Investigating emotion perception using expertise:

A multidisciplinary approach between cognitive neuroscience and performing arts

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Dance is the hidden language of the soul of the body.
The body says what words cannot.

Martha Graham (1894-1991)
American modern dancer and choreographer

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Thesis Abstract

Dance expertise has been found to influence neural and psychophysiological responses to emotion processing, action observation and body awareness. Whether this enhanced emotion sensitivity is specific only to their familiar stimuli or can be generalised to everyday forms of emotion expression remains unclear and, so, our primary aim was to investigate the role of dance as motor and artistic expertise on facial emotion perception. The first experiment compared neural activity of dancers and non-dancers controls performing a visual emotion recognition task and provided novel supportive evidence for the dance expertise effect on the visual and somatosensory processing of facial emotion and the embodied emotion theory more generally with significant effects and interactions with group, emotion and task both on the Somatosensory and the Visual Evoked Potentials across most of our selected time windows. Our secondary aim was to better understand how dancers perceive their own bodies and emotions exploring the effect of dance on interoceptive markers and their relation to emotion processing. For our second experiment we investigated for the first time the heart- brain interactions on dancers and controls on the same visual emotion recognition task and compared the relationships between heartbeat, visual and somatosensory evoked potentials and the interoceptive abilities between groups. No emotion or dance expertise modulation was found on Heartbeat Evoked Potentials, but dance expertise was strongly related to interoceptive abilities and Heartbeat Evoked Potential was strongly related to personality traits for both groups. The third experiment was an online pilot study comparing dancers and controls on a visual emotion discrimination task informed by the visual object recognition literature. Dance expertise was strongly related with behavioural performance, empathy and interoceptive awareness. The fourth experiment focused on the distinct embodiment signatures for different emotion and the potential influence of psychological traits on embodiment providing evidence for significantly different somatosensory processing of angry and happy facial expressions and

the influence of the Somatosensory Evoked Potential of anger by the levels of alexithymia. Our results suggest an enhanced general emotion sensitivity in dance experts beyond their motor acquired skill and are discussed in the light of the current theoretical and methodological approaches in relation to dance neuroscience, emotion perception and interoception.

Chapter 1: General Introduction

1.2 Facial emotion perception

Emotions are deeply rooted in our animal nature; they are part of our identities and social interactions with others and the world around us. We communicate emotions, speak about them, regulate them, inform our decision making based on them all the time in our everyday life. The idea of emotions has baffled philosophers from millennia. And yet, here we are today, still the hardest thing for a researcher working on emotion perception is to actually define what emotion is. Many have tried to explain it but a consensus is yet to be reached (Adolphs, Mlodinow, & Barrett, 2019; Engelen & Mennella, 2018). One of the key debates on emotion is the classic nature versus nurture debate: do we have hard wired neurobiological mechanisms of emotion perception a priori? Are emotions natural or are socially constructed concepts? Research evidence exist for both sides of the argument and the truth might be somewhere in the middle, a combination of biological natural origins and social constructivism. One of the first to provide evidence for the naturality of emotions was Charles Darwin in his book 'The Expressions of Emotions in Man and Animals' concluding that emotions such as fear, happiness, anger and sadness seem to be natural and common across species (Darwin, 1872). A few years later, William James in his famous essay (James, 1884) argued that emotions are rather our feelings caused by physiological changes in our bodies e.g., faster heart rate following an event e.g., seeing suddenly a bear in front of us. Later, Carl Lange argued that these exact physiological changes are the emotions (Lange, 1885). Nowadays the James – Lange theory is considered one of the most important theories of emotion and the notion that bodily feedback modulates emotion experience is its most important contribution that is still taken into account today (Dalgleish, 2004; Friedman, 2010). Later, Panksepp created the term 'affective neuroscience' and also proposed that there are four natural basic emotion systems across species and these are fear, anger, seeking and rage, each one associated with its own neurotransmitter and neural structures (Panksepp 1998 & 2011). Nowadays, we have been able to find supportive evidence for the natural aspect of emotions also from facial expressions of blind people, albeit with some contradictory results (Roch-Levecq, 2006; Valente, Theurel, & Gentaz, 2018).

Some of the most important research on the origins of emotions has come from the studies investigating the universality of emotions across the world. Paul Ekman was a pioneer on this field claiming that there are six basic universal emotions: happiness, fear, sadness, disgust, surprise and anger after comparing facial expressions in various societies across the globe including more remote ones with minimal to no connection to western world (Ekman, 1993; Ekman & Friesen, 1971). One remark they made though was that surprise and fear as well as disgust and anger were not found be consistently different in all cultures and this was consistent in later studies too (Jack, Sun, Delis, Garrod, & Schyns, 2016). Two significant limitations of the studies by Ekman and colleagues are firstly, that their findings have failed sometimes to be replicated (e.g. see Barrett, 2006; Jack et al., 2016) and secondly, they refer to universality of emotions, but only focused on facial expressions (Barrett, 2006; Barrett & Satpute, 2019; Duran & Fernandez-Dols, 2021).

There might not be one exact definition of emotion yet, but there is a broad consensus that emotion is not a state, but a rather complex process with potentially five parts: the bodily signals, the cognitive appraisal or evaluation of the related event, the facial and body expression, the feeling (as the subjective evaluation of the bodily state) and the action tendency (Adolphs, 2010; Oatley & Johnson-Laird, 2014). The current thesis adopts the notion above and focuses on the facial expressions of emotions acknowledging that these represent an important but not the only component of emotion expression. This view of emotion as a process with separate parts and not as a state is adopted also by the appraisal theories of emotion. These theories take a more cognitivist approach aiming to explain how the same event can cause different emotions in different people or under different circumstances by focusing on appraisal (Moors, Ellsworth, Scherer, & Frijda, 2013). These theories view appraisal as a process assessing environmental factors and their influence on the person's wellbeing allowing space for individual, cultural and developmental differences (Moors et al., 2013).

In contrast to the above, a new theory has emerged the last years, namely the theory of constructed emotion by Feldman Barrett (2017). This theory takes a social constructivism approach and re-defines emotion through the predictive framework and active inference of interoception and categorisation/ conceptualisation. In a nutshell, this framework suggests that the brain makes continuously predictions and prediction errors based on the internal signals, past experiences and the external environment, it constructs concepts to identify the input, to explain its cause and act upon them. Feldman Barrett argues that emotions are concepts constructed in the moment resulting in an 'instance of emotion'(Feldman Barrett, 2017).

Studies using electrophysiology (EEG), event related potentials (ERP) and functional magnetic resonance imaging (fMRI) have reported consistently an early processing of facial expression in occipital and temporal cortices. ERP studies using visual stimuli showing people with various facial expressions have found that emotional facial expressions modulated the ERPs related to visual processing as early as 50-90 milliseconds (Adolphs, 2002). Theoretical modelling papers such as Bruce and Young (1986) and Haxby and colleagues (Haxby, Hoffman, & Gobbini, 2000) have proposed that these effects most probably concern the categorisation of visual features, an early possibly autonomic processing. ERP components are commonly named based on their positive or negative amplitude and the timing they occur. The ERPs we focus on for the visual processing of facial expressions occur at 120 milliseconds after the visual stimulus onset with a positive amplitude (P120), at 170 ms after the onset with a negative amplitude (N170) and at 200 ms after the visual onset with a positive amplitude again (P200). These ERP components, the P120, the N170 and P200, are excessively reported in ERP studies showing significant interactions with emotion perception (Batty & Taylor, 2003; Eimer & Holmes, 2007; Eimer, Holmes, & McGlone, 2003; Joyce & Rossion, 2005; Linkenkaer-Hansen et al., 1998; Mermillod et al., 2018; Rossion, 2014). Adolphs (2002) suggested that P120 could be activity in midline occipital cortex to distinguish between emotional facial expressions followed by temporal cortical activity for the N170 near the fusiform face area. Regarding N170, Hinojosa and colleagues (Hinojosa, Mercado, & Carretié, 2015) conducted a meta-analysis on 128 studies looking at N170 in response to emotional and neutral expressions. They confirmed the N170 sensitivity to emotional faces and found that the N170 amplitude seem to be larger for anger, fear and happy in that order, with no significant contrasts between sadness and disgust with neutral.

The areas that have been commonly shown to be engaged in emotion processing in fMRI studies are the limbic system, the amygdala, basal ganglia, insula, the somatosensory and orbitofrontal cortices. These areas are not active in the same way nor at the same time and not for all emotions. Although there is evidence that most of these areas are involved in all emotions, they might show different activation pattern. Amygdala for example is activated during emotion processing, but the highest interaction seems to be mostly with anger and potentially sadness (Adolphs, Tranel, Damasio, & Damasio, 1994; Adolphs, 2002, 2006; Adolphs, Damasio, Tranel, & Damasio, 1996; Batty & Taylor, 2003; Sprengelmeyer, Rausch, Eysel, & Przuntek, 1998; Winston, O'Doherty, & Dolan, 2003). For reviews of fMRI studies, see Adophs (2002, 2006, 2010), Sabatinelli and colleagues (Sabatinelli et al., 2011).

1.2 Embodiment

Embodied cognition or embodiment theory is one of the most influencing theories on emotion perception, the perspective of which is adopted in the current thesis. Since the discovery of mirror neurons in monkeys and later in humans showing that the motor and premotor cortices respond similarly both while doing an action and while observing the same action performed by someone else (Gallese, Fadiga, Fogassi & Rizzolatti, 1996), Keysers, Kaas and Gazzola (2010) in a key review showed that somatosensory cortices in humans also have mirror properties related to processing observed body stimuli (not only related to action observation). Embodied cognition theory postulates that these vicarious responses of the somatosensory system drive the processing of other people's sensations, feelings and bodies (Keysers & Gazzola, 2009; Keysers, Kaas and Gazzola, 2019; de Vignemont, 2011). Based on this theory we perceive emotions of others by simulating them 'as if it were us experiencing it in the first place' (Niedenthal & Maringer, 2009). As Paula Niedenthal describes it, 'perceiving and thinking about emotion involve perceptual, somatovisceral, and motoric reexperiencing' (Niedenthal, 2007). Individual and cultural differences can be taken into account for these theories, as it is considered that we build up on our experience (Niedenthal & Maringer, 2009). A large amount of neuroscientific research has provided supportive evidence for the theory of embodied emotion from TMS, fMRI and ERP, EMG and lesion studies (Keysers, Kaas & Gazzola, 2010, Wood, Rychlowska, Korb, & Niedenthal, 2016). Adolphs and colleagues (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000) provided causal evidence for the role of right somatosensory cortex by testing visual emotion perception on patients with lesion in somatosensory areas. An example of supportive evidence for embodiment theories from fMRI studies comes from Winston and colleagues (Winston et al., 2003) who reported increased activation in the somatosensory cortices of the participants while conducting event-related fMRI. Pourtois and colleagues (Pourtois et al., 2004) and Pitcher and colleagues (Pitcher, Garrido, Walsh, & Duchaine, 2008) applied TMS in the somatosensory cortices disrupting the early stages of facial emotion processing and providing causal evidence for embodied cognition theories and the early involvement of nonvisual cortical areas in the facial expression processing.

Inspired by the above TMS work, Alejandra Sel and colleagues analysed visual and somatosensory evoked potentials from a facial emotion perception task employing a novel analysis method and demonstrated for the first time the independent contribution of the somatosensory cortex (Sel, Forster, & Calvo-Merino, 2014). Specifically, in an ERP experiment Sel and colleagues measured activity in the somatosensory and visual areas while participants completed a visual emotion or gender discrimination task. Inspired by the results of Pitcher et al. (2008), in 50% of the trials they applied a tactile stimulation on the participants' left index finger or left cheek at 105 ms after the visual stimulus onset (the timing where participants' performance was worsened following TMS in Pitcher et al. (2008) study) to evoke Somatosensory Evoked Potentials (SEPs). The single subject averaged amplitude on the somatosensory electrodes from the visual only conditions (without a tactile stimulation) was later removed from the visual-tactile conditions (conditions with the tactile stimulation) to remove the visual carry-over effect resulting in SEPs free from the Visual Evoked Potentials. The tactile probe was task irrelevant and helped in enhancing the activity over the somatosensory cortices. The subtraction method was necessary to isolate the visually driven (as participants complete a visual task) processing of body stimuli in non-visual areas which was otherwise masked by the visual processing that is much stronger in amplitude (for more information on subtraction methods on ERPs see Dell'Acqua, Jolicoeur, Pesciarelli, Job & Palomba, 2003, for a detailed review on this specific technique see Galvez-Pol, Calvo-Merino & Forster, 2020). By applying this novel method, Sel et al. (2014) were able to analyse and show for the first time the independent contribution of the somatosensory cortex in emotion processing, with facial emotion modulating the SEPs. Importantly, similar response was evoked in the SEPs by emotion for both tactile conditions (finger and cheek) which was stronger than the somatotopic effect and so, the two conditions were later combined in the analysis. The tactile probe (on the left index finger only after Sel et al. (2014)) and subtraction method has been used in later studies with body stimuli in order to better understand the independent role of the somatosensory cortices in emotion processing in population with Autism Spectrum Disorder (Fanghella, Gaigg, Candidi, Forster and Calvo-Merino, 2022) and in bodily stimuli perception (Arslanova, Galvez-Pol, Calvo-Merino & Forster, 2019; Galvez-Pol, Calvo-Merino, Capilla & Forster, 2018, Galvez-Pol et al., 2020). The Chapters 2 and 5 of this thesis drew inspiration and continued the line of work set by Sel and colleagues (2014) using the same tactile stimulation and ERP subtraction method to investigate the somatosensory processing of facial emotion.

Importantly, based on the idea that emotions are modulated by our own bodily feedback, as suggested by James-Lange theory and the evidence on the vicarious brain representations of others and the self, it has been proposed that the perception of our own emotions and of others is linked to our ability to perceive our own bodily signals; that is, interoception (Craig, 2003). Indeed, emotion perception and interoception seem to be localised in similar brain areas such as somatosensory and insular cortices (Craig, 2003; Craig 2009; Weins, 2005) and research has been providing with supporting evidence for the modulation and the importance of the interoceptive processing in understanding the external social environment (Critchley & Garfinkel, 2017; Park & Blanke, 2019). Chapter 3 provides a detailed review on the state -of-the-art on interoception, heart-brain interaction and the link to emotion perception.

1.3 Expertise

Research on visual face and object perception has provided us with very important insights on how we process faces, facial emotion and whether faces involve unique perceptual mechanisms. A very influential approach on face recognition was the visual expertise framework which states that what makes faces unique is that we are all considered to be experts in face recognition (Bukach, Gauthier, & Tarr, 2006). An in depth literature overview on the topic of visual expertise can be found in Chapter 4. Two excellent reviews have been written by Xu (2005) and Harel (2016) supporting the concept of visual expertise after extensive domain specific visual object experience.

Another domain of expertise research is the motor expertise. Many researchers have turned to elite athletes and sometimes musicians, as motor experts to study action observation, motor processing and motor imagery. In a key study, Aglioti and colleagues investigated action anticipation and motor resonance in elite basketball players (as visuo-motor experts), coaches and sport journalists (as visual only experts) and novices (Aglioti, Cesari, Romani & Urgesi, 2008). The authors found that elite athletes predicted more accurately and much earlier the anticipated action (the success of free shots) than both the visual experts and novices and that motor evoked potentials were modulated for both the visuo-motor and the visual experts. In a later fMRI study (Abreu et al., 2012) with elite basketball players and novices, they provided evidence for expertise modulation beyond the fronto-parietal Action Observation Network with activations in the extrastriate body area, inferior frontal gyrus, right anterior insular cortex suggesting stronger embodiment of the observed action and higher body awareness for the experts. Another fMRI study tested professional piano players and non-musicians while watching videos of piano performances either in ‘correct’ condition (focus on technique) or in ‘enjoyment’ condition (focus on pleasure) and showed similar results, with stronger activations over the mirror neuron network for the experts and even more so in the ‘enjoyment’ condition (Hou et al., 2017).

Another example of motor expertise that has provided the means for this research domain to flourish in the last decades is professional ballet dance which was also used in the current study. Before briefly presenting the rich literature, it is important to explain how dance expertise is defined in the current thesis and what are the important benefits of using dance and not another type of motor or artistic expertise. Firstly, the common practice in the dance neuroscience literature that was followed in the studies of the present thesis too is to test specifically ballet dancers who work professionally (freelancing, in a dance company, or teaching) or are in professional training for 5 years or more. They can be trained or work in other dance styles as well, but the main professional training needs to be in ballet. The reason for this criterion is because, in contrast to most other dance styles, ballet has a very strict academic professional training programme of several years that offers the respective qualification in addition to the 10-15 years dancers might be attending ballet classes in an amateur level. Even though there are professional qualifications for styles such as contemporary or latin dance, only ballet requires such an extensive and strict training which allows researchers to control for years, type and similarity of motor training across expert participants. Secondly, dance is a unique type of expertise and this uniqueness makes dance such an important domain to study: both motor and artistic that cannot be found in other professions, using their own body to produce their work and express their emotions. For example, athletes are motor experts, but not artistic, do not train professionally to express emotions with their bodies and their motor expertise varies depending on the sport (if it is a team sport or not, if they use only their bodies like swimmers do or use an instrument like basketball or football players do). Similarly, musicians are both motor and artistic experts and do express emotions but through the use of an instrument. Actors are artistic experts that do learn to express/reproduce emotions but are not motor experts. Therefore, only dance combines motor, art and emotion expression expertise in such unique way making it the perfect example to study not only motor skills but also, topics that are the focus on the present thesis, namely emotion perception, body awareness and interoception-exteroception interplay.

Briefly, dance has been used to study the effects of motor expertise on action observation with modulation on behavioural responses, ERPs, frequency analyses and functional activations in sensorimotor areas (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Ehrenberg, Leung, & Haggard, 2010; Cross, Hamilton, & Grafton, 2006; Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008; Orlandi & Proverbio, 2019; Orlandi, Zani, & Proverbio, 2017, Sevdalis & Keller, 2010), joint action with evidence supporting an aesthetic preference for joint movements (e.g., Vicary, Sperling, von Zimmermann, Richardson & Orgs, 2017, Monroy, Imada, Sagiv & Orgs, 2021), social cognition, empathy and the role of dance in society throughout history (Bläsing et al., 2012; Bläsing, 2014; Christensen, Cela-Conde, & Gomila, 2017; Fink, Bläsing, Ravignani, & Shackelford, 2021; Sevdalis & Keller, 2011), body awareness and proprioception with strong evidence on improved performance by dancers than non-dancers control participants (albeit only on domain specific proprioceptive tasks, in new lab based tasks dancers do not always perform significantly better, see Beck, Saramandi, Ferrè, & Haggard, 2020; Christensen, Gaigg, & Calvo-Merino, 2017; Ramsay & Riddoch, 2001; Rein, Fabian, Zwipp, Rammelt, & Weindel, 2011; Sevdalis & Raab, 2014; Van Wieringen, Veer, And, & Ader, 1982), emotion with evidence showing similarly a modulation on psychophysiological affective responses of dancers in comparison to non-dancers control participants (Christensen, Gomila, Gaigg, Sivarajah, & Calvo-Merino, 2016; Christensen, Pollick, Lambrechts, & Gomila, 2016; Sevdalis & Keller, 2012) and lately, (neuro) aesthetics with studies on exploring the dance expertise effect on aesthetic preference of dance movements (Calvo-Merino, Jola, Glaser, & Haggard, 2008; Christensen & Calvo-Merino, 2013; Cross, Kirsch, Ticini, & Schütz-Bosbach, 2011; Kirsch & Cross, 2018; Kirsch, Dawson, & Cross, 2015; Kirsch, Snagg, Heery & Cross, 2016; Kirsch, Urgesi, & Cross, 2016; Orlandi, Cross, & Orgs, 2020; Vicary et al., 2017). The current thesis focuses on dance expertise and in- depth reviews of the literature can be found in chapters 2, 3 and 4.

1.4 Thesis overview and structure

The primary aim of the current thesis was to investigate the role of dance as motor and artistic expertise on facial emotion perception. This aim was based on the evidence for a differential neural and psychophysiological response of dancers while viewing affective dance movements in comparison to non-dancers (e.g., Christensen et al. 2016) but also on the lack of evidence on how dance modulates emotion perception outside of the familiar dance domain. In my first experiment dancers and non-dancers control participants performed a visual emotion recognition task while recording their EEG activity. Chapter 2 is focused on the dance expertise effect on the visual and somatosensory processing of facial emotion providing supportive evidence for the embodied emotion theory and, importantly, for differential processing of dancers on everyday facial emotions. A secondary aim was to better understand how dancers perceive their own bodies and emotions exploring the effect of dance on interoceptive markers and their relation to emotion processing. This aim was informed by and attempted to replicate and expand the work by Christensen et al. (2017) where dancers were shown to have better interoceptive abilities in comparison to controls. Chapter 3 explored for the first time the heart-brain interactions on dancers and controls on the same visual emotion recognition task and compared the relationships between heartbeat, visual and somatosensory evoked potentials and the interoceptive abilities between groups. Chapter 4 contributes to the primary aim of the thesis again. This time we tested dancers and controls on an online pilot of a visual emotion discrimination task employing the face inversion effect to better understand the emotion enhancement of dancers following the lines of visual perception expertise literature. With this study, we took a different approach on dance expertise focusing for the first time on potential differences at a visual perception and behavioural level on domain-general facial expression stimuli.

Throughout these studies the psychological state of the participants and the connection they have with their bodies were always taken into consideration. For that reason, the third aim of the thesis was exactly to investigate the role of psychological markers on emotion perception. This aim is informed by the latest research showing on one hand, the importance of interoceptive signals in exteroceptive processing (e.g., see Craig, 2003) and on the other hand, how psychological factors might affect emotion perception (e.g., Ihme, 2014). Participants' psychological states and traits were collected to control for as many variables as possible between the control and expert group. Chapter 5 is dedicated to this aim, looking at individual differences in psychological characteristics and interoception and their effect of embodiment of emotion. In contrast to the other experimental chapters, in chapter 5 participants from general population were recruited without collecting details about motor or artistic expertise. The main reason for this difference is the different perspective of this chapter. This study was the next step after Sel et al. (2014) study aiming to investigate the somatosensory processing of emotion more in depth in terms of more specific direct analysis in comparison to Sel et al. (2014) (one sample t-tests of only the values of interest were used instead of repeated measures ANOVA) and more in breadth including firstly more and different emotions than Sel et al. (2014) study and secondly, investigating the role of psychological factors to emotion embodiment. Even though dancers are not included in the study, chapter 5 provides two very crucial elements in this thesis: firstly, provides additional evidence in support of the embodied cognition theory and the timeline of somatosensory processing of different emotions and secondly, is dedicated to the third aim of the thesis investigating the role of psychological factors of emotion processing. Information on the participants' psychological characteristics and body awareness were collected also in Chapter 2, 3 and 4. In all 3 chapters potential relations between these markers, emotion perception and dance expertise were investigated.

Finally, in Chapter 6 all findings are discussed in the light of the current theoretical and methodological approaches and future directions are suggested in relation to dance neuroscience, emotion perception and interoception.

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Chapter 2: Dance your emotions: Expertise modulates visual and embodied emotion

This chapter includes the manuscript: Meletaki, V., Forster, B., Calvo-Merino, B. (2022) Dance your emotions: Expertise modulates visual and embodied emotion. (in prep). The structure is according to Nature Neuroscience publication guidelines with Methods as the last and online only section.

Abstract

Dance expertise modulates visual, sensorimotor and psychophysiological responses to affective body movements. We investigated if the enhanced expert emotion sensitivity is domain-specific or general to other forms of emotional expression by comparing neural responses to happy, fearful, neutral facial expression in professional dancers/experts and non-dancers. Visual Evoked Potentials (VEPs) and Somatosensory Evoked Potentials (SEPs) were measured in the somatosensory cortex while participants performed a visual emotion/ gender discrimination task on emotional faces. Our results showed distinct group differences and group x emotion interactions over the occipital lobe for the VEPs (P1, N170 and P2) and in the SEPs (P50, N80, P100 and N140) suggesting a differential embodied response to facial expression between experts and non-experts. This data suggests an enhanced general emotion sensitivity in experts that is reflected beyond the observation of their motor acquired skill but onto general and everyday emotional expressions. These results point towards new venues for emotional sensitivity training based on engaging motor and artistic knowledge.

2.1. Introduction

Emotions encompass our lives often through nonverbal communication, with facial expressions and body language. Facial emotional expressions have been studied widely in the past offering us invaluable information on how the brain processes such visual stimuli and/ to identify emotional facial expressions (e.g. Calvo & Nummenmaa, 2016; Liu, Liu, Zheng, Zhao, & Fu, 2021). The question whether faces per se are unique in their perceptual process in the brain or not has resulted in a rich literature on visual object recognition expertise showing that expertise does not apply only to faces. Studies have shown that similar cortical activity for face perception has been observed for birds, cars, chess displays, dogs, fingerprints, radiology, minerals and visual creatures (the 'Greebles') among others after extensive visual experience and, therefore, visual expertise is a skill that can be learned (Bukach, Gauthier, & Tarr, 2006; Diamond & Carey, 1986; Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Gauthier & Tarr, 1997; Gilaie-Dotan, Harel, Bentin, Kanai, & Rees, 2012; Harel, 2016; Martens, Bulthé, van Vliet, & Op de Beeck, 2018; Taylor & Tanaka, 1991; Xu, 2005). With the current study we questioned whether the domain specific sensorimotor expertise of professional ballet dancers can modulate everyday visual and somatosensory emotion perception.

Embodied emotion theory argues that emotion involves *perceptual, somatovisceral and motoric (re-)experiencing* (Niedenthal, 2007: 1002; Niedenthal & Maringer, 2009; Pitcher, Garrido, Walsh, & Duchaine, 2008). Supportive evidence for embodied emotion has shown the necessary involvement of the somatosensory cortices in early stages of facial emotion processing (Fanghella, Gaigg, Candidi, Forster, & Calvo-Merino, 2022; Keysers, Kaas & Gazzola, 2010, Pitcher et al., 2008; Pourtois et al., 2004; Sel, Forster, & Calvo-Merino, 2014). This contribution of the SCx is merely somatic, independent from the visual processing and it concerns not only emotion processing but also attention and working memory tasks involving bodily stimuli (Arslanova, Galvez-Pol, Calvo-Merino, & Forster, 2019; Galvez-Pol, Calvo-Merino, Capilla, & Forster, 2018; Galvez-Pol, Calvo-Merino, & Forster, 2020). Recent studies from the lab suggest that specifically the neural index of embodied anger and happiness have significantly distinct signatures in the right somatosensory cortex and embodied anger is partially predicted by the observer's level of alexithymia (Arslanova, Meletaki, Calvo-Merino, Forster, in prep).

If our bodies are necessary to process emotions, could focusing on expressive motor expertise offer us an insight on emotion perception? The art of dance is exemplary for the emotion expression and communication through the body. Dance has been the means to investigate topics from social interactions (e.g. Christensen, Gaigg, & Calvo-Merino, 2017; Fink, Bläsing, Ravignani, & Shackelford, 2021), to body movement memory processing (e.g. Vicary, Robbins, Calvo-Merino, & Stevens, 2014) and neuroaesthetics (Calvo-Merino, Jola, Glaser, & Haggard, 2008; Cross, Kirsch, Ticini, & Schütz-Bosbach, 2011; Cross & Ticini, 2012; Kirsch, Dawson, & Cross, 2015; Kirsch, Urgesi, & Cross, 2016; Kirsch, Snagg, Heerey & Cross, 2016). Relevant literature has shown that dance expertise modulates neural responses on familiar movements and action observation (Bläsing et al., 2012; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Calvo-Merino, Ehrenberg, Leung, & Haggard, 2010; Cross, Hamilton, & Grafton, 2006; Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008; Orlandi & Proverbio, 2019; Orlandi, Zani, & Proverbio, 2017). Dance expertise has been associated with structural neuroplasticity in the sensorimotor network (Hänggi, Koeneke, Bezzola, & Jäncke, 2010) and with effects on white matter diffusivity in sensorimotor pathways (of both professional dancers and musicians; Giacosa, Karpati, Foster, Penhune, & Hyde, 2016). Strong evidence suggests that professional dancers show significantly different psychophysiological responses during observation of familiar affective body movements than control participants without former dance experience (Christensen, Gomila, Gaigg, Sivarajah, & Calvo-Merino, 2016; Christensen, Pollick, Lambrechts, & Gomila, 2016; Kirsch, Drommelschmidt, & Cross, 2013). Furthermore, dancers have shown enhanced somatosensory abilities and body awareness including better interoceptive abilities than participants without prior dance training (Beck, Saramandi, Ferrè, & Haggard, 2020 for dancers showing more susceptibility; Christensen, Cela-Conde, & Gomila, 2017; Christensen, Gaigg, et al., 2017; Golomer & Dupui, 2000; Jola, Davis, & Haggard, 2011; Ramsay & Riddoch, 2001; Rein, Fabian, Zwipp, Rammelt, & Weindel, 2011; Sevdalis & Keller, 2011 for a review).

The current study aimed to investigate if this enhanced emotion sensitivity is domain specific (i.e., only related to emotion expressed on familiar dance movements) or can be generalized to other forms of emotional expressions (i.e., everyday facial expressions) and if it affects psychophysiological and neural responses to emotional expressions of others. 26 professional ballet dancers and 26 age and gender-matched control participants with no prior dance expertise completed an emotion or gender (as a control task) discrimination task showing neutral, afraid and happy facial expressions on male and female faces while measuring their EEG activity. In half of the trials a tactile stimulation was received on their left index finger to enhance the activity over the somatosensory cortices. The specific paradigm and emotions were used to expand the line of work of Sel and colleagues (2014) in a way that is easily comparable and potentially replicable. Additionally, regarding the emotions, afraid and happy expressions offer a great balance between a positive and negative emotion on a similar level of valence, with neutral serving as a baseline. Neutral, afraid and happy are the expressions most easily recognisable and most used in the literature and worked as a stepping stone in broadening up the research on dancers to domain-general stimuli. The somatosensory evoked potentials over the somatosensory cortices and the visual evoked potentials over the occipital electrodes were later averaged and compared between the groups in repeated measures ANOVA with factors: group (dancers, controls), task (emotion or gender discrimination task), emotion (neutral, afraid, happy), hemisphere (right or left), region (anterior, central, posterior) and site (dorsal, dorsolateral, lateral). Levels of behavioural accuracy during the task were collected, subjective ratings of the emotion and gender, as well as levels of depression, alexithymia, state-trait anxiety, prosopagnosia, interoceptive awareness, past music experience and for dancers only, level of dance expertise. For more details about the methods, please see the methods section 2.4.

2.2. Results

2.2.1. Behavioural accuracy in the visual emotion and gender recognition task during EEG recording

The task (2 levels) x group (2 levels) ANOVA resulted in a significant main effect of task, F (1, 48) = 5.337, p = .025, η_p^2 = .100 with the gender discrimination to have significantly higher accuracy (M = .96, SD = .04) than the emotion task (M = .95, SD = .04). The task x group interaction was also significant, F (1, 48) = 7.666, p = .008, η_p^2 = .138 with dancers being significantly more accurate in the gender discrimination task than the control participants (on gender task dancers were 98% accurate and controls 95% and on emotion task dancers were 94% accurate and controls 95%). The main effect of group was not statistically significant, p = .488, η_p^2 = .01.

2.2.2. Subjective Ratings of visual emotion and gender intensity

On the emotion task results showed a main effect of emotion, F (2, 98) = 1750.52, p < .001, η_p^2 = .973 with Bonferroni post hoc comparisons showing a significant difference between the three emotions (M = 11, SD = 7.1 for afraid, M = 50.6, SD = 2 for neutral and M = 91, SD = 6.9 for happy, all p < .001). No significant differences were found between groups (group effect p = .565 and emotion x group interaction p = .792. The ANOVA on the gender task showed a main effect of gender, F (1, 49) = 4634.33, p < .001, η_p^2 = .99 with Bonferroni post hoc comparisons showing a significant difference between ratings for male and female faces, (M = 4.87, SD = 5.5 for female and M = 95, SD = .4.9 for male, p < .001). No significant group effect (p = .639) or gender x group interaction (p = .331) was found.

2.2.3. Somatosensory activity (SEP, VEPs free) during Face Emotion and Gender Visual Recognition Task

Regarding topography, we did have a main effect of region, main effect of site and interactions between hemisphere, region, and site across all time windows. Hemisphere had a significant main effect on P50 and N80. Below we unfold the key results involving group and emotion.

2.2.3.1. P50

We have a group x emotion x hemisphere x region interaction, *F* (3.17, 155.53) = 3.321, *p* = .019, η_p^2 = .063. Dancers showed the emotion x hemisphere x region interaction (*F* (2.88, 72.03) = 4.261, *p* =.009, η_p^2 = .146) with a main effect of emotion in central region of both hemispheres (right *p* = .046, n. s. post hoc emotion comparisons, left *p* = .024 with neutral being significantly different than afraid, *p* = .006, see Figure 2.1). Controls did not show any significant emotion effects.

2.2.3.2. N80

The first interaction to unfold is the group x task x hemisphere x region interaction (*F* (2, 94) = 5.747, *p* = .004, η_p^2 = .105). Dancers showed a task x hemisphere x region interaction, *F* (2 ,50) = 8.454, *p* = .001, η_p^2 = .253 which on the right hemisphere led to a task x region interaction at *p* = .005 and on the left hemisphere an overall main effect of task, *F* (1, 25) = 4.830, *p* = .037, η_p^2 =.162, see Figure 2.2. Controls did not show any significant effects.

The second interaction is group x task x hemisphere x site, *F* (1.77, 86.75) = 5.412, *p* = .008, η_p^2 = .099. Dancers showed a task x hemisphere x site interaction (*F* (2, 50) = 3.606, *p* = .034, η_p^2 = .126) and then on the right hemisphere a task x site interaction and on the left the main effect of task. Controls did not show any significant effects.

The third interaction is group x emotion x hemisphere x site, *F* (3.07, 150.51) = 4.736, *p* = .003, η_p^2 = .088. Dancers had a main effect of emotion overall (*F* (2, 50) = 4.834, *p* = .012, η_p^2

= .162) with the neutral/ afraid post hoc comparison to be significant, p = .014 and the paired samples t-test on emotion index (afraid- neutral and happy- neutral), t (25) = 2.435, p = .022.

The control participants had an emotion x hemisphere interaction and an emotion x hemisphere x site interaction, F (2, 48) = 3.404, p = .044, η_p^2 = .124 and F (2.69, 62.2) = 4.084, p = .014, η_p^2 = .145 respectively. We found a main effect of emotion on the left hemisphere overall (p = .019, n. s. for the right) with the neutral/ afraid post hoc comparison to be significant, p = .036. Additionally, we found a main effect of emotion for the lateral site on both hemispheres (p = 038, η_p^2 = .128 and p = .027 η_p^2 = .139 respectively) and the neutral/ happy post hoc comparison to be significant on the right, p = .048 (n. s. post hoc comparisons on the left, see Figure 2.1.).

Altogether, dancers showed a significant main effect of task on the left hemisphere, task interactions with region and site with no significant follow-ups and a significant main effect of emotion overall with differences between neutral and afraid and the afraid index with happy index of emotion. Control participants showed a main effect of task on the left hemisphere and the lateral site on both right (with neutral significantly different from afraid) and left hemisphere with no significant follow-ups.

2.2.3.2.1. Additional Effects on Emotion and Task on N80

The main effect of emotion was significant, F (2, 100) = 5.449, p = .006, η_p^2 = .098. The neutral/ afraid Bonferroni post hoc comparison and the paired samples t-test on emotion index (afraid – neutral and happy – neutral) were significant at p = .002 and t (50) = 2.006, p = .05. Following up the hemisphere x emotion interaction (F (2, 98) = 3.878, p = .024, η_p^2 = .073), we found a main effect of emotion only at the left hemisphere, F (2, 100) = 10.479, p < .001, η_p^2 = .173 (n. s. for the right) with neutral/ afraid and neutral/ happy post hoc comparisons to be significant at p < .001 and p = .048 respectively.

2.2.3.3. P100

The group x emotion x task x hemisphere x region interaction was significant, F (2.96, 144.92) = 3.843, p = .011, η_p^2 = .073. Dancers showed an emotion x task x hemisphere x region interaction, F (2.66, 66.53) = 4.497, p = .008, η_p^2 = .152. By hemisphere, no significant results were found on the right. On the left, there was a main effect of emotion on the central (p = .012, η_p^2 = .227, n. s. post hoc comparisons) and the posterior region (p = .006, η_p^2 = .269, afraid/ happy post hoc comparison was significant, p = .041). Control participants showed a task x hemisphere interaction (p = .041, η_p^2 = .163, n. s. follow ups for both factors as it was an inverse interaction).

The emotion x group x emotion x hemisphere x site from N80 continued to P100, F (3.02, 147.85) = 3.259, p = .023, η_p^2 = .083. Dancers had no significant follow-ups. Control participants had an emotion x hemisphere x site interaction (p = .016, η_p^2= .135) leading into a main effect of emotion on the left lateral site only (p = .044, η_p^2= .122, n. s. post hoc comparisons).

Altogether, dancers showed a main effect of emotion on the left central (n. s. post hoc comparisons) and posterior region (with the afraid / happy post hoc comparison to be significant). Dancers showed an inverse task by hemisphere interaction and a main effect of emotion on the left lateral site with no significant follow-ups.

2.2.3.3.1. Additional Effects on Emotion and Task on P100

The hemisphere x emotion interaction, F (2, 98) = 3.287, p = .042, η_p^2= .063, continued from N80 to P100 finding similarly a main effect of emotion on the left hemisphere, F (2, 100) = 5.209, p = .007, η_p^2 = .094 (n. s. for the right). The pairwise neutral / afraid comparison was significant, p = .006 and the paired samples t-test on emotion index (afraid – neutral and happy – neutral), t (50) = 2.247, p = .029.

2.2.3.4. N140

The first interaction is group x emotion x task x region (*F* (2.28, 111.83) = 3.466, *p* = .029, η_p^2 = .066). Dancers showed an emotion x task x region interaction (*p* = .008, η_p^2= .164) and then on happy a task x region interaction, *p* = .028, ηp^2 = .162. Controls had no significant results. The second interaction is group x emotion x task x site (*F* (2.76, 135.32) = 5.287, *p* = .002, η_p^2 = .097). Control participants showed an emotion x task x site interaction (*p* = .014, ηp^2 = .142) and on gender task only a main effect of site for neutral and happy emotions (*p* = .013 and *p* = .009 respectively). No significant results for dancers.

Altogether, dancers showed a significant task x region interaction on the amplitude on happy and the controls showed a main effect of site on the amplitudes of neutral and happy on the gender task only.

2.2.3.5. Source Localisation

The statistical non – parametric mapping comparing average somatosensory activity (VEP free) of dancers on emotion and gender discrimination task showed significant results: one-tailed t – test (emotion < gender task) *t* = -2.243, *p* <.001 and two – tailed – test (emotion <> gender task) *t* = 2.308, *p* =.001. The sLORETA topographic results showed as best match at 1mm the Brodmann area 30 within the cingulate gyrus, the posterior cingulate and the limbic lobe (MNI coordinates: X =-20, Y = -60, Z = 11, Figure 2.3.).

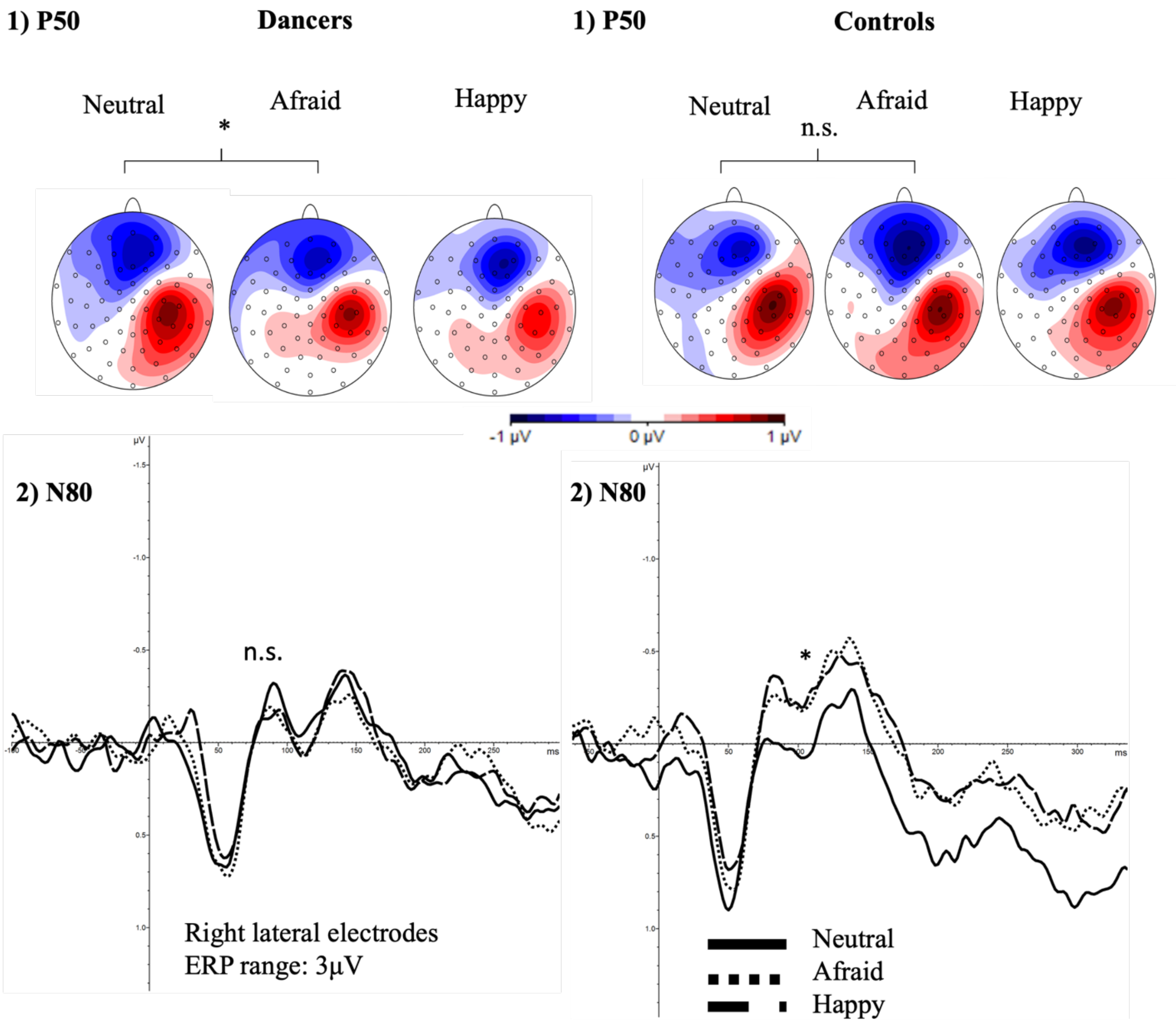

Figure 2.1: *Somatosensory Evoked Potentials results (VEP free)*

Notes: 1) Topographical maps of the electrophysiological activity at P50 showing the significant emotion effect for dancers in central electrodes after averaging task. 2) Grand averaged difference in somatosensory activity showing the localised significant effect of emotion for controls only on the right lateral electrodes 23, 24, and 25 at N80.

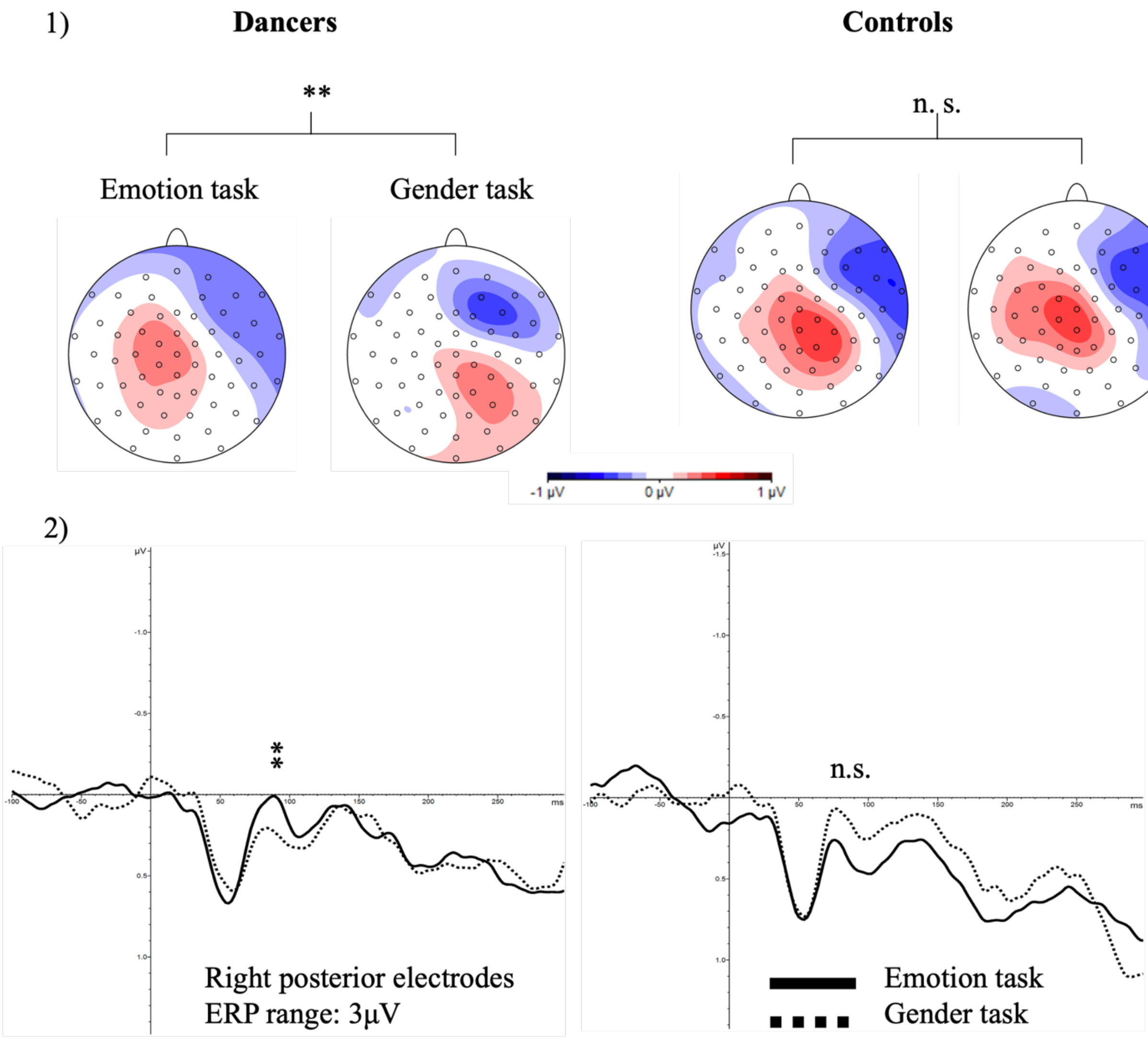

Figure 2.2: *Somatosensory Evoked Potentials results (VEP free)*

Notes: 1) Topographical maps of the electrophysiological activity at N80 showing the significant task effect for dancers only and not for controls. 2) Grand averaged difference in somatosensory activity showing the task effect at N80 at the right posterior electrodes 4, 12, 25 for dancers and not for the controls.

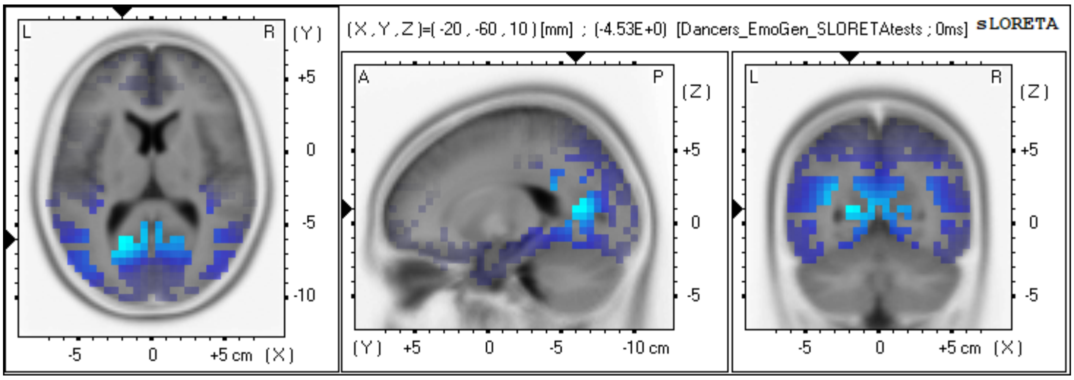

Figure 2.3: *Source Localisation analysis*

Notes: sLORETA identified as best match at 1mm the Brodmann area 30, the posterior cingulate and the limbic lobe for the task comparison at N80 on SEPs (VEP free) for the dancers.

2.2.4. Visual activity (VEPs) during Face Emotion and Gender Visual Recognition Task

Regarding topography, we had a significant main effect of electrode, all $p < .001$ for the three time windows, a main effect of hemisphere at P2 ($p = .050$) and a hemisphere x electrode interaction at P1 and P2 ($p < .001$ and $p = .006$ respectively).

2.2.4.1. P120

In P1, group interacted with electrode (F (1.36, 66.54) = 7.72, $p = .003$, $\eta_p^2 = .136$) indicating a main effect of group on the right occipital electrode 42, F (1, 49) = 4.794, $p = .033$, $\eta_p^2 = .089$.

2.2.4.1.1. Additional Effects on Emotion and Task on P120

The main effect of emotion was significant, F (2, 98) = 10.481, $p < .001$, $\eta_p^2 = .176$ with Bonferroni pairwise comparisons afraid/ neutral and afraid/ happy to be significant ($p = .001$ and $p = .018$). The paired samples t-test comparing the emotion index (afraid – neutral and happy – neutral) was significant, t (50) = -2.862, $p = .006$.

The emotion x hemisphere interaction (F (2, 98) = 7.994, $p = .001$, $\eta_p^2 = .14$) led to a significant main effect of emotion for both hemispheres with the Bonferroni comparisons on afraid/neutral and afraid/ happy to be significant but the paired samples t-test comparing the emotion index between afraid – neutral and happy – neutral was statistically significant only for the right hemisphere, t (50) = -5.68, $p < .001$.

2.2.4.2. N170

The group x emotion hemisphere x electrode interaction (F (3.144, 154.077) = 2.711, p = .044, $\eta_p^2 = .052$) was significant. Both dancers and controls had a significant main effect of emotion, see Figure 2.4. For dancers, F (2, 50) = 9.784, p = .000, $\eta_p^2 = .281$, with the neutral/afraid, p = .004 and neutral/happy p = .007 Bonferroni comparisons to be significant. For controls, F (2, 48) = 16.858, $p < .000$, η_p^2.413, with all the Bonferroni comparisons to be significant, neutral/ afraid $p < .001$, afraid/happy p = .009, neutral/ happy p = .032, including the paired samples t- test on emotion index, p = .003. No further significant results were found for dancers. Controls showed the emotion x hemisphere x electrode interaction, F (4, 96) = 3.448, p = .011, $\eta_p^2 = .126$, with a significant emotion x electrode interaction on the right hemisphere, F (4, 96) = 4.332, p =.003, $\eta_p^2 = .153$.

Broken by emotion, on neutral a significant group x electrode interaction was found, F (1.29, 63.011) = 4.100, p = .037, p = .037, $\eta_p^2 = .077$. We averaged the homologous electrodes (42-44, 54-58 and 55-57) and found a main effect of group for the averaged electrodes 54-58, F (1, 50) = 6.452, p = .014.

2.2.4.2.1. Additional Effects on Emotion and Task on N170

The main effect of emotion was significant (F (1.79, 89.68) = 24.150, $p < .001$, $\eta_p^2 = .326$) with all the Bonferroni pairwise comparisons to be significantly different from each other (neutral/ afraid and neutral/ happy, $p < .001$ and afraid/ happy, p = .008). The paired samples t-test comparing the emotion index (afraid – neutral and happy – neutral) was also significant, t (50) = -3.156, p = .003.

2.2.4.3. P200

The group x emotion x hemisphere x electrode interaction continued to P2 (F (4, 196) = 3.197, p = .014, η_p^2 = .061), see Figure 2.4. The main effect of emotion was significant both for dancers (F (2, 50) = 3.959, p = .025, η_p^2 = .137) with significant afraid/ happy Bonferroni comparison, p = .026 and the paired samples t-test between the emotion index (afraid – neutral and happy – neutral), t (25) = -2.842, p = .009) and for controls (F (2, 48) = 9.924, p < .001 η_p^2= .293) with significant the neutral / afraid comparison, p = .002 and afraid / happy, p = .013 and the paired samples t-test for emotion index (afraid – neutral and happy – neutral), t (24) = -3.143, p =.004). For the dancers, we followed up the emotion x electrode interaction (F (4, 100) = 4.622, p = .002, η_p^2 = .156) averaging the homologous electrodes and found a main effect of emotion for the 55 & 57 pair (p = .011, afraid/ happy comparison, p = .017 and emotion index paired t-test, p = .006) and the 54 & 58 pair (p = .004, neutral/ afraid comparison, p = .041, afraid/ happy comparison, p = .002 and emotion index paired t-test, p = .001). Control participants showed an emotion x hemisphere x electrode interaction (F (4, 96) = 2.988, p = .023, η_p^2 = .111. On the right hemisphere there was a main emotion effect, p = .007 (neutral/ afraid comparison at p = .020 and emotion index t-test at p < .001) and an emotion x electrode interaction, p = .006 and on the left a main emotion effect, p < .001 (neutral/ afraid comparison at p = .001, afraid/ happy at p = .005 and emotion index t-test at p = .002). Controls also had an emotion x electrode interaction (F (4, 96) = 2.624, p = .039, η_p^2 = .099) leading to a significant main effect of emotion for the 55 & 57 pair and 54 & 58 pair, p < .001 for both, neutral/ afraid comparison at. p =.002 and p = .005, afraid/ happy comparison at p = .038 and p = .004 and the emotion index t – test at p = .013 and p = .001, respectively.

2.2.4.3.1 Additional emotion effects on P2

The main effect of emotion was significant, $F\ (2, 100) = 11.775$, $p < .001$, $\eta_p^2 = .191$ with the neutral/ afraid and afraid/ happy comparison to be significant, $p < .001$ and the paired samples t-test on emotion index (afraid – neutral and happy – neutral), $t\ (50) = -4.223$, $p < .001$.

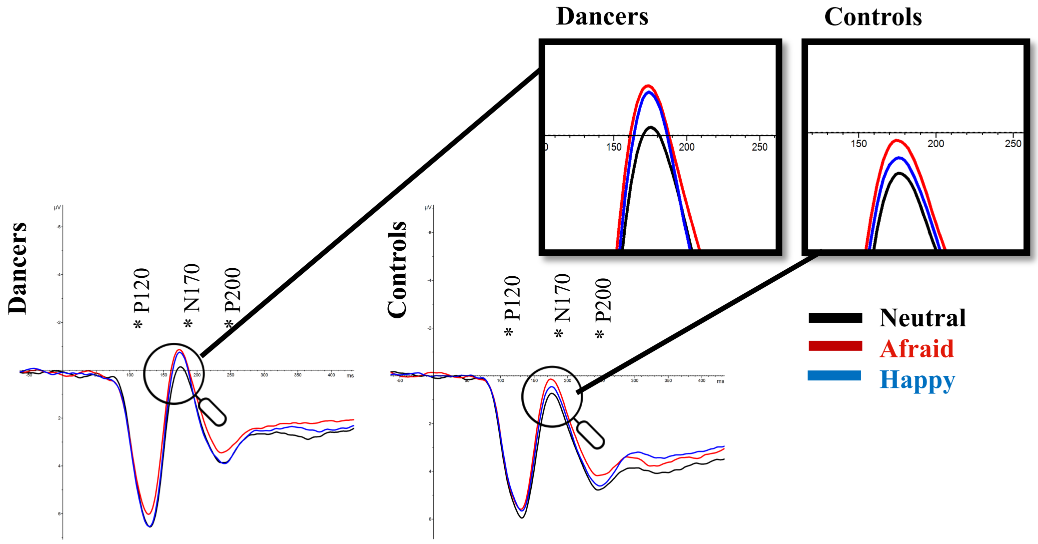

Figure 2.4: *Visual Evoked Potentials results*

Notes: Grand averaged activity over the six occipital electrodes 42, 44, 54, 55, 57, 58. At N170 dancers had a main effect of emotion with neutral significantly different from afraid and happy and controls had a main effect of emotion with all post hoc comparisons significant. At P2 dancers had an emotion effect with afraid being significantly different than happy and controls had an emotion effect with amplitude over afraid expression to be significantly different than neutral and happy.

2.3. Discussion

Previous studies have established the visual and psychophysiological sensitivity of professional dancers to domain specific affective stimuli (e.g. Christensen, Gomila, et al., 2016; Christensen, Pollick, et al., 2016). The aim of the current study was to investigate if this affective sensitivity is only domain specific or general, i.e., to facial emotion expressions. In accordance with our hypotheses, our results showed that expertise modulated both the visual and the somatosensory processing of facial emotion with group effects unfolding through all the time- windows.

Specifically for SEPs, at P50 dancers had an emotion effect in the central region. At N80, dancers showed a task effect in both hemisphere and an emotion effect overall with afraid expression being the significantly different from neutral and happy. Dancers showed an emotion x task interaction at P100 too and a task effect on happy expression at N140. Controls showed an emotion effect localised at the lateral electrodes at N80 and P100 and different topography for neutral and happy expressions within the gender task at N140.

Specifically for the VEPs, both groups had emotion effects. However, for dancers the neutral expression was processed significantly differently than afraid and happy at N170 and at P200 afraid expression was significantly different than happy. For controls, all emotions were processed differently from each other for N170 and for P200 afraid differed from neutral and happy.

The main effect of emotion over P1, N170 and P2 is in accordance with the well-established literature on visual processing of facial expressions and confirms our visual manipulation (Conty, Dezecache, Hugueville, & Grèzes, 2012; Williams et al., 2004; Williams, Palmer, Liddell, Song, & Gordon, 2006). The emotion effect over N80 agrees with previous literature on emotion embodiment (Arslanova et al., in prep.; Fanghella et al., 2022; Sel et al., 2014; Sel, Calvo-Merino, Tsakiris, & Forster, 2020).

We provide the first empirical evidence that dance expertise modulates early activations over the somatosensory and visual areas while observing facial emotion expressions. Dancers seem to be more sensitive than control participants; following up the group interactions, we could see that the pattern unfolding showed more spread activations for dancers both at a visual and at a somatosensory level with main emotion and task effects. For example, emotion effects were present irrespective of the task which was not the case for the control participants. Control participants, on the other hand, confirmed previous literature and showed more localised and task specific emotion effects. It is noteworthy that in both groups the afraid expression was the one that stood out and differed significantly from other emotion conditions confirming previous evidence for the dominance of fear in emotion processing (Batty & Taylor, 2003; Pegna, Landis, & Khateb, 2008). Even though the Source Localisation Analysis did not show as a best match for the somatosensory activity (VEP free) of the dancers over the task effect on N80 the somatosensory areas as expected, the suggested areas still correspond to areas that are often found in fMRI literature on emotion processing (e.g. LeDoux, 2000, Molenberghs, Cunnington & Mattingley, 2012). As this is the first time testing motor and artistic expertise on facial emotion, more research is needed to better understand and localise the roots of the differential somatosensory activity. The novel neuroimaging methods can be very beneficial in localising the activity in real time with great spatial and temporal accuracy.

The novelty of our results offers an important new perspective on the meaning of 'expertise' and specifically motor expertise such as dance. Moreover, our findings align perfectly with the literature that has established dance expertise modulation on motor processing, psychophysiological responses on domain specific affective stimuli and motor specific anatomical differences in comparison to non-dancers controls and/ or experts on a different motor domain. The current study adds to the literature that dance expertise affects how we embody and process visual facial emotions that are not domain specific but everyday facial expressions. We were also able to support previous findings suggesting that dancers have stronger interoceptive abilities, with our dancers participants showing significantly higher averages on MAIA than controls (Christensen, Gaigg, et al., 2017; but see Sokol-Hessner et al., 2022 for beter interoceptive metcognition on actors). As shown in the supplementary material, MAIA was a significant predictor of emotion embodiment in different patterns for dancers and controls.

Following a holistic approach and considering other psychological characteristics in addition to dance expertise, we provide strong evidence that our results are only due to dance expertise. No other significant group difference was found on behavioural accuracy or levels of depression, anxiety, alexithymia and no participant had high levels of prosopagnosia. Applying the subtractive method to remove the visual carry-over effect from the somatosensory processing, we could show how dancers embody facial emotion differently than controls and how visual processing followed a distinct pattern from the somatosensory.

Our novel results offer new directions in the field of dance expertise and emotion perception. Future research could explore more deeply the roots of expertise studying the progression timeline of expertise and whether emotion and interoceptive sensitivity are skills that can be taught through training. Increasing emotion and interoceptive sensitivity through training can be highly beneficial especially for people with ASD and alexithymia. Lastly, future research could investigate how dancers and other motor or art experts process emotions following the predictive account of constructed emotion (Feldman Barrett, 2017).

2.4. Methods

2.4.1. Participants

Twenty-six ballet dancers (in professional training or working) (1 left-handed, 22 females, aged 19-38; *M*= 25.61, *SD*= 5.3) and twenty-six participants with no prior dance experience (2 left-handed, 22 females, aged 21-35; *M*= 25.59, *SD*= 4.44) naïve to the objective of the experiment reported normal or corrected-to-normal vision and participated in the study for a small time reimbursement (£8/hour). The control participants were matched for age and gender with the dancers, and they were recruited through an online psychology website (SONA Inc.). Further details about the participants are provided in Table 1. All participants gave their written informed consent, and the study was approved by the Ethics Committee, School of Arts and Social Sciences, City, University of London.

Table 2.1: *Participants' demographics*

Group	Age (years)	Age range (years)	Dance style			
			Ballet			Other *
			Professional experience (years)	Experience (total-years)	Hours/week training	Hours/week training
Dancers	25.61 (5.3)	19-38	4.86 (4)	17.38 (6.8)	7 (5.4)	9.97 (6.15)
Controls	25.59 (4.4)	21-35	0		0	0

Notes: Data show the means and the standard deviations in brackets. Other styles include contemporary (for all dancers), jazz, tap, street, modern, traditional among other styles.

2.4.2. Materials

2.4.2.1. Stimuli

A set of 60 pictures with faces depicting happy, afraid, and neutral expressions (half male) were taken from the Karolinska Directed Emotional Faces set (Lundqvist, Flykt, & Ohman, 1998). All faces were grey scaled and presented in a rectangular frame (1.4 x 1.57 inches). The photos used for happy and afraid expressions had been rated highly in valence and the neutral ones very low in a previous experiment (Sel et al., 2014).

2.4.2.2. Psychometric measures

We administered the following psychometric measures: for levels of depression, the Beck Depression Inventory II (Beck, Brown, Steer, Eidelson, & Riskind, 1987); for alexithymia, the Twenty Item Toronto Alexithymia Scale-II (Bagby, Taylor, & Parker, 1994), for levels of anxiety as a mental state or as a personal characteristic, the State-Trait Anxiety Inventory for Adults (Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983) and for the interoceptive awareness of the participants, the Multidimensional Assessment of Interoceptive Awareness (MAIA) (Mehling et al., 2012). Finally, the 20-Item Prosopagnosia Index (PI-20) (Shah, Gaule, Sowden, Bird, & Cook, 2015) was administered to check for possible developmental prosopagnosic traits. In table 2.2 below the means and standard deviations are shown for each group and in table 2.3 the correlations between the questionnaires.

Table 2.2: *Mean, Standard Deviation, Minimum and Maximum scores on the questionnaires (TAS, STAI- state, STAI- trait, BDI, MAIA and the 20-item prosopagnosia index) for control participants and dancers*

Dancers	**TAS**	**STAI-state**	**STAI-trait**	**BDI**	**MAIA**	**PI-20**
Mean	41.04/37.5	36.81	42.04	8/6	3.69	36.19
SD	12.18/51	7.99	10.31	6.08/18	.48	7.61
Minimum	27	21	25	1	2.68	25
Maximum	82	51	65	19	4.75	56
Controls	**TAS**	**STAI-state**	**STAI-trait**	**BDI**	**MAIA**	**PI-20**
Mean	45.68	36.32	42.29	5.96	2.71	37.12
SD	12.01	11.11	12.36	5.87	.66	10.96
Minimum	21	20	21	0	1.49	22
Maximum	72	56	73	23	3.82	70

Note: TAS: Toronto Alexithymia Scale, STAI-state: State Trait Anxiety Inventory- State scale, STAI-trait: State Trait Anxiety Inventory- Trait scale, BDI: Beck Depression Inventory, MAIA: Multidimensional Assessment of Interoceptive Awareness. N = 24 for STAI – trait anxiety for controls because the data for one control participant was not recorded. The second values shown on TAS and BDI for dancers correspond to the median and range respectively due to normality tests showing non normal distribution, D (26) = .18, p =.027 for TAS and D (26) = .18, p = .029 for BDI (Kolmogorov-Smirnov test was utilized based on sample size).

Table 2.3: *Correlations between the questionnaire scores*

Dancers	**TAS**	**STAI-state**	**STAI-trait**	**BDI**	**MAIA**
TAS	1	.353	.412*	.111	-.277
STAI-state		1	.721**	.600**	-.314
STAI-trait			1	.767**	-.251
BDI				1	-.171
MAIA					1
Controls	**TAS**	**STAI-state**	**STAI-trait**	**BDI**	**MAIA**
TAS	1	.421*	.532*	.233	-.530**
STAI-state		1	.675**	.648**	-.214
STAI-trait			1	.793**	-.228
BDI				1	-.265
MAIA					1

Note: $^*p \leq .05$, $^{**}p \leq .001$ Controls' responses on MAIA and STAI-S did not violate any assumption. On TAS there were three outliers (participants 7, 16 and 38), on STAI -T one outlier (participant 6), on BDI data were positively skewed and there was one outlier (participant 14). For the dancers, MAIA, STAI-S and STAI-T did not violate any assumptions. BDI and TAS were not normally distributed, and the latter had one outlier (participant 20).

One-way ANOVAs were computed to investigate group differences in behavioural scores. Dancers had significantly higher mean (M = 3.7, SD = .48) in average MAIA score than controls ($M = 2.71$, $SD = .66$), $F(1, 49) = 36.88$, $p \leq .001$, and in 6 out of the 8 MAIA subscales: noticing, attention regulation, emotion awareness, self-regulation, body listening and trusting the body. Correlation and regression analyses were computed to identify potential predictors of the emotion modulation of the visual and somatosensory activity using the questionnaire scores, physiological data (heartbeat per minute) and dance expertise for dancers. The correlations and selected regression analyses are included in the supplementary material.

2.4.3. Procedure

Participants were seated in a dimly lit sound attenuated electromagnetically shielded room looking at a computer monitor in a distance of 80 cm. Tactile stimulation was applied using one 12 V solenoid driving a metal rod with a blunt conical tip that touched the skin of the tip of the left index finger of the participants when current passed through the solenoid that was attached to the skin with a microporous tape. White noise masked the noise of the tactile stimulators using one loudspeaker 90cm away from the participant's head. Participants were asked to ignore the tactile stimulations and the white noise.

Trials started with a fixation cross (500ms) followed by a neutral, happy, or afraid face (600ms). During the visual-tactile conditions, participants received a tactile stimulation on their left index finger at 105ms after the visual onset (Fanghella et al., 2022; Pitcher et al., 2008; Sel et al., 2014). To control for the visual carry-over effect over the somatosensory response, half of the trials were the visual-only condition where the visual stimuli were presented without the tactile stimulation (Galvez-Pol et al., 2020). In 20% of the trials in both conditions, participants were asked if the last face they saw was happy/afraid (emotion discrimination task) or if it was male/female (gender discrimination task). Each task consisted of 600 trials presented in three blocks with breaks in between (see Figure 2.5 for the procedure). Participants were asked to focus on the visual stimuli and answer verbally yes or no (to avoid the motor preparation artifact in the EEG) as soon as possible after the question was presented. Before the two tasks, participants completed a short practise session to ensure they understood the procedure. The visual stimuli were presented centrally on a black background using the E-prime 2.0 software (Psychology Software Tools) on a Windows 7 desktop.

As a control measure, after the completion of the emotion and discrimination tasks, participants were presented with the same stimuli at the centre of the screen and below a visual analogous scale (VAS) with the word ‘happy’ on the left end, ‘neutral’ in the middle and ‘afraid’ on the right end or with the word ‘male’ on the left end and ‘female’ on the right end. Their task was to discriminate between the emotions or the gender by clicking on the appropriate side of the bar. The accuracy of their ratings was measured. The Beck Depression Inventory, the Toronto Alexithymia Scale, the State-Trait Anxiety Inventory, the MAIA and the 20-Item Prosopagnosia Index were administered using the online software tool Qualtrics (Qualtrics XM Platform™). The order of the tasks was counterbalanced across participants.

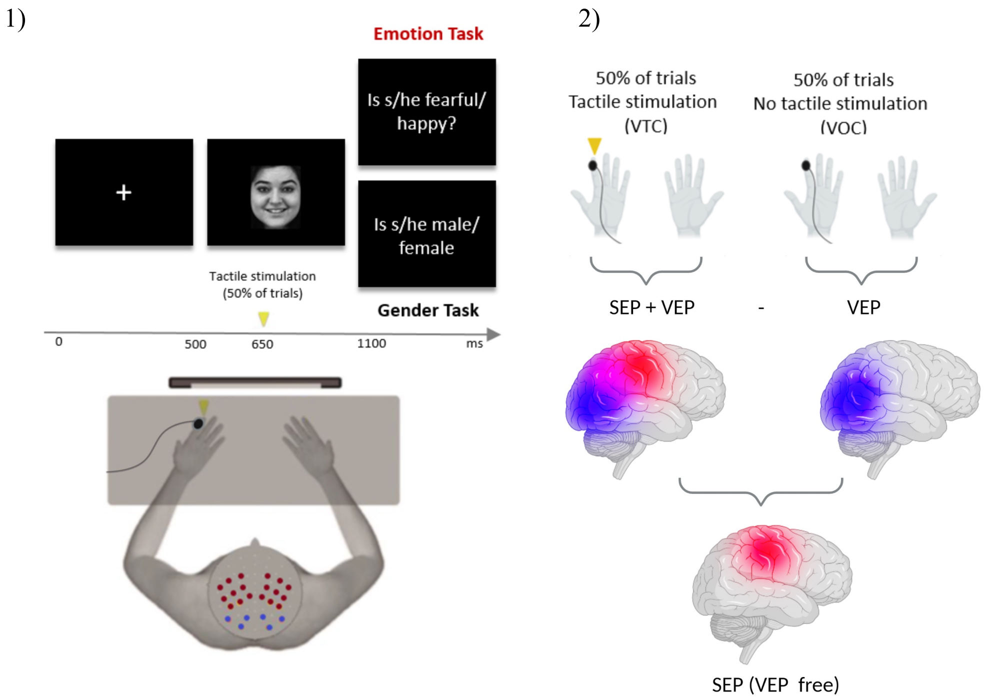

Figure 2.5: *Experimental Design*

Notes: 1) Task: face stimuli were presented at 500 ms from fixation cross onset and in 50% of trials tactile stimulation was delivered on the left index finger at 105 ms after the face onset (605 ms after fixation cross onset). In 10% of trials, a question appeared after 1100 ms. for Emotion Task: «Is s/he fearful? » Or «Is s/he happy? »; for Gender Task: «Is s/he male? » Or «Is s/he female? ». The electrodes in red were selected for analysis on Somatosensory Evoked Potentials and the electrodes in blue were selected for analysis on Visual Evoked Potentials. 2) Subtraction of Visual-Only Condition (VOC), with no tactile stimulation, from Visuo-Tactile Condition (VTC), when tactile stimulation was delivered. This method allowed us to isolate pure somatosensory evoked activity from visual carry-over effects (VEP + SEP) – (VEP) = SEP (VEP free). Figure adapted from Fanghella et al. (2022) and used with permission.

2.4.4. EEG recording and data analysis

EEG was recorded during the whole experiment from 64 active electrodes mounted equidistantly on an elastic electrode cap (M10, EasyCap GmBH, Herrsching, Germany). All electrodes were referenced online on the right earlobe and re-referenced offline to the average of all electrodes. Vertical and bipolar horizontal electrooculogram was recorded for eye movement tracking and artifact correction purposes. For the horizontal electrooculogram an electrode was placed next to the outer canthi of each eye and for the vertical, an electrode was placed below the right eye. One electrode was placed just under the left collarbone to record the electrocardiogram (ECG) throughout the experiment. Continuous EEG was recorded using a BrainAmp amplifier (500Hz sampling rate) and BrainVision Recorder while the offline EEG analysis was performed using BrainVision Analyser 2.1 (BrainProducts) on a Windows 10 desktop. Electrodes with extensive noise or flat lines were spline interpolated using their neighbouring channels. The data were digitally filtered at 0.1 - 30Hz (order 2, Butterworth zero phase shift) before re-referencing to the average to avoid spreading any noise. The EEG signal was epoched into 700ms segments starting 100ms before the tactile onset for the visual-tactile conditions for the SEPs or before the visual onset for the visual only conditions for the VEPs. Segments were then baseline corrected to the first 100ms. Ocular correction was performed for vertical and horizontal eye movements (Gratton, Coles, & Donchin, 1983) and artifacts with amplitude exceeding 100µV were removed from the analysis.

Single-subject ERPs and averages were computed for each condition (visual-tactile, visual only), emotion (happy, afraid, neutral) and task (emotion or gender discrimination). To keep the pure somatosensory response VEP-free, the single-subject averages of the visual-only conditions were subtracted from the single-subject averages of the visual-tactile conditions (see below for more details on the method). The resulting single-subject SEP VEP-free averages were used to calculate grand averages including all dancers and all control participants for neutral, happy, and afraid. The mean amplitude of the difference somatosensory evoked activity was computed.

For the visual- tactile condition our analysis focused on the 18 electrodes over the somatosensory cortices (electrodes corresponding to Fc1/2, Fc3/4, Fc 5/6, C1/2, C3/4, C5/6, Cp1/2, Cp3/4, Cp5/6 of the 10/20 system). Following visual inspection of the grand average across all emotions and conditions for each group time windows were exported for P50 (38-68" after the tactile stimulation onset), N80 (69-99"), P100 (99-119") and N140 (119-145"). Analysis was conducted for the visual evoked potential (VEPs) from the visual only condition to ensure that we replicate previous findings in the literature (e.g Sel et al., 2014; Williams et al., 2004, 2006). The time windows exported were focused on the P120 (110-150" after the visual stimulus onset), the N170 (155-195") and the P200 (222-262") and our analysis for this condition concerned only the electrode sites 44/42, 57/55 and 58/54 (corresponding to O1/2, O9/10 and PO9/10) over the occipital cortex (see Figure 2.5). The time windows were determined by visual inspection of the grand average across both tasks and all emotions (Luck & Gaspelin, 2017). The factors of the SEP analysis were group (dancers or controls), task (emotion or gender discrimination), hemisphere (right or left), region (anterior, central, posterior), site (dorsal, dorsolateral, lateral) and emotion (neutral, afraid, happy). Repeated-measures ANOVAs were conducted separately for each time window. Where appropriate, Greenhouse-Geisser values were used, and *p* values were corrected for multiple comparisons. One participant was an outlier (defined as >3 SD) in most conditions and was excluded from the analysis.

2.4.5. ERP signal-to-noise ratio

To ensure that the levels of signal-to-noise ratio across the conditions were not significantly different, repeated-measures ANOVA with factors task (emotion/ gender), condition (touch/ no touch) and emotion (neutral/ afraid/ happy) were conducted for the SEPs. The results showed no significant main effect of task, F (1, 50) = .756, condition, F (1, 50) = .005, p = .943, emotion, F (2, 100) = .586, p = .559 nor interaction between the factors. Paired t-tests showed no significant difference in the number of trials overall between the visual-tactile and visual-only conditions neither in emotion discrimination task, t (50) = .22, p = .827 nor in the gender discrimination task, t (50) = -.090, p = .929. These results suggest that the signal-to-noise ratio did not differ between the two conditions and therefore could not bias the results of further analyses and the ERP subtraction.

2.4.6. ERP subtraction

The visual processing of facial emotional expressions has been studied extensively in the literature (Calvo & Nummenmaa, 2016; Güntekin & Başar, 2014; Kragel & LaBar, 2016; Kragel, Reddan, Labar, & Wager, 2019; Y. Liu, Wang, Gozli, Xiang, & Jackson, 2021; Phan, Wager, Taylor, & Liberzon, 2002; Saarimäki et al., 2016). The aim of this study was to further our understanding on how we embody facial emotions, therefore we were interested in the somatosensory responses over the primary and secondary somatosensory cortex. Because the visual evoked potential spreads above the posterior cortex potentially masking the somatosensory response over the body-related information (Luck, 2014, Arslanova et al., 2019; Galvez-Pol et al., 2018), we applied mechanical stimulation by using the tactile taps on the visual-tactile conditions. The tactile probes were sent 105ms after the visual onset based on the studies of Sel et al. (2014) and Pitcher et al. (2008). The tactile stimulation was task-irrelevant, and it enhanced the activity over the SCx eliciting SEPs and allowing us to measure and investigate the somatosensory processing to facial emotion. To isolate the somatosensory evoked potential from the still ongoing visual processing we subtracted the brain activity of the visual only conditions from the visual-tactile conditions. That way, we could isolate the SEPs that were VEP-free (Arslanova et al., 2019; Galvez-Pol et al., 2018, 2020).

2.4.7. Source Localisation

The standardised low resolution brain electromagnetic tomography (sLORETA) software was used to compute the cortical three-dimensional distribution of current density (publicly available at http://www.uzh.ch/keyinst/loreta.htm; Pascual-Marqui, Esslen Kochi, & Lehmann, 2002; Pascual-Marqui, Michel, & Lehmann, 1994). This software uses the MNI152 template (Jurcak, Tsuzuki, & Dan, 2007) for a realistic head model (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002) and includes 6239 cortical grey matter voxels at 5mm resolution with results compatible with Talairach coordinates based on the probabilistic Talairach atlas (Oostenveld

& Praamstra, 2001). The sLORETA was performed on the SEPs (VEP free) and specifically the N80. After creating the Talairach coordinates and the transformation matrix, we performed statistical non - parametric mapping analysis comparing dancers' average activity during emotion and gender discrimination task to investigate the task effect. Based on the statistical results, the sLORETA images were obtained representing the best match at that time window.

2.4.8. Behavioural accuracy in the visual emotion & gender discrimination task

The mean accuracy of each participant was calculated including both tasks with a value from 0% (no correct answers) to 100% (100% correct answers). A task x2 x group x2 ANOVA was computed.

2.4.9. Subjective Ratings of visual emotion and gender intensity

To ensure that participants were able to distinguish between the three emotions and the gender of the faces presented, we scored their responses in a separate emotion and gender discrimination task in a visual analogue scale. An emotion x3 (neutral, afraid, happy) x group x2 ANOVA was computed for the emotion task and a gender x2 x group x2 ANOVA for the gender task.

2.5. Supplementary Material

2.5.1. Behavioural and physiological data as predictors of SEP and VEP emotion modulation

One sample t-tests computed to confirm the reliability of the emotion modulation. Correlation and regression analyses were computed to identify potential predictors of the reliable emotion modulation of the somatosensory and visual activity using the behavioural scores (Multidimensional Assessment of Interoceptive Awareness, Beck Depression Inventory, Toronto Alexithymia Scale (TAS-20), State- Trait Anxiety Inventory for Adults and the average interoceptive accuracy score on heartbeat counting task), physiological data (heartbeat per minute) and dance expertise for dancers.

2.5.1.1. Behavioural and physiological data as predictors of SEPs

2.5.1.1.1.P50

For the dancers, in the right central region SEP activity for neutral, afraid and happy expressions was significant (one sample t test p <.001 for neutral and afraid, p = .007 for happy). In the left central region, SEP activity for neutral, p = .001 and for afraid emotion index was significant, p = .002. Based on the significant results from the correlations (see table 2.4. below), we ran regression analyses. The amplitude for afraid expression over the right central electrodes (3, 11 and 24) was predicted by the MAIA subscale on not worrying, R^2 = .208, F (1, 24) = 6.315, p = .019. Over the same electrodes the amplitude for neutral was predicted by STAI- trait and STAI- state, R^2 = .274, F (2, 23) = 4.331, p = .025. SEP activity over left central electrodes for neutral was predicted by MAIA subscale on noticing, R^2 = .384, F (1, 24) = 14.940, p = .001 and for the afraid emotion index was best predicted by TAS identifying feelings, R^2 = .222, F (1, 24) = 6.842, p = .015. No results are reported for the controls.

Table 2.4: *Correlations between SEP emotion modulation of dancers with behavioural scores*

Measures	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
1. Right central Neutral	1											
2. Right central Afraid	.387	1										
3. Left central Neutral	.307	-.271	1									
4. Left central Afraid index	-.201	.090	-.531**	1								
5. STAI-state	.408*	.020	.199	-.391*	1							
6.STAI-trait	.521**	.013	.207	-.298	.721**	1						
7. BDI	.463*	.089	.125	-.225	.600	.767**	1					
8. MAIA not worrying	-.180	-.456*	.234	-.032	-.052	.058	-.007	1				
9. MAIA noticing	.364	.119	.619**	-.290	-.038	.062	.022	-.081	1			
10. TAS total	.219	.065	.211	-.494*	.353	.412*	.111	-.156	.196	1		
11. TAS describing feelings	.272	.126	.225	-.392*	.102	.392*	.184	-.274	.350	.808**	1	
12. TAS identifying feelings	.229	.081	.120	-.471*	.463*	.439*	.174	-.317	.169	.915**	671**	1

Note: * Correlation is significant at .05 level. ** correlation is significant at .01 level. No significant interactions are reported for SEP activity of happy expression on right central region.

2.5.1.1.2. N80

One sample t-test confirmed the main effect of emotion across all participants with significant SEP modulation for Afraid, $p < .001$ and afraid emotion index, $p = .001$. Based on the emotion x hemisphere interaction and the emotion effect on the left, we ran one sample t-tests on both hemispheres and only on the left the SEP activity of afraid ($p < .000$) and for happy ($p = .004$) was significant. The SEP activity on the left for happy expressions correlated with STAI trait, $r = .289$, $p = .041$ and MAIA not worrying, $r = -.318$, $p = .023$. MAIA not worrying was the best predictor, $R^2 = .159$, $F\ (2, 47) = 4.437$, $p = .015$.

Focusing on the dancers, from the main emotion effect, the SEP activity on afraid and afraid emotion index was significant, both at $p = .005$. From the task effect, SEP activity over the right posterior region on gender task ($p = .024$) and on emotion task over the left hemisphere ($p = .004$) was significant. SEP activity for afraid expressions correlated with MAIA subscale on not noticing, $r = .415$, $p = .035$ (regression model: $R^2 = .172$, $F\ (1, 24) = 4.997$, $p = .035$). Afraid emotion index correlated with STAI state, $r = .\text{-}447$, $p = .022$, STAI trait, $r = -.486$, $p =$ 012 and MAIA subscale on attention regulation, $r = .435$, $p = .027$ (regression model including all three predictors: $R^2 = .236$, $F\ (1, 24) = 7.420$, $p = .012$).

Focusing on the controls and the emotion effect on the left hemisphere, the SEP activity on afraid, on happy, on afraid and happy emotion index was significant ($p = .011$, p =.010, $p =$ .012, $p =.031$ respectively). From the emotion effect on the lateral sites, SEP amplitude on right happy emotion index was significant, $p = .016$ and on the left afraid, happy and afraid emotion index ($p = .009$, $p = .014$, $p = .018$ respectively). Average TAS score predicted afraid emotion index on the left, $R^2 = .163$, $F\ (1, 23) = 4.473$, $p = .045$. TAS subscale on identifying feelings predicted happy emotion index on the left hemisphere, $R^2 = .188$, $F\ (1, 23) = 5.330$, $p = .030$ and on the right lateral site, $R^2 = .180$, $F\ (1, 23) = 5.053$, $p = .034$. MAIA subscale on not distracting and the average heartbeat per minute predicted the left lateral activity for afraid emotion index, $R^2 = .313$, F (2, 22) = 5.021, $p = .016$. The table 2.5 below summarises the significant correlations.

Table 2.5: *Correlations between SEP emotion modulation of controls with behavioural scores*

Measures	1.	2.	3.	4.	5.	6.	7.	8.	9.
1. Left Afraid emotion index	1								
2. Left Happy emotion index	.575**	1							
3. Right lateral happy emotion index	-.407*	-.451*	1						
4. Left lateral afraid emotion index	.684**	.491*	-.243	1					
5. TAS total	.403*	.258	-.239	-.086	1				
6. TAS identifying feelings	.359	.434*	-.424*	-.072	.822**	1			
7. MAIA not worrying	-.104	-.178	.113	-.083	-.259	-.200	1		
8. MAIA not distracting	.221	.028	-.108	.398*	-.178	-.133	-.257	1	
9.HB/minute	-.212	-.103	.330	-.475*	.269	.128	-.084	-.230	1

Note: * Correlation is significant at .05 level. ** correlation is significant at .01 level. No significant interactions are reported for SEP activity of afraid and happy expression and on the left lateral site for afraid and happy expressions.

2.5.1.1.3. P100

For the dancers one sample t tests confirmed the emotion effect on the left central and posterior region with SEP amplitude on afraid to be significant, $p = .017$ and $p = .004$ respectively. No significant correlations are reported. For the control participants the one sample t-tests on the emotion effect on the left lateral site were not significant, $p < .100$.

2.5.1.1.4. N140

For the dancers the one sample t-tests ran on the SEP amplitude of happy on emotion and gender task over the anterior, central and posterior region were not significant, $p < .090$. No further results are reported for dancers and control participants.

2.5.1.2. Behavioural and physiological data as predictors of VEPs

2.5.1.2.1. P1

Based on the group effect over the averaged activity on occipital electrode 42, we ran one sample t-tests which were significant both for dancers and controls, both $p < .001$. For the dancers, averaged activity over electrode 42 correlated with dance experience ($r = -.390$, $p = .049$), MAIA subscale on body listening ($r = .399$, $p = .044$) and TAS subscale on externally oriented thinking ($r = -.420$, $p = .033$). Backward regression model showed the TAS subscale as the best predictor, $R^2 = .176$, F (1, 24) = 5.136, $p = .033$.

For the control participants, averaged activity over electrode 42 correlated with MAIA average score ($r = -.427$, $p = .033$) and MAIA subscale score on self-regulation ($r = -.417$, $p = .038$), with the latter to be the best predictor (regression model: $R^2 = .182$, F (1, 23) = 5.120, $p = .033$.

2.5.1.2.2. N170

Based on the main emotion effect in each group, we ran one sample tests for both groups. On dancers, the emotion modulation was significant for the afraid and happy emotion index, $p = .001$ and $p = .002$ respectively. Afraid emotion index correlated with resting heartbeat per minute, $r = .483$, $p = .012$, MAIA subscale on attention regulation, $r = -.405$, $p = .040$, MAIA subscale on emotion awareness, $r = -.406$, $p = .040$, MAIA subscale on trusting, $r = -.407$, $p = .039$ and MAIA average score, $r = -.432$, $p = .028$. The best regression model showed average MAIA score and resting heartbeat per minute as the strongest predictors, $R^2 = .351$, F (2, 23) = 6.228, $p = .007$.

On controls, the emotion modulation was significant for neutral, $p = .003$, happy, $p = .038$, afraid emotion index, $p < .001$ and happy emotion index, $p = .011$. Afraid emotion index correlated with MAIA subscale on not distracting, $r = .481$, $p = .015$, regression model: $R^2 = .231$, $F(1, 23) = 6.926$, $p = .015$.

2.5.1.2.3. P200

Based on the main emotion effect in each group, we ran one sample tests for both groups. On dancers, the emotion modulation was significant for neutral, afraid, happy expression (all $p < .001$) and afraid emotion index, $p = .035$. Afraid emotion index correlated with MAIA average score, $r = -.424$, $p = .031$ and MAIA subscale score on trusting, $r = -.495$, p = .010. The latter seemed to be the strongest predictor, $R^2 = .245$, $F(1, 24) = 7.781$, $p = .010$.

Similarly on controls, the emotion modulation was significant for neutral, afraid, happy expression (all $p < .001$) and afraid emotion index, $p = .001$. No significant correlations are reported.

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Chapter 3: Heart – brain interactions during facial emotion processing and interoceptive abilities on professional dancers and controls

This chapter includes the manuscript: Meletaki, V., Galvez-Pol, A. Forster, B., Calvo-Merino, B. (2022) Heart -brain interactions and cardiac activity on emotion processing on professional dancers and controls. (in prep)

Abstract

The heartbeat evoked potential (HEP) has often been used as a neural marker of visceral activity. Growing empirical evidence suggests that the cardiac cycle and HEP as a cortical marker play a critical role in visual perception, emotion and consciousness more broadly supporting embodied cognition theories (e.g. Park and Blanke, 2019). Previous studies from our lab provided strong evidence for expertise effect comparing the visual and somatosensory evoked potentials on facial emotion expressions for professional dancers and control participants. In the present study EEG and ECG of dancers and controls were recorded while watching neutral, afraid and happy expressions and their levels of alexithymia, stress, body awareness and depression were collected. We questioned firstly, how emotion and personality traits interact with HEP and secondly, how these dynamics are modulated by dance expertise. HEP was found to be strongly related to personality traits for both groups and was modulated by task only for controls. No emotion or dance expertise modulation was found on HEP but dance expertise was strongly related to interoceptive abilities. This study aims to contribute to the HEP and brain-viscera interaction literature offering valuable evidence on how visual emotion, expertise and personality characteristics may modulate the HEP.

3.1. Introduction

The first main difference between an amateur and a professional dancer is the technical know-how. The second main difference is this extraordinary ability built over the years to connect movement with breath. To dance is to feel and express emotions through the body; but only when the dancer tunes into their heartbeat and breath, dance becomes a piece of art and acquires flow. After years of intensive training, do dancers have indeed a stronger ability to tune into their bodies and heart?

Interoception, the ability to perceive our bodily signals (Craig, 2002), has increasingly been the focus of the fields from experimental psychology to computational neuroscience and behavioural economics. It has been proposed to be our 'sixth sense' (Zagon, 2001). Poor interoceptive abilities have been linked to poor mental health (depression, alexithymia), autism spectrum disorder, and personality disorders such as depersonalization (for example see Brewer, Murphy, & Bird, 2021; Khalsa et al., 2018; Murphy, Brewer, Hobson, Catmur, & Bird, 2018; Sedeño et al., 2014).

Garfinkel and colleagues (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015) have proposed three levels of interoception: firstly, the interoceptive accuracy referring to one's performance level on the objective interoceptive measures, secondly, the interoceptive sensibility referring to the self- evaluation scores on subjective measures and thirdly, the interoceptive awareness referring to the metacognitive awareness of interoceptive accuracy such as the participants' confidence on their accuracy on objective measures.

The current state of the art in the literature offers behavioural tasks for cardiac, gastric and respiratory interoception and psychometric measures for an overall ability to perceive bodily sensations. The latter and the cardiac interoception tasks have been the most commonly used with the heartbeat counting task to be the most popular.

The Heartbeat Counting Task initially developed by Schandry (1981) requires participants to focus and count their heart beating while staying as still as possible and without physically taking their pulse for four different time durations. After each trial participants report the number of heartbeats they counted, their level of confidence for their answer and, in some cases, where in their body they felt their heartbeat the most. The interoceptive accuracy score is based on their reported and real recorded heartbeat. This task albeit widely used has been a subject of criticism (Desmedt et al., 2020).

In response to the criticism over the heartbeat counting task, new tasks measuring cardiac accuracy have been developed. One of them is the heartbeat discrimination task where participants are asked to report whether an auditory or visual signal was synchronous or asynchronous with their heartbeat. The heartbeat discrimination task has appeared in the literature with different variations such as a two alternative forced choice procedure or six alternative forced choice complicating the comparison between studies (Hickman, Seyedsalehi, Cook, Bird, & Murphy, 2020). Another task recently developed by Plans et al. (2021) is the Phase Adjustment Task. This task is a smartphone app that records the heartbeat from the participants' finger that is touching the smartphone's camera and plays a beat tone coming asynchronously with the heartbeat but at the same frequency. Participants need to adjust the beat tone through a dial appearing on the screen until they feel it's synchronous with their heartbeat. New tasks on cardiac accuracy keep being created as our theoretical knowledge and methodological tools is progressing, such as the heart discrimination task following adaptive Bayesian psychophysics (Legrand et al., 2022). New tasks measuring gastric (see review by Prentice & Murphy, 2021) and respiratory interoception have been developed such as the respiratory resistance sensitivity task (Nikolova et al., 2021), the respiratory occlusion discrimination task (Van Den Houte et al., 2021), the details of which, however, are out of the scope of the present thesis.

Furthermore, a classic way to measure interoceptive abilities more generally has been by administering questionnaires such as the Multidimensional Assessment of Interoceptive

Awareness (MAIA) by Mehling et al. (2012), MAIA 2 (Mehling, Acree, Stewart, Silas, & Jones, 2018) and the Body Perception Questionnaire by Porges (1993). These questionnaires focus on the interoceptive and body awareness which questions about if and how participants perceive different bodily signals and sensations such as thirst or pain. They have been validated and used across healthy and clinical populations (Flasinski et al., 2020; Slotta, Witthöft, Gerlach, & Pohl, 2021; Torregrossa, Amedy, Roig, Prada, & Park, 2021).

3.1.1 Heartbeat Evoked Potentials

In the last few years, in addition to searching for new more robust behavioural interoceptive tasks, research has started looking on better understanding the heart – brain interactions and the effect of cardiac cycle on exteroception - interoception interplay. To do so, researchers use scalp EEG, intracranial EEG or MEG and ECG simultaneously and then analyse the Heartbeat Evoked Potentials (HEPs). HEPs are neural responses time locked to the R peak of the antecedent heartbeat and they seem to be linked to the cardiac nerves and to the mechanoreceptors and baroreceptors reacting to cardiac contractions. Azzalini, Rebollo, & Tallon-Baudry (2019) and Park & Blanke (2019) offer an excellent in depth review of the physiological and biological bases of the heart- brain interactions. Importantly, with the recent shift of the literature to Bayesian brain and interoceptive predictive coding to explain interoception and its role to perception (Barrett & Simmons, 2015; Critchley & Garfinkel, 2018; Marshall, Gentsch, & Schütz-Bosbach, 2018; Petzschner et al., 2019; Seth, 2013; Seth, Suzuki, & Critchley, 2012), HEPs have been proposed to reflect prediction or prediction errors based the previous heartbeat (e.g. Marshall, Gentsch, & Schütz-Bosbach, 2020; Petzschner et al., 2019). HEPs have been used to test hypotheses on bodily self-consciousness, first – person perspective, attentional shift between interoception and exteroception, somatosensory processing, even signs of consciousness in post-comatose patients (Al et al., 2020; Azzalini, Buot, Palminteri, & Tallon-Baudry, 2021; Azzalini et al., 2019; Babo-Rebelo, Buot, & Tallon-

Baudry, 2019; Babo-Rebelo, Richter, & Tallon-Baudry, 2016; Candia-Rivera et al., 2021; Park et al., 2016; Park, Correia, Ducorps, & Tallon-Baudry, 2014; Petzschner et al., 2019; Weijs, Daum, & Lenggenhager, 2022).

Only very recently studies shifted their attention to heart – brain interactions in relation to emotion processing using various designs making it harder to draw more general conclusions. However, evidence so far suggest that HEPs are modulated by external emotional stimuli. In one study, Marshall and colleagues (Marshall, Gentsch, Jelinčić, & Schütz-Bosbach, 2017) in a repetition suppression paradigm found that a repetition suppression effect in HEPs and VEPs for repeating angry faces, a repetition enhancement of HEPs on repeating neutral faces and a correlation between the HEP repetition suppression and VEP attenuation. In a series of similar studies in 2018 (Marshall, Gentsch, Schröder, & Schütz-Bosbach, 2018), they found an increased HEP amplitude for repeated sad and pained faces, a decreased HEP amplitude for repeated angry faces and a correlation between suppression on HEP and VEPs on repeated angry faces only. No significant effects were reported for positive facial expressions. In a modified repetition task, Gentsch and colleagues (Gentsch, Sel, Marshall, & Schütz-Bosbach, 2019) where the second affective stimulus was either expected or unexpected, HEP amplitude decreased on expected negative faces with no similar effect on expected neutral faces. These studies provided evidence on how neural responses to internal bodily signals are modulated by predictions on our external environment and especially socially relevant such as facial emotions. In other study using dynamic natural affective scenes, Couto and colleagues (Couto et al., 2015) found emotion modulation on HEP within fronto-insular- temporal areas.

3.1.2. The present study

Despite the spike in HEP and viscera – brain interaction research, many questions remain answered on how socially relevant information such as the facial emotional expressions of others might be interfering with our heart beating and the neural responses to it. Surprisingly, research comparing different populations are very sparse, with only a handful of them testing clinical population (Müller et al., 2015; Salamone et al., 2018). To our knowledge, until now there has not been a study investigating such a big pool of interoception indices between professional ballet dancers and non – dancers control participants. The present study aimed to compare group differences on interoceptive abilities and how facial emotion expressions as exteroceptive stimuli might modulate neural responses to heartbeat. For the two groups, EEG and ECG data were collected during a visual emotion or gender discrimination task using happy, afraid and neutral faces. Additionally, participants completed the Heartbeat Counting Task for cardiac accuracy and the MAIA for interoceptive sensibility.

3.2. Methods

3.2.1. Participants

As described in section 2.2.1., twenty-six ballet dancers (in professional training or working) (1 left-handed, 22 females, aged 19-38; *M*= 25.61, *SD*= 5.3) and twenty-six participants with no prior dance experience (2 left-handed, 22 females, aged 21-35; *M*= 25.59, *SD*= 4.44) naïve to the objective of the experiment reported normal or corrected-to-normal vision and participated in the study for a small time reimbursement (£8/hour). The control participants were matched for age and gender with the dancers, and they were recruited through an online psychology website (SONA Inc.). Due to evidence showing enhanced interoception accuracy levels for professional musicians (Schirmer-Mokwa et al. 2015), the music experience of all participants was recorded; sixteen control participants had no music experience and only four had between 10-15 years of experience. Ten dancers had no experience and eight had at least 10 years of experience. Further details about the participants are provided in section 2.2.1. All participants gave their written informed consent, and the study was approved by the Ethics Committee, School of Arts and Social Sciences, City, University of London.

3.2.2. Materials

3.2.2.1. Stimuli

As described in section 2.2.2.1., a set of 60 pictures with faces depicting happy, afraid, and neutral expressions (half male) were taken from the Karolinska Directed Emotional Faces set (Lundqvist et al., 1998). All faces were grey scaled and presented in a rectangular frame (1.4 x 1.57 inches). The photos used for happy and afraid expressions had been rated highly in valence and the neutral ones very low in a previous experiment (see Sel et al. 2014).

3.2.2.2. Psychometric measures

As described in section 2.2.2.2., we administered the following psychometric measures: for levels of depression, the Beck Depression Inventory II was used (Beck et al., 1987); for alexithymia, the Twenty Item Toronto Alexithymia Scale-II (Bagby et al., 1994), for levels of anxiety as a mental state or as a personal trait, the State-Trait Anxiety Inventory for Adults (Spielberger et al. 1983), and the 20-Item Prosopagnosia Index (PI-20) (Shah et al., 2015) was administered to check for possible developmental prosopagnosic traits. To measure their interoceptive abilities, participants filled in the Multidimensional Assessment of Interoceptive Awareness (MAIA) by Mehling et al. (2012). This 32-item battery consists of eight factors: noticing, not-distracting, not-worrying, attention regulation, emotional awareness, self-regulation, body listening and trusting (Mehling et al., 2012). The group means with standard deviation are presented in Table 2.2.

We ran correlations for the BDI, TAS, MAIA and STAI state and trait for controls and dancers separately and we were able to replicate previous findings suggesting strong correlations between levels of anxiety both as a mental state and a trait with levels of alexithymia and depression (Hendryx, Haviland , & Shaw, 1991; Honkalampi, Hintikka, Tanskanen, Lehtonen, & Viinamäki, 2000; Van der Velde et al., 2013). The correlations between the questionnaire scores are reported in Table 2.3. Additionally, we ran one-way ANOVAs to investigate for group differences in their psychological traits and states. Further details about the group differences are reported in section 2.2.2.

3.2.3. EEG and ECG recording

Continuous EEG was recorded from 64 active electrodes placed equidistantly on an elastic electrode cap (M10, EasyCap, GmBH, Herrsching, Germany) using a BrainAmp amplifier (500Hz sampling rate) and BrainVision Recorder (BrainProducts). The electrodes were referenced online on the right earlobe. Vertical and bipolar horizontal electrooculogram was recorded to correct for eye movements offline. The horizontal electrooculogram was recorded from one electrode placed next to the outer canthi of each eye and the vertical from one electrode placed below the right eye. Electrocardiogram was recorded throughout the experiment from one electrode placed just under the left collarbone.

3.2.4. EEG and ECG pre-processing

EEG pre-processing was performed on BrainVision Analyser 2.1 on a Windows 10 desktop. Electrodes with extensive noise or flat lines were spline interpolated using their neighbouring channels. The data were digitally filtered at 0.1-30Hz (order 2, Butterworth zero phase shift) and re-referenced to the average. Vertical and horizontal ocular correction was performed (Gratton, Coles & Donchin, 1983) and the ECG markers were individually applied per participant using the automated algorithm EKG Markers solution on BrainVision Analyser. Two participants had to be removed from the analysis because the EKG markers algorithm was not fully applied due to noisy data. The EEG signal was epoched into 1100ms segments (duration of each trial before any following stimulus) starting at the visual stimulus onset for each emotion condition (neutral, afraid, and happy). No baseline correction was applied at this stage to avoid distorting the R peak and adding noise from the previous heartbeat cycle into the segmented data. Artifacts with amplitude exceeding 100µV were removed from the analysis. The data were epoched again based on R peak (-100ms to 600ms post R peak) and baseline corrected (-100ms to 0ms). Single subject HEP averages for each emotion condition were then created.

3.2.5. ERP signal-to-noise ratio

Ran repeated measures ANOVA task x2 x emotion x3 on the segments used for average and the results were non-significant, $F(1, 48) = .066$, $p = -.798$ for task, $F(2, 96) = 2.115$, $p = .126$ for emotion and $F(2, 96) = 1.217$, $p = .301$ for the task x emotion interaction. Paired samples t-tests on the task averages confirmed the non-significant results for both groups, $t(49) = .279$, $p = .782$ and for each group separately, (controls, $t(25) = -.5$, $p = .620$, dancers, $t(25) = .145$, $p = .886$.

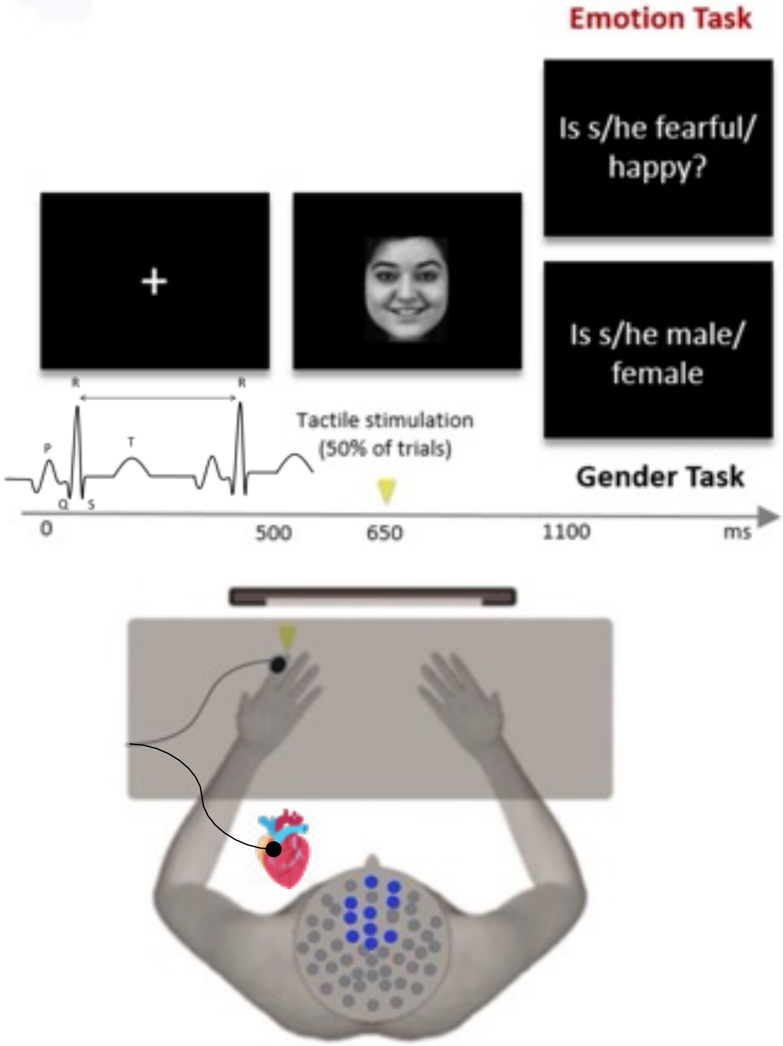

Figure 3.1 *Full experimental procedure for the emotion and gender discrimination task as explained in chapter 2*

Note: The electrodes shown in blue were selected for the HEP analysis. During the whole experiment the EEG and ECG was recorded. Only the Visual Only conditions were analysed for the current study to avoid contamination from somatosensory processing. The HEP was based on the R peak of the cardiac cycle. Figure adapted and used by permission from Fanghella and colleagues (Fanghella, Gaigg, Candidi, Forster, & Calvo-Merino, 2022).

3.2.6. Group level EEG and ECG analysis

Based on the R peak the heartbeat per minute per participant was calculated during the emotion and gender recognition task. A repeated measures task (emotion, gender) x emotion (neutral, afraid, happy) x group (controls, dancers) ANOVA comparing the group averages showed a significant main effect of group, *F* (1, 48) = 8.901, *p* = .004 with an average heartbeat per minute for controls *M* = 75.31 (*SD* = 2.27) and for dancers *M* = 66.64 (SD = 1.75).

Following previous literature (e.g. Petzschner et al., 2019), statistical analysis was conducted on two ERP components: the first from 200ms to 400ms and the second from 400ms to 600ms post R peak. Based on Petzschner and colleagues (2019), we compared the ECG amplitude between groups and emotion conditions running a repeated measures task x2 emotion x3 x group x2 ANOVA on each time window of interest. On the 200-400ms time window, the emotion x group interaction was significant, F (2, 96) = 3.234, p = .044 η_p^2 = .063 with non-significant follow ups by group (three one-way ANOVAs comparing group means per emotion) or emotion (repeated measures emotion x3 ANOVA per group). On the 400-600ms the ANOVA did not yield any statistically significant results (all results $p < .2$).

To identify the most active electrodes, we ranked the averaged amplitude values for each group, condition and time window and selected the electrodes with the most positive and most negative amplitude. Two clusters were formed; a frontal one with the electrodes 35, 36, 34, 21 and 8 (equivalent to Fpz, Fp2, AF3, AF4 and Fz of the 10/20 system) and a central one with the electrodes: 19, 2, 3, 7 and 1 (equivalent to FC3, FCz, FC2/C2, FC1/F1 and Cz). On these electrodes a repeated measures ANOVA task x2 (emotion, gender) x region x2 (frontal, central) x electrode x5 (frontal: 35, 36, 34, 21, 8 and central: 19, 2, 3, 7 and 1) x emotion x3 (neutral, afraid, happy) x group x2 (dancers, controls) was computed and post hoc tests were performed. In case of a sphericity violation, Greenhouse-Geisser values are reported. Correlation and regression analyses were run to identify the potential predictors on the statistically significant HEP results of the ANOVA.

3.2.7. Heartbeat Evoked Potential modulation by psychological traits and states

We ran correlation and regression analyses for each group to identify potential predictors of the heart-brain interactions during visual facial emotion processing utilising the behavioural scores namely Beck Depression Inventory, State- Trait Anxiety Inventory, Toronto Alexithymia Scale and Multidimensional Assessment of Interoceptive Awareness, physiological data (heartbeat per minute during the task) and expertise for dancers.

3.2.8. Interoception tasks

To measure the interoceptive abilities of the participants, first, they completed the widely used heartbeat counting task (Garfinkel et al., 2015, Schandry ,1981). Participants were asked to silently count their heartbeat for four time intervals of 25, 35, 45 and 100 seconds. The order of the time intervals was randomised. They were explicitly told not to physically take their pulse or guess based on their average resting heart rate. Participants were instructed to press 'Enter' when they were ready. Then, a red cross would appear in the middle of the screen (see Figure 3.1 for the experimental procedure). When the cross became green, participants had to count their heartbeat until the cross became red again. Subsequently, they had to answer three questions: the first was 'How many heartbeats did you count?', the second 'How confident you are for your answer in a scale from 0 (no confident at all) to 10 (very confident)?' and the third was 'where did you pay mostly attention to on your body?'. Participants typed down their answers using the keyboard. EEG and their heartbeat were recorded for the whole experiment. For each trial, an interoceptive accuracy score was calculated, as defined by Hart et al. (2013): $1-|nbeats_{real} - nbeats_{reported}|/ - (nbeats_{real} - nbeats_{reported})/2$. These scores were then averaged across the four trials resulting in one average value per participant.

Two more tasks were included involving time and touch counting that have been shown to be accurate control tasks for the HCT (Christensen, Gaigg, & Calvo-Merino, 2017; Desmedt et al., 2020). For the time counting task, participants were asked to count silently seconds for the same four time intervals using the same paradigm as for the heartbeat counting. After each interval, they were asked to report how many seconds they counted. All participants were asked to remove their watch if they had one at the time of the EEG preparation. The touch counting task followed the same paradigm but this time the tactile stimulator was connected back to the tip of the participants' left index finger with current passing through every 0.8 seconds and they were asked to count how many taps they felt. The purpose of the touch counting task was to measure the exteroceptive abilities of the participants. An average accuracy score was created per participant for each task applying the same formula as for the HCT. The group means with standard deviations on the interoception tasks, the real and estimated heartbeat per minute during the interoception tasks are reported in the table 4 below. For the statistical analysis the methodological approach of Christensen et al. (2017) was followed.

Table 3.1:

The means with Standard Deviation on the interoception tasks for control participants and dancers

Dancers	**IAcc**	**Conf**	**Time Acc**	**Touch Acc**	**Real HBpm**	**Estimated HBpm**
Mean	.62	5.67	.9	1.34/1.44	60.17	42.77
SD	.33	1.58	.2	.38/1.97	7.7	13.12
Controls	**IAcc**	Conf	**Time Acc**	**Touch Acc**	**Real HBpm**	**Estimated HBpm**
Mean	.61	5.11	.86	1.41	68.44	47.85
SD	.26	1.77	.31	.05	10.38	14.92

Note: IAcc = average of interoceptive accuracy score, Conf = average confidence score on their reported heartbeat, Time Acc = average of accuracy score on the time counting task, touch Acc = average score on touch counting task, real HBpm = real heartbeat per minute during the IAcc task, estimated HBpm = estimated heartbeat per minute (calculated based on the estimated heartbeats form the participants declared during the IAcc task).
The second values on the average touch accuracy scores on dancers correspond to the median and range due to the Kolmogorov – Smirnov test showing normality violation, D (24) = .38, $p < .001$. The KS test was non-significant for all the remaining group averages.

3.2.9. Interoception modulation by psychological traits and states

We ran correlation and regression analyses for each group to identify potential predictors of interoception using the behavioural scores namely Beck Depression Inventory, State- Trait Anxiety Inventory, Toronto Alexithymia Scale and Multidimensional Assessment of Interoceptive Awareness, years of music experience, physiological data (heartbeat per minute during the task) and expertise for dancers. In case of violation of the parametric assumptions, Spearman's Rho is reported instead of Pearson's r.

3.2.10 Interoception and Somatosensory and Visual processing of facial emotions

We were interested to explore potential relationships between the interoceptive abilities of the two group and their somatosensory and visual processing of facial emotions. We used the statistically reliable SEP and VEP emotion modulations as shown in chapter 2 and for this reason the results are based on the participants included in the chapter 2 ($n = 51$). No outliers were found at the heartbeat counting task used for this analysis. Pearson's correlations were computed between the significant SEP and VEP modulations and the average IAcc scores of the participants.

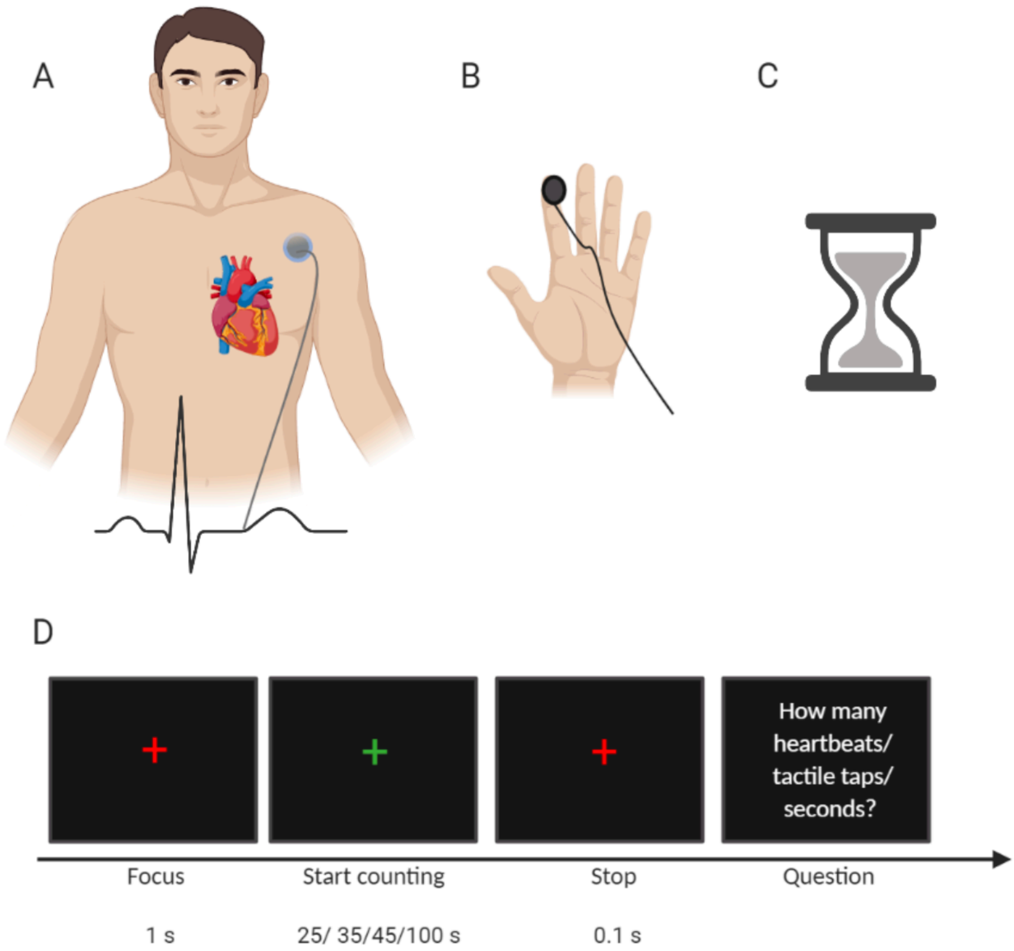

Figure 3.2: *Experimental procedure for the interoception tasks*

A. For the Heartbeat Counting task participants were instructed to count their own heartbeat without actively taking their pulse or guessing. The real heartbeat was recorded from an electrode placed on the left side of the chest above the collar bone. B. For the Touch Counting task, a mechanical stimulator was used to deliver tactile taps on the left index finger. C. For the Time Counting task, participants counted seconds. D. For all the three tasks, participants were asked to count their heartbeat or taps on their finger or seconds for four time intervals (25, 35, 45, 100 seconds) while the cross in the middle of the screen in front of them was green. As soon as it became red, they stopped and were asked to report how many heartbeats/ taps on the finger/ seconds they counted. Figure adapted and used with permission from Fanghella and colleagues (2021).

3.3. Results

The results on the behavioural accuracy on the visual emotion and gender recognition task during the EEG recording and the subjective ratings of visual emotion and gender intensity are reported in sections 2.3.1. and 2.3.2. respectively.

3.3.1. Heartbeat evoked potentials (HEPs) during Facial Emotion and Gender Visual Recognition Task

3.3.1.1. 200-400ms

Regarding topography, there was a significant main effect of region F (1, 48) = 25.065, $p <$ .001 $\eta_p^2 = .343$, of electrode F (2.69, 129.23) = 7.490, $p < .001$, $\eta_p^2 = .135$ and a significant region x electrode interaction F (2.35, 112.55) = 5.698, $p = .003$, $\eta_p^2 = .063$. The task x region interaction was significant, F (1, 48) = 4.785, $p = .034$, $\eta_p^2 = .091$ which when broken down task, showed a significant main effect of region $p < .001$ for both tasks.

Two group interactions were significant: task x electrode x group interaction F (2.96, 141.97) = 2.775, $p = .044$, $\eta_p^2 = .055$ and the task x region x electrode x group F (2.5, 119.7) = 3.873, $p = .016$, $\eta_p^2 = .075$ which were both followed up by group and topography. The follow up by group (repeated measures task x2 x electrode x3 ANOVA on each group) of the first interaction on the dancers showed a significant main effect of electrode, $p = .031$ and region $p < .001$. On the controls it showed a significant main effect of task, F (1, 25) = 4.374, $p = .047$, $\eta_p^2 = .149$ and of electrode p =.031. When we broke down the first interaction by electrode (paired homologous electrodes and ran repeated measures task x2 x group ANOVA on five electrode pairs separately), the task x group interaction was significant for the 36 & 3 electrode pair F (1, 48) = 5.525, $p = .023$, $\eta_p^2 = .103$ and non-significant for the other four pairs.

Following up the task x region x electrode x group interaction by group (repeated measures task x2 x region x2 x electrode x3 ANOVA on each group), dancers resulted in a significant main effect of region $p < .001$ and electrode p =.002. Control participants resulted in the aforementioned main effect of task, a task x region interaction F (1, 25) = 7.685, $p = .01$, η_p^2

= .235, task x region x electrode interaction F (4, 100) = 5.474, p = .003, η_p^2 = .180, main effect of region p = .004 and of electrode p =.022. The task x region interaction follow ups by region on control participants only showed a main effect of task on the frontal region F (1, 25) = 7.159, p = .013, η_p^2 = .223, not in the central one, p = .911 and by task it showed a main effect of region on the emotion task only, p =.001 and not in the gender task, p = .078. The task x region x electrode interaction followed up by region showed on the frontal area the same main effect of task, a significant main effect of electrode p =.044 and a task x electrode interaction, p =.005, with non-significant results in the central region, all $p < .08$.

Following up this task x region x electrode x group interaction by region, on the frontal we found a significant main effect of electrode p < .001 and a task x electrode x group interaction, F (4, 192) = 5.172, p = .006, η_p^2 = .072 and on the central a significant main effect of electrode, p = .009 and a task x electrode interaction, F (4, 192) = 2.564, p = .040, $\eta^2 p$ = .051. The task x electrode x group interaction of the frontal region broken down by group showed on the controls a significant main effect of electrode p = .011 and the significant main effect of task and the task x electrode interaction mentioned above and, on the dancers, the significant main effect of electrode.

3.3.1.2. 400-600ms

The main effects of region, of electrode and the region x electrode interaction were significant, all $p < .001$. No results regarding task, emotion or group were statistically significant for this time window, all $p < .14$.

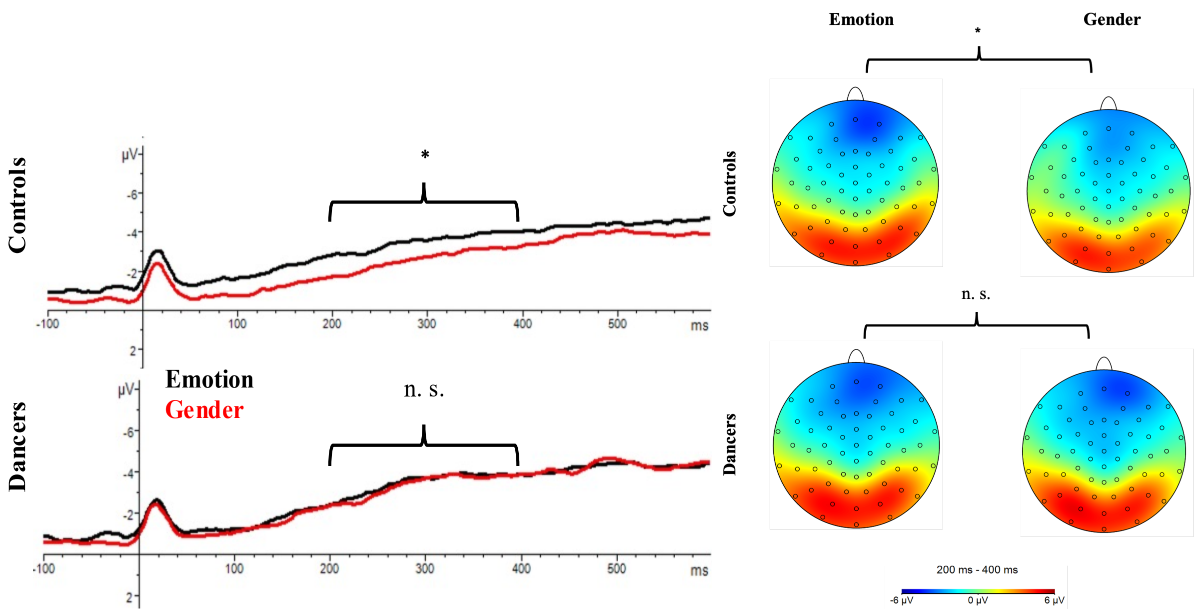

Figure 3.3 *The HEP results for controls and dancers*

The main effect of task was significant for control participants at the 200-400ms ERP component as it is seen on the top figures in the ERP waveforms and the topographical maps during the same 200-400ms time window below. Dancers did not reveal significant results on emotion or task.

3.3.1.3. Heartbeat Evoked Potential modulation by psychological traits and states

For the heartbeat, we averaged the heartbeat per minute between the two tasks for each group was used as the paired samples t-tests on each group separately did not show a significant difference on the heartbeat per minute between emotion and gender task (p = .428 for controls and p = .280 for the dancers). Only the statistically significant HEP emotion modulations of the 200-400ms time window were included in analyses. One sample t-tests confirmed the reliable HEP modulations: for controls only averaged frontal activity on emotion task t (25) = -8, p < .001 and gender task t (25) = -7.39, p < .001, while averaged central activity on emotion task t (25) = 10.88, p < .001 and gender task t (25) = -9.32, p < .001. On dancers averaged frontal activity on emotion task t (23) = -7.21, p < .001 and gender task t (23) = -12.01, p < .001, while averaged central activity on emotion task t (23) = 8.48, p < .001 and gender task t (23) = -12.01, p < .001. Due to a missing value on STAI- trait from one of the control participants, correlation analysis between HEP and STAI trait was run separately with 25 instead of 26 control participants.

For control participants only, the MAIA subscale score on not distracting was a predictor of averaged central activity on gender task, $R^2 = .291$, $F(1, 24) = 8.579$, $p = .004$ as shown on the figure 3.4. Averaged central activity on emotion task as well as averaged frontal activity for both emotion and gender discrimination task did not correlate significantly with the remaining behavioural and physiological variables.

For dancers only, averaged frontal activity on emotion task negatively correlated with average IAcc score, $r(24) = -.429$, $p = .036$ and the score on MAIA not distracting, $r(24) = -444$, $p = .030$. Hierarchical regression model showed that the model including both average IAcc score and MAIA subscale score on not distracting was a strong predictor of average frontal activity on emotion task, , $R^2 = .291$, $F(2, 21) = 4.304$, $p = .027$ as shown on the Figure 3.4. Central activity on emotion task did not yield significant correlations.

Averaged frontal activity on the gender task was predicted by average BDI scores, $R^2 = .204$, $F(1, 23) = 5.654$, $p = .027$. Averaged central activity on the gender task negatively correlated with averaged TAS sore, $r(24) = -.422$, $p = .040$, TAS subscale score on describing feeling, $r(24) = -.457$, $p = .025$ and TAS subscale score on identifying feelings, $r(24) = -.440$, $p = .031$. Hierarchical backward regression did not yield any significant models combining the TAS scores (model with the three potential predictors: $p = .104$). However, separate linear regressions for each TAS score showed that averaged central activity on gender task was significantly predicted by TAS subscale score on describing feelings, $R^2 = .2049$, $F(1, 22) = 5.822$, $p = .025$, by TAS subscale score on identifying feelings, $R^2 = .194$, $F(1, 22) = 5.290$, $p = .031$ and by average TAS score , $R^2 = .178$, $F(1, 22) = 4.780$, $p = .040$, as shown on the Figure 3.4. No other significant correlations were found between HEP and the behavioural and physiological variables.

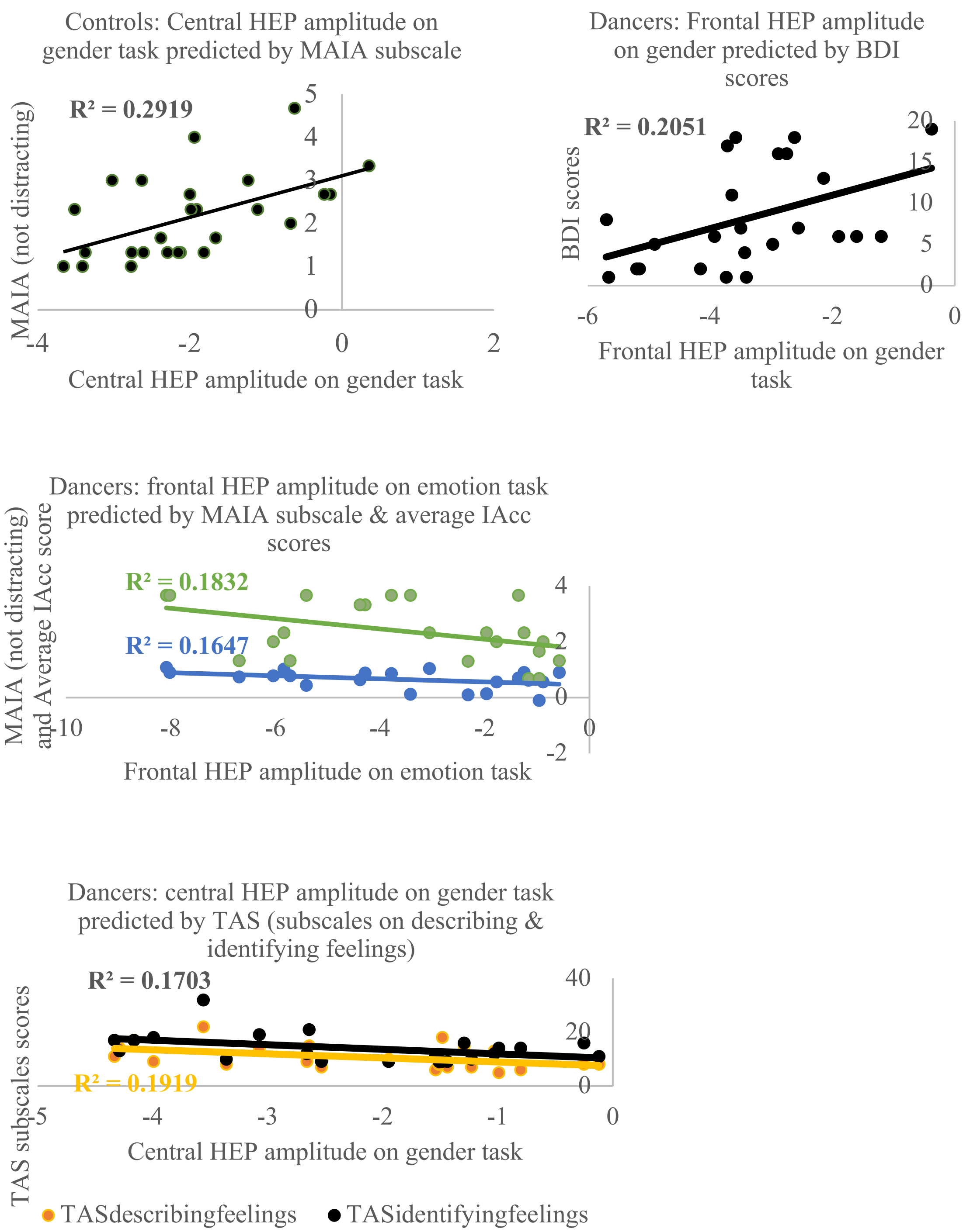

Figure 3.4: *Scatterplots showing the regression analyses for the HEP modulation by psychological states and traits on controls and dancers for the 200-400ms time window*

3.3.2. Interoception

3.3.2.1. Heartbeat Counting task

The duration x4 (25, 35, 45 and 100 seconds) x group x2 (controls, dancers) did not show any significant main effects (duration p = .299, group p = .934) or duration x group interaction, p

= .830. A one-way ANOVA comparing the averaged group means confirmed the non-significant results, p = .934. Following Christensen's work (Christensen et al., 2017), we performed a median split (median = 17.5, range 5- 33) for the dancers based on years on dance expertise resulting in two groups, the juniors and the senior dancers with 12 participants in each group. We re-ran the repeated measures ANOVA with the three groups this time and the duration x group interaction was significant, F (6, 141) = 2.190, p = .047, η_p^2 = .085. The effects of duration and group did not reach significance, p = .208 and p = .172 respectively. Following up the interaction, we ran one-way ANOVAs for each of the four time intervals and the average IAcc score. The IAcc score for the 35 second interval was significant, F (2, 47) = 4.442, p = .017, η_p^2 = .159, with the senior dancers achieving the highest interoception score (*M* = .85, *SD* = .31) and significantly different from junior dancers (p = .015), the control participants achieving the second higher score (*M* = .62, *SD* = .09) and the junior dancers having the lowest interoception score (*M* = .46, *SD* = .41) on this interval. The rest of the pairwise comparisons and the group performance in the remaining time windows did not reach significance, IAcc score for 25 seconds p = .087, for 45 seconds p = .689, for 100 seconds p = .820 and the average IAcc p = .172. Figure 3.5 shows the score distribution for the three groups. The same duration x4 (25, 35, 45 and 100 seconds) x group x2 (controls, dancers) repeated measures ANOVA was conducted for the confidence levels during the heartbeat counting task. We found a significant main effect of duration, F (3, 144) = 5.027, p = .002, $\eta^2 p$ = .095 with the confidence levels of the 25 second interval being significantly higher (*M* = 5.99) than the 45 second interval (*M* = 5.09) at p = .014 and the 100 second interval (*M* = 5.08) at p = .017. The main effect of group and the duration x group interaction did not reach significance, p = .254 and p = .226 respectively. A one-way ANOVA comparing the group means confirmed the non-significant group differences in confidence ratings, p = .254.

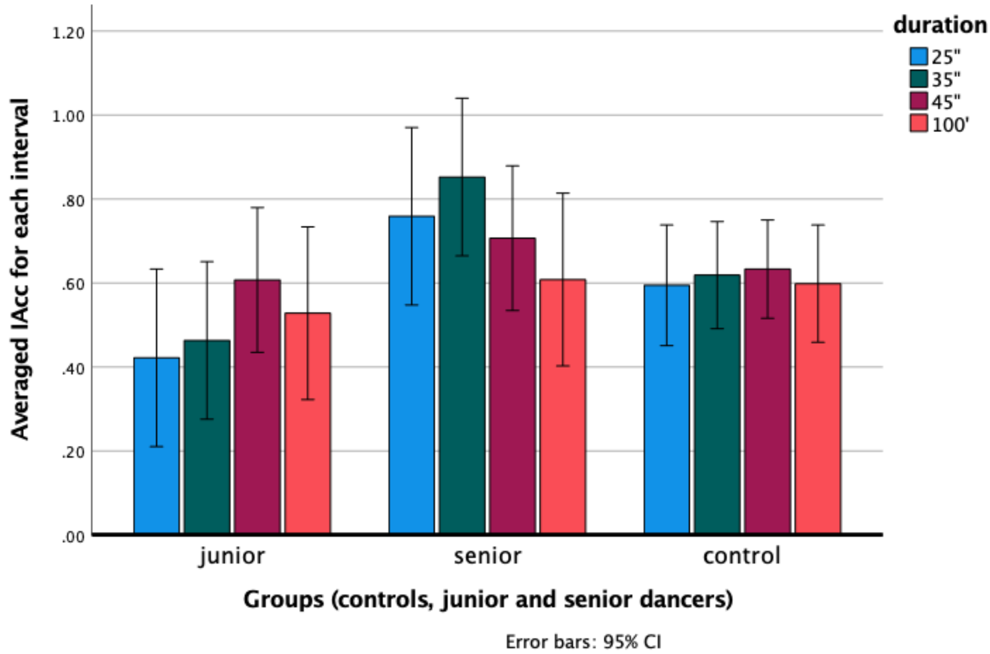

Figure 3.5: *Averaged IAcc scores for 25", 35", 45" and 100" time intervals after median split on dancers resulting in three groups: controls, junior and senior dancers*

3.3.2.1.1. Heartbeat perception on the body

At the end of each trial of the heartbeat counting task, participants were instructed to write down where in their body they felt their heartbeat the most. The responses of one dancer and one of the four responses from one control participant were not recorded. Dancers' responses were much more specific in their descriptions, more diverse in the body parts but more focused in the left side. After thematic analysis (grouping the similar words), five themes were apparent for both groups: chest was the strongest(including keywords: chest, heart and left chest), then neck (keywords: neck and throat), hands (keywords: hand(s), left/right hand, arm, wrist), abdomen (keywords: belly and stomach), ribs and head with the words foot and ear to appear once. Dancers did show similar themes with chest (keywords: chest, heart, "chestback") to be the most common, but still mentioned less times than in controls. Other themes included hands (keywords: hand(s), arm, left forearm, left hand, left index finger, wrist and left wrist), ribs (with a few participants specifying the exact locations on the ribs), abdomen (keywords: lungs, stomach, abdomen, diaphragm and sternum), right ear and back with the words big toe, mouth and head to appear once. As a general remark, most participants in both groups declared a stronger sensation of their heartbeat either in the areas around the heart such as chest or abdomen or in their limbs. An explanation for the sensation in the back or limbs might be the touch; the touch of the body on the chair or the floor or the hands resting on their laps.

3.3.2.2. Interoception control tasks

Moving to the time counting control task of interoception, the same duration x4 (25, 35, 45 and 100 seconds) x group x2 (controls, dancers) repeated measures was computed based on the accuracy scores of the participants following the same analysis as for the heartbeat counting tasks for consistency. The duration x group interaction was significant, F (1.52, 72.91) = 3.619, p = .043, η_p^2 = .070. The main effects of duration and group did not reach significance, p = .807 and p = .089 respectively. Following up on the duration x group interactions, one-way ANOVAs were computed comparing the group means for each time interval. The groups' time accuracy scores were significantly different for the 25 second interval (controls: M = .96, SD = .3, dancers: M = .8, SD = .23) F (1, 48) = 4.784, p = .034, η_p^2 = .091 and for the 100 second interval (controls: M = .93, SD = .3, dancers: M = .8, SD = .18) F (1, 48) = 4.126, p = .048, η_p^2 = .079. For the 35 and 45 second time interval the group differences were not statistically significant, p = .058 and p = .710 respectively.

Moving to the touch counting task of interoception, due to assumption violations with outliers and not normally distributed data, the non-parametric Mann- Whitney test was preferred to compare the group distributions on touch accuracy. The test did not yield any significant group differences on the average score (p =.086) or the scores for the 25, 35, 45 and 100 second intervals. (p = .193, p = .531, p = .203 and p =.444 respectively).

Lastly, we ran a task (IAcc scores, time accuracy and touch accuracy scores) repeated measures ANOVA to investigate group differences on the performance between the tasks. The group effect and task x group interaction were not statistically significant (p =.941 and p = .554), but the main effect of task was, $F\,(2, 96) = 111.105$, $p < .001$, $\eta_p{}^2 = .698$ with the post hoc pairwise comparisons showing significant differences across all task combinations, all at $p < .001$. However, the Mann- Whitney test comparing the group distributions across the three tasks did not yield statistically significant results (IAcc p =.669, time accuracy p = .332 and touch accuracy p = .086).

3.3.2.3. Interoception modulation by psychological traits and states

For the control participants only, the average IAcc score positively correlated with the participants' estimated heartbeat per minute, $r = .862$, $p < .001$. The average touch accuracy scores correlated positively with the MAIA subscale score on trusting, Spearman's Rho = .527, $p = .006$ and average time accuracy scores correlated negatively with the MAIA subscale score on body listening, $r = -.531$, $p = .028$. No more significant correlations are reported.

For the dancers, average IAcc scores correlated positively with dance expertise, $r = .44$, $p = .031$, their estimated heartbeat per minute, $r = .915$, $p < .001$ and with the TAS subscale score on describing feelings, $r = -.538$, $p = .007$. Hierarchical regression showed that the model including dance expertise, estimated HB per minute and the TAS subscale score on describing feelings significantly predict the average IAcc score, $R^2 = .906$, $F\,(3, 20) = 64.171$, $p < .001$ (the coefficient of dance expertise $p = .003$, of estimated HB per minute $p < .001$ and of the TAS subscale score $p = .349$) . The regression model including only dance expertise as a predictor of average IAcc score was also significant but explained a smaller proportion of the variance, $R^2 = .194$, $F\,(1, 22) = 5.279$, p =.031. Furthermore, participants' estimated heartbeat per minute during IAcc task correlated negatively with the TAS subscale on describing feelings, $r = -.478$, $p = .018$. Average time accuracy scores correlated negatively with BDI scores, $r = -.417$, $p = .043$ and the TAS subscale on externally oriented thinking, $r = .410$, p =.047. Lastly, music experience negatively correlated with TAS identifying feelings, $r = -.396$, $p = .045$.

3.3.2.4. Interoception and somatosensory and visual processing of facial emotions

The Pearson's correlations showed that at the P2 ERP component of VEPs on dancers only the averaged VEP amplitude on afraid emotion index (afraid – neutral) significantly correlated with the averaged IAcc score on Heartbeat Counting Task, r = -.429, p = .029, as well as with the averaged MAIA score, r = -.424, p = .031 and the MAIA subscale on trusting, r = -.495, p = .010. A hierarchical backward regression showed that the model explaining the largest variance of the VEP amplitude on afraid emotion index included all three variables relating to interoception (IAcc score, averaged MAIA score and MAIA subscale score), R^2 = .358, F (3, 22) = 4.093, p =.019, see Figure 3.6. The model including the IAcc score alone explained 18,4% of the variance, p = .029. No other significant correlations are reported for VEPs and SEPs on both dancers and control participants.

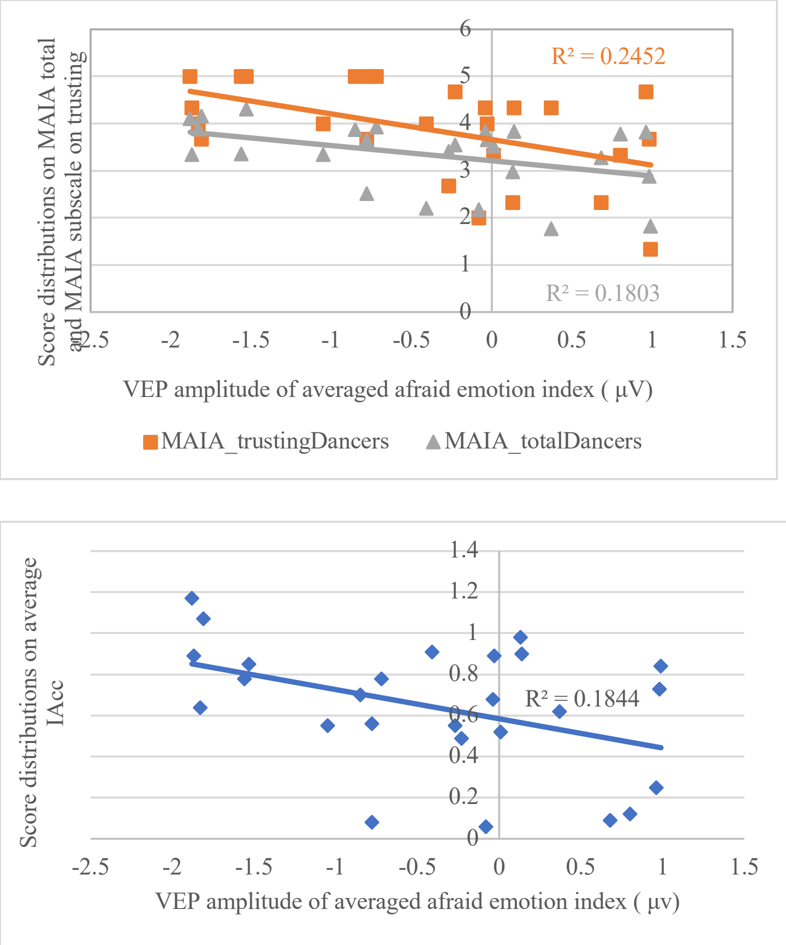

Figure 3.6: *Modulation of VEPs on dancers by interoceptive abilities*

Note: At P2 IAcc score, average MAIA score and MAIA subscale on trusting significantly predicted the VEP amplitude on afraid emotion index (afraid - neutral) on dancers.

3.4. Discussion

The overall purpose of this study was an attempt to answer if and how dancers as sensorimotor experts and artists have developed different or better abilities to tune into their body and whether this is reflected in their neural processing. Dancers are the only artists whose bodies are their tool and canvas simultaneously offering a tremendous opportunity to explore the role of the body and bodily self in interoceptive and exteroceptive perception.

We hypothesised that HEP would be modulated by group and emotion. Although the effect of group and emotion did not reach significance, we were able to show that at the first 200-400ms the frontal HEP amplitude on control participants was modulated by task; hence by focusing their attention on facial features regarding gender and not emotional valence. It should be acknowledged that in figure 3 the ERP waveforms for each group do seem to be similar pattern from time 0 throughout the time windows. As it was mentioned earlier, baseline correction was not performed following the guidelines by Petzschner and colleagues (Petzschner et al., 2019). We decided to perform a paired samples t-test comparing the mean frontal HEP amplitude between emotion and gender task at the baseline level (time 0) which came out significant, $t(25) = -2.21$, $p = .037$.

Our second hypothesis was that dancers would have better interoceptive abilities; meaning they would show significantly higher interoceptive accuracy in the HCT and higher interoceptive sensibility in MAIA. Our aim here was to replicate previous findings by Christensen and colleagues (Christensen et al., 2017). Although we were not able to replicate their significant effect of group overall, our results still provide supportive evidence for higher levels of interoceptive abilities for professional dancers in comparison to controls. Dance expertise was a strong and the only predictor of interoceptive accuracy for dancers and in the secondary analysis with the median split, senior dancers performed significantly better than the novices, although only for one of the four time intervals. In the latter analysis also controls showed a higher accuracy than junior dancers but this difference, although puzzling, was not statistically significant. One potential explanation for it could be the learning curve while dancers learn how to trust themselves and their bodies during their training, but this can only be a speculation and further research is needed including dancers at different training levels. We did not find group differences at the control tasks for interoception. Our hypothesis for higher interoceptive sensibility on dancers was strongly confirmed with significantly higher scores on dancers than controls for the average MAIA score and in 6 of the 8 MAIA subscales, namely noticing, attention regulation, emotion awareness, body listening, trusting the body.

At a more exploratory level, we searched for potential associations between interoception and visual or somatosensory evoked potentials inspired by the work of Fanghella and colleagues (Fanghella et al., 2022) and we found that the VEP amplitude on afraid emotion index at P2 on control participants was predicted by the averaged IAcc score, averaged MAIA score and the score on MAIA subscale on trusting.

As far as the HCT is concerned, the last few years it has received a lot of scepticism (Desmedt, Luminet, & Corneille, 2018; Ring & Brener, 2018; Zamariola, Maurage, Luminet, & Corneille, 2018) and awareness has been raised over the importance of clear task instructions and control tasks to check that participants truthfully completed the task and did not report counted seconds or a guessed number based on their average heartbeat per minute. In the present study, there was no interaction between real heartbeat of participants with their IAcc scores. Therefore, physical fitness as measured by their real heartbeat per minute and general knowledge of dancers for their own heartbeat do not significantly explain dancers' interoceptive accuracy scores. Another factor that could influence dancers' IAcc scores is any potential difference on body and emotion related characteristics as measured by questionnaires. Dancers did score significantly higher on the average scores of MAIA and most of its subscales, but MAIA was not a significant predictor of IAcc scores for neither of the two groups. In order to control for the possibility of the participants reported seconds instead of heartbeats, we used the time counting task where participants had to count and report seconds and no significant group difference was found. One consideration, nonetheless, for future research would be to investigate other control measures with added difficultly as this task seemed to be too easy and we observed a ceiling effect. Time perception gives the floor for new ways to investigate interoception thanks to evidence for shared mechanisms (Richter & Ibáñez, 2021).

3.4.1. Methodological considerations and future research ideas

Research on HEP is still growing and there are not yet specific guidelines on how to analyse HEP, but the analysis is still rather at an exploratory level. One of the suggestions from current literature is to control for differences in heartbeat and ECG amplitude between groups or conditions depending on the research design, which we did. The heartbeat per minute during the visual emotion task was significantly different between groups, but this was expected. We tested professional ballet dancers who are physically very fit and have been under intensive physical training every day for years. One important consideration for future study would be to collect information on fitness level for both groups and potentially run a test measuring cardiovascular fitness as a physiological control, as HEPs do seem to be modulated by the level of physical training (Perakakis, Luque Casado, Ciria, Ivanov, & Sanabria, 2017). One limitation of our study that could be implemented in the future is to measure the heartbeat per minute during rest too and not only during the tasks. In our study, we calculated the heartbeat per minute during the visual emotion/gender task and during the HCT but not at rest. As the group difference on the heartbeat per minute was expected based on fitness level, we also compared the ECG amplitude between groups which did not show any significant difference. Furthermore, it should be noted that this expected difference in heartbeat per minute did not seem to affect the HEP results, given that we focused on each group separately, as there wasn't an overall main effect of group.

There has been evidence showing a modulation of interoceptive abilities by psychological traits and states such as depression and anxiety (e.g. Smith et al., 2021), but we did not replicate this finding. A possible explanation for this is that we did not recruit participants based on a diagnosis of depression, generalized anxiety disorder or alexithymia as our focus was on the sensorimotor dance expertise. Therefore, participants' scores distribution on BDI, STAI and TAS were not surprisingly mostly skewed on lower levels. Importantly though, a newly published meta-analysis and literature review found no association between HCT performance, trait anxiety, depression and alexithymia questioning previous evidence (Desmedt & Corneille, 2022). The same group has raised important considerations about the commonly used interoceptive sensibility questionnaires too, as their latent factor analyses showed distinct constructs being measured for each questionnaire, making their results less compatible between them (Desmedt et al., 2022).

3.4.2. Conclusion

The present study aimed to investigate firstly, HEP modulations by emotion (neutral, afraid and happy), task (emotion and gender) and group (professional dancers and controls) and secondly, group differences on interoceptive abilities by means of interoceptive accuracy on HCT and interoceptive sensibility by means of the MAIA questionnaire.

For the first hypothesis, our results showed a task effect for the frontal HEP amplitude early on at the 200-400ms time window with no further significant results. For our second hypothesis, our results provided supportive evidence with dance expertise predicting interoceptive accuracy and dancers showing significantly higher interoceptive sensibility with higher scores in almost all subscales.

To our knowledge, this is the first study comparing interoception and heart – brain interactions in expert populations and in a comprehensive way incorporating a full range of neural, physiological and behavioural measures. Despite the limitations and methodological considerations, we have been able to provide supportive evidence for all our hypotheses, both for HEPs and interoception. The contrary could be argued for HEP as the task effect was found only on controls. However, firstly, we should highlight that we did not have a directional hypothesis given that it had not been tested before. Secondly, these findings can actually be in line with the findings in chapter 2 where on one hand, dancers showed overall effects both for emotion effect and for task and, on the other hand, controls showed emotion effects much more localised in time and space.

Further research is needed to better understand heart – brain interactions in general in a comprehensive way, for example looking at HEPs and the effect of cardiac cycle activity on perception. Expert populations such as professional dancers are of exceptional value offering us insights thanks to their expertise in visual, sensorimotor processing and artistic expertise. Finally, in view of the still ongoing discussions on how to better approach and analyse HEPs, in the present study there was an active effort to be as open as possible for our methodological and analytical approach aiming for a better and more reproductible science in the future.

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Chapter 4: The role of motor expertise on behavioural performance in the visual facial emotion processing: An online pilot study on the face inversion effect

Abstract

Dance expertise has been shown to enhance emotion processing, empathy and interoception. Dancers elicit differential neural and psychophysiological responses to emotional body movements and stimuli familiar to them and, recently, similar results were found for facial emotions. However, it remains unclear whether this facilitation is part of the perceptual processes found at the behavioural level or is mostly rooted at the neural level. To answer this question, we compared professional ballet dancers and non- dancers controls on an online pilot study using a facial emotion discrimination task. Accuracy, reaction times and sensitivity (d') were calculated and levels of empathy and interoceptive awareness were measures. Dancers were faster but less accurate and sensitive than controls on the emotion discrimination task. Dance expertise was strongly related with behavioural performance, empathy and interoceptive awareness. Lastly, empathy and interoceptive awareness were strong predictors of behavioural performance. Overall, this pilot study provides supportive evidence for the dance expertise effect on emotion processing and empathy, but more work is needed to better understand its role on the behavioural and perceptual mechanisms of emotion perception.

4.1. Introduction

The notion and study of visual expertise, that is visual recognition of a specific object, has occupied the visual perception literature for many decades. This has resulted in a large volume of research on how we process faces and facial emotions (examples of reviews: Calder & Young, 2005; Hadders-Algra, 2022). One of the most interesting aspects of studying face perception is the inversion effect. According to the face inversion effect, whole faces are harder to be perceived and recognised when viewed in inverted orientation in comparison to upright orientation (Farah, Tanaka, & Drain, 1995). This effect is much stronger for whole faces than for face parts or other objects with no facial features such as houses or cars and it is observed even from the first months of life (Hills & Lewis, 2018; Turati, Sangrigoli, Ruel, & de Schonen, 2004) but not on people with prosopagnosia (Farah, Wilson, Maxwell Drain, & Tanaka, 1995) supporting theories for face-specific perceptual mechanisms (Rossion et al., 1999).

It was generally assumed that humans possess unique visual perceptual processes for faces due to our expertise on faces until Gauthier and Tarr showed that humans have actually similar effects on other stimuli (Gauthier & Tarr, 1997). The authors invented the 'Greebles', novel objects to study face expertise. After intensive visual training of the participants the researchers were able to show similar behavioural responses and neural activations on the fusiform face area (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999) providing for the first time evidence for the visual expertise hypothesis (Bukach, Gauthier, & Tarr, 2006), even for people with prosopagnosia (Rezlescu, Barton, Pitcher, & Duchaine, 2014). The expertise hypothesis postulates that the neural and perceptual processes found for faces are not unique to faces per se but to visual expertise (Diamond & Carey, 1986; Taylor & Tanaka, 1991; Valentine, 1988). Nowadays we have rich and strong evidence in favour of the expertise hypothesis coming from research with real world experts and laboratory studies showing that after intensive visual training on a specific domain, the domain specific object perception is similar to the face perception (Harel, 2016; Xu, 2005). Some fascinating examples of visual expertise include dogs, birds, cars, chess, minerals, fingerprints and radiology (Duyck, Martens, Chen, & Op de Beeck, 2021; Gauthier, Skudlarski, Gore, & Anderson, 2000; Gilaie-Dotan, Harel, Bentin, Kanai, & Rees, 2012; Martens, Bulthé, van Vliet, & Op de Beeck, 2018; Weiss, Mardo, & Avidan, 2016).

Domain specificity is not a unique feature of visual expertise. On the contrary, it is in the core of motor processing too and specifically on mirror neuron network and dance has been a tremendous example to study motor processing thanks to the domain specific motor expertise of the dancers. Several key studies have established the role of motor expertise on modulating neural and psychophysiological responses on familiar body movements and action observation on dancers including differences in action observation network and visual areas activations and frequency desynchronisation (Bläsing et al., 2012; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Calvo-Merino, Urgesi, Orgs, Aglioti, & Haggard, 2010; Cross, Hamilton, & Grafton, 2006; Cross, Kirsch, Ticini, & Schütz-Bosbach, 2011; Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008; Orlandi & Proverbio, 2019; Orlandi, Zani, & Proverbio, 2017). One study found similar findings even for visually experienced dance spectators without having motor expertise (Jola, Abedian-Amiri, Kuppuswamy, Pollick, & Grosbras, 2012). Another characteristic of dance that make it unique to study is that dance is both motion and emotion. Dancers learn to project emotions through their own bodies. This has provided the opportunity to study emotion perception using dance movements and comparing different populations. The research evidence has pointed towards strong differences between experts and non-experts with professional dancers eliciting enhanced neural, psychophysiological and behavioural responses on emotional body movements (Christensen, Azevedo, & Tsakiris, 2021; Christensen, Cela-Conde, & Gomila, 2017; Christensen, Gomila, Gaigg, Sivarajah, & Calvo-Merino, 2016; Christensen, Pollick, Lambrechts, & Gomila, 2016; Grosbras, Tan, & Pollick, 2012; Van Dyck, Vansteenkiste, Lenoir, Lesaffre, & Leman, 2014).

Moving away from the familiar motor stimuli, professional dancers have shown higher interoceptive abilities and higher levels of emotional sensitivity and empathy (Christensen, Gaigg, & Calvo-Merino, 2017; Sze, Gyurak, Yuan, & Levenson, 2010). Evidence for the latter though has also been found in musicians and actors (Goldstein & Bloom, 2011; Petrides, Niven, & Mouskounti, 2006; Schmidt, Rutanen, Luciani, & Jola, 2021; Sevdalis & Keller, 2011; Sevdalis & Raab, 2014, 2016; Sokol-Hessner et al., 2022). Besides, art and dance specifically are very common tools in psychotherapy successfully applied to improve social skills, psychological state, well- being for clinical populations or to improve movement abilities (Bräuninger, 2012; Carapellotti, Stevenson, & Doumas, 2020; Koch, Kunz, Lykou, & Cruz, 2014; Mala, Karkou, & Meekums, 2012; McGarry & Russo, 2011; Millman, Terhune, Hunter, & Orgs, 2020),

Nevertheless, most of the studies testing dancers have used stimuli familiar to them. A recent study showed for the first time evidence on dancers' differential neural activity using emotional faces- stimuli that we are all considered experts of with dancers processing facial emotion differently both on visual and somatosensory level even from early perceptual stages (see Chapter 2).

Taken together, it is clear that dance expertise facilitates emotion processing including the visually presented facial emotion, but it still remains unclear whether this facilitation can be found at the behavioural responses too in addition to the changes found at the neural level. To answer the above question, we compared professional dancers and controls on an emotion discrimination task.

4.1.1 The present study

The aim of the present study was threefold. Primarily we were interested how professional ballet dancers as motor and art experts perceive visually and behaviourally facial emotion expressions in comparison to control participants with no or minimal prior dance, music and sports experience. For this we used an emotion discrimination task and incorporated the inversion effect as a measure of visual perception by presenting our facial emotional stimuli both in upright and inverted orientation. We also used d' as an overall means of behavioural sensitivity. The secondary aim was to compare levels of empathy and interoceptive sensibility between dancers and controls and search whether these could be indicators of better visual emotion perception. Thirdly, we wanted to explore whether dancers and controls differ on localising emotions on their body using a custom made version of the body maps of emotions. The body maps of emotions have been broadly administered to general population but their use on more special populations (clinical, experts) is rather sparse, with only one study to our knowledge using them with patients with schizophrenia (Torregrossa et al., 2019). We hypothesised that dancers would have a better performance on the emotion discrimination task by means of higher accuracy rates, faster reaction times and higher d-prime as a measure of sensitivity. Additionally, we hypothesised that levels of empathy and interoceptive awareness would correspond to better performance overall and that dancers would have higher scores on empathy and interoception. The task on the body maps of emotion was exploratory and, so no directional hypothesis was a priori made but we did expect to find differences on the localisation between groups.

4.2. Methods

4.2.1. Participants

Twenty – nine professional ballet dancers in professional training or working with 4 years of professional experience or more (all right handed, 1 male, aged 20-40; $M = 29.1$, $SD = 3.64$, all had participated in music classes and all in sports classes expect for one) and twenty control participants with no or minimal prior dance experience (all right handed, 13 males, aged 19-49; $M = 27$, $SD = 7.9$, 12 had participated in dance or music classes and 13 in sports classes) naïve to the objective of the experiment participated in the study for a small time reimbursement (£8/hour). The Testable platform was used for the experiment (Rezlescu, Danaila, Miron, & Amariei, 2020). Dancers were recruited through social media and were given an Amazon voucher upon completion of the study and the control participants were recruited through Testable Minds platform and were matched for age and gender. Before the start of the experiment, all participants were pre-screened to ensure they fulfilled the inclusion criteria. Dancers filled in an adapted version of the Art experience questionnaire (Chatterjee, Widick, Sternschein, Smith, & Bromberger, 2010) that was used in studies presented in chapters 2 and 3 and the Dance Aesthetic Fluency Scale by (DAFS; Fernández- Cotarelo, 2021). Further details about dancers' experience were provided in Table 4.1 and Table 4.2. All participants gave their informed consent online and the study was approved by the Ethics Committee, School of Arts and Social Sciences, City, University of London.

Table 4.1 *Dancers' experience based on the adapted Art Experience Questionnaire.*

Dance Years	Prof years	Train (h/w)	Attend dance performances	Watch dance (h/w)	Read dance (h/w)	h/w spent dancing
11.2 (3.4)	6.3 (1.3)	25.2 (7.2)	3.5 (0.7)	4.5 (0.7)	4.1 (0.7)	4.7 (0.5)

Note: The table shows the means and the standard deviations in brackets. In the question whether they attend dance performances the response options were 1 = almost never, 2 = once a year, 3 = once every six months, 4 = once a month, 5 = once a week. In the following questions, we measured the hours per week they watch/read about dance and spend time dancing with the response options being 1= none, 2 = some time but less than 10 minutes, 3 = between 10 minutes and 1 hour, 4 = between 1 and 5 hours and 5 = more than 5 hours.

Table 4.2 *Dancers' responses on the Dance Aesthetic Fluency Scale*

Pas de bourrée	Pina Bausch	Ballet	Contemporary Dance	Alicia Alonso	Modern Dance	George Balanchine	Plié	Isadora Duncan	Release
2.6 (0.5)	3.1 (0.4)	4 (0.4)	4.8 (0.6)	4.1 (0.5)	3.2 (0.7)	3.6 (0.8)	3.9 (1.2)	3.4 (0.6)	3.7 (1.1)
Contact	Merce Cunningham	Martha Graham	Vaslav Nijinsky	Understand dance	Expert about dance	Knowledgeable about dance	Average		
3.7 (0.6)	3 (0.7)	3.3 (0.8)	3.4 (1)	3.1 (0.9)	4.8 (0.5)	4.3 (0.6)	3.7 (0.3)		

Note: The table shows the means and the standard deviations in brackets. The response options for all questions except the last three were 1 = I have never heard of this artist or term, 2 = I have heard of this, but I don't really know what or who it is, 3 = I have a vague idea about what or who it is, 4 = I understand the artist, discipline or concept when discussing it, 5 = I can talk about it competently. For the last three questions the response options were 1 = strongly disagree, 2 = disagree, 3 = neutral, 4 = agree, 5 = strongly agree.

4.2.2. Materials

4.2.2.1. Stimuli on visual emotion discrimination task

A set of 60 pictures with faces depicting happy, afraid, and neutral expressions (20 happy, 20 afraid and 20 neutral, half male) were taken from the Karolinska Directed Emotional Faces set (Lundqvist, Flykt, & Ohman, 1998). All faces were grey scaled and presented in a rectangular frame (1.4 x 1.57 inches). The photos used for happy and afraid expressions had been rated highly in valence and the neutral ones very low in a previous experiment (Sel, Forster, & Calvo-Merino, 2014). A set of 60 pictures of bodies depicting similarly happy, afraid and neutral expressions (20 neutral, 20 afraid and 20 neutral, half male) were taken from the Bodily Expressive Action Stimulus Test (de Gelder & Van den Stock, 2011).

4.2.2.2. Psychometric measures

The Dance Aesthetic Fluency Scale (DAFS; Fernández- Cotarelo, 2021) was administered to the dancers to verify and measure their dance expertise. DAFS measures declarative knowledge on dance and procedural (i.e., knowing key dance figures and dance terminology) on a 5-point Likert scale with 1 meaning having no knowledge and 5 having good knowledge. The average score per participant was used.

To measure empathy and emotional awareness, the Interpersonal Reactivity Index (IRI) was administered (Davis, 1980). IRI has four subscales on perspective taking, fantasy, empathic concern and personal distress with seven items each subscale and 28 in total. With a 5-point Likert scale (0 for 'does not describe me well' to 4 for 'describes me very well), the average score per participant was used as a measure of general empathy and the average sub-totals for a score on each subscale. Dancers had a slightly higher average IRI score (*M* = 2.7, SD = .26) than controls (*M* = 2.14, *SD* = .34).

The Multidimensional Assessment of Interoceptive Awareness version 2 was used to measure participants' interoceptive abilities (Mehling, Acree, Stewart, Silas, & Jones, 2018). MAIA includes 8 subscales on noticing, not distracting, not worrying, attention regulation, emotional awareness, self-regulation, body listening and trusting totalling 37 items on a 6-point Likert scale from 0 ('never') to 5 ('always'). The average on each factor and a total average was calculated for the level of body awareness per participant. The two groups showed similar results with controls *M* = 2.8, *SD* = .82 and dancers *M* = 2.8, *SD* = .23)

4.2.2.3. Body maps of emotion

An adapted version of the Body maps of emotions was used as shown on Sel and colleagues (Sel, Calvo-Merino, Tsakiris, & Forster, 2020). The Embody tool is a standardised self-report tool localising emotions and mental states with specific body locations with consistent results across cultures (Nummenmaa, Glerean, Hari, & Hietanen, 2014; Nummenmaa, Hari, Hietanen, & Glerean, 2018). It has been used with clinical populations too and specifically participants with schizophrenia showing a differentiation in localising emotions in the body (Torregrossa et al., 2019). In our adapted version, participants viewed on the left a body silhouette and on the right each of the faces depicting neutral, afraid and happy emotion from the emotion discrimination task. Participants had to click where within the body silhouette they felt firstly, the most, and secondly, the least, the facial emotion shown each time on the right. Only one click was allowed per trial due to technical constraints on the testing platform. Afterwards, the body silhouette was split in four areas: head, upper body, arms and legs to analyse where dancers and control participants localise happiness, fear and neutral the most and least on their bodies.

4.2.3. Procedure

All participants gave their informed consent before commencing the study. Then they were presented with the screening questionnaire to verify that they fulfilled the inclusion criteria. Expert dancers needed to have 4 or more professional dance experience and non- dancers control participants needed to have no or minimal dance experience and not to have professional music or sport experience. If they did not fill in the pre-screening criteria, they were later removed from the analysis. Then the visual emotion discrimination task started which consisted of 384 trials in total with 8 blocks of 48 trials each. Both face and body stimuli were presented for four blocks each, two blocks for upright orientation (one block for male and one for female stimuli) and similarly two for inverted orientation. The order of the blocks and the order of the stimuli within each block was randomised. A practice block of 8 trials was completed before the start of the experiment.

For the visual emotion discrimination task, the first stimulus was shown for 100ms followed by a mask for 250ms, then the second stimulus for another 100ms which depicted a congruent or incongruent emotion with the first stimulus following with a question after each trial whether the two images showed the same or different emotion (see Figure 4.1). Participants had to reply yes or no by pressing the button 1 for same or 2 for different emotion. Reaction times and accuracy were recorded.

After the first 4 experimental blocks, participants filled in the IRI. After the last 4 blocks, they filled in the MAIA-2 and then the task with the body maps of emotion was completed (see

Figure 4.2). The experiment in total lasted approximately 45’ and all participants were debriefed at the end.

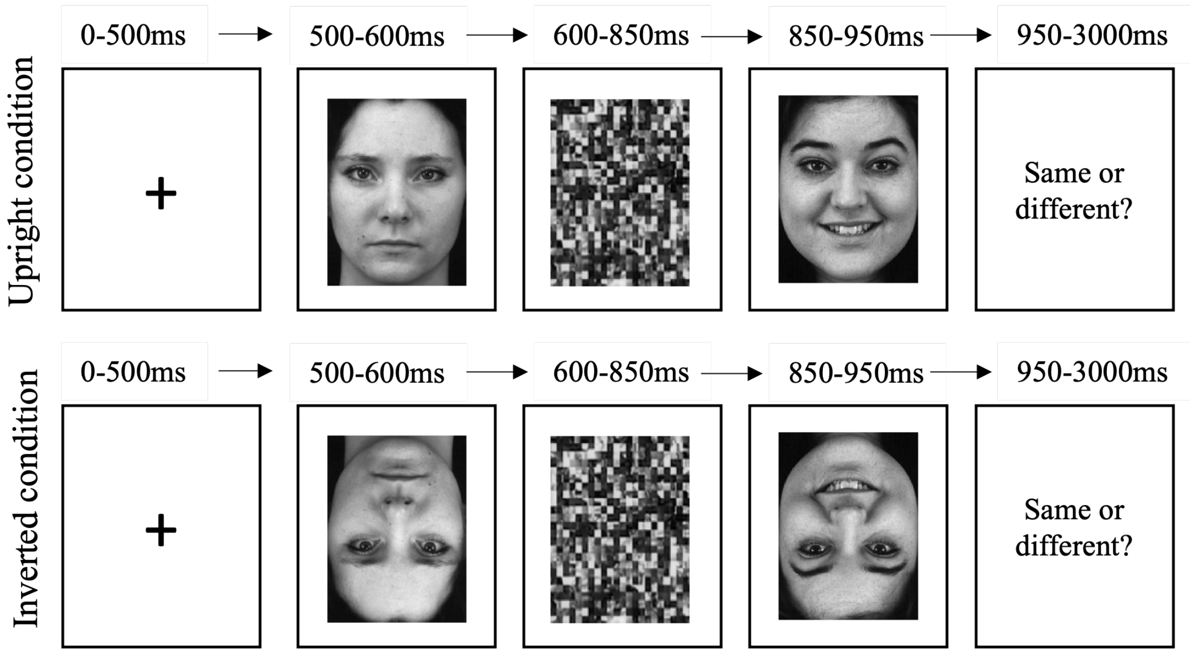

Figure 4.1 *Experimental procedure for the visual emotion discrimination task*

Note: The task involved two conditions with the same stimuli shown in upright and inverted orientation. For both conditions, participants were shown a cross for 500ms followed by the first face stimulus for only 100ms depicting neutral, afraid or happy emotion expression. Then, a mask was shown for 250ms followed by the second face stimulus for 100ms depicting a congruent or incongruent emotion expression with the preceding first image. At the end of the trial, participants were asked whether the two faces they saw showed the same (congruent) or different (incongruent) emotion. Each trial lasted 3 seconds in total. If participants did not respond by pressing button 1 (same) or 2 (different), it was counted as a ‘timeout’ and the next trial was shown.

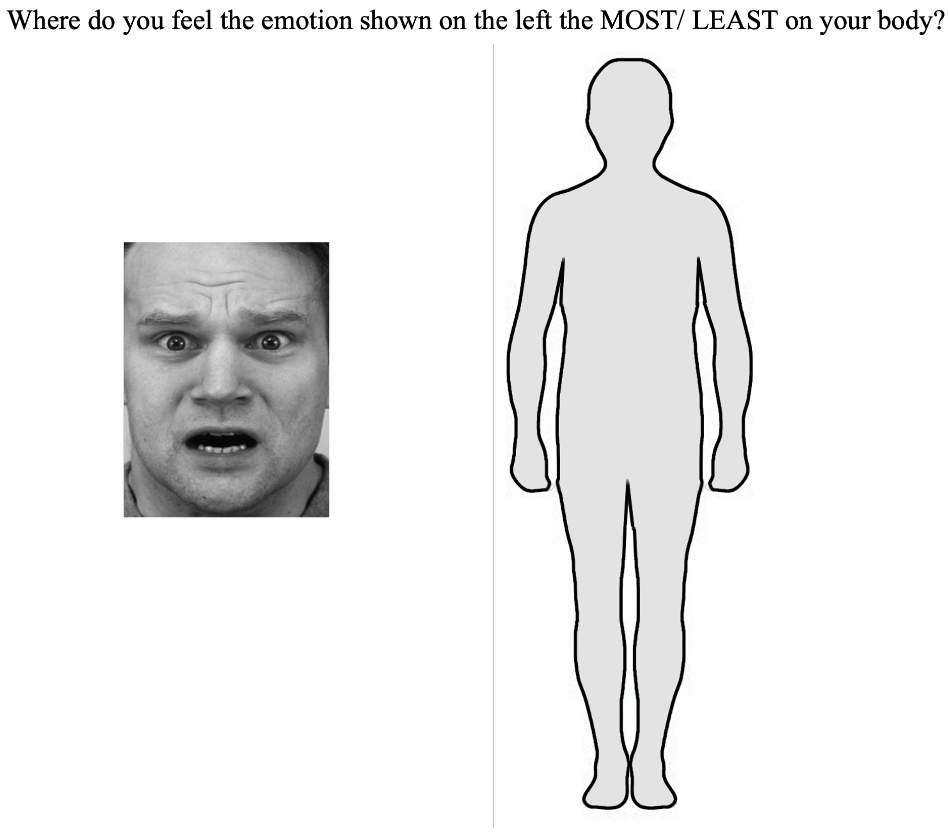

Figure 4.2: *Body Maps of Emotion*

Note: For the task on body maps of emotion, the face stimulus was shown on the left of the screen and a body silhouette on the right. Participants were asked to click once on the body silhouette to indicate where they felt the emotion shown on the face stimulus on their body the most and the least. The task consisted of 60 trials including all face stimuli that were shown twice (once for 'the most' condition and once for 'the least' condition). All face stimuli were shown on upright orientation.

4.2.4. Data analysis

In the present study only the trials with face stimuli are included. The mean accuracy and reaction times of each participant was calculated for upright and inverted stimuli. Participants only with 70% or more accuracy rate and reaction times of 350ms of more were included in the analysis. For the analysis 4 control participants were removed due to reported total dance experience of more than 5 years resulting in 16 controls and 29 dancers. D-prime was calculated per participant to measure sensitivity applying the equation of signal detection theory as per d' = z (Hits) – z (False Alarms) for each orientation and gender condition. A repeated measures orientation x2 (upright, inverted) x gender x2 (female, male) x group (controls, dancers) ANOVA was run for accuracy, reaction times and d' prime separately. One-way ANOVAs were run for group differences on our psychometric measures IRI and MAIA-2. Greenhouse – Geisser values are reported if the sphericity assumption is violated. Correlations, linear and stepwise regression analyses for each group were used to identify potential relations between the psychometric measures and the behavioural performance. Spearman's Rho is reported in case of violation of normality assumptions and the values reported have not been corrected for multiple comparisons. Regarding the body maps of emotion, due to a technical issue the data of only 4 dancers were suitable to be used. Given the low number, no statistical comparisons were run but all the datapoints of both groups were plotted to visualise where controls and dancers localise emotion sensations in the body.

4.3. Results

4..3.1. Behavioural performance in the visual emotion discrimination task

4.3.1.1. Accuracy

The orientation (upright, inverted) x gender (female, male) x group (controls, dancers) repeated measures ANOVA on accuracy overall resulted in a significant main effect of orientation, F (1, 43) = 15.886, $p < .001$, $\eta_p^2 = .27$, significant main effect of group, F (1, 43) = 2253.487, $p < .001$, $\eta_p^2 = .981$ and a significant orientation by group interaction, F (1, 43) = 4.241, $p = .046$, $\eta_p^2 = .09$. Upright orientation overall resulted in higher accuracy rates ($M = .66$, $SD = .18$) in comparison to inverted ($M = .63$, $SD = .15$). Control participants irrespective of orientation and gender of stimulus shown were more accurate ($M = .82$, $SD = .06$) than dancers ($M = .54$, $SD = .11$). Post hoc pairwise comparisons following the orientation by group interaction showed that the group means are significantly different both for upright (controls $M = .85$, $SD = .07$, dancers $M = .55$, $SD = .12$) and inverted condition (controls $M = .8$, $SD = .06$, dancers $M = .53$, $SD = .1$), all $p < .001$. The post hoc comparisons also showed that the accuracy rates for control participants were significantly different between conditions (upright $M = .85$, $SD = .07$, inverted $M = .8$, $SD = .06$), $p < .001$, but not for the dancers (upright $M = .54$, $SD = .12$, inverted $M = .53$, $SD = .1$), $p = .114$. Figure 4.3 below shows the group distribution for accuracy scores.

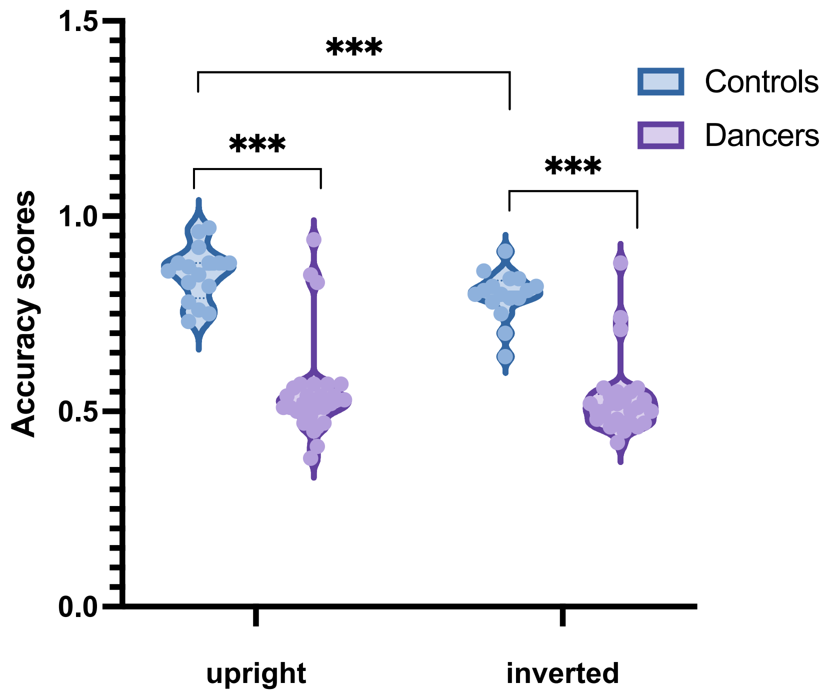

Figure 4.3 *Group distributions for accuracy scores on upright and inverted orientation.*
Note: * for p < .05, ** for p < .005 and *** for p < .001. Made with Prism 9.

4.3.1.2. Reaction times

The orientation (upright, inverted) x gender (female, male) x group (controls, dancers) repeated measures ANOVA on reaction times only on the correct responses resulted in a significant main effect of orientation, F (1, 43) = 12.564, $p < .001$, $\eta_p{}^2 = .226$, a significant orientation by group interaction, F (1, 43) = 11.225, $p = .002$, $\eta_p{}^2 = .207$ and a significant sex by group interaction, F (1, 43) = 8.851, $p = .005$, $\eta_p{}^2 = .171$. The main effect of group was not statistically significant, p = .097. Upright orientation overall resulted in higher reaction times ($M = 824.58$, $SD = 191.91$) in comparison to inverted ($M = 785.99$, $SD = 142.64$). Post hoc pairwise comparisons following the orientation by group interaction showed that the group mean reaction times are significantly different for upright (controls $M = 907.8$, $SD = 218.08$, dancers $M = 778.56$, $SD = 161.96$), $p = .023$ but not for inverted condition (controls $M = 805.08$, $SD = 188.79$, dancers $M = 775.46$, $SD = 112.04$), $p = .502$. The post hoc comparisons also showed that the reaction times for control participants were significantly different between conditions (upright $M = 907.8$, $SD = 218.08$, inverted $M = 805.08$, $SD = 188.79$), $p < .001$, but not for the dancers (upright $M = 778.56$, $SD = 161.96$, inverted $M = 775.46$, $SD = 112.04$), $p = .871$. The post hoc pairwise comparisons following the sex by group interaction showed that in the female face condition the control mean reaction times were significantly higher than the dancers' mean (controls $M = 886.19$, $SD = 227.5$, dancers $M = 768.93$, $SD = 137.52$), $p = .036$ but not for male face condition (controls $M = 835.11$, $SD = 176.26$, dancers $M = 785.1$, $SD = 133.16$), $p = .289$. Additionally, the control mean reaction times were significantly higher for female faces than for male faces (female $M = 886.19$, $SD = 227.5$, male $M = 835.11$, $SD = 176.26$), $p = .007$, but not dancers (female $M = 768.93$, $SD = 137.52$, male $M = 785.1$, $SD = 133.16$), $p = .237$. Figure 4.4 shows the group distributions for the reaction times.

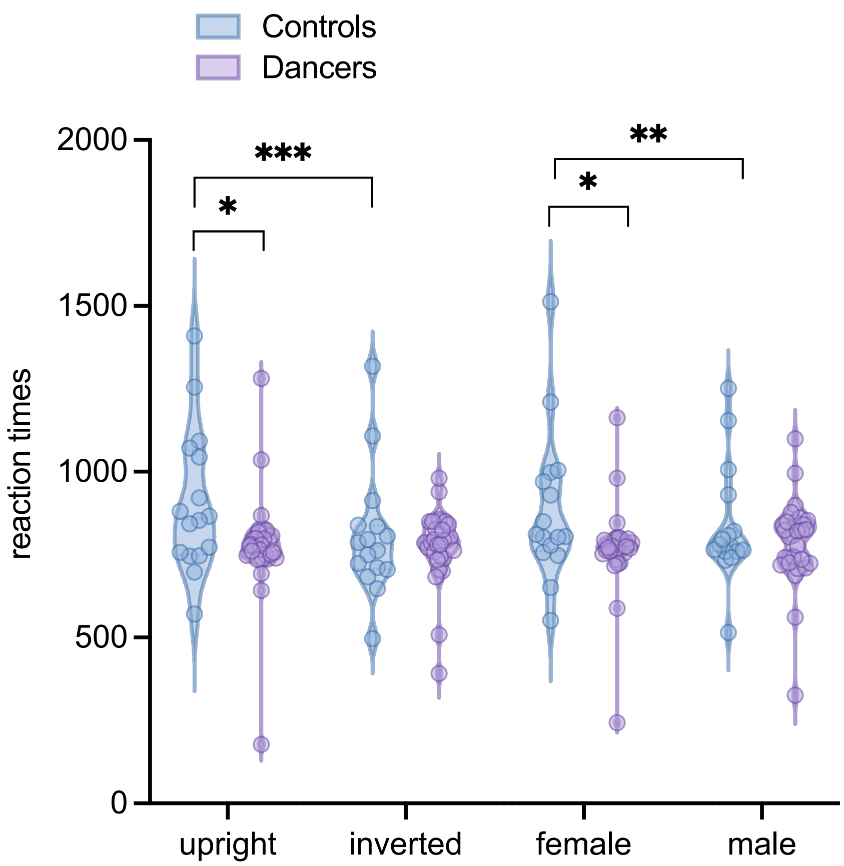

Figure 4.4 *Group distributions for reaction times on upright and inverted orientation and for female and male face stimuli (irrespective of orientation).*

Note: * for p < .05, ** for p < .005 and *** for p < .001. Made with Prism 9.

4.3.1.3. D prime

The orientation (upright, inverted) x gender (female, male) x group (controls, dancers) repeated measures ANOVA on d' overall resulted in a significant main effect of orientation, F (1, 43) = 6.823, p = .012, η_p^2 = .14, significant main effect of group, F (1, 43) = 122.562, p < .001, η_p^2 = .740 and a significant orientation by group interaction, F (1, 43) = 7.447, p = .009, η_p^2 = .15. Upright orientation had a higher detection rate (*M* = .98, *SD* = 1.32) than inverted orientation (*M* = .78, *SD* = .96) and control participants similarly had a higher detection (*M* = 2, *SD* = .41) than dancers (*M* = .23, *SD* = .61) overall. Following the orientation x group interaction, controls had a higher detection rate than dancers for both upright (controls *M* = 2.34, *SD* = 1.19, dancers *M* = .23, *SD* = .59), p < .001 and inverted condition (controls *M* = 1.75, *SD* = .42, dancers *M* = .24, *SD* = .72), p < .001. Additionally, controls' detection rates were significantly different between conditions (upright *M* = 2.34, *SD* = 1.19, inverted *M* = 1.75, *SD* = .42), p = .002 but not for dancers (upright *M* = .23, *SD* = .59, inverted *M* = .24, *SD* = .72), p = .922. Figure 4.5 below visualizes the group distributions on d'.

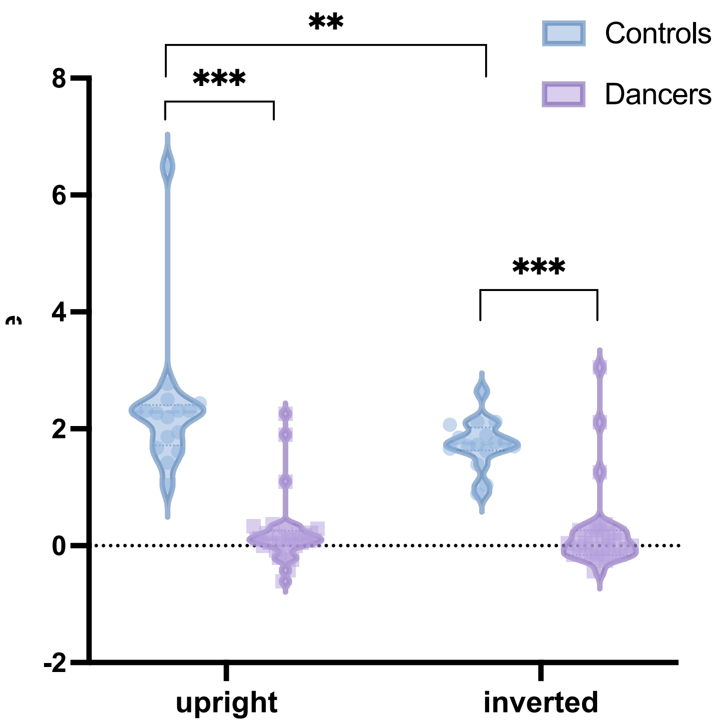

Figure 4.5 *Group distributions for d' on upright and inverted orientation.*

Note: * for p < .05, ** for p < .005 and *** for p < .001. Made with Prism 9.

4.3.2. Psychometric measures

Dancers had significantly higher scores on Interpersonal Reactivity Index average score, F (1, 43) = 40.292, $p < .001$, $\eta^2 = .48$ and all four subscales than controls, F (1, 43) = 17.303, $p < .001$, $\eta^2 = .29$ for Fantasy, F (1, 43) = 29.729, $p < .001$, $\eta^2 = .41$ for Empathic concern, F (1, 43) = 6.201, $p = .017$, $\eta^2 = .13$ for Perspective taking and F (1, 43) = 41.532, $p < .001$, $\eta^2 = .49$ for Personal Distress. Results on interoceptive sensibility are mixed with dancers having higher scores on MAIA subscale on self-regulation F (1, 43) = 4.458, $p = .041$, $\eta^2 = .09$ and body listening, F (1, 43) = 15.704, $p < .001$, $\eta^2 = .27$ and controls having higher scores on not distracting subscale, F (1, 43) = 50.418, $p < .001$, $\eta^2 = .54$. Table 4.3 shows the Means and SD for each group on MAIA and IRI.

Table 4.3 *Group Means and SD for MAIA and IRI averages and subscales*

Questionnaires	Controls	Dancers
IRI total	2.14 (.34)	2.7 (.26)
IRI Fantasy	2.13 (.587)	2.7 (.329)
IRI Empathic concern	2.07 (.36)	2.78 (.44)
IRI Perspective taking	2.39 (.49)	2.73 (.40)
IRI Personal distress	1.96 (.413)	2.63 (.29)
MAIA total	2.8 (.82)	2.81 (.23)
MAIA Noticing	3.13 (1.19)	3.19 (.45)
MAIA Not distracting	2.97 (1.03)	1.51 (.31)
MAIA Not worrying	2.35 (.87)	2.13 (.62)
MAIA Attention regulation	2.56 (1.24)	3.07 (.52)
MAIA Emotion Awareness	3.2 (1.3)	3.18 (.43)
MAIA Self - regulation	2.66 (1.11)	3.17 (.53)
MAIA Body listening	2 (1.24)	3.14 (.69)
MAIA trusting	3.5 (1.04)	3.06 (.577)

4.3.3. Psychometric measures as predictors of behavioural performance in visual facial emotion perception

Correlation and regression analyses were run between the significant measures of behavioural performance and the questionnaires for each group. For control participants, the average accuracy score on upright stimuli correlated with average MAIA score, Rho = -.516, p = .041 and the average score on inverted stimuli with IRI subscales on Fantasy, Rho = - 610, p = .012 and on Perspective Taking, Rho = - .544, p = .029. Reaction times with upright male stimuli correlated with IRI subscale on personal distress, Rho = - 581, p = .018. The reaction times for the remaining conditions (inverted male stimuli, upright and inverted female stimuli and averaged reaction times for upright and inverted stimuli) did not yield any significant correlations. d' prime for upright stimuli correlated with MAIA average score, Rho = - 513, p = .042 and the subscale on attention regulation, Rho = - 508, p = .045. d' prime for inverted stimuli correlated with IRI average score, Rho = - 659, p = .006 and the IRI subscales on Fantasy, Rho = - 653, p = .006 and perspective taking, Rho = - 588, p = .017. Regression analysis showed IRI subscale on Fantasy as a significant predictor of d' prime on inverted stimuli, R^2 = .3, F (1, 14) = 5.983, p = .028.

For the dancers, the average accuracy score on inverted stimuli correlated with the MAIA subscale on attention regulation, Rho = - 434, p = .019 and the IRI subscale on fantasy, Rho = - 370, p = .048. The regression model showed both the MAIA and IRI subscales as significant predictors of the average accuracy on inverted stimuli, R^2 = .55, F (1, 27) = 15.81, p < .001. Reaction times on inverted stimuli correlated with MAIA subscales on attention regulation, Rho = - 371, p = .048 and self-regulation, Rho = - 411, p = .027. Reaction times specifically for inverted female stimuli correlated with MAIA subscales on emotion awareness, Rho = - 390, p = .036 and self-regulation, Rho = - 376, p = .044. Reaction times for upright male stimuli also correlated with and were predicted by MAIA subscale on self-regulation, Rho = - 453, p = .014 and R^2 = .14, F (1, 27) = 4.558, p = .042. d' prime on upright stimuli correlated with and were predicted by MAIA subscale on trusting, Rho = - 404, p = .03 and R^2 = .27, F (1, 27) = 9.751, p = .004. d' prime on inverted stimuli was predicted by and correlated with MAIA subscale on attention regulation, Rho = - 491, p = .007 and R^2 = .34, F (1, 27) = 13.747, p < .001. Figure 4.6 visualises all the significant regressions reported above.

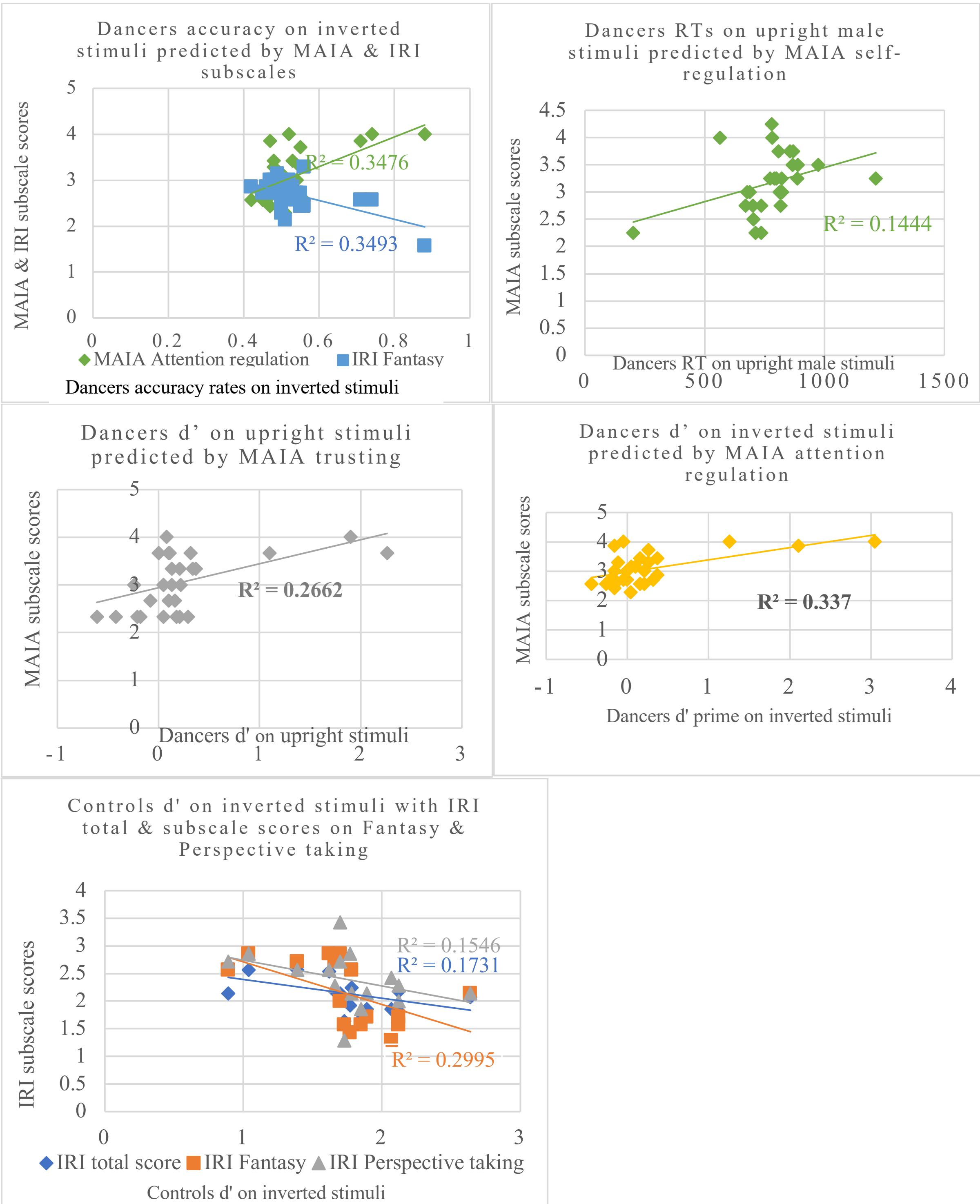

Figure 4.6 *Plots for controls and dancers showing the significant predictors of behavioural performance.*

Continuing our focus on dancers, we searched if behavioural performance on the emotion discrimination task and levels of empathy and interoceptive awareness were related to the level of expertise. We ran non – parametric correlations between the years of total and professional dance experience and the DAFS items on declarative level of dance expertise and the markers of behavioural performance (accuracy, reaction times and d') and questionnaires totals and subtotals. Table 4.4 summarises the correlations.

Table 6.4

Correlations between measures of dance expertise, behavioural performance and levels of empathy and interoceptive awareness

Measures	Dance total years	Prof. dance years	Understand dance	Dance Expert	Dance knowledgeable
Dance total years	1				
Prof. dance years	.506**	1			
Understand dance	-.201	.390*	1		
Dance Expert	-.171	-.054	.148	1	
Dance knowledgeable	.285	-.151	-.469	.206	1
Acc. Up. Female	.103	.394*	.206	-.236	-.209
Acc. Up. Male	.188	.225	.036	-.416*	.040
Acc. Inv. Female	.224	.518**	.469*	-.377*	-.329
Acc. Inv. Male	.080	.403*	.388*	-.067	-.236
Acc. Inv. Total	.138	.430*	.494**	-.221	-.334
Accuracy total	.265	.366	.275	-.370*	-180
RT Up. Male	.045	.656**	.495**	.121	-.377*
RT Up. Total	-.076	.578**	.440*	.142	-.264
RT Inv. Female	.253	.541**	.208	-.047	-.238
RT Inv. Male	-.023	.551**	.378*	.131	-.359
RT Inv. Total	.101	.672**	.443*	-.005	-.451*
RT Female	.071	.565**	.262	-.047	-.324
RT Male	-.050	.595**	.485**	.152	-.414*
d'	.264	.365	.282	-.370*	-.180
d' Up. Female	.204	.472**	.275	-.221	-.296
d' Inv. Female	.150	.427*	.319	-.371*	-.217
d' Inv. Male	.127	.430*	.247	-.205	-.148
d' Inv. Total	.114	.421*	.378*	-.352	-.316
IRI total	.455*	.000	-.218	.033	.389*
IRI Fantasy	.358	-.162	-.298	.137	.454*
IRI Emp. Con.	.413*	.036	-.263	-.056	.517**
IRI Pers. Dist.	.453*	-.003	.093	.154	-.073
MAIA Att. Reg.	-.137	.232	.462*	-.159	-.198
MAIA Self Reg.	.106	.359	.399*	.073	-.180

Note: * correlation is significant at p < .05. ** correlation is significant at p < .001

4.3.4. Body maps of emotions

Most clicks for where both groups felt an emotion the most are concentrated on the head and upper body, while for the least, they are mostly on the lower part, hands and legs. Although there are no statistical comparisons, from visual inspection it could be easily argued that for both groups the afraid emotion is located both in the head and in the trunk and chest, while for the neutral and happy emotions, most data points are focused on the head only. Figure 4.7 below visualises all the data points of control participants and dancers entered on the body silhouette localising neutral, afraid and happy emotions on the body.

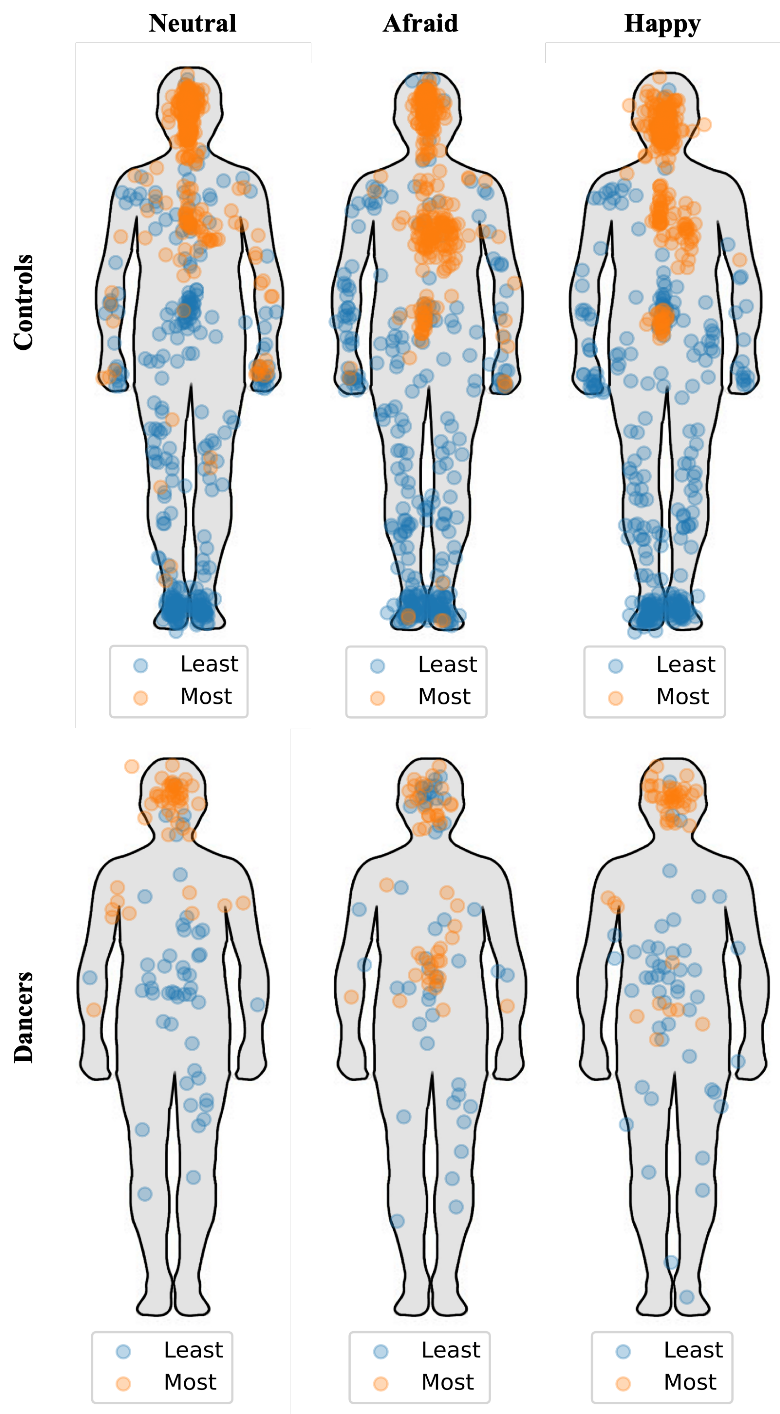

Figure 4.7 *Plots of the body silhouettes including all the points controls and dancers clicked on to localise neutral, afraid and happy emotions.*

Note: Made with custom made Python code by Iason Papapanagiotakis Bousy.

4.4. Discussion

The present study aimed primarily at investigating the effect of dance as motor and art expertise on behavioural perception of visual facial emotion. The behavioural performance of professional dancers and controls on a facial emotion discrimination task was measured by means of accuracy rates, reaction times (only on correct responses) and perceptual sensitivity. Following paradigms of visual perception literature, neutral, afraid and happy face stimuli were shown both in upright and inverted position to look for the inversion effect. We hypothesised that dancers would show significantly higher accuracy rates, fastest reaction times and better sensitivity than controls. Our results revealed main effects and interactions with group but not always in the direction we hypothesized. Regarding accuracy, there was a main effect of group and a group by orientation interaction with controls having better accuracy scores than dancers. Upright condition was more accurately predicted than inverted for all participants and for controls specifically (orientation by group interaction), but not for dancers. Regarding reaction times, group interacted both with orientation and stimulus gender with faster reaction times for dancers on upright orientation and on female faces. Reaction times for inverted orientation were faster than upright overall. Regarding sensitivity, there was a main effect of group and a group by orientation interaction with controls having higher d' than dancers overall and the upright orientation showing higher sensitivity rates than inverted both overall and for controls specifically but not for dancers. Overall, dancers were faster but less accurate and less sensitive discriminating between emotions contradictory to our hypotheses.

The second aim of the study was to compare the levels of empathy and interoceptive awareness between groups and look for potential predictors of behavioural performance hypothesising that dancers will have higher levels of empathy and interoceptive awareness. Here again our results were mixed with dancers indeed showing significantly higher levels of empathy by means of IRI average score and all IRI four subscales. On MAIA, however, dancers were better on the self – regulation and body listening subscales, but controls were better at attention regulation subscale. Importantly, dance expertise was found to correlate with behavioural performance on the emotion discrimination task and on empathy. This finding goes in line with previous evidence on emotion enhancement and better interoceptive abilities found on dancers (e.g. Christensen et al., 2016). However, given the low performance and mixed results from the dancers, more work is needed for more robust and conclusive results.

Our third aim was to explore whether dancers localise emotions on their body differently than non- experts. Due to the technical error resulting in 4 dancers, we cannot make an argument on group differences. From the controls' body maps though we would suggest that afraid emotion seemed to be spread in the head and the trunk similarly to previous findings (L. Nummenmaa et al., 2014), while neutral and happy emotions are mostly concentrated on the head.

Overall, our results do not allow us to make a conclusive argument on the effect of dance expertise on the behavioural perception of emotion based on our emotion discrimination task. Although dance expertise correlated with behavioural performance, dancers were faster but less accurate and sensitive to the task. Dancers' performance was close to chance levels which was unexpected based on the type of the task and the literature. Given that both groups were asked to perform exactly the same task under similar conditions (monitor screen, keyboard), we would assume that participants from the dancers group were not engaged enough with the task and paid less attention to the stimuli and their responses. Previous work on dance expertise and emotion has provided us with overwhelming evidence on enhancement on emotion perception (Camurri, Lagerlöf, & Volpe, 2003; Christensen, Cela-Conde, et al., 2017; Christensen, Pollick, et al., 2016; Sze et al., 2010). Therefore, more work would be needed using paradigms from visual perception literature to identify the perceptual mechanisms involved in this emotion enhancement. Nevertheless, our results showed higher empathy levels for dancers than controls partially confirming previous findings for dance expertise effect on emotional awareness, empathy and interoception (e.g. Christensen, Gaigg, et al., 2017; Sevdalis & Keller, 2011).

Interestingly, in our study empathy and interoceptive awareness did predict albeit partially the different measures of behavioural performance going in line with previous findings, such as Chick and colleagues where interoceptive accuracy correlated with perceptual sensitivity (d') and facial mimicry on a facial expression discrimination task (Chick, Rounds, Hill, & Anderson, 2020). These results add to the evidence supporting the account for mirroring and empathy on social perception (Decety & Jackson, 2006; Hess & Blairy, 2001; Rymarczyk, Zurawski, Jankowiak-Siuda, & Szatkowska, 2016).

4.4.1 Limitations and future work

Due to the covid -19 pandemic, an in person experiment was not possible at the time of preparing this study. Therefore, the present is a pilot study to test our paradigm in a small sample before conducting a larger one in the lab settings. As an online study, it was much harder to control for participants' attention and whether they properly followed instructions. To that end, we speculate that dancers' faster but less accurate performance across the task might be a case of improper task engagement paying less attention to the task and its instructions. The latter and the few technical difficulties resulted in removing participants to preserve as high data quality as possible. Another limitation of the online study is that physiological measures are much harder to be measured and, so, questionnaires only were administered to measure empathy and interoceptive abilities.

It would be interesting to run the same study again in the future adding attention checks and extra measures to ensure as high engagement of the participants as possible. The next step for this line of work would be to recruit and compare for the first time different art and motor experts: professional dancers, musicians and athletes as an example of motor but not emotion or art experts. Behavioural, psychophysiological (cardiac data, galvanic skin responses) and neural indices (visual and somatosensory processing by means of ERPs) of facial emotion perception would be collected.

4.4.2. Conclusion

The present study investigated the dance expertise effect on visual facial emotion perception. Our results showed strong group effects, but they are rather mixed, with dancers being faster but less accurate and less sensitive to the emotion discrimination task. However, they did have higher empathy levels and dance expertise did correlate with their behavioural performance. As a pilot work, this study can be the stepping stone for more interdisciplinary work between perception, neuroscience and arts in order to provide a still missing holistic perspective on how artists and/ or motor experts perceive emotions around them.

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Chapter 5: Emotion embodiment: Other's emotion expressions are uniquely presented in somatosensory activations

This chapter includes the manuscript: Arslanova, I., Meletaki, V., Calvo-Merino, B., Forster, B. (2022) Emotion embodiment: Other's emotion expressions are uniquely presented in somatosensory activations. (in prep)

Author Contributions

V.M. performed the data analyses under the supervision of B.F. and B.CM.. The following text was written by V.M. to be included in the present thesis and it is not the same manuscript drafted by B.F. to be submitted for publication.

Abstract (as appears in the manuscript)

Understanding other's emotions is fundamental for smooth social interactions. Recent research has shown that one's own somatosensory cortex (SCx) plays a crucial role during facial emotion discrimination. Participants completed an alexithymia questionnaire (TAS-20) and performed a heartbeat counting task followed by an emotion judgment task of angry, happy, sad and neutral faces while their EEG was recorded. We extracted the pure, embodied emotion effect and show reliable and distinct modulations of SCx activity in response to angry and happy faces. We show that different emotion expressions elicit unique SCx patterns of activation and further that such neural embodiment of others' emotion is shaped by personality trait but not interoceptive abilities. Moreover, individual differences in trait alexithymia predicted the embodied anger response. Thus, the emotional expressions of other's are uniquely presented in the observer's SCx sub serving early perceptual processes in social interactions.

5.1. Introduction

Emotions are an integral part of our everyday life and our social interactions with the external environment. We often express our emotions nonverbally through body language and facial expressions. The latter has long been a research topic of interest from Darwin suggesting that the emotions of fear, anger, disgust, sadness, and happiness are innate, universal and common across species (Darwin, 1872) and Ekman and colleagues later (e.g. Ekman, 1993; Ekman & Friesen, 1971) suggesting that happiness, sadness, anger, surprise, fear, and disgust are the six basic emotions whose expressions are universally recognized. Later studies have contradicted these results pointing towards the important role of culture, exposure, and personality characteristics among other factors (Barrett, Adolphs, Marsella, Martinez, & Pollak, 2019; Calvo, Gutiérrez-García, Fernández-Martín, & Nummenmaa, 2014; Elfenbein & Ambady, 2003; Nummenmaa & Calvo, 2015). Nevertheless, emotion perception is that deeply wired that we can perceive facial expressions from infancy (dependent on mother's engaging behaviour, see review by Ilyka, Johnson, & Lloyd-Fox, 2021), in case of blindness (congenital or later in life e.g. see review by Valente, Theurel, & Gentaz, 2018) or without awareness (Leiberg & Anders, 2006) or full consciousness (Pegna, Landis, & Khateb, 2008). Neuroimaging studies have shown concrete evidence that facial emotion perception seems to involve a large cortical and subcortical brain network involving the visual areas (occipital and fusiform gyrus), limbic and frontal areas (amygdala, striatum, ventromedial prefrontal cortex), the insular and somatosensory cortices (e.g. Adolphs, Damasio, Tranel, & Damasio, 1996; Phan, Wager, Taylor, & Liberzon, 2002). Differences in timing and location of neural processing between distinct emotion expressions have also been well evidenced (Batty & Taylor, 2003; Williams et al., 2004; Williams, Palmer, Liddell, Song, & Gordon, 2006).

One of the key theories of emotion processing, namely the theory of embodied emotion stipulates that we perceive emotions of others through *perceptual, somatovisceral and motoric (re-)experiencing* (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; Niedenthal, 2007:1002; Niedenthal & Maringer, 2009; Sato, Kochiyama, & Uono, 2015; Wood, Rychlowska, Korb, & Niedenthal, 2016). The recent neuroimaging studies have offered supportive evidence for the embodied emotion theory showing the importance and necessity of the somatosensory cortices' involvement in the early stages of facial emotion processing (D. Pitcher, Garrido, Walsh, & Duchaine, 2008; Pourtois et al., 2004; A. Sel, Forster, & Calvo-Merino, 2014). Later studies in our lab have provided further evidence for this contribution of the somatosensory cortices as purely somatic, independent from the visual processing concerning tasks from attention and working memory involving bodily stimuli (Arslanova, Galvez-Pol, Calvo-Merino, & Forster, 2019; Galvez-Pol, 2017; Galvez-Pol, Calvo-Merino, Capilla, & Forster, 2018; Galvez-Pol, Calvo-Merino, & Forster, 2020) to facial emotion processing (Fanghella, Gaigg, Candidi, Forster, & Calvo-Merino, 2022; A. Sel et al., 2014). Importantly, the latter studies provided supportive evidence for the involvement of somatosensory cortices while focusing on the emotion in comparison to the gender of a face and for differentiation in somatosensory processing based on the facial emotion expression shown, specifically between embodied happy emotion (SCx amplitude of happy minus SCx amplitude of neutral) and embodied fearful emotion SCx amplitude of fearful minus SCx amplitude of neutral).

The first aim of the current study is to investigate more deeply and establish a link between different facial emotions and their unique and reliable neural signatures of embodiment. The second aim is to explore the influence of alexithymia and the observer's interoceptive abilities in embodiment of emotion. Alexithymia is a personality trait characterized by difficulty in recognizing, identifying and verbalizing emotions of ourselves and others. It has been linked with lower levels of empathy (Alkan Härtwig, Aust, Heekeren, & Heuser, 2020), reduced and/or inaccurate theory of mind (Pisani et al., 2021), higher levels of depression (Honkalampi, Hintikka, Tanskanen, Lehtonen, & Viinamäki, 2000), autism spectrum disorder (Mul et al., 2018), even psychopathy (Burghart & Mier, 2022). Previous literature has provided with strong evidence between alexithymia and difficulties in emotion perception tasks (Ihme et al., 2014; Jongen et al., 2014; Parker & Bagby, 1993; Reker et al., 2010; Rosenberg et al., 2020). People with higher alexithymia levels also exhibit differential neural activations in their emotion network during emotion perception/recognition tasks (Jongen et al., 2014; Reker et al., 2010; Rosenberg et al., 2020). Van der Velde et al. (2013) in their meta-analysis found a diminished activation over the amygdala, motor and premotor areas for negative stimuli and a diminished activation over the insula for positive stimuli. Ihme et al. (2014) found increased activation over the somatosensory and supplementary motor areas for angry in comparison to fearful faces. Even though these studies have shown a strong link between areas involved in emotion embodiment and alexithymia, the exact timing of these neural differences remain unclear. Therefore, the second aim of the current study was to shed light into whether these differences take place early at the time of the emotional stimulus visual onset or reflect post-perceptual processes.

Apart from alexithymia, we were interested in investigating the role of interoception in emotion embodiment. Growing evidence has been provided for a positive relation between emotion perception and embodiment with interoceptive abilities involving similar neural networks; having a stronger awareness of one's own body seems to facilitate emotion perception of others (Chick, Rounds, Hill, & Anderson, 2020; Critchley & Garfinkel, 2017; Füstös et al., 2013; Grynberg & Pollatos, 2015; Herbert & Pollatos, 2012; Herbert, Pollatos, & Schandry, 2007; Shah, Catmur, & Bird, 2017). Interoception has also been linked negatively with alexithymia levels with studies showing lower interoceptive abilities for people with higher alexithymia levels (Bonaz et al., 2021; Brewer, Cook, & Bird, 2016; Herbert, Beate M.; Cornelia, Herbert; Pollatos, Herbert, Herbert, Pollatos, & Herbert, Beate M.; Cornelia, Herbert; Pollatos, 2011; Quadt, Critchley, & Garfinkel, 2018; Trevisan et al., 2019). However, other studies have provided contradicting evidence raising the need for further research on the link between interoception and alexithymia (Murphy, Brewer, Hobson, Catmur, & Bird, 2018; Nicholson et al., 2018).

Based on the previous literature, we hypothesised firstly that different facial emotion expressions will evoke distinct somatosensory and visual emotion effects and secondly that alexithymia and interoceptive abilities will modulate these somatosensory and visual emotion effects.

5.2. Methods

5.2.1. Participants

Thirty- five volunteers naïve to the experiment objective were recruited through an online psychology website (SONA Inc.) and participated in the study for a small time reimbursement. The data of five participants were excluded from the analysis (see section 5.2.5). The remaining 30 participants (16 women) were all right- handed with age range 18- 66 years (mean age = 27.61) and reported normal or corrected to normal vision. One further participant was excluded for the interoception analysis only (see section 5.2.5.). The study was approved by the Psychology Research Committee of City, University of London and all participants gave informed consent before the start of experiment.

5.2.2. Materials

5.2.2.1. Stimuli

A set of 80 pictures with faces depicting happy, angry, sad, and neutral expressions (20 per emotion, half male) were taken from the Karolinska Directed Emotional Faces set (Lundqvist, Flykt, & Ohman, 1998) All faces were grey scaled and presented in a rectangular frame (1.4 x 1.57 inches) excluding most of hair and non -facial characteristics.

5.2.2.2. Psychometric measures

Participants were asked to fill in the Toronto Alexithymia Scale to measure their alexithymia levels (Bagby, Taylor, & Parker, 1994) and the Beck Depression Inventory (Beck, Ward, Mendelson, Mock, & Erbaugh, 1961) for levels of depression. The latter was measured as a control variable in the analysis as depression has been associated both with alexithymia (Hendryx, Haviland, & Shaw, 1991; Honkalampi et al., 2000; Li, Zhang, Guo, & Zhang, 2015) and with impaired emotion processing (Bourke, Douglas, & Porter, 2010; Carballedo et al., 2011). Participants' mean score on BDI was 5.6 (SD = 6.14) which is well below the threshold signifying clinical depression (> 17).

5.2.2.3. Interoception measures

To measure the interoceptive abilities, the widely used Heartbeat Counting Task was completed (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015; Schandry, 1981). Participants silently counted their heartbeat for four time intervals of 25, 35, 45 and 100 seconds. The order of the time intervals was randomised. They were explicitly told not to physically take their pulse or guess based on their average resting heart rate. Participants were instructed to press 'Enter' when they were ready. Then, using E – prime 2.0 software (Psychology Software Tools, Pittsburgh, PA) a red cross would appear in the middle of the screen (see figure 5.1 for the experimental procedure). When the cross became green, participants had to count their heartbeat until the cross became red again. Subsequently, they had to answer two questions: the first was 'How many heartbeats did you count?' and the second 'How confident you are for your answer in a scale from 0 (no confident at all) to 10 (very confident)?' (see figure 5.1C for the experimental procedure). Participants typed down their answers using the keyboard. Before the experimental task started, a 10 second practice was given. Their heartbeat was recorded for the whole experiment. For each trial, an interoceptive accuracy score was calculated, as defined by Hart et al. (Hart et al., 2013): 1-|nbeatsreal - nbeatsreported|/ -

(nbeatsreal - nbeatsreported)/2. These scores were then averaged across the four trials resulting in one average value per participant. Participants' interoceptive awareness was calculated using Pearson correlation between the counting accuracy and confidence scores.

5.2.3. Procedure

Participants were seated in a dimly lit sound attenuated electromagnetically shielded room looking at a 60 Hz computer monitor in a distance of 80 cm. First, the Beck Depression Inventory and the Toronto Alexithymia Scale were administered using the online software tool Qualtrics (Qualtrics XM Platform™). Then, the facial emotion judgement task was introduced. Through E – prime 2.0 tactile stimulation was applied using 12 V solenoids (5 mm in diameter) attached with microporous tape to the tip of the left index finger. When a current passed through the solenoid tactile stimulation lasting 2ms was delivered by driving a metal rod with a blunt conical tip that contacted participants' fingertip. White noise masked the noise of the tactile stimulators using one loudspeaker 70cm away from the participant's head. Participants were asked to ignore the tactile stimulations and the white noise.

Trials started with a fixation cross (500ms) followed by a neutral, happy, angry or sad face (600ms). During the visual-tactile conditions, participants received a tactile stimulation on their left index finger at 105ms after the visual onset (D. Pitcher et al., 2008; A. Sel et al., 2014). To control for the visual carry-over effect over the somatosensory response, half of the trials were the visual-only condition where no tactile stimulation followed the visual stimuli were presented (Alejandro Galvez-Pol, Calvo-Merino, & Forster, 2020). In 10% of the trials, participants were asked if the last face they saw was happy, sad or angry. In total 800 trials (200 trials for each emotion) were presented in four blocks with breaks in between (see Figure 5.1 for the procedure). Participants were asked to focus on the visual stimuli and answer verbally yes or no (to avoid the motor preparation artifact in the EEG) as soon as possible after the question was presented. Before the task, participants completed a short practise session with 20 trials that did not contain experimental material to ensure they understood the procedure. The visual stimuli were presented centrally on a black background using the E-prime 2.0 software (Psychology Software Tools) on a Windows 7 desktop. Lastly, the Heartbeat Counting Task was completed.

5.2.4. EEG and ECG recording

EEG and ECG was recorded from 64 Ag/AgCL active electrodes mounted equidistantly on an elastic electrode cap (M10 montage, EasyCap GmBH, Herrsching, Germany). All EEG electrodes were referenced online on the right earlobe and re-referenced offline to the average of all electrodes. Bipolar horizontal electrooculogram was recorded for eye movement tracking and artifact correction purposes with an electrode placed about 1cm lateral to the outer canthi of each eye. One electrode was placed about 2cm under the left collarbone to record the electrocardiogram (ECG) throughout the experiment. Continuous EEG was recorded using a BrainAmp amplifier (BrainProducts, amplified bandpass 0.06 – 100Hz) with 500Hz sampling rate and BrainVision Recorder while the offline EEG analysis was performed using BrainVision Analyser 2 (BrainProducts). The data were digitally low-pass filtered at 30Hz (order 2, Butterworth zero phase filters). The EEG signal was epoched into 600ms segments starting 100ms before to 600ms after the tactile onset for the visual-tactile conditions for the somatosensory evoked potentials or the visual onset for the visual only conditions for the visual evoked potentials. Segments were then baseline corrected to the first 100ms. Ocular correction was performed for eye movements (Gratton, Coles, & Donchin, 1983) and trials with amplitude artifacts exceeding ± 100μV at any electrode relative to baseline were removed from the analysis.

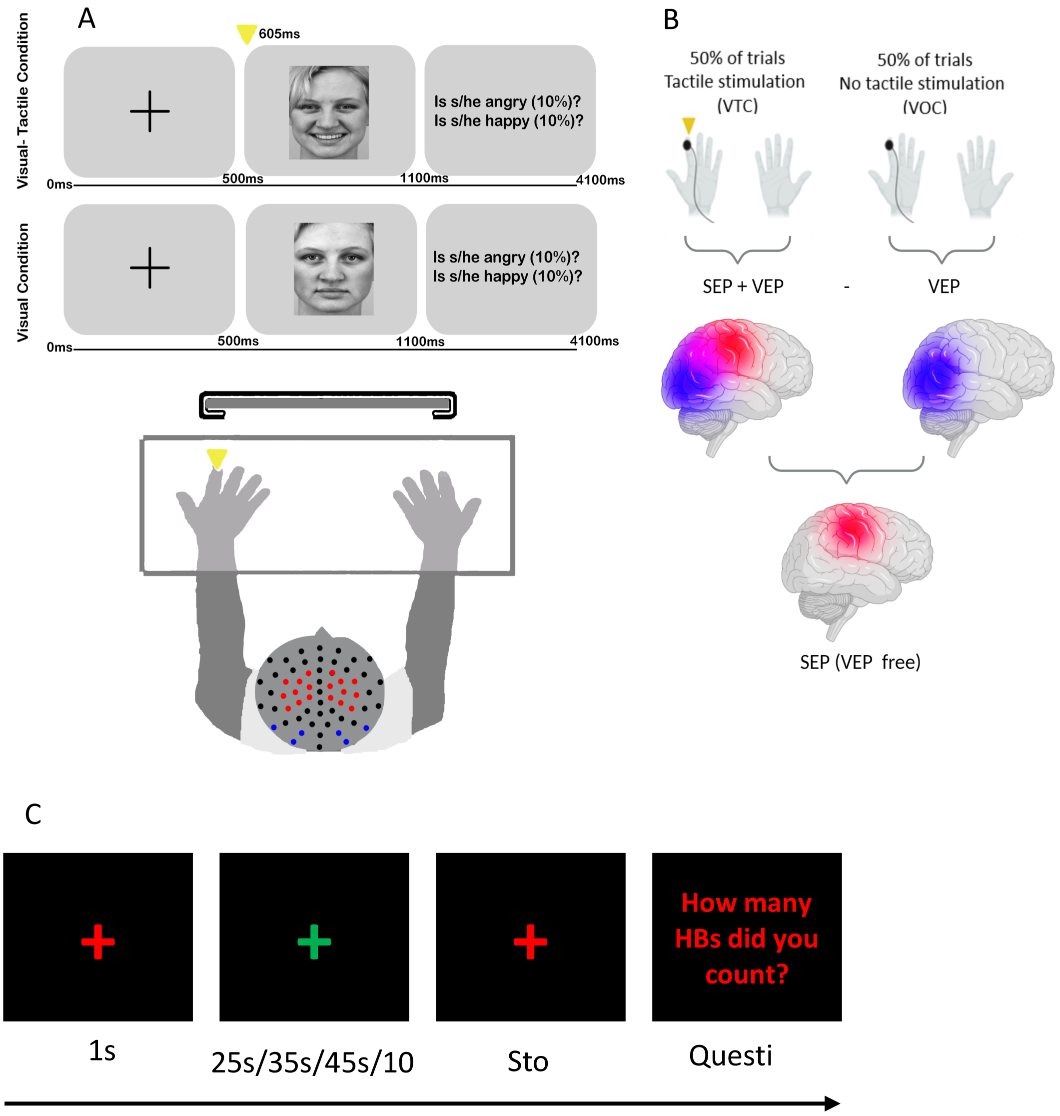

Figure 5.1 *Experimental Design*

A. Facial Emotion Judgement Task: faces were presented at 500 milliseconds from fixation cross onset and in 50% of trials tactile stimulation was delivered on the left index finger at 105 ms after the face onset (605 ms after fixation cross onset). In 10% of trials, a question appeared after 1100 ms: “Is s/he angry?” or “Is s/he happy?”. The electrodes in red were selected for analysis on Somatosensory Evoked Potentials and the electrodes in blue were selected for analysis on Visual Evoked Potentials.
B. Subtraction of Visual-Only Condition (VOC), with no tactile stimulation, from Visuo-Tactile Condition (VTC), when tactile stimulation was delivered. This method allowed us to isolate pure somatosensory evoked activity from visual carry-over effects (VEP + SEP) – (VEP) = SEP (VEP free). Figure adapted from Fanghella et al. (2021) and used with permission.
C. Heartbeat Counting Task: Participants saw a red cross. When it became green, they were asked to count their heartbeat until the cross became red again for four time intervals: 25/35/45/100 seconds. Then they were asked to reply how many heartbeats did they count and how confident they were for their answer.

5.2.5. EEG and ECG data analysis

Single-subject ERPs and averages were computed for each condition (visual-tactile, visual only) and emotion (happy, angry, sad and neutral). Firstly, to keep the somatosensory response VEP-free, the single-subject averages of the visual-only conditions were subtracted from the single-subject averages of the visual-tactile conditions. This is a validated method allowing us to examine the somatosensory processing cleared from any visually evoked activity, hence VEP- free (Arslanova et al., 2019; A. Galvez-Pol et al., 2018; Alejandro Galvez-Pol et al., 2020; A. Sel et al., 2014). To ensure a similar level of signal – to – noise ratio between the visual – tactile and visual only conditions, we ran a paired samples t – test which was not significant, t (29) = -1.23, p = .23). Two participants were excluded from the analysis due to a large difference (>45 trials) in accepted trials between the two conditions. Secondly, to isolate the pure embodied emotion effect in SEPs, the mean amplitudes of the neutral condition was subtracted from the each of the three emotion conditions (happy, angry and sad).

Previous literature (A. Sel et al., 2014) has shown modulation of the somatosensory cortex from visual facial emotion at early and mid – latency somatosensory components, namely P45, N80 and P100. Therefore, to minimise type I errors (Luck & Gaspelin, 2017), SEPs (VEP free) were pooled together only from the electrode sites localised on the right somatosensory cortex 9, 10, 23, 3, 10, 24, 4, 12 and 25 (corresponding to FC2, FC4, FC6, C2, C4, C6, CP2, CP4 and CP6 of the 10/10 system) where these ERP components have been shown (Fanghella et al., 2022; Sel et al., 2014). 3 participants were excluded from the analysis due to no clear SEP components across all emotion conditions. The resulting single-subject SEP VEP-free emotion effect averages were used to calculate grand averages for each emotion condition. Following visual inspection of the grand averages, three time windows were exported for analysis of these early and mid – latency ERP components: P45 (40 – 60ms), N80 (66 – 92ms) and P100 (94 - 124ms). To confirm statistically reliable embodiment of emotion effects (amplitudes on happy, angry, and sad minus the amplitude from neutral face trials), one sample t-tests were computed.

Lastly, Pearson's correlations were used to examine the relationships between the mean amplitude values of reliable SCx emotion indexes and alexithymia and cardiac interoception. Regression analyses were then run based on the significant correlations to further investigate the proportion of variance explained by the predictor models.

Additionally, analysis was conducted for the visual evoked potential (VEPs) on the occipital cortex from the visual only condition for each emotion following previous literature (A. Sel et al., 2014; Williams et al., 2004, 2006). The time windows exported were focused on the P120 (115 -165ms after the visual stimulus onset), the N170 (167 – 199ms) and the P200 (215-270ms) and our analysis for this condition concerned only the electrode sites 44/42, 57/55 and 58/54 (corresponding to O1/2, O9/10 and PO9/10) over the occipital cortex (see Figure 1 on experimental design for the electrode map visualisation). The time windows were determined by visual inspection of the grand average across all emotions. In a similar approach as for the SEPs, in order to examine the pure VEP emotion effect, the mean amplitudes of the neutral condition were subtracted from the each of the three emotion conditions (happy, angry and sad). To confirm statistically reliable visual emotion effects (amplitudes on happy, angry, and sad minus the amplitude from neutral face trials), one sample t-tests were computed for each of the VEP emotion expression based on mean amplitudes pooled over the electrodes of interest for each of the three VEP components. As for SEPs, Pearson's correlations were used to investigate relationships between the mean amplitude values of reliable VEP emotion indexes and alexithymia and cardiac interoception. The significant correlations were then investigated for causal relationship by running regression analysis.

For the ECG signal during the Heartbeat Counting Task, we applied the Vision Analyser 2 EKG detection macro to identify the R peaks for each counting interval. One participant was excluded from this analysis due to no R peaks detected from the algorithm.

5.3. Results

5.3.1. Behavioural performance in the EEG visual emotion recognition task

The behavioural performance was calculated from the 10% of the trials that included the emotion recognition question. Participants overall performance across emotion condition was very high at 87%. More specifically happy faces had the highest recognition rate at 96%, following by sad faces at 89%, 84% angry and 79% for neutral faces.

5.3.2. Psychometric scores

Participants showed a wide range on TAS- 20 questionnaire and scored on average 45.62 (SD = 10.03). 17 participants showed low levels of alexithymia scoring ≤51, and 13 participants high levels of alexithymia scoring ≥52 (Franz et al., 2008).

5.3.3. Performance on Heartbeat Counting Task

Participants average interoceptive accuracy on the heartbeat counting task was 0.62 (*SD* = 0.18), average confidence score was 5.7 (*SD* = 1.62) and their average interoceptive awareness score was 0.26 (*SD* = 0.56). Based on the R peaks counted by the EKG markers algorithm, the average heartbeat per minute of participants was 86.2.

5.3.4. Somatosensory emotion effect

The one sample t-tests performed on the SEP emotion effect showed a significant expression effect of anger in the N80 component, $t\ (29) = 2.07$, $p = .047$, $d = .38$) and an expression effect of happy faces in the P100 component, $t\ (29) = -2.13$, $p = .042$, $d = .39$. No statistically reliable emotion effect was found in the P45 component, and the sad emotion did not show a significant somatosensory modulation in any of the three ERP components (all $t\ (29) < .832$, $p > .412$, $d < .142$). These results showed that the pure emotion effect of anger and happiness at different time points modulated somatosensory activity with amplitudes significantly different from zero, while the emotion effect of sad emotion did not reach significance. Figure 5.2 shows the averaged SEPs (VEP free) before (Figure 5.2A) and after (Figure 5.2B) the subtraction of amplitude from neutral face trials and the corresponding topographical maps for SEP angry and happy emotion effect and N80 and P100 respectively (Figure 2D).

5.3.4.1. Alexithymia and interoception as predictors of SEP emotion modulation

Pearson correlation analyses were run between the statistically reliable SEP emotion effect and the average alexithymia score and cardiac accuracy score. Alexithymia as measured by TAS significantly correlated with the SEP effect of anger over N80, r (28) = .395, p =.031, but not with the SEP effect of happy at P100, r (28) = -.073, p =.70. Then, regression analysis was performed with the averaged amplitude of SEP emotion effect of anger as dependent variable and the averaged alexithymia score as independent variable and the model was significant, $F(1,28) = 5.18$, $p = .031$, $R^2 = .156$; *beta* = 0.023); A second regression model was calculated adding the averaged depression score in BDI as covariate and it was even stronger, $R^2 = .148$; *beta* = 0.569; t (27) = 2.63, $p = .014$. Figure 5.2C shows the correlation plot between N80 SEP anger emotion effect and average alexithymia scores.

Interoception by means of the averaged cardiac accuracy and awareness scores did not correlate significantly with the N80 SEP emotion effect of anger (accuracy: r (27) = -.147, p = .44, awareness: r (27) = -.035 p = .857), or the P100 SEP happy emotion effect (accuracy: r (27) = -.205, p = .286, awareness: r (27) = .118, p = .544). The degrees of freedom are different for the interoception correlation analyses due to one participant being excluded.

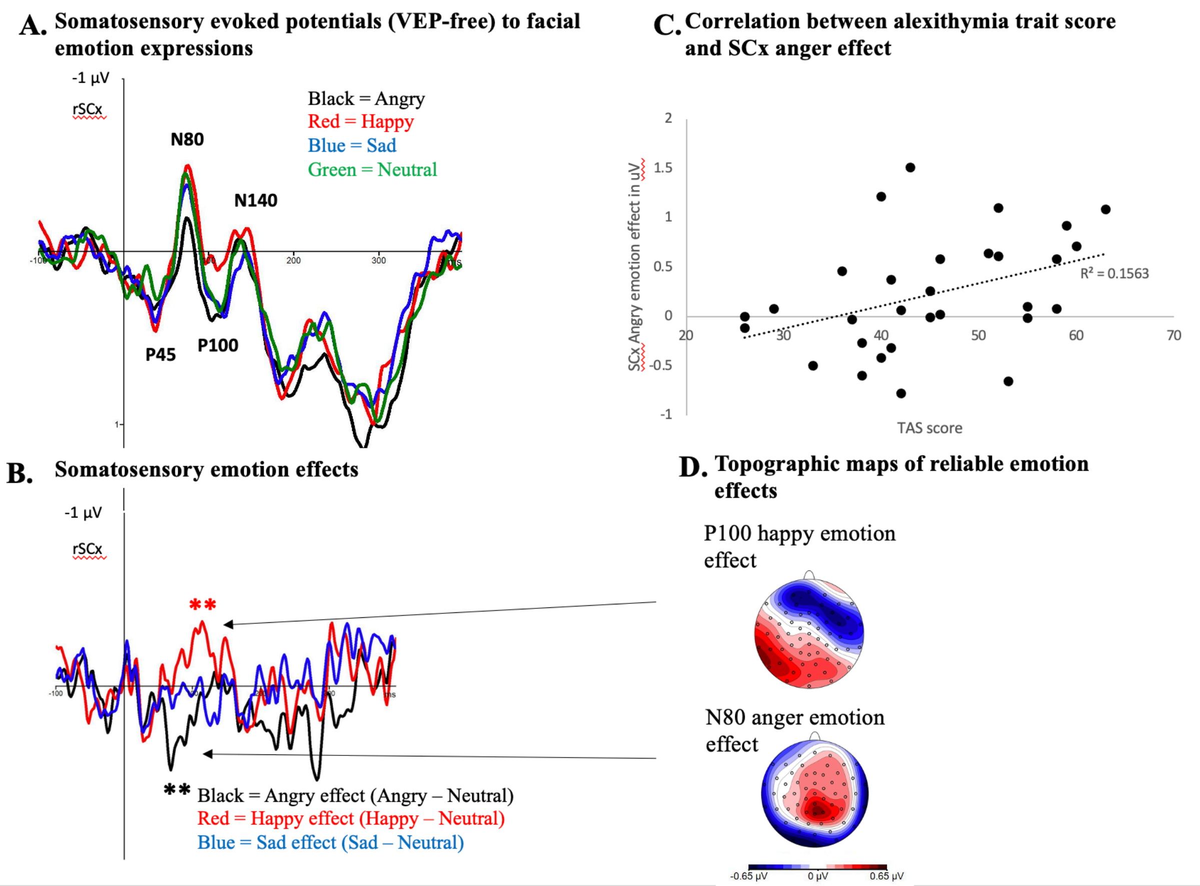

Figure 5.2 *Somatosensory evoked potentials results*

A. Somatosensory evoked potentials (VEP free) to facial emotion expressions averaged across the nine right somatosensory cortex electrodes before the subtraction of amplitude on neutral face trials.

B. SEP emotion effects to angry, happy and sad faces averaged across the nine right somatosensory cortex electrodes after the subtraction of amplitude on neutral face trials

C. Plot showing the significant correlation between the SEP emotion effect of anger at N80 with the averaged alexithymia scores.

D. Topographic maps of the statistically reliable SEP emotion effects of angry at N80 and happy faces at P100.

5.3.5. Visual emotion effects

The one sample tests performed on the visual emotion effects showed that that visual emotion effect of anger at P2 was statistically reliable, t (29) = -3.46, p = .002, d = -.63. No further statistically reliable visual emotion effects were found in P1, N170 and P2 for angry, happy or sad emotion expression (all p >.13). In Figure 3 the averaged VEPs across all the 6 occipital electrodes are shown before (Figure 5.3A) the subtraction of the amplitude during neutral expression trials and after (Figure 5.3B).

5.3.5.1. Alexithymia and interoception as predictors of VEP emotion modulation

Pearson correlation analyses were run between the statistically reliable VEP emotion effect on anger, the average alexithymia score and cardiac accuracy and awareness scores. The correlations were not statistically significant, for alexithymia r (28) = -.02, p = .93, and for interoception scores, accuracy r (27) = -.05, p = .79, awareness r = .02, p = .92).

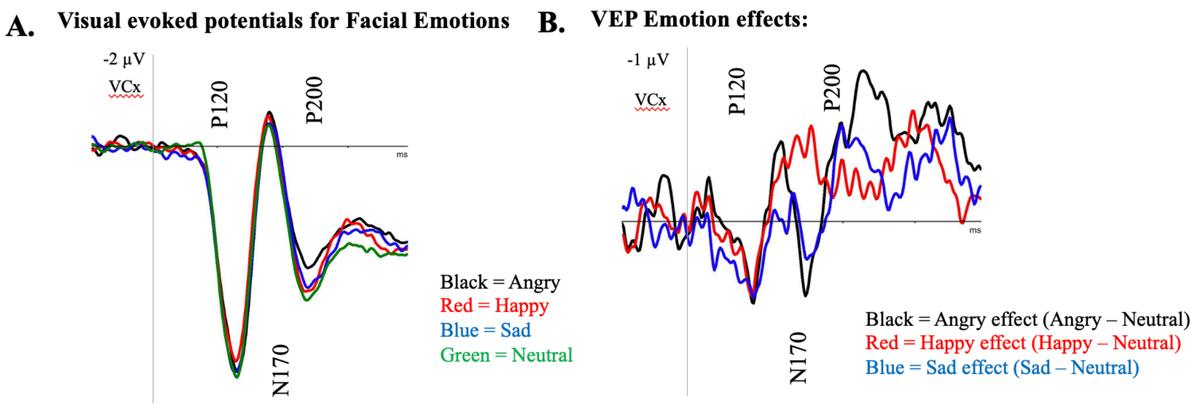

Figure 5.3 *Visual Evoked Potentials results*

A. Visual Evoked Potentials to facial emotion expressions averaged across the six occipital cortex electrodes before subtraction of amplitude from neutral face trials.
B. Visual Evoked Potentials to facial emotion expressions averaged across the six occipital cortex electrodes after subtraction of amplitude from neutral face trials.

5.4. Discussion

Considering how much emotions are rooted in our everyday life, emotion perception and expression is crucial for smooth social interactions. Following previous studies demonstrating the necessary and independent contribution of the somatosensory cortices in emotion perception in support of the embodied emotion theories (Pitcher et al., 2014; Pourtois et al., 2004; Sel et al., 2014), the current study aimed to investigate firstly whether facial emotion expressions evoke differential and statistically reliable embodied and visual emotion effects and secondly, the role of alexithymia and interoceptive abilities in emotion embodiment. Taking advantage of the good temporal resolution of EEG, we were able to record the exact time course of emotion processing from the very early stages. Our innovative methodological approach (Galvez-Pol et al., 2020; Sel et al., 2014) allowed us to isolate the non-visual somatosensory processing of emotion by applying task irrelevant touch on the left index finger and then, by subtracting the amplitude of neutral faces, to focus only on the pure emotion embodiment.

The results confirmed our first hypothesis for reliable and distinct emotion embodiment effect with a statistically significant SEP emotion effect for anger over the N80 ERP component and for happiness over the P100 ERP component. These results are in accordance to previous studies from the lab demonstrating different somatosensory activity on emotion discrimination tasks in comparison to gender discrimination task, on fearful in comparison to happy emotion expression and on anger in comparison to sad emotion effects (Fanghella et al., 2022; Sel et al., 2014; Sel, Calvo-Merino, Tsakiris, & Forster, 2020). It should be noted that discrimination between embodied emotions has been found not only on neurotypical populations, but also in participants with ASD (Fanghella et al, 2022) and in professional ballet dancers (see chapter 2). Due to the spatial limitations of EEG, future research could combine our novel ERP technique with fMRI to explore simultaneously the exact topographical path and localisation in addition to the timing of emotion embodiment. It would also be interesting to investigate whether there are differences on the embodiment of emotions on clinical populations such as patients with high levels of disembodiment experiences.

In addition to the SEP emotion effect of anger, the VEP emotion effect of anger was also statistically reliable at the P2 ERP component. This result is in accordance to previous research on early visual emotion processing (e.g. Sel et al., 2014; Williams et al., 2004, 2006).

Interestingly, the SEP emotion effect of anger at N80 (66- 92 ms after the tactile stimulus onset and 171-197ms after the visual onset) precedes the VEP emotion effect of anger at P2 (110-165 after the tactile stimulus onset and 215-270 after the visual onset) establishing the independent and necessary contribution of somatosensory cortices in emotion processing.

The results supported our second hypothesis with the average alexithymia scores significantly, though partially, predicting the SEP emotion effect of anger at N80 while controlling for depression as a confound variable. No further relationships were found between alexithymia and embodied or visual emotion processing. The positive relationship between alexithymia and SEP anger emotion effect are in accordance to previous literature showing a modulation of alexithymia on emotion processing potentially because the higher the alexithymia levels the higher the cognitive effort for emotion recognition (e.g. Ihme et al., 2014; Rosenberg et al., 2020, among others). It should be noted that this modulation was found at a very early ERP component and only on the SEP and not the VEPs. Thus, we could claim that alexithymia seems to be involved in the early perceptual processes of emotion and specifically the embodiment of facial emotion and not the visual or the later perceptual processes related to re-appraisal and more conscious processing. However, more research is needed to investigate this claim including clinical population as well, as in our study participants were from the general population and were not recruited based on their alexithymia levels.

Apart from alexithymia, we also investigated the contribution of interoceptive abilities to embodied emotion hypothesising a positive correlation. However, the results yield no statistically significant correlations between interoceptive accuracy and awareness with embodied and visual emotion effects. This result did not confirm with our hypothesis and the literature suggesting a positive relationship between interoception and emotion perception (Chick et al., 2020; Critchley & Garfinkel, 2017; Füstös et al., 2013; Grynberg & Pollatos, 2015; Herbert & Pollatos, 2012; Herbert et al., 2007; Shah et al., 2017) but adds to the existing literature questioning this relationship (e.g. Ainley, Maister, & Tsakiris, 2015). Moreover, the Heartbeat Counting Task has received a fair amount of criticism in the recent years and there has been an increasing awareness on the need for more robust interoception and control measures (Desmedt, Luminet, & Corneille, 2018; Ring, Brener, Knapp, & Mailloux, 2015; Zamariola, Maurage, Luminet, & Corneille, 2018) with a recent large meta-analysis failing to confirm links between the heartbeat counting task and theoretically- relevant mental health risk factors (Desmedt & Corneille, 2022). Lastly, in our study interoception accuracy and awareness did not correlate with alexithymia either (r = .01, p = .98) also in line with other studies providing conflicting results (Trevisan et al., 2019). Future studies could incorporate a range of psychophysiological and behavioural measures of interoception investigating their role to alexithymia and emotion perception.

5.5. Conclusion

Taken together, our study showed unique and reliable embodied emotion effects for angry and happy facial emotion expression at N80 and P100 ERP components respectively supporting and extending previous findings on the independent role of SCx in emotion processing (Fanghella et al., 2022; Pitcher et al., 2008; Sel et al., 2014; Sel et al., 2020). The visual emotion effect for angry facial emotion expression was also statistically reliable at P200 ERP component. Additionally, we were also able to show that alexithymia modulates, even partially, the embodied anger emotion effect. Therefore, the embodied neural response when observing other's emotions in SCx is unique to the observed emotion and, at least for anger, is shaped by the observer's personality trait alexithymia.

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Chapter 6: Discussion

6.1 General Discussion

The overarching objective of the current thesis was to systematically examine the role of dance expertise on emotion perception. Specifically, the aim was threefold; firstly, to investigate the role of dance as motor and artistic expertise on perceiving facial emotion on a visual and somatosensory level; secondly, to explore how dancers perceive their bodies and emotions by investigating the effect of dance expertise on interoceptive abilities and their relation to emotion processing; thirdly, to investigate the role of psychological markers on emotion perception more generally. The studies were informed by the theoretical framework of embodied cognition proposing that we perceive emotions and other social cues through somatovisceral, perceptual and motor re-experience (Keysers, Kaas, & Gazzola, 2010; Niedenthal, 2007) and overall, the research outcomes have been in support of and accordance to this theory and line of research. In my first experiment professional ballet dancers and control participants with no prior dance or music experience performed a visual facial emotion expression (neutral, afraid and happy emotion) or gender (male or female) recognition task while recording their brain activity. Given that dancers have shown differential activity in the sensorimotor areas in previous studies (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Calvo-Merino, Ehrenberg, Leung, & Haggard, 2010; Hänggi, Koeneke, Bezzola, & Jäncke, 2010; Kirsch et al., 2009) and enhanced emotion sensitivity to familiar to them emotional stimuli (Christensen, Gomila, Gaigg, Sivarajah, & Calvo-Merino, 2016; Christensen, Pollick, Lambrechts, & Gomila, 2016, Kirsch, Snagg et al. 2016), we were interested whether this enhanced sensitivity is only domain – specific to their expertise or can be generalised to everyday emotion expressions. We focused in the visual and somatosensory processing of facial emotions and to better study the SEPs, in 50% of the trials we applied a tactile stimulation irrelevant to the task (Galvez-Pol, Calvo-Merino, & Forster, 2020; Sel, Forster, & Calvo-Merino, 2014; Sel, Calvo-Merino, Tsakiris, & Forster, 2020). An expertise effect on emotion embodiment and visual perception was hypothesised and indeed our results confirmed our hypothesis.

Expertise modulated both the visual and somatosensory facial emotion processing with group effects and interactions throughout all the time windows. Concerning the SEPs (VEP free) dancers had a strong main effect of emotion at P50 and N80 and a task effect at N80 too. Significant Interactions with emotion and task were found also for P100 and N140. Controls had more localised emotion effects in N80, P100 and N140. As for the VEPs, both controls and dancers had emotion effects at N170 and P200 with afraid emotion expression mostly differentiating from neutral and happy.

This study provides the first empirical evidence that dance expertise modulates early activations over the somatosensory and visual areas while observing facial emotion expressions. Our findings align with the previous literature on dance expertise modulation on motor and emotion processing on their familiar stimuli and aid us to suggest that dance is more than motor skill expertise. Professional ballet dancers embody and process visually everyday facial emotions that are not specific to their domain. Importantly, taking into consideration other psychological traits such level of anxiety and alexithymia, we have been able to show that our findings are based on dance expertise only as no other groups differences were found, apart from the interoceptive awareness on MAIA, in line with previous studies (Christensen, Gaigg, & Calvo-Merino, 2017).

In my second study the same paradigm as in the first one was used but this time I focused on the heart - brain interactions during facial emotion processing, interoception and the role of psychological characteristics on professional dancers and controls. I focused on the heartbeat evoked potential which has only recently started to be used in the literature and is considered a neural marker of visceral activity (Park & Blanke, 2019). I was interested in how visual emotion and psychological traits interact with HEP and whether these relationships are modulated by dance expertise. EEG and ECG was collected to calculate HEP, levels of alexithymia, stress, body awareness and depression levels were measured, as well as cardiac interoceptive accuracy and awareness based on the Heartbeat Counting Task. Following the line of our previous work (Chapter 2), we expected to find a dance expertise effect on HEP and interoception task. Our results showed a task modulation on HEP but only for controls, no dance expertise or emotion modulation was found. However, HEP was strongly related to psychological traits for both groups and dance expertise did predict interoceptive abilities adding up to the strong evidence for better interoception and body awareness of the dancers. This study is the first endeavour to provide empirical evidence on heart -brain interactions in experts and a more exploratory and holistic approach was taken incorporating a wide range of measurements at a neural, psychophysiological and behavioural level. Although dance expertise did not seem to modulate HEP as we expected, we would argue that our findings still project group differences as controls showed this localised effect on HEP, similar to the SEPs on the previous study, while the effects on dancers seemed to be more generalised. Research in interoception and heart – brain interactions is in the midst of methodological and technological advancements and further research should incorporate newly developed tools in order to better understand the effect of brain – heart coupling on social cognition and the effect of dance as sensorimotor and art expertise.

With the third study, we decided to turn our perspective on the visual object recognition literature. Our paradigm was informed by the visual expertise framework which suggests that the visual perception mechanisms attributed to faces are also involved in other domain specific objects which people might have extensive visual experience with (Bukach, Gauthier, & Tarr, 2006). Dance expertise has been found to modulate motor processing, interoception, empathy and emotion processing, including everyday facial emotions. My third experiment searched whether this modulation is found at a behavioural level of vision perception, or it is more deeply rooted at the neural level. To this aim, we ran an online pilot study testing professional dancers and controls on a visual facial emotion discrimination task that tested among others the classic inversion effect (Diamond & Carey, 1986). Dancers were found to be faster in their reaction times, less accurate and less sensitive to the task (by means of d') in comparison to controls. Dance expertise was strongly related with behavioural performance, empathy and body awareness. Our results on dancers' behavioural performance were mixed and not in perfect alignment with the previous findings. However, they did support previous literature on enhanced empathy and body awareness for dancers. As this was an online pilot study, more research is needed in the future to offer a more comprehensive and conclusive account on the behavioural and perceptual mechanisms involved in the dance expertise effect on visual emotion perception.

The fourth and last study moves away from dance expertise and focuses more in depth on embodiment of emotion. Participants performed a visual emotion (neutral, sad, happy, angry) recognition task where in half of the trials they received a task irrelevant tactile stimulation (Galvez-Pol et al., 2020) and the heartbeat counting task. Their levels of alexithymia and depression were measured. We aimed to better understand firstly, how different facial emotions are embodied in the somatosensory cortices and, secondly, the influence of alexithymia and interoception in embodied emotion perception. We expected to find firstly, differential somatosensory and visual processing between emotions and secondly, a modulation on this neural processing by alexithymia and interoception. In accordance with our first hypothesis, the somatosensory processing of anger was significant at N80 and of happiness at P100. As for the VEPs, there was a significant emotion effect for anger at P2 as well. Our second hypothesis was partially confirmed with the SEP emotion effect of anger being significantly predicted by alexithymia levels. Interoception abilities did not predict emotion embodiment. With this experiment we were able to show novel evidence that observing emotions of others elicit unique and reliable embodied emotion effects, at least for anger and happiness and that these effects seem to be partially predicted by the observer's psychological traits.

The aim to understand the influence of psychological traits and states to emotion perception was incorporated not only in chapter 5, but in all studies of the current thesis. By gathering data from different populations across different studies, we have observed interesting findings for dancers and control population. For dancers, interoceptive awareness by means of MAIA average and subscale scores was found to be a strong predictor of somatosensory emotion processing (for example predicting average SEP (VEP free) amplitude on afraid and afraid emotion index at N80), of visual emotion processing (for example predicting average VEP amplitude on afraid emotion index at N170 and P200) and heartbeat evoked potentials related to emotion processing (average frontal HEP amplitude on emotion discrimination task at 200-400ms time window). Average interoceptive accuracy did predict together with MAIA the average VEP amplitude on afraid emotion index at P200. State or trait anxiety by means of STAI-S/T predicted somatosensory emotion processing (average SEP (VEP free) right amplitude on neutral at P50 and average amplitude on afraid at N80). Alexithymia by means of the TAS average and subscale scores predicted somatosensory emotion processing (average SEP VEP-free left central activity on afraid at P50) and visual emotion processing (average activity over electrode 42 at P120). For controls, interoceptive awareness by means of MAIA predicted somatosensory emotion processing (SEP VEP free average left lateral activity on afraid at N80), visual emotion processing (average activity over electrode 42 at P120 and average activity on afraid emotion index at N170) and heartbeat evoked potentials related to emotion processing (average central HEP amplitude on gender discrimination task at 200-400ms time window). State – trait anxiety was not a significant predictor of somatosensory, visual or heartbeat evoked potentials for controls. Alexithymia by means of TAS predicted somatosensory emotion processing (SEP VEP free average left activity on afraid and happy emotion index at N80). Alexithymia was also strong predictor of SEP VEP free average activity on anger at N80 in chapter 5 (participants were recruited from general population, no data on dance or other motor or artistic expertise were collected). Overall, psychological characteristics do seem to influence emotion processing in multiple ways (somatosensory, visual and heartbeat evoked potentials). Interestingly, although in our current studies dancers did not differ significantly than controls in levels of alexithymia, depression and state-trait anxiety but only interoceptive awareness, we could see differences unfolding on how psychological factors modulate emotion processing in each group. It was evident that interoceptive awareness played a key role for both groups, albeit it was more often a predictor for dancers, but alexithymia was a more common predictor in controls than in dancers and state-trait anxiety was less common in both groups. Further studies are needed in the future to provide more evidence on how and when psychological factors influence emotion processing by including in an elaborative way a variety of psychological measures both to general and to expert population. This will help us to better identify potential differences between general and expert population both in respect to psychological and personality traits and in respect to emotion processing and body awareness.

6.2 Conclusion and future directions

Overall, these studies aimed at expanding our knowledge on facial emotion perception using dance expertise. It is now evident that social perception and our ability to understand other people’s behaviour are far more complex and multifactorial than previously imagined. Our own bodies play a determining role in these processes as we seem to perceive others through ourselves: on the one hand, there have been extensive evidence for the theory of embodied cognition and the necessity of the somatosensory cortices in social perception (Keysers et al., 2010; Niedenthal & Maringer, 2009; Wood, Rychlowska, Korb, & Niedenthal, 2016). On the other hand, recently there has been a growing recognition on the significant influence of physiological signals and interoceptive afferents on social (but not limited to) cognition (Critchley & Garfinkel, 2018; Park et al., 2018; Park & Blanke, 2019). Combining these frameworks and in the context of the continuously developing predictive coding account could offer us important new insights on social perception and facial emotion perception more specifically (Feldman Barrett & Simmons, 2015; Feldman Barrett, 2017; Gentsch, Sel, Marshall, & Schütz-Bosbach, 2019; Seth, 2013).

As it has been well established in this thesis, through its complexity and versatility dance has been a great example of studying a wide range of topics in cognition and perception. Importantly, professional ballet dancers were the best suited population for our research questions because they are the only population that has motor and artistic expertise that have be found to affect their neural responses in action observation (e.g., Calvo-Merino et al., 2005), their structural neuroplasticity in sensorimotor pathways (e.g., Hänggi, Koeneke, Bezzola, & Jäncke, 2010), their affective psychophysiological responses to familiar emotional stimuli (e.g., Christensen et al., 2016) and their interoceptive, proptioceptive abilities and body awareness (e.g. Beck, Saramandi, Ferrè, & Haggard, 2020; Christensen, Gaigg, & Calvo-Merino, 2017). Their special training differentiates them from other motor only experts such as athletes or musicians that have both artistic and motor expertise but use additional equipment. The strict training of dancers also ensures that our population has similar motor and artistic background which can be harder to control for while testing people from other dance, music or sport background. Morover, part of professional dance training is to learn how to express emotions using the body and face, even in an extravagant way, to be visible enough in a theatre setting for the spectators. Taking into consideration that our aim was to investigate the effects of motor and artistic expertise on emotion perception and body awareness, the expertise of professional ballet dancers was the best model for our research questions.

Our studies are the first to our knowledge studying domain general emotional stimuli using dance expertise and the results so far have been very promising regarding the dance expertise influence. We aspire to give the floor to many new directions in the field of dance expertise and emotion perception. In the present studies facial emotion perception was tested for the first time. The next steps could focus on aiming to replicate our findings on somatosensory, visual and heartbeat evoked potentials on dancers and controls and/ or to investigate the expertise effect on full body emotion expressions but not dance related. The latter would be particularly interesting because although professional ballet dancers use their full body to dance, emotional body movements can be used from standardised stimuli libraries such as the Bodily Expressive Action Stimulus Test (de Gelder & Van den Stock, 2011) that are not dance related. One exciting dimension for future research is to explore more deeply the roots of expertise through longitudinal studies following the progression timeline of expertise (from a very young age, amateur level and amateur dance companies until professional training and working professional as dancers) and whether emotion and interoceptive sensitivity are skills that can be taught through training. This type of studies would be tremendously useful in clinical practice informing current dance therapy techniques and potentially building up new types of training targeting on improving emotion and interoceptive sensitivity for example for people with ASD and alexithymia.

Thanks to the advances of the neuroscientific methods, future studies could put in place new paradigms in order to expand our understanding on the brain connectivity involved in the dance expertise modulation on emotion perception. These methodologies would offer us valuable insights on the time course and localisation of facial emotion processing and embodiment.

Finally, one of the ideas that could not be realised due to covid restrictions but would be of a great interest is to perform further interdisciplinary studies involving art and motor experts from different backgrounds: dancers, musicians, actors and athletes and provide a holistic overview on how art and motor expertise influence body awareness and emotion perception. As Agnes De Mille (1905-1993), American dancer and choreographer, said : 't*he truest expression of a people is in its dance and its music*', there could not be a better example to study emotions than art and specifically the art of dance.

6.3 References

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