 and Klimesch, 2012 for reviews). During Stick Figure, the changes on the alpha band are diminished during fast movement when compared to the slow movement, and mainly occur between the fronto-central and parieto-occipital electrodes referring to changes in the visual observation and attention (Hobson and Bishop, 2016). Indeed, 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. Also, the emotions interpreted by dance movement are better recognized from more naturalistic moving body (Ross et al., 2012). During Dance, 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.

When professional dancers watch dance, they pay attention and evaluate the movement from a different perspective than laymen (Bläsing, 2015). In Study IV, laymen were the only group with systematic changes in synchrony related to the dance movement. Their changes in synchrony are in accordance to the results of earlier studies, in which alpha and beta synchrony decreased during movement observation (Di Nota et al., 2017; Hobson and Bishop, 2016; Rizzolatti and Craighero, 2004 for a review). Observation of vast dance movement (High in comparison to Low Acceleration) with music decreased the alpha and beta synchrony in laymen referring to the processing of rhythm and movement. Beta power is shown to be reduced with observation and imagination of complex dance movement when compared to simple non-dance movements indicating higher cognitive load (Di Nota et al., 2017). Absence of the alpha and beta desynchronization in experts might refer to more efficient neural processing when wacthing dance. During efficient processing, the alpha and beta synchrony stay at similar levels as during other stimuli, such as music. Experts may also adapt faster to the dance stimuli which would decrease changes in synchrony, or they may guide their attention to music during the audio-visual stimulus. These might be the underlying causes that no systematic changes in synchrony emerged in experts during dance.

In silence, especially when watching the nearly motionless dancer, laymen had increased theta and gamma synchrony when compared to the absence of visual stimulus. The nearly still body transmitted presence and internal dance which also had a strong aesthetic value. Dancers are used to such a minimalistic bodily expression and may have interpreted the character according to the storyline. Musicians also are familiar to implicit and atmospheric storytelling through arts, and may have focused on the protagonist in that context. On the other hand, laymen may have observed the dancer from a general social perspective considering her intentions, thoughts and emotions, or observed her in the spatial context.

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. Indeed, the enhanced cortical synchrony of dancers might reflect the processes involved in recognizing emotions from the whole-body movement. Interestingly, in Study III this enhancement 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 MNS (Oberman et al., 2007).

Thus, the emotional content of human movement might not be understood via the MNS but rather via the same pathways as other non-corporal emotional stimuli. Since changes in theta power have been linked to the hippocampal-cortical pathway (Ekstrom et al., 2005; Klimesch, 1996), the autobiographical memory might be crucial in emotional processing also in human movement. Observed movement might evoke processes of episodic memory and emotions related to these memories (Phelps, 2004 for a review). This approach would challenge the prevailing, though recently criticized (Caramazza et al., 2014; Lamm and Majdandzic, 2015 for reviews), theory of understanding emotions from human movement via activation of the MNS due to instant mental imitation of the observed movement. Alternatively, the processes of episodic memory and mental movement imitation could both contribute to the emotional understanding of human movement.

5.6 LIMITATIONS

The replicability of the ERP method developed for this dissertation was proven by Studies I and II when receiving robust results with different groups of participants and different musical and multimodal stimuli. For the phase-synchrony method, developed in Studies III and IV, the replication study is still lacking. Therefore, the results should be treated with caution. To correct this deficit, a sequential study for the phase synchrony method is already in process.

The ERP method still requires further development to understand the relevance of different elements, such as intensity change during the fast change of a musical feature, to the evoked responses. It is important to note that in Studies I and II at the time points of rapid change, both the intensity and the feature value changed drastically. Further studies need to be performed to extract the subcomponents related to the intensity and the feature value from the ERP components. In addition, the number of the ERP epochs was remarkably smaller than in traditional ERP studies. Also, the location of the ERP responses should be defined with a method such as sLORETA (Pascual-Marqui, 2002) which would help in interpreting the results in relation to the traditional ERP literature.

Methodologically, this dissertation focused on ERP and phase synchrony. Other methods, such as time-frequency representation, amplitude power, and source-level analysis would complement the methods chosen for this dissertation. By combining different methodological approaches, cortical functions in expertise could be understood in a more profound way.

Also, the heterogeneity of the groups of experts may have influenced to the results. The dance style, in which each dancer was specialized, may have an influence on the early auditory processing of changes in the musical features. The dance style may also influence to the phase synchrony in different frequency bands over a longer time-window. Familiarity with the composition or with the musical genre in general may play a role in these individual differences (Jacobsen et al., 2005). Such specialization of brain functions and structure has previously been shown in musicians (Vuust et al., 2012, Tervaniemi et al., 2016; for a review, see Tervaniemi, 2009). Also, a strong background in dance improvisation may have an influence on the preattentive and continuous auditory processing. Improvisation skills may enhance the movement imagery when listening to music even if it is not associated to a learned choreography. These skills may augment the sensitivity to the musical cues, the auditory-motor brain processes, and the general state of alertness. The composition used in Studies II, III and IV was played by string instruments with occasional percussion.

Thus, the musicians specialized in string instruments might have had enhanced brain responses to the fast changes in the musical features and altered cortical synchrony if compared to musicians with biography in non-string instruments (Margulis et al., 2009).

By means of non-musical and non-dance stimuli, it could be studied whether the sensitization of dancers and musicians is related to the musical sounds and dance movement only or to the sensory information in general. However, it is increasingly common to use non-musical sounds, such as environmental sounds or digital sounds, as well as non-dance movements, such as walking or interpreting daily gestures, in the creation of contemporary dance. Familiarity with the composition or with the dance style used in our studies could modify the uni- and multimodal processing (Calvo-Merino et al., 2005; Olshansky et al., 2015). Our participants had a versatile background in dance. Thus, a follow-up study in which expertise in specific dance styles are compared, would be important to analyse the effect of familiarity of sound space and of movement language to the early auditory responses and cortical synchronies when watching a dance piece and the unimodal components of it. In addition, a longitudinal study would be important to investigate whether the functional changes found in dancers' brain in comparison to musicians and laymen is caused by dance training or some other factor, such as genes or personality traits (Pantev and Herholz, 2011 for a review in musicians). These other factors might have an influence that certain type of people become professional dancers.

5.7 CONCLUSIONS

These four studies discussed in this dissertation introduce methodological possibilities in analyzing continuous EEG of artistic stimuli. The methods developed for this dissertation can detect changes in cortical processes both on lower (primary sensory processing) and higher (multimodal processing, perception of human movement, emotions, expertise) level. Based on the results, multisensory integration, movement quantity and expertise can be studied with the methods of ERP and phase synchrony during continuous dance and music. This kind of artistic stimuli induce simultaneous sensory, cognitive and affective processes in the brain. Challenge with such comprehensive stimuli is to know which results are related to which one of the several overlapping brain processes - or to which kind of combination of them. The extensive literature of traditional ERPs and cortical synchrony for simplified stimuli assists in interpreting the results gained with naturalistic stimuli. Despite not giving straightforward answers, the literature combined to the results of this dissertation guide to study further the interactions of human movement, episodic memory, embodied emotions and empathy.

Based on the results of Studies II, III and IV, dancers seem to have enhanced cortical processing of dance and music when compared to musicians and laymen. Also, the synchronous activity of musicians differs from dancers and laymen during music listening. These results combined with the results of Jola and colleagues (2012), in which experienced dance spectators had stronger corticospinal excitability than novices when watching live dance, direct our attention to the subcortical processes related to expertise. Dancers had enhanced theta phase synchrony over fronto-central electrodes when compared to musicians and laymen when watching the multimodal dance performance of *Carmen*. Theta synchrony is suggested to have its origin in the hippocampal structures (Ekstrom et al., 2005; Klimesch, 1996). Also, the cortico-basal ganglia loops are suggested to be strengthened in dancers (Li et al. 2015) which may play a role in enhanced P50 in dancers when listening to music. The basal ganglia are crucial in both conducting voluntary and involuntary movements as well as inhibiting excessive movements (Mink, 2003). Hippocampus is essential in memory consolidation and retrieval (Dudai et al., 2015). Thus, both movement and memory processes might be enhanced in professional dancers.

In sequential studies, it is important to investigate the possible synchrony between theta and gamma bands, which individually had enhanced synchrony among dancers (both frequencies during music listening and on the theta band during audio-visual dance). If the cross-frequency coupling on theta and gamma bands was enhanced in dancers, it would open a whole new field in the possible advantages of dance training. Brain synchrony - theta-gamma cross-frequency synchrony in particular - is suggested to be strongly related to the brain functions in health and disease (Voytek and Knight, 2015). Therefore, if the path of cortical cross-frequency synchronies pointed out in this dissertation was successfully explored, we would have 1) a method in detecting changes in the malfunctioning brain (phase-amplitude coupling of cross-frequency synchrony; Canolty and Knight, 2010 for a review), and 2) possible treatments in treating such conditions (dance-based therapy interventions such as dance movement therapy; Chaiklin and Wengrower, 2009).

All in all, the methods of ERP and phase synchrony can be applied in versatile clinical contexts, such as in patients with disorders of consciousness or the ones receiving expressive therapies based on dance and music for conditions such as Parkinson's, dementia, stroke, autism, or pain or mood disorders. In the artworld, these methods can be directly used in spectators and performing musicians during a live performance of dance and music, and, with the development of EEG technology in the near future, in performing dancers. When considering the ground-breaking application possibilities, the methods developed for this Doctoral dissertation are well worth to be investigated and developed further.

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APPENDIX

Table A1 *Age and musical background of each participant in Study I.*

Code of participant	**Age**	**Years of musical activity**	**Instrument**	**Years of activity in dance**	**Type**
kh2	20	15	Piano/singing	None	
kh3	23	13	Piano/flute	None	
kh4	23	16	Cello	None	
kh5	23	None		6	Ballet
kh6	24	None		None	
kh7	20	2	Piano	None	
kh8	42	15	Alto saxophone	None	
kh9	46	None		None	
kh11	22	7	Piano	None	
kh12	21	None		None	
kh13	34	6	Piano/keyboards	None	
kh14	31	5	Piano	None	
kh20	25	7	Piano/violin	7	Folk dance/ street dance
kh23	25	None		None	
kh25	24	3	Piano	None	
kh26	31	5	Computer music	None	

Table A2 *Detailed background information of the participants in Studies II, III and IV. To protect the anonymity of the participants, in some cases the specific information of the institute is replaced with XXX.*

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

F, 32	Professional		2013	Theater Academy, University of Arts, Helsinki	Contemporary dance	13
F, 28	Professional		2010	Arts Academy, XXX University of Applied Sciences	Circus	ballet: 7v
M, 30	Professional		2010	Theater Academy, University of Arts, Helsinki	Contemporary dance	15
M, 27	Self-taught				Stree dance	19
M, 23	Self-taught				Popping	17
F, 29	Student	2013		Tanssivintti, Alexander Theater, Helsinki	Contemporary dance	11
F, 30	Professional	2007		BA (Hons), London	Contemporary dance	12
M, 25	Self-taught				Locking	16
Musicians						
Gender, age	**Student/professional**	**Studies started**	**Graduated**	**Education**	**Instrument**	**Age when started to play**
M, 27	Student	2008		Sibelius Academy, University of Arts, Helsinki	Choir leader	piano: 7v
M, 20	Student	2013		Sibelius Academy, University of Arts, Helsinki	Jazz piano	10
M, 26	Student	2008		Sibelius Academy, University of Arts, Helsinki	Music education	guitar, piano: 8v
F, 24	Student	2008		Sibelius Academy, University of Arts, Helsinki	Recorder	6
F, 22	Student	2013		Sibelius Academy, University of Arts, Helsinki	Electric base guitar	11
F, 26	Student	2011		Sibelius Academy, University of Arts, Helsinki	Pop & jazz singing	14

F, 27	Student	2012		Sibelius Academy, University of Arts, Helsinki	Pop & jazz singing	piano: 7v
F, 31	Professional		2012	Sibelius Academy, University of Arts, Helsinki	Classical singing	piano: 4v
M, 28	Student	2008		Sibelius Academy, University of Arts, Helsinki	Recorder	singing: 8v
F, 24	Student	2010		Sibelius Academy, University of Arts, Helsink	N/A	N/A
F, 29	Student	2008		Sibelius Academy, University of Arts, Helsinki	Music education	violin: 6v
F, 24	Student	2011		Sibelius Academy, University of Arts, Helsinki	Viola	5
F, N/A	Student	2010		Sibelius Academy, University of Arts, Helsinki	Oboe	piano: 4v
F, 21	Student	2013		Sibelius Academy, University of Arts, Helsinki	N/A	N/A
F, 23	Student	2013		Sibelius Academy, University of Arts, Helsinki	Saxophone	10
F, 23	Student	2009		Sibelius Academy, University of Arts, Helsinki	Music education	piano: 4v
F, 23	Student	2012		Sibelius Academy, University of Arts, Helsinki	Piano	5
F, 26	Student	2007		Sibelius Academy, University of Arts, Helsinki	Music education	violin: 6v
M, 25	Student	2011		Sibelius Academy, University of Arts, Helsinki	N/A	N/A
Laymen						
Gender, age	**Student/professional**	**Education**				

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

Table A3 *Study I: Presentation of the characteristics of the triggers for the features brightness, RMS, zero-crossing rate and spectral flux of songs Astor Piazzolla: Adios Nonino, Kira Kira: Bless and Len Faki: My Black Sheep Radio Slave.*

Song and feature	**Number of triggers**	**Preceding Low-Feature Phase (PLFP) duration**	**Mean value of the feature across the whole song**	**Magnitude of the rapid increase (MoRI) of the feature value, from –X % to +X % of the mean value**
Astor Piazzolla: Adios Nonino				
Brightness	8	750 ms	0.3272	-20 % -> +20 %
RMS	8	500 ms	0.04827	-10 % -> +10 %
Zero-crossing rate	8	500 ms	1089	-15 % -> +15 %
Spectral flux	8	1000 ms	13.30	-15 % -> +15 %
Kira Kira: Bless				
Brightness	8	500 ms	0.3300	-15 % -> +15 %
RMS	7	875 ms	0.09500	-15 % -> +15 %
Zero-crossing rate	8	500 ms	987.3	-10 % -> +10 %
Spectral flux	8	1000 ms	24.25	-20 % -> +20 %
Len Faki: My Black Sheep Radio Slave				
Brightness	7	500 ms	0.2046	-10 % -> +10 %
RMS	8	500 ms	0.2846	-15 % -> +15 %
Zero-crossing rate	8	500 ms	471.1	-15 % -> +15 %
Spectral flux	8	312.5 ms	85.93	-10 % -> +10 %

Table A4 *Study I: T-tests of the N100 component (time window from 80 milliseconds to 150 milliseconds of the stimulus onset) over the Cz electrode for the features brightness, RMS, zero-crossing rate and spectral flux of songs Astor Piazzolla: Adios Nonino, Kira Kira: Bless and Len Faki: My Black Sheep Radio Slave.*

t-test	**t_{15}**	**p**
Astor Piazzolla: Adios Nonino		
Brightness	-6.40	0.000012
RMS	-2.97	0.0095
Zero-crossing rate	-7.35	0.00000239
Spectral flux	-4.68	0.000297
Kira Kira: Bless		
Brightness	-1.56	0.14
RMS	0.56	0.58
Zero-crossing rate	-2.76	0.015
Spectral flux	-0.39	0.70
Len Faki: My Black Sheep Radio Slave		
Brightness	-3.06	0.0079
RMS	-1.24	0.24
Zero-crossing rate	-2.53	0.023
Spectral flux	0.56	0.59

Table A5 *Study I: T-tests of the P200 component (time window from 150 milliseconds to 350 milliseconds of the stimulus onset) over the Cz electrode for the features brightness, RMS, zero-crossing rate and spectral flux of songs Astor Piazzolla: Adios Nonino, Kira Kira: Bless and Len Faki: My Black Sheep Radio Slave.*

t-test	**t_{15}**	**p**
Astor Piazzolla: Adios Nonino		
Brightness	7.41	0.00000218
RMS	8.16	0.000000675
Zero-crossing rate	6.92	0.00000491
Spectral flux	7.52	0.00000184
Kira Kira: Bless		
Brightness	9.29	0.000000131
RMS	6.33	0.0000134
Zero-crossing rate	4.43	0.000485
Spectral flux	8.58	0.000000359
Len Faki: My Black Sheep Radio Slave		
Brightness	3.73	0.0020
RMS	5.55	0.0000560
Zero-crossing rate	3.83	0.0016
Spectral flux	6.02	0.0000234

Table A6 *Study II: P50 response (time window from 30 milliseconds to 90 milliseconds of the stimulus onset). T-tests over the averaged signal of the 16 electrodes in the fronto-central region for musicians, dancers and laymen in the auditory and audio-visual condition of the musical features brightness, RMS, zero-crossing rate and spectral flux.*

t-test	**t_{17}**	**p**
Musicians		
Brightness		
Auditory stimulus	0.63	0.54
Auditory-visual stimulus	3.97	0.0010
RMS		
Auditory stimulus	5.71	0.000025
Auditory-visual stimulus	3.43	0.0032
Zero-crossing rate		
Auditory stimulus	2.75	0.014
Auditory-visual stimulus	1.67	0.11
Spectral flux		
Auditory stimulus	3.40	0.0034
Auditory-visual stimulus	1.74	0.10
Dancers		
Brightness		
Auditory stimulus	4.82	0.00016
Auditory-visual stimulus	3.49	0.0028
RMS		
Auditory stimulus	4.38	0.00041
Auditory-visual stimulus	3.45	0.0031
Zero-crossing rate		
Auditory stimulus	6.12	0.000011
Auditory-visual stimulus	0.28	0.79
Spectral flux		
Auditory stimulus	0.77	0.45
Auditory-visual stimulus	2.06	0.055
Laymen		
Brightness		
Auditory stimulus	0.44	0.66
Auditory-visual stimulus	3.91	0.0011
RMS		
Auditory stimulus	4.28	0.00050
Auditory-visual stimulus	3.91	0.0011
Zero-crossing rate		
Auditory stimulus	3.30	0.0043
Auditory-visual stimulus	-0.13	0.90
Spectral flux		
Auditory stimulus	3.09	0.0067
Auditory-visual stimulus	3.61	0.0021

Table A7 *Study II: N100 response (time window from 50 milliseconds to 150 milliseconds of the stimulus onset). T-tests over the averaged signal of the 16 electrodes in the fronto-central region for musicians, dancers and laymen in the auditory and audio-visual condition of the musical features brightness, RMS, zero-crossing rate and spectral flux.*

t-test	**t_{17}**	**p**
Musicians		
Brightness		
Auditory stimulus	-5.82	0.000021
Auditory-visual stimulus	-3.00	0.0089
RMS		
Auditory stimulus	-2.32	0.033
Auditory-visual stimulus	-1.43	0.17
Zero-crossing rate		
Auditory stimulus	-4.30	0.00048
Auditory-visual stimulus	-5.90	0.000017
Spectral flux		
Auditory stimulus	-5.78	0.000022
Auditory-visual stimulus	-1.76	0.096
Dancers		
Brightness		
Auditory stimulus	-2.72	0.015
Auditory-visual stimulus	-1.93	0.070
RMS		
Auditory stimulus	-2.34	0.032
Auditory-visual stimulus	-3.30	0.0042
Zero-crossing rate		
Auditory stimulus	-5.00	0.00011
Auditory-visual stimulus	-4.34	0.00044
Spectral flux		
Auditory stimulus	-1.80	0.089
Auditory-visual stimulus	-3.34	0.0038
Laymen		
Brightness		
Auditory stimulus	-7.12	0.0000017
Auditory-visual stimulus	-4.61	0.00025
RMS		
Auditory stimulus	-3.34	0.0039
Auditory-visual stimulus	-1.05	0.31
Zero-crossing rate		
Auditory stimulus	-5.45	0.000043
Auditory-visual stimulus	-6.13	0.000011
Spectral flux		
Auditory stimulus	-3.52	0.0026
Auditory-visual stimulus	-2.36	0.031

Table A8 *Study III: 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**.*

4 – 8 Hz Electrode pair	**F(2,51)**	**pGG**	**Multiple comparison (Bonferroni)**	**pFDR**	**Q**
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
FC4 – FC5	10.28	0.00018	Dancers > Musicians **p=0.00032** Dancers > Laymen **p=0.0023** Laymen > Musicians p=1.0	0.0041	0.0041
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
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

Table A9 *Study III: 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).*

Dance					
8 – 13 Hz Electrode pair	**F(1,51)**	**pGG**	**Multiple comparison (Bonferroni)**	**pFDR**	**Q**
FC6 – FC4	13.32	0.00062	Low > High Acceleration p=0.00062	0.0064	0.0064
FC6 – FCz	6.59	0.013	Low > High Acceleration p=0.013	0.041	0.041
FC4 – FCz	18.32	0.000082	Low > High Acceleration p=0.000082	0.0013	0.0013
FC4 – FC3	10.15	0.0025	Low > High Acceleration p=0.0025	0.0019	0.0019
FC3 – C3	7.28	0.0094	High > Low Acceleration p=0.0094	0.037	0.037
FC3 – Fp1	6.05	0.017	Low > High Acceleration p=0.017	0.049	0.049
FC3 – Fp2	6.74	0.012	Low > High Acceleration p=0.012	0.043	0.041
FC5 – C3	9.03	0.0041	High > Low Acceleration p=0.0041	0.026	0.026
FC5 – Fp1	8.45	0.0054	Low > High Acceleration p=0.0054	0.028	0.028
FC5 – Fp2	7.31	0.0093	Low > High Acceleration p=0.0093	0.041	0.037
Fp1 – Fp2	19.47	0.000053	Low > High Acceleration p=0.000053	0.0017	0.0013
Dance & music					
8 – 13 Hz Electrode pair	**F(1,51)**	**pGG**	**Multiple comparison (Bonferroni)**	**pFDR**	**Q**
CPz – C3	5.10	0.028	Low > High Acceleration p=0.028	0.0072	0.0072
CPz – PO1	7.47	0.0086	Low > High Acceleration p=0.0086	0.0033	0.0033
C4 – FC4	6.88	0.011	Low > High Acceleration p=0.011	0.0038	0.0038
C4 - FCz	11.78	0.0012	Low > High Acceleration p=0.0012	0.00075	0.00075
C4 – FC3	6.01	0.018	Low > High Acceleration p=0.018	0.0049	0.0049

C4 – Fp2	4.61	0.036	Low > High Acceleration p=0.036	0.0087	0.0087
FC6 – FC4	13.63	0.00054	Low > High Acceleration p=0.00054	0.00047	0.00047
FC6 - FCz	12.93	0.00073	Low > High Acceleration p=0.00073	0.00050	0.00050
FC6 – FC3	10.20	0.0024	Low > High Acceleration p=0.0024	0.0013	0.0012
FC6 – Fp1	13.81	0.00050	Low > High Acceleration p=0.00050	0.00050	0.00047
FC6 – Fp2	10.72	0.0019	Low > High Acceleration p=0.0019	0.0011	0.0011
FC6 – PO1	8.12	0.0063	Low > High Acceleration p=0.0063	0.0027	0.0027
FC4 – FCz	22.06	0.000020	Low > High Acceleration p=0.000020	0.00014	0.00012
FC4 – FC3	19.63	0.000050	Low > High Acceleration p=0.000050	0.00015	0.00012
FC4 – Fp1	13.10	0.00068	Low > High Acceleration p=0.00068	0.00052	0.00050
FC4 – Fp2	7.62	0.0080	Low > High Acceleration p=0.0080	0.0032	0.0032
FC4 – PO1	16.52	0.00017	Low > High Acceleration p=0.00017	0.00029	0.00029
FCz – PO1	6.13	0.017	Low > High Acceleration p=0.017	0.0048	0.0048
FC3 – Fp1	14.82	0.00033	Low > High Acceleration p=0.00033	0.00038	0.00038
FC3 – Fp2	6.27	0.016	Low > High Acceleration p=0.016	0.0049	0.0048
FC3 – PO1	4.76	0.034	Low > High Acceleration p=0.034	0.0083	0.0083
FC3 – PO2	9.35	0.0035	Low > High Acceleration p=0.0035	0.0016	0.0016
FC5 – Fp1	19.60	0.000050	Low > High Acceleration p=0.000050	0.00012	0.00012
FC5 – Fp2	7.08	0.010	Low > High Acceleration p=0.010	0.0036	0.0036
FC5 – PO2	7.15	0.010	Low > High Acceleration p=0.010	0.0036	0.0036
C3 – Fp1	4.48	0.039	Low > High Acceleration p=0.039	0.0090	0.0090
Fp1 – Fp2	15.64	0.00024	Low > High Acceleration p=0.00024	0.00033	0.00033

Fp1 – PO2	6.13	0.017	Low > High Acceleration p=0.017	0.0050	0.0048
Fp2 – PO1	5.92	0.019	Low > High Acceleration p=0.019	0.0049	0.0049
Fp2 – PO2	10.16	0.0025	Low > High Acceleration p=0.0025	0.00012	0.00012
PO1 – PO2	4.22	0.045	Low > High Acceleration p=0.045	0.0100	0.0100
Stick figure					
8 – 13 Hz Electrode pair	**F(1,51)**	**pGG**	**Multiple comparison (Bonferroni)**	**pFDR**	**Q**
FC6 – Fp1	5.81	0.020	Low > High Acceleration p=0.020	0.049	0.049
FC4 – FCz	8.37	0.0056	Low > High Acceleration p=0.0056	0.016	0.016
FC4 – Fp1	8.95	0.0043	Low > High Acceleration p=0.0043	0.015	0.015
FC4 – PO1	10.28	0.0023	Low > High Acceleration p=0.0023	0.014	0.014
FCz – PO1	9.57	0.0032	Low > High Acceleration p=0.0032	0.014	0.014
FC3 – PO2	0.30	0.00017	Low > High Acceleration p=0.00017	0.0015	0.0015
Fp1 – Fp2	23.17	0.000014	Low > High Acceleration p=0.000014	0.00024	0.00024

Table A10 *Study IV, Dancers: Electrode pairs with significant synchronization differences for the main factor Music (Music Off, Music On) over the frequency bands theta (4-8 Hz), beta (13-30 Hz) and gamma (30-48 Hz). In the table, pGG indicates the p-value with a Greenhouse-Geisser adjustment and pFDR the p-value according to the False Discovery Rate.*

4 – 8 Hz Electrode pair	**Condition**	**F(1,51)**	**pGG**	**pFDR**	**Q**	
CPz – FCz	Music	5.80	0.020	0.018	0.018	Music On > Music Off
CPz – Fp1	Music	6.84	0.012	0.015	0.015	Music On > Music Off
C4 – PO1	Music	4.55	0.038	0.021	0.021	Music On > Music Off
FC6 – FC5	Music	6.05	0.017	0.017	0.017	Music On > Music Off
FC6 – PO2	Music	7.74	0.0076	0.014	0.014	Music On > Music Off
FC4 – FC3	Music	6.98	0.011	0.016	0.015	Music On > Music Off
FC4 – FC5	Music	11.76	0.0012	0.0054	0.0039	Music On > Music Off
FC4 – Fp1	Music	5.29	0.026	0.021	0.019	Music On > Music Off
FCz – FC3	Music	14.30	0.00041	0.0037	0.0037	Music On > Music Off
FCz – FC5	Music	11.57	0.0013	0.0039	0.0039	Music On > Music Off
FCz – Fp1	Music	6.36	0.015	0.017	0.017	Music On > Music Off
FC3 – FC5	Music	4.62	0.036	0.022	0.021	Music On > Music Off
FC5 – C3	Music	5.19	0.027	0.019	0.019	Music On > Music Off
FC5 – Fp1	Music	4.83	0.032	0.021	0.021	Music On > Music Off
FC5 – PO2	Music	10.79	0.0018	0.0041	0.0041	Music On > Music Off
C3 – PO2	Music	5.22	0.027	0.020	0.019	Music On > Music Off
13 – 30 Hz	**Condition**	**F(1,51)**	**pGG**	**pFDR**	**Q**	

FC4 – Fp1	Music	8.98	0.0042	0.031	0.031	Music On > Music Off
30 – 48 Hz Electrode pair	**Condition**	**F(1,51)**	**pGG**	**pFDR**	**Q**	
CPz – C4	Music	8.81	0.0046	0.0029	0.0018	Music On > Music Off
CPz – FC6	Music	4.49	0.039	0.0023	0.0018	Music On > Music Off
CPz – FC4	Music	4.33	0.043	0.0021	0.0018	Music On > Music Off
CPz – FCz	Music	4.81	0.033	0.0030	0.0018	Music On > Music Off
CPz – C3	Music	5.35	0.025	0.0032	0.0018	Music On > Music Off
CPz – PO2	Music	4.51	0.039	0.0025	0.0018	Music On > Music Off
C4 – FC6	Music	4.26	0.044	0.0020	0.0018	Music On > Music Off
C4 – FC4	Music	4.65	0.036	0.0026	0.0018	Music On > Music Off
C4 – FCz	Music	7.03	0.011	0.0023	0.0018	Music On > Music Off
FC6 – FCz	Music	5.31	0.025	0.0027	0.0018	Music On > Music Off
FC6 – PO2	Music	4.44	0.040	0.0021	0.0018	Music On > Music Off
FC4 – FCz	Music	5.53	0.023	0.0036	0.0018	Music On > Music Off
FCz – FC3	Music	4.69	0.035	0.0028	0.0018	Music On > Music Off
FCz – C3	Music	4.26	0.044	0.0019	0.0018	Music On > Music Off
FCz – Fp1	Music	8.16	0.0062	0.0020	0.0018	Music On > Music Off
Fp1 – Fp2	Music	4.20	0.045	0.0018	0.0018	Music Off > Music On

Table A11 *Study IV, Musicians: Electrode pairs with significant synchronization differences for the main factor Music (Music Off, Music On) over the frequency bands alpha (8-13 Hz) and beta (13-30 Hz). In the table, pGG indicates the p-value with a Greenhouse-Geisser adjustment and pFDR the p-value according to the False Discovery Rate.*

8 – 13 Hz Electrode pair	**Condition**	**F(1,51)**	**pGG**	**pFDR**	**Q**	
FC3 – C3	Music	5.27	0.026	0.0094	0.0026	Music Off > Music On
13 – 30 Hz Electrode pair	**Condition**	**F(1,51)**	**pGG**	**pFDR**	**Q**	
CPz – PO1	Music	4.82	0.033	0.0012	0.00047	Music Off > Music On
FC4 – FC3	Music	5.54	0.023	0.0010	0.00047	Music Off > Music On
FCz – C3	Music	4.38	0.041	0.0010	0.00047	Music Off > Music On
FC3 – FC5	Music	4.76	0.034	0.0010	0.00047	Music Off > Music On
FC3 – C3	Music	6.98	0.011	0.0017	0.00047	Music Off > Music On
FC5 – C3	Music	4.27	0.044	0.00095	0.00047	Music Off > Music On
PO1 – PO2	Music	4.93	0.031	0.0016	0.00047	Music Off > Music On

Table A12 *Study IV, Laymen: Electrode pairs with significant synchronization differences for the main factors Music (Music Off, Music On) and Dance (Dance Off, Low Acceleration, High Acceleration) and the Music*Dance interaction over the frequency bands theta (4-8 Hz), alpha (8-13 Hz), beta (13-30 Hz) and gamma (30-48 Hz). In the table, pGG indicates the p-value with a Greenhouse-Geisser adjustment and pFDR the p-value according to the False Discovery Rate.*

4 – 8 Hz Electrode pair	**Condition**	**F(1,51)**	**pGG**	**pFDR**	**Q**	
FC6 – Fp1	Music	14.08	0.00045	0.013	0.013	Music On > Music Off
4 – 8 Hz Electrode pair	**Condition**	**F(2,51)**	**pGG**	**pFDR**	**Q**	**Multiple comparison (Bonferroni)**
C4 – PO1	Dance*Music	4.75	0.013	0.012	0.012	Music Off: Low Acceleration > Dance Off p=.047
FC6 – PO1	Dance*Music	9.65	0.00028	0.0010	0.0010	Music Off: Low Acceleration > Dance Off p=.027
FC5 – Fp1	Dance*Music	10.42	0.00016	0.0011	0.0010	Music Off: Low Acceleration > Dance Off p=.0026 Music Off: High Acceleration > Dance Off p=.040
FC5 – Fp2	Dance*Music	6.28	0.0037	0.0087	0.0069	Music Off: Low Acceleration > Dance Off p=.019
8 – 13 Hz Electrode pair	**Condition**	**F(2,51)**	**pGG**	**pFDR**	**Q**	**Multiple comparison (Bonferroni)**
CPz – FC3	Dance	4.44	0.017	0.044	0.033	Dance Off > Low Acceleration p=.024
CPz – FC5	Dance	4.12	0.022	0.039	0.033	Dance Off > High Acceleration p=.038
FCz – Fp2	Dance	4.14	0.022	0.046	0.033	Dance Off > High Acceleration p=.031

FC3 – Fp2	Dance	4.11	0.022	0.033	0.033	Dance Off > High Acceleration p=.018
FC5 – Fp2	Dance	5.72	0.0057	0.030	0.027	Dance Off > High Acceleration p=.0044
C3 – Fp1	Dance	5.39	0.0075	0.027	0.027	Dance Off > Low Acceleration p=.045 Dance Off > High Acceleration p=.010
C3 – Fp2	Dance	6.90	0.0022	0.023	0.023	Dance Off > Low Acceleration p=.018 Dance Off > High Acceleration p=.0032
8 – 13 Hz Electrode pair	**Condition**	**F(2,51)**	**pGG**	**pFDR**	**Q**	**Multiple comparison (Bonferroni)**
C4 – PO1	Dance*Music	3.44	0.040	0.015	0.015	Music On: Dance Off > High Acceleration p=.016
FC6 – FC4	Dance*Music	7.81	0.0011	0.0073	0.0037	Music On: Dance Off > High Acceleration p=.011
FC6 – FCz	Dance*Music	3.57	0.035	0.016	0.015	Music On: Dance Off > High Acceleration p=.0091
FC6 – FC3	Dance*Music	4.98	0.011	0.0088	0.0079	Music On: Dance Off > High Acceleration p=.038
FC6 – PO1	Dance*Music	4.83	0.012	0.0079	0.0079	Music On: Dance Off > High Acceleration p=.014
FC4 – PO1	Dance*Music	5.36	0.0077	0.0073	0.0073	Music On: Dance Off > High

						Acceleration p=.024
FC3 – Fp1	Dance*Music	3.60	0.035	0.016	0.015	Music On: Dance Off > High Acceleration p=.023
Fp1 – Fp2	Dance*Music	4.26	0.020	0.012	0.012	Music On: Dance Off > High Acceleration p=.043
Fp2 – PO1	Dance*Music	7.80	0.0011	0.0037	0.0037	Music On: Dance Off > High Acceleration p=.025
13 – 30 Hz Electrode pair	**Condition**	**F(2,51)**	**pGG**	**pFDR**	**Q**	**Multiple comparison (Bonferroni)**
C4 – FC5	Dance*Music	5.39	0.0075	0.034	0.033	Music On: Dance Off > High Acceleration p=.028 Music On: Dance Off > Low Acceleration p=.023
30 – 48 Hz Electrode pair	**Condition**	**F(1,51)**	**pGG**	**pFDR**	**Q**	
C4 – Fp1	Music	11.421	0.0014	0.029	0.029	Music On > Music Off
C3 – Fp2	Music	8.1547	0.0062	0.043	0.043	Music On > Music Off
30 – 48 Hz Electrode pair	**Condition**	**F(2,51)**	**pGG**	**pFDR**	**Q**	**Multiple comparison (Bonferroni)**
C4 – FC3	Dance*Music	6.2303	0.0038	0.0010	0.0010	Music Off: Low Acceleration > Dance Off p=.026