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Somatosensory processing in social cognition: from an individualistic to an interactionist approach

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In allem Chaos ist Kosmos und in aller Unordnung geheime Ordnung.

Carl Gustav Jung

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Chapter 1

Introduction

1.1 State of the art

Embodied social cognition

Embodied accounts of social cognition propose that high-order social skills are grounded in low-level somatic, motor and visceral representations of self and others' mental states (Gallese et al., 2004; A. Goldman and de Vignemont, 2009; J. M. Kilner et al., 2007a; J. Kilner and Lemon, 2013). Pioneering studies on single-cell recordings in monkeys reported "mirror" neurons in the area F5 of monkey's premotor cortex, firing both when an action was performed and when it was observed being performed by another agent (Gallese et al., 1996; Rizzolatti et al., 1996, but see Heyes, 2010). Importantly, it has been shown that somatosensory areas have mirror properties, responding also to events related to others' bodies (Keysers and Gazzola, 2009). In monkeys, shared representations of self and others' somatic experience are implemented in multimodal neurons with mirror properties in the posterior parietal and premotor cortices (Ishida et al., 2010; Sharma et al., 2018). Studies on humans provided evidence supporting the idea of a mirror-like mechanism in somatosensory areas of humans (Blakemore et al., 2005; Bolognini et al., 2011, see Keysers and Gazzola, 2009; Keysers et al., 2010 for reviews and Molenberghs et al., 2012 for a meta-analysis of brain regions with mirror properties in humans).

The somatosensory system and adjacent sensorimotor and multisensory areas are crucially involved in social cognition, such as recognising others' emotions (Adolphs et al., 2000; Pitcher et al., 2008; Pourtois et al., 2004; Rudrauf et al., 2009; Sel et al., 2014; Sel et al., 2020) or understanding and predicting their actions (Avikainen et al., 2002; Coll et al., 2017; Del Vecchio et al., 2020; Ferri et al., 2015; see Dijkerman and de Haan, 2007 for a review). Before describing recent evidence highlighting how somatosensory information contributes to social cognition, I will introduce current accounts suggesting that somatosensation is processed within the brain (de Haan and Dijkerman, 2020; Keysers et al., 2010).

Somatosensation is processed in a distributed system

Current models based on evidence from studies on primates and humans describe the cerebral areas and structures implicated in processing somatic information as a distributed cortico-subcortical-cerebellar system organized in several anatomical and functional networks, involving the primary (S1) and secondary (S2) somatosensory cortices (Eickhoff et al., 2008; Fitzgerald, 2004; Kaas et al., 1979; Ruben, 2001), insular cortex (Burton et al., 1993; Mazzola et al., 2006), primary motor cortex (M1) (Kaas, 2004), dorsal and ventral premotor cortices (Avanzini et al., 2018), supplementary motor areas (Lim et al., 1994), superior and inferior parietal lobules (Huang et al., 2012; Sakata et al., 1973; Young et al., 2004), orbitofrontal cortex (Hagen et al., 2002), the cingulate cortex (Arienzo et al., 2006) and the cerebellum (Boillat et al., 2020).

In a series of pioneering studies, Penfield and colleagues first described the somatotopic organisation of the primary somatosensory cortex and other areas implicated in processing sensorimotor information, such as the primary motor area, the secondary somatosensory area, the insular cortex and the supplementary motor area (Penfield & Boldrey, 1937; Penfield, 1950; Penfield & Faulk, 1955; Penfield & Rasmussen, 1950). A recent work from Saadon-Grosman and colleagues (Saadon-Grosman et al., 2020) expanded Penfield's early observations of the somatosensory

homunculus (Penfield & Boldrey, 1937) and described multiple somatotopic maps in distributed fronto-parietal cortical areas, responding to continuous tactile stimulation. Specifically, the authors identified cortical responses to tactile stimulation in parietal somatosensory regions, secondary somatosensory and insular-opercular areas, motor and supplementary motor cortices and high-order prefrontal areas, suggesting that different structures may be implicated in processing specific facets of somatic information (Saadon-Grosman et al., 2020). Another recent research identified double somatotopic body representations in the cerebellum, organised similarly to the motor and sensory areas of the cerebral cortex, but ipsilateral to the stimulated body part (Boillat et al., 2020).

Moreover, in a recent review, De Haan and Dijkerman identified five anatomical and functional networks implicated in somatosensation (haptic object recognition and memory, body perception, body ownership, affective processing, and action), proposing that the somatosensory system is essentially an interactive, distributed framework (de Haan & Dijkerman, 2020).

Shared representations of self and others' feelings and emotions

Vicarious responses in the somatosensory system are involved in processing others' sensations and feelings (de Vignemont, 2014; Keysers et al., 2010), and have been described in several contexts, for instance, during visual perception of touch in infants (Addabbo et al., 2020; Meltzoff et al., 2018) and adults (Blakemore et al., 2005; Lee Masson et al., 2020; Schaefer et al., 2012b; Schirmer and McGlone, 2019), or during observation of others' pain (Bufalari et al., 2007; Gallo et al., 2018; Han et al., 2009; Marcoux et al., 2013) or emotions (Adolphs et al., 2000; Adolphs et al., 1996; A. I. Goldman & Sripada, 2005).

In particular, the role of the somatosensory system in processing emotional expressions have been recently addresses through lesions (Adolphs et al., 2000), TMS (Pitcher et al., 2008; Pourtois et al., 2004) and EEG (Sel et al., 2014; Sel et al., 2020) studies (see also Bastiaansen et al., 2009). Remarkably, Pitcher and colleagues

(Pitcher et al., 2007) confirmed previous lesion studies highlighting a causal role of the right somatosensory cortex in recognising facial emotional expressions (Adolphs et al., 2000) showing that repetitive transcranial magnetic stimulation (rTMS) sequentially delivered over the right occipital face area (rOFA) (60-100 ms after visual stimuli onset) and the right somatosensory cortex (rSCx) (100-140 and 130-170 ms after visual stimuli onset) disrupted performance in emotion recognition, but not identity recognition. Another study investigating with EEG somatosensory and visual responses to facial emotional expressions (Sel et al., 2014), by dissociating somatosensory from visual evoked responses through a subtraction of visual only activity from visual and somatosensory responses (Dell’acqua et al., 2003; see Galvez-Pol, Calvo-Merino, and Forster, 2020 for an in-depth explanation of this method), showed enhanced somatosensory responses during emotion processing over and above visual carryover effects.

Importantly, it has been proposed that the somatosensory cortex and other related areas, such as the insular cortex, are involved in processing the somatic feelings associated to the experience of emotions (Critchley and Nagai, 2012; A. Damasio and Carvalho, 2013; A. R. Damasio, 1999). This idea has its roots in William James’ theory of emotions, suggesting that the conscious experience of emotional feelings has its roots in perceiving the visceral, somatic and motor patterns associated to a certain emotional state (James, 1884). For this reason, it has been proposed that the ability to perceive and understand self and others’ emotional feelings is tightly linked to interoception (i.e., the inner sense of the physiological signals of the body) (Craig, 2003; Critchley and Garfinkel, 2017; Wiens, 2005), processed in insular, somatomotor and cingular cortices (Berntson and Khalsa, 2021; Critchley et al., 2004). Moreover, it has been shown that difficulties in interoception are associated with alexithymia, a condition characterised by difficulties in by difficulties identifying and describing the bodily feelings associated with one’s own emotions (see Brewer et al., 2016 for a review). Importantly, emotion processing and interoception seem to operate differently in individuals with autism spectrum disorder (ASD) (Bird and

Cook, 2013; Shah, Catmur, et al., 2016; Silani et al., 2008; Sucksmith et al., 2013). However, the debate on whether these difficulties are associated to autism per se, or they are a byproduct of concurrent alexithymia, is still ongoing (Bird & Cook, 2013; R. Cook et al., 2013; Gaigg et al., 2016; Mul et al., 2018; Poquérousse et al., 2018; Shah, Catmur, et al., 2016; Shah, Hall, et al., 2016).

Reduced embodiment and interoception in autism spectrum disorder

Growing evidence revealing the role of somatosensory processing in social cognition has prompted the idea that the somatosensory system and adjacent motor, premotor and insular cortices might respond differently to social stimuli in people with difficulties in navigating the social world, such as autistic individuals (Masson et al., 2019; Minio-Paluello et al., 2009 see Eigsti, 2013 for a review) .

Autism Spectrum Disorder (ASD) is a neurodevelopmental condition characterized by multiple facets of difficulties in the domain of social interactions, including reduced emotional sharing (Gaigg, 2012; Kanner, 1943; Loveland, 2005) and difficulties in interpersonal coordination (Bolis et al., 2017; Curioni et al., 2017; Gallagher, 2004), possibly linked to difficulties in predicting and adjusting to others' behaviour (Balsters et al., 2017; Bolis & Schilbach, 2018; von der Lühe et al., 2016).

In particular, individuals with ASD experience difficulties in the domain of facial emotion recognition (Dawson et al., 2005; Uljarevic & Hamilton, 2013), possibly related to atypical visual processing of emotional expressions (Aoki et al., 2015; Apicella et al., 2013; Black et al., 2017; Dawson, Webb, Carver, et al., 2004; Dawson et al., 2005; Deeley et al., 2007; Martínez et al., 2019). Nevertheless, alternative accounts proposed that atypical embodied resonance of emotional expressions may underlie difficulties in emotion processing in Autism Spectrum Disorder (Dapretto et al., 2006). More broadly, it has been shown that reduced embodied resonance (Gallese & Sinigaglia, 2018) of others' somatic states might underlie some of the difficulties in social cognition exhibited by individuals with ASD (Iacoboni and Dapretto, 2006; Minio-Paluello et al., 2009; Oberman et al., 2007; Oberman et al.,

2008, but see A. F. d. C. Hamilton, 2013).

In addition, individuals with autism show difficulties in interoception (Petzschner et al., 2021) and often struggle with recognising their own and other people's emotions (Silani et al., 2008. Remarkably, a study by Garfinkel and colleagues (Garfinkel et al., 2016) showed that individuals with autism have reduced interoceptive accuracy, (i.e., the objective measure of people's ability to detect their inner feelings), quantified through the heartbeat detection task (i.e., a test quantifying participants' ability to count their heartbeats in specific time intervals, focusing on their inner feelings (Schandry, 1981)). Moreover, results highlighted that individuals with ASD had excessive confidence in their subjective perception of bodily sensations, measured through self-report questionnaires, such as the Porges Body Perception Questionnaire (Porges, 1993). Interestingly, the discrepancy between objective (interoceptive accuracy) and subjective (interoceptive sensitivity) measures of interoception correlated with deficits in emotion processing and anxiety symptoms.

Importantly, it has been proposed that difficulties in processing the somatic patterns associated to different kinds of affective information characterising Autism Spectrum Disorder may arise as a consequence of atypical engagement in early relationships with the caregivers (Elsabbagh & Johnson, 2016; R. P. Hobson & Hobson, 1993).

Social interactions shape bodily representations

It has been suggested that the neural circuits underlying our capacity to process social information develop in an interactive, experience-dependant manner during infancy (Johnson, 2001, 2003, 2011). According to Meltzoff (Meltzoff, 2007), early interactions with the caregiver are essential for the creation of somatic maps, which form the basis for acknowledging the equivalence between self and others. Similarly, other authors argued that engaging with the social world during early stages of development is essential for the emergence of interpersonal representations grounded in shared bodily maps, which are the foundation of social cognition (Fotopoulou & Tsakiris, 2017; Gallagher, 2004; R. P. Hobson, 2008; Marshall & Meltzoff, 2015).

It has been proposed that the atypical developmental trajectory of these emerging processes, primarily grounded in early reduced engagement with the social world, contributes to the social difficulties experienced by individuals with Autism Spectrum Disorder (ASD) (Chevallier et al., 2012). A decreased engagement in social interactions with their caregivers may originate from autistic toddlers' decreased innate orientation towards the social environment (Dawson et al., 1998; Dawson, Toth, et al., 2004). According to this framework, reduced social interactions during early infancy might have cascade effects on atypical development of the social brain, thus causing difficulties in processing social information in adults with autism. This interpretation emphasises the role of experience-dependent dynamics in triggering atypical processing of social information in ASD, rather than innate differences in how socio-cognitive mechanisms operate, as proposed by others accounts (Baron-Cohen, 2000).

Importantly, investigating how social interactions can shape bodily representations, and how this may have implications for high-order social cognition, is relevant not only to understand the dynamics of typical and atypical neurodevelopment, but also for expanding our understanding of the mechanisms underlying interpersonal interactions in neurotypical adults.

Shared representations of the body and the peripersonal space

In the past decade, it has been argued that a shift from an individualistic towards an interactionist approach is necessary to elucidate the neural underpinnings of social cognition in an ecological context (De Jaegher et al., 2010; Gallotti & Frith, 2013; Hari et al., 2015; Hari & Kujala, 2009; Redcay & Schilbach, 2019; Schilbach et al., 2013). Interactive paradigms, focusing on dyads, rather than single individuals, innovatively contributed to elucidate the neurocognitive mechanisms underlying interpersonal coordination and mutual understanding in ecological contexts (Dumas et al., 2010; Era et al., 2018; Moreau et al., 2020; Novembre et al., 2014; Sacheli, Candidi, Era, et al., 2015).

Several brain areas and networks supporting joint action, such as those involved in visuo-motor integration (Era, Aglioti, Mancusi, et al., 2020; Sacheli et al., 2012) (Sacheli et al., 2012; Era et al., 2020) or error monitoring (Moreau, Candidi, Era, Tieri, & Aglioti, 2018; Moreau et al., 2020), have been revealed through interactive paradigms. However, the role of bodily representations in interpersonal interactions are still poorly investigated.

Recently, behavioural evidence of plastic changes of bodily representations during motor interactions has been provided (Soliman et al., 2015). It has been suggested that interacting with a partner triggers the formation of a joint body schema, which supports mutual coordination during motor interactions. Specifically, the authors suggested that, during motor interactions, we 'incorporate' the partner's limb in our body schema to form a shared representations of our own movements and sensations and those of our partner, to achieve interpersonal coordination. A similar proposal has also been raised by Pezzulo and colleagues (Pezzulo et al., 2013), who argued that, during motor interactions, the mechanisms for sensorimotor transformation and multisensory integration learn to incorporate information relative to the co-actor, exploiting mechanisms similar to those inducing tools' incorporation after their use. Interestingly, individuals with autism seem to experience difficulties in interpersonal coordination (Curioni et al., 2017), and reduced malleability of body and PPS representations (Noel, Cascio, et al., 2017; Noel, Paredes, et al., 2020). However, the neural dynamics underlying the creation of a shared framework to process self and others' bodily and spatial representations in typical and atypical development have not been investigated yet.

Predictive coding accounts of actions and interactions

The somatosensory system is recruited during action monitoring (Avikainen et al., 2002; Coll et al., 2017; Ferri et al., 2015) and also during observation of events occurring in self and others' peripersonal space (PPS), Schaefer et al., 2012a, defined as the space immediately surrounding the body, which is a 'multisensory interface'

between the body and the environment Serino, 2019. For instance, an fMRI study showed that not only touch received on the body, but also in the space immediately surrounding the body, activated the primary somatosensory cortex (Brodmann Area 2) both in a first and third person perspective (Schaefer et al., 2012a).

Interestingly, several computational models has been proposed with the aim of describing how low-level, sensorimotor responses may contribute to high-order processing of others' intentions, mental states, and goals (Giese and Rizzolatti, 2015), thus linking somatosensory processing to high-order social skills. An influential model proposed by Kilner and colleagues (J. M. Kilner et al., 2007a, 2007b) explains the relationship between corporeal and cognitive aspects of other agents' understanding within the predictive coding account (K. Friston, 2003, 2005; Rao & Ballard, 1999), a unified model of neural and cognitive functioning based on Bayesian inference (K. Friston, 2003). Within this framework, it is proposed that, when we observe someone performing an action, the information is processed hierarchically in the brain by low-level sensory level and high-level cognitive areas, which are interconnected via forward and backward connections (K. Friston, 2005). Through recurrent iterations within this hierarchical architecture, the most likely cause of the observed actions can be inferred by minimizing the prediction error at each level of the cortical hierarchy (J. M. Kilner et al., 2007b).

Encompassing action observation, predictive coding accounts have also been proposed to explain vicarious somatosensory processing of others' body representations (Ishida et al., 2015), occurring in somatosensory and insular cortices and parieto-premotor networks (Brozzoli et al., 2013; Thomas et al., 2006), linking somatosensation to high-order social skills. Indeed, it has been extensively shown that vicarious somatosensory processing of others' somatic states has important implications for social cognition (see Keysers et al., 2010) for a review). Importantly, predictive coding may elucidate not only the dynamics underlying other agents' understanding during passive observation, but also during active interactions with a partner (K. Friston and Frith, 2015). Consistent with this background, the purpose of my thesis

is to provide theoretical and empirical work to elucidate the role of the somatosensory system in processing social information during passive observation of others' emotions and in the context of on-line interpersonal interactions, in typically developing individuals and in individuals with autism.

1.2 Aims and structure of the thesis

Somatosensory processing of emotions in autism

In the first part of my PhD, I investigated through traditional 'individualistic' approaches the role of the somatosensory system in representing others' emotional expressions in typically developing individuals and ASD.

It is known that the somatosensory system is involved in processing the corporeal aspects of emotional information (Adolphs et al., 2000; Pitcher et al., 2008; Sel et al., 2014; Sel et al., 2020), contributing to embodiment of the observed expression (Niedenthal, 2007; Niedenthal et al., 2005). However, reduced somatosensory processing of emotional expressions in ASD have not been investigated yet. In the first experiment, described in Chapter 2, I employed a novel methodology based on probing the state of activity of the somatosensory cortex during visual perception of emotional expressions by delivering task-irrelevant tactile taps to evoke Somatosensory Evoked Potentials (SEP) concomitant to visual stimuli (Galvez-Pol, Calvo-Merino, & Forster, 2020; Sel et al., 2014). This technique allows to dissociate somatosensory activity from visual carryover effects by subtracting visual activity from concurrent visual and somatosensory responses, following previous studies employing subtractive methods to isolate cortical sources of ERPs (Dell'acqua et al., 2003). Specifically, I tested if adults with a diagnosis of ASD show reduced modulations of somatosensory activity during an emotion discrimination task and a control gender task, compared to Typically Developing (TD) individuals. In addition, I explored the relationship between levels of somatosensory emotional embodiment, associated to an increase of SEP amplitudes during perception of emotional expres-

sions, and personality traits (autism, alexithymia, and interoceptive awareness). The objective of the second empirical study, described in Chapter 3, was to explore the associations between interoceptive accuracy, emotional embodiment, and personality traits (autism, alexithymia, and interoceptive awareness). Interoception is the ‘inner sense’ of the physiological states of the body (Pace-Schott et al., 2019). Indeed, it has been suggested that interoception is implemented in neural circuits also underlying emotional experience (i.e., insula, somatosensory and cingulate cortices (Berntson & Khalsa, 2021; Critchley & Harrison, 2013; Critchley et al., 2004)) and can modulate the quality of affective experience (Critchley & Garfinkel, 2017; Garfinkel et al., 2015). Moreover, individuals with autism often experience difficulties both in the domain of emotions and interoception (Garfinkel et al., 2016; Shah, Catmur, et al., 2016). In this study, two matched groups of TD and ASD, who previously participated in experiment 1, performed a heartbeat counting task (Christensen et al., 2017; Garfinkel et al., 2016; Schandry, 1981), a tactile counting task, and a control time counting task, to measure their interoceptive and exteroceptive (tactile) accuracy. Specifically, I explored associations between the levels of somatosensory embodiment of emotional expressions, measured with EEG, personality traits, and interoceptive accuracy.

Shared somatosensory representations in social interactions

In the second part of this thesis, I move from an individualistic towards an interactionist approach to social cognition (Gallotti & Frith, 2013; Hari et al., 2015; Schilbach et al., 2013). Part of this work is dedicated to develop a novel theoretical framework, which highlights the centrality of bodily and spatial shared representations during joint action.

In Chapter 4, I propose that interpersonal interactions are grounded in shared bodily representations, which are characterized by plastic reorganization of the body schema and the peripersonal space. Specifically, I hypothesise that predictive multisensory processing of the partner’s action is embedded in a joint self-other corporeal and

spatial framework, where the somatosensory (i.e. proprioception, touch) and spatial features of the two interactive bodies are represented in a ‘we mode’ (Gallotti & Frith, 2013). Moreover, I argue that interpersonal alignment of bodily and spatial maps are functional to predictions and mutual adaptation of behaviour between partners, and I outline how this mechanisms may operate differently in individuals with autism spectrum disorder.

The project also aimed at testing this hypothesis experimentally. Therefore, during my PhD, I developed an interactive paradigm inspired from a recent behavioural study (Soliman et al., 2015) to investigate with EEG the neural basis of the ‘entangled’ body schema arising as a consequence of joint action (Soliman et al., 2015). The task involves cutting a candle with a rope, either in a joint or in a solo condition, and then engaging in an interpersonal visuo-tactile integration task. This experimental paradigm, and the expected results, are described in Chapter 5. Unfortunately, due to the Covid-19 pandemic, it was not possible to run the experiment. Hopefully, in the next months, the social distancing circumstances will improve, and we will manage to start with the data collection.

Chapter 2

Somatosensory evoked potentials reveal reduced embodiment of emotional expressions in autism

2.1 Introduction

Autism Spectrum Disorder (ASD) is a neurodevelopmental disorder characterised by differences in processing social and sensory information and by repetitive patterns of interests and behaviours (Association, 2013). Within social perception, autistic individuals often demonstrate difficulties in facial emotion recognition (Harms et al., 2010; Loth et al., 2018; Uljarevic and Hamilton, 2013 but see R. Cook et al., 2013), which have often been associated to reduce sensitivity to emotional expressions in visual cortices (Apicella et al., 2013; Black et al., 2017; Dawson et al., 2005; Deeley et al., 2007; Martínez et al., 2019).

Studies in Typically Developing (TD) individuals suggest that beyond the visual analysis of faces, perceiving emotional expressions triggers embodied resonance

(Gallese & Sinigaglia, 2018) in sensorimotor regions, which implies re-enacting the visceral, somatic proprioceptive and motor patterns associated with the observed expressions (A. I. Goldman & Sripada, 2005; Heberlein & Atkinson, 2009; Niedenthal, 2007). Research using TMS (Pitcher et al., 2008; Pourtois et al., 2004) and lesion methods (Adolphs et al., 2000; Adolphs et al., 1996) has shown the causal role of the right Somatosensory Cortex (rSCx) in facial emotion recognition. Importantly, EEG studies directly measuring SCx activity combining Visual and Somatosensory Evoked Potentials (V/SEP), have shown SCx engagement in facial emotion recognition over and above any visual carry-over activity (Sel et al., 2014; Sel et al., 2020) proving neural evidence of embodiment of emotional expressions beyond the visual analysis of emotions.

These embodied simulative mechanisms operate differently in ASD. FMRI studies comparing autistic and TD individuals have shown reduced embodied resonance of vicarious affective touch in the SCx (Masson et al., 2019), and decreased activity in the Premotor Cortex, the Amygdala and the Inferior Frontal Gyrus during perception of dynamic bodily emotional expressions (Grèzes et al., 2009). In another TMS study, ASD participants showed significantly reduced modulations of Motor Evoked Potentials (MEP) during observation of painful stimuli delivered to someone's hand (Minio-Paluello et al., 2009). Together with studies suggesting reduced mirror activity in autistic individuals during observation and imitation of actions (Oberman et al., 2005; Oberman et al., 2008) and emotional expressions (Dapretto et al., 2006; Greimel et al., 2010), the evidence suggests that some of the differences in social-emotional cognition that characterise Autism Spectrum Disorder are related to reduced simulation of the observed actions or feelings. However, the specific processes involved remain the topic of debate, partly because of methodological challenges in dissociating the multiple neural underpinnings of the perception and understanding of other's emotional expressions.

This study aims to investigate whether the differential mechanisms of emotion processing in ASD are associated with reduced somatosensory activations, over and

above differences in visual responses. To this aim, we recorded simultaneous visual and somatosensory evoked potentials by means of electroencephalography (EEG) in two groups of autistic individuals and matched TD controls during a visual emotion discrimination task and a control task, where participants judged the gender of the same facial stimuli utilized in the emotion task. Importantly, we directly measured somatosensory activity by evoking task-irrelevant SEP (Auksztulewicz et al., 2012) during the visual tasks. Based on previous research, we used a subtractive method to isolate somatosensory responses from visual carry-over effects (Arslanova et al., 2019; Dell’acqua et al., 2003; Galvez-Pol et al., 2018; Galvez-Pol, Forster, et al., 2020; Sel et al., 2014; Sel et al., 2020), and we directly probed the dynamics of somatosensory activity during discrimination of emotional expressions. Moreover, we explored how differences in embodiment of emotional expressions relate to autistic traits, and to additional measures related to conditions which are often in co-morbidity with ASD, such as alexithymia (R. Cook et al., 2013) or reduced interoception (Garfinkel et al., 2016). We predicted to observe stronger modulations of SEP amplitudes (free from visual processing) during emotion discrimination, compared to the control task, in TD compared to ASD, as an index of increased recruitment of the somatosensory cortex during emotion processing, which would reflect stronger embodiment of emotional expressions in TD compared to autistic individuals. Moreover, we tested if distinct patterns of somatosensory responses were associated to different emotions in TD and ASD individuals.

2.2 Materials and methods

Participants. Twenty-two adult participants with a diagnosis of Autism Spectrum Disorder (ASD) and Twenty-two Typically Developing (TD) adults matched for IQ, age and gender took part in the experiment. Datasets from two participants (1 ASD, 1 TD) were not included in the final dataset because markers were accidentally not recorded during data collection. We excluded two additional ASD participants

	TD	ASD	Results	Cohen's d
<i>Age</i>	40.84 \pm 12.25	40.47 \pm 8.87	t(36)=.11, p=.92	-
<i>VIQ</i>	113.58 \pm 17.80	108.56 \pm 15.38	t(35)=.92, p=.37	-
<i>PIQ</i>	117.42 \pm 13.98	111.17 \pm 14.75	t(35)=1.32, p=.19	-
<i>SRS-2</i>	49.29 \pm 5.91	69.12 \pm 11.37	t(32)=-6.38, p=.000***	2.19
<i>AQ</i>	17.61 \pm 8.79	34.89 \pm 7.76	t(34)=-6.25, p=.000***	2.08
<i>TAS-20</i>	40.42 \pm 8.76	54.33 \pm 14.18	t(34)=-6.25, p=.001**	1.18
<i>MAIA-2</i>	3.15 \pm .68	2.66 \pm .81	t(36)=-3.437, p=.048*	.66

Table 2.1. Demographics and questionnaires scores for Typically Developing (TD) and Autism Spectrum Disorder (ASD) participants. Age (M \pm SD): mean age of participants for each group. VIQ (M \pm SD): Verbal Intelligence Quotient. PIQ (M \pm SD) Performance Intelligence Quotient. SRS-2 (M \pm SD): Social Responsiveness Scale, Second Edition; AQ (M \pm SD): Autism Quotient; TAS-20 (M \pm SD): Twenty-Item Toronto Alexithymia scale; MAIA-2 (M \pm SD): Multidimensional Assessment of Interoceptive Awareness, Version 2.

(M: Mean; SD: Standard Deviation. *p<.05; **p<.01; ***p<.001).

because of excessive artefacts in the EEG data (drift due to sweat and artefacts caused by muscular tension) and two TD participants because they scored above cut off in Social Responsiveness Scale (SRS-2) and Autism Quotient (AQ) respectively. The final sample was thus composed by 19 ASD (17 right handed, 1 female, mean age 40.47 \pm 8.865) and 19 TD participants (19 right handed, 1 female, mean age 40.84 \pm 12.249). All participants in the ASD group had a formal diagnosis of autism spectrum disorder from qualified professional clinicians based on the DSM criteria. To control for IQ we tested all our participants with a short version of the Weschler Adult Intelligence Scale (WAIS), and obtained a Verbal IQ (VIQ) and Performance IQ (PIQ) for each participant. Moreover, participants completed the adult self-report form of the Social Responsiveness Scale (SRS-2, Constantino, 2002), the Autism Spectrum Quotient (AQ; Baron-Cohen et al., 2001a), the Toronto Alexithymia Scale (TAS-20; Taylor et al., 2003) and the Multidimensional Assessment for Interoceptive Awareness (MAIA-2; Mehling et al., 2018). Unfortunately, SRS-2 scores from four participants and AQ scores from two participants are missing. For a summary of tests and questionnaires scores, see Table 2.1.

		SRS-2	AQ	TAS-20	MAIA-2
<i>SRS-2</i>	<i>r</i>	1	.877,	.412,	-.590,
	<i>p</i>		.000***	.015*	.000***
	<i>n</i>	34	32	34	34
<i>AQ</i>	<i>r</i>	.877	1	.587	.542
	<i>p</i>	.000***		.000***	.001**
	<i>n</i>	32	36	36	36
<i>TAS-20</i>	<i>r</i>	.412	.587	1	-0.214
	<i>p</i>	.015*	.000***		.196
	<i>n</i>	34	36	38	38
<i>MAIA-2</i>	<i>r</i>	-.590	-.542	-.214	1
	<i>p</i>	.000***	.001**	.196	
	<i>n</i>	34	36	38	38

Table 2.2. Correlations between questionnaires scores in all participants. SRS-2: Social Responsiveness Scale, Second Edition; AQ: Autism Quotient; TAS-20: Twenty-Item Toronto Alexithymia scale; MAIA-2: Multidimensional Assessment of Interoceptive Awareness, Version 2.
(*r*: Pearson's correlation coefficient; **p*<.05; ***p*<.01; ****p*<.001).

Stimuli. We used a set of pictures depicting neutral, fearful and happy emotions used in a previous study (Sel et al., 2014), originally selected from the Karolinska Directed Emotional Faces set (Lundqvist et al., 1998). The grayscale faces were enclosed in a rectangular frame (140 x 157 inches), excluding most of the hair and non-facial contours.

Task. Participants sat in an electrically shielded chamber (Faraday's cage) in front of a monitor at a distance of 80 cm. Visual stimuli were presented centrally on a black background using E-Prime software (Psychology Software Tools). Trials started with a fixation cross (500 ms), followed by the presentation of a face image (neutral, fearful or happy, either male or female) for 600 ms. The experiment consisted of 1200 randomised trials, presented in two separate blocks of 600 trials, which included 200 neutral, 200 fearful and 200 happy faces (half male and half female), presented

		SRS-2	AQ	TAS-20	MAIA-2
<i>SRS-2</i>	<i>r</i>	1	.798	-.176	-.579
	<i>p</i>		.000***	.500	.015*
	<i>n</i>	17	16	17	17
<i>AQ</i>	<i>r</i>	.798	1	0.009	-.626
	<i>p</i>	.000**		0.971	.005**
	<i>n</i>	16	18	18	18
<i>TAS-20</i>	<i>r</i>	-.176	.009	1	-.024
	<i>p</i>	.500	.971		.923
	<i>n</i>	17	18	19	19
<i>MAIA-2</i>	<i>r</i>	-.579	-.626	-.024	1
	<i>p</i>	.015*	.005**	.923	
	<i>n</i>	17	18	19	19

Table 2.3. Correlations between questionnaires scores in the ASD group. SRS-2: Social Responsiveness Scale, Second Edition; AQ: Autism Quotient; TAS-20: Twenty-Item Toronto Alexithymia scale; MAIA-2: Multidimensional Assessment of Interoceptive Awareness, Version 2.
(*r*: Pearson's correlation coefficient; **p*<.05; ***p*<.01; ****p*<.001).

in random order. In the emotion task (block 1), participants were instructed to attend to the emotional expression of the faces, while in the gender task (block 2) they needed to attend to the gender of the faces. The order of presentation of the two blocks was counterbalanced across participants. To ensure participants were attending to the stimuli, in 20% of emotion block trials, participants were asked whether the face stimulus was fearful (Is s/he fearful?) or happy (Is s/he happy?), or whether it depicted a female (Is s/he female?) or male (Is s/he male?) during the gender block trials. When a question was presented, participants had to respond vocally (yes/no) as soon as possible. Responses were recorded with a digital recorder and manually inserted by the experimenter, who was able to hear the participant from outside the Faraday's cage through an intercom. Before starting each block, participants completed a practice session with 12 trials (4 neutral, 4 happy, 4 fearful, half male/female).

To evoke SEP during the task, in 50% of trials (Visual-Tactile Condition; VTC), participants received task-irrelevant tactile taps on their left index finger 105 ms after face onset (Sel et al., 2014). In the Visual-Only Condition (VOC, 50% of

trials), the same visual facial stimuli were presented without any concurrent tactile stimulation (see Figure 2.1 for an illustration of a trial). VTC and VOC were equally distributed in each block across the stimulus types (emotion, gender). Tactile taps were delivered using two 12 V solenoids driving a metal rod with a blunt conical tip that contacted with participants' skin when a current passed through the solenoids. Participants were instructed to ignore the tactile stimuli. To mask sounds made by the tactile stimulators, we provided white noise through one loudspeaker placed 90 cm away from the participants' head and 25 cm to the left side of the participants' midline (65 dB, measured from the participants' head location with respect to the speakers).

After completing the experimental task, every participant completed a brief rating task in which they rated the previously observed expressions from 0 (extremely happy) through 50 (neutral) to 100 (extremely fearful) using a Visual Analogue Scale (VAS). On separate trials they also rated gender from 0 (extremely female) to 100 (extremely male).

EEG recording and data pre-processing. We recorded EEG from a 64 electrodes cap (M10 montage; EasyCap). All electrodes were on-line referenced to the right earlobe and off-line re-referenced to the average of all channels. Vertical and bipolar horizontal electrooculogram and heartbeats were also recorded. Continuous EEG was recorded using a BrainAmp amplifier (BrainProducts; 500 Hz sampling rate).

Analysis of the EEG data were performed using BrainVision Analyzer software (BrainProducts). The data was digitally low-pass-filtered at 30 Hz and high-pass-filtered at 0.1 Hz. Ocular correction was performed (Gratton et al., 1983) and the EEG signal was epoched into 700 ms segments, starting 100 ms before visual (for VEP analysis) and tactile (for SEP analysis) stimulus onsets. We performed baseline correction using the first 100 ms before stimulus onsets. Artefact rejection was computed eliminating epochs with amplitudes exceeding 100 μ V. Single-subject

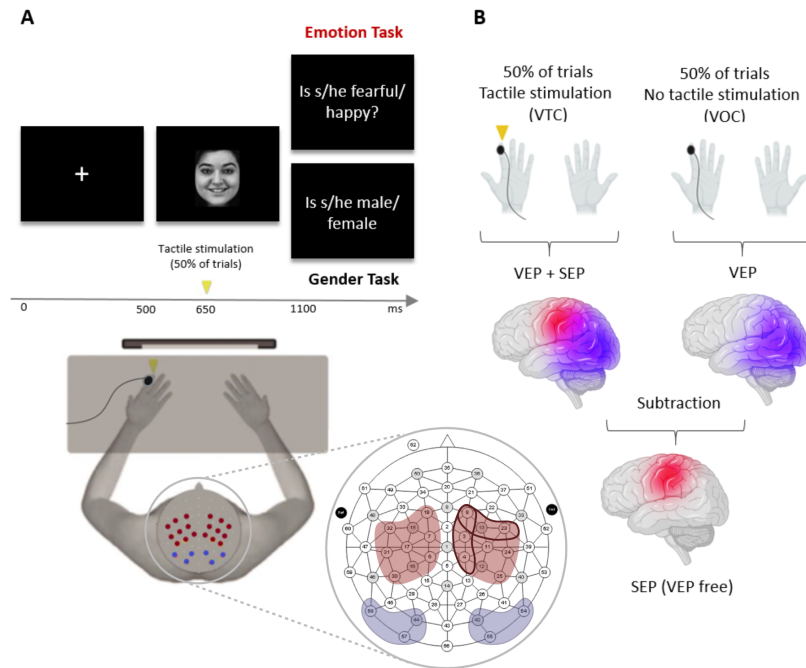


Figure 2.1. Experimental Design. **A. Task:** faces were presented at 500 ms from fixation cross onset and in 50% of trials tactile stimulation was delivered on the left finger after 605 ms. In 10% of trials, a question appeared after 1100 ms (Emotion Task: «Is s/he fearful?» Or «Is s/he happy?»); Gender Task: «Is s/he male?» Or «Is s/he female?»). **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. The topographical map highlights the electrodes placed over occipital areas (blue) and fronto-parietal areas (red) which were considered during the statistical analysis. In SEP analysis, vertical (Site) and horizontal (Region) clusters of fronto-parietal electrodes were included as factors (e.g., dorsal site (vertical) and frontal region (horizontal) in the right hemisphere are circled by red lines).

grand-averaged ERPs for each condition (VOC and VTC), task (emotion, gender) and emotion (neutral, fearful, happy) were computed. For SEP, after pre-processing, single-subject averages of VOC trials were subtracted from single-subject averages of VTC trials, in order to isolate somatosensory evoked responses from visual carryover effects (Galvez-Pol, Calvo-Merino, & Forster, 2020). This subtractive method is described in Figure 2.1.

Statistical analysis

Accuracy of catch-trials: we extracted the mean accuracy for each participant,

expressed in a value in a range between 0 (0% of correct answers) and 1 (100% correct answers). Exclusion criteria was set to accuracy below 50%. We computed a linear mixed model with group (TD, ASD) and Task (Emotion, Gender) as fixed effects and a random intercept for each participant. Before running the test, assumptions of normality of residuals, homoscedasticity, linearity, and collinearity were tested. We chose to run this analysis because it is more robust to violations of assumptions of normality compared to a mixed repeated-measures ANOVA (Schielzeth et al., 2020) and therefore is often used to analyse datasets unsuitable for classic linear models (Casals et al., 2014). Significant effects are reported in type II anova via Satterthwaite's degrees of freedom (Winter, 2013).

VAS ratings: we computed two mixed repeated-measured ANOVAs for emotion and gender ratings separately. For emotion ratings, factors were group (TD, ASD) as between factor and emotion (Neutral, Fearful, Happy) as within factor. For gender ratings, factors were group (TD, ASD) as between factor and gender (Female, Male) as within factor.

Amplitude of Somatosensory Evoked Potentials (SEP): we computed mean amplitudes of SEP in four consecutive time windows of 30 ms length starting from 40 ms up to 160 ms after tactile stimulus onset (occurring after 105 ms of visual stimulus onset). These time windows were centred on the P50 (40-70 ms), N80 (70-100 ms), P100 (100-130 ms) and N140 (130-160 ms) peaks (Bufalari et al., 2007; Eimer et al., 2005; Schubert et al., 2008). Analyses were restricted to 18 electrodes located over sensorimotor areas (corresponding to Fc1/2, Fc3/4, FC5/6, C1/2, C3/4, C5/6, Cp1/2, Cp3/4, CP5/6, of the 10/20 system) (Sel et al., 2014). We selected the time windows from the grand average of all conditions and participants (Luck, 2014). SEP mean amplitudes were analysed through mixed repeated-measures ANOVAs in SPSS. Factors of the ANOVAs were: between-group factor: group (TD, ASD); within-group factors: task (Emotion, Gender), emotion (Neutral, Fearful, Happy), hemisphere

(Left, Right), site (Dorsal, Dorsolateral, Lateral), region (Frontal, Central, Posterior). We applied Greenhouse-Geisser (G-G) correction when appropriate (Keselman & Rogan, 1980) and post-hoc tests were corrected for multiple comparisons (Bonferroni).

Amplitudes of Visual Evoked Potentials (VEP): we used single-subject averages of VEP on the data corresponding to the visual-only condition and free from any contamination from SEP. Analyses were computed on 30 ms time windows, centred on the visual components P1 (120-150 ms), N2 (170-200 ms) and P3 (240-270 ms). ERPs were computed at occipital sites (corresponding to O1/2, O9/10, PO9/10 electrodes of the 10/20 system) (Conty et al., 2012). We selected the time windows from the grand average of all conditions and participants (Luck, 2014). VEP mean amplitudes were analysed through mixed repeated-measures ANOVAs in SPSS, including the factors group (TD, ASD), task (Emotion, Gender) hemisphere (Left, Right), electrode (corresponding to O1/2, O9/10, PO9/10 electrodes of the 10/20 system) and emotion (Neutral, Fearful, Happy). We applied Greenhouse-Geisser (G-G) correction for non-sphericity when appropriate (Keselman & Rogan, 1980) and post-hoc tests were corrected for multiple comparisons (Bonferroni).

Correlations and linear regressions between personality traits and SEP and VEP amplitudes: we computed correlations in SPSS with the aim to explore linear relationships between autism, alexithymia and interoception, and somatosensory and visual responses to emotional faces. Specifically, we tested if individual scores to questionnaires measuring autistic traits (Social Responsiveness Scale (SRS-2) and Autism Quotient (AQ)), alexithymia (Toronto Alexithymia Scale (TAS- 20)) and interoceptive awareness (Multidimensional Assessment of Interoceptive Awareness (MAIA-2)) significantly correlated with SEP and VEP amplitude during emotion and gender tasks. Because we were interested in further exploring the relationship between somatosensory processing of emotions and autistic traits, as well as conditions often associated to ASD, such as alexithymia and poor interoception, we ran this analysis

only on the SEP and VEP components and clusters of electrodes where robust statistical differences between ASD and TD were found. We first ran correlations on the whole sample (e.g., Masson et al., 2019), following recent literature describing autistic traits as a continuum of clinical and subclinical features (Bölte et al., 2011; Caldwell-Harris & Jordan, 2014) and suggesting that the Social Responsiveness Scale (SRS) and Autism Quotient (AQ) can effectively detect the strength of autistic traits both in clinical and non-clinical populations (Constantino & Todd, 2003, 2005; Ruzich et al., 2015). However, because correlational analysis between autistic traits and behaviour or neural responses on clinical populations only are also common in the literature (e.g., Dapretto et al., 2006; Minio-Paluello et al., 2009), we ran the same analysis on the ASD group only. Following the same rationale, we ran multiple linear regressions, on the whole sample and then the on ASD group only, selecting SEP amplitudes as dependent variable and adding the scores to the four questionnaires (SRS-2, AQ, TAS-20 and MAIA-2) as predictors.

Source Reconstruction. We performed source reconstruction of SEP with SPM 12 (Ashburner et al., 2013) using a standard MRI template with the COH – Smooth Priors method (K. Friston et al., 2008), a source reconstruction method assuming locally coherent and distributed sources (Bonaiuto et al., 2018) equivalent to LORETA (R. D. Pascual-Marqui, 2002; R. Pascual-Marqui et al., 1994). We performed source analysis on segments of 150 ms, 200 ms and 300 ms length, starting from tactile onset. The segments were grand-averaged across subjects (Fogelson et al., 2014; Ranlund et al., 2016) for each group and task. We specified two conditions for each group (Emotion Task and Gender Task) which were source reconstructed separately. After inverting the three models, we selected the model with the highest log-evidence or marginal likelihood (K. Friston et al., 2008). We extracted the MNI coordinates of the voxel showing the strongest level of activity for each SEP peak of interest (P50: 50 ms; N80: 90 ms; P100: 110 ms; N140: 145 ms) and converted in Brodmann areas with the Atlas Bioimage Suite Web (Papademetris et al., 2006).

2.3 Results

Behavioural results

Behavioural Performance on Face Emotion and Gender catch trials during EEG recording: the linear mixed model revealed a main effect of group $F(1,36)=5.396$, $p=.026$, explained by an overall decreased accuracy for the ASD ($M=.886$, $SE=.019$) compared to the TD group ($M=.950$ $SE=.019$). No further significant effects were found (main effect of task, $p=.392$; group by task interaction, $p=.185$), suggesting the behavioural differences between the two groups were not task dependent (i.e., ASD were overall less accurate, compared to TD).

Subjective ratings of Emotion and Gender intensity: results highlighted a main effect of emotion $F(1.10, 41.77) = 764.861$, $\eta^2 = .955$, $p=.000$). Post-hoc pairwise comparisons showed a significant difference between mean ratings of neutral, fearful and happy expressions (all $ps < .001$). The two groups did not show statistically significant differences in how they rated the emotional expressions, as highlighted by non-significant Group*Emotion interaction ($p=.372$) and non-significant main effect of group ($p=.519$).

Moreover, we found a significant main effect of gender ($F(1,36) = 915.433$, $\eta^2 = .962$, $p=.000$), and post-hoc pairwise comparison showed a difference between ratings to female and male ($p=.000$). The Task*Group interaction was also significant ($F(1,36) = 5.703$, $\eta^2 = .137$, $p=.022$). We computed two independent-sample t-tests for female and male faces. Results suggested a significant difference in how TD and ASD rated male faces ($t(26.074)=-2.600$, $p=.015$, Cohen's $d = .603$; TD: $M=.95.76$, $SD = 5.51$; ASD: $M = 88.23$, $SD = 11.34$), but not female faces ($p=.064$).

EEG results

Amplitudes of Somatosensory Evoked Potentials (SEP, VEP free): somatosensory processing was isolated from concomitant visual activity by subtracting the visual only condition from the visuo-tactile condition (i.e., visual-tactile minus visual-only

trials). We only report significant interactions and main effects including the factors of interest (i.e., group, task, emotion).

Early sensitivity of SEP to emotional expressions (P50, N80)

P50: Results from the mixed repeated-measures ANOVA highlighted a significant interaction between Group*Site*Region ($F(3.19, 114.94) = 3.026$; $\eta^2 = 0.078$; $p = .030$). Because we were interested in exploring group differences in somatosensory responses, we followed-up the Group*Site*Region interaction by performing three mixed repeated-measures ANOVAs for each Region (Frontal, Central, Parietal) and Site (Dorsal, Dorsolateral, Lateral), but no significant interactions involving the factor group emerged from these analyses (all $ps > .05$).

Moreover, the analysis yielded a significant Task*Emotion*Hemisphere*Site*Region interaction ($F(5.82, 209.36) = 2.353$; $\eta^2 = 0.06$; $p = .033$). To explore general differences in emotion processing during emotion and gender task, we computed two mixed repeated-measures ANOVAs for the emotion and gender tasks, collapsing the non-significant between-factor Group. In the emotion task, results highlighted a significant Emotion*Site*Region interaction ($F(8, 896) = 3.026$; $\eta^2 = 0.076$; $p = .003$), showing different emotional patterns in the SCx during emotion but not gender processing (Sel et al., 2014). To follow-up the Emotion*Site interaction, we performed repeated-measures ANOVAs with the factors Emotion and Site for each dorsal, dorsolateral and lateral sites including the factors emotion (Neutral, Fearful, Happy) and Region (Frontal, Central, Posterior). This revealed a significant Emotion*Region interaction in the dorsal sites ($F(4, 148) = 2.710$; $\eta^2 = 0.068$; $p = .032$). However, further follow-up, performed computing three repeated-measures ANOVA with the factor Emotion (Neutral, Fearful, Happy) for each region did not highlight further significant effects of emotion (all $ps > .05$).

N80: The analysis highlighted significant Group*Emotion*Hemisphere*Site*Region ($F(5.26, 189.71) = 2.236$; $\eta^2 = 0.058$; $p = .049$) and Emotion*Site ($F(4, 140) = 5.005$; $\eta^2 = 0.122$; $p = .000$) interactions. Because in a previous study on typically develop-

ing individuals significant interactions involving the factor emotion were found in this time window, (Sel et al., 2014), we computed two repeated-measures ANOVAs for the ASD and TD groups separately including the factors emotion, hemisphere, site and region. In the TD group, we found a significant cross-over interaction involving the factor emotion (Emotion*Site ($F(2.657, 47.828) = 4.123$; $p\eta^2 = 0.186$; $p = .014$)), but further follow-up running three separate ANOVAs for dorsal, dorsolateral and lateral sites failed to highlight a significant main effect of emotion (Dorsal Site: $p=.133$; Dorsolateral Site: $p=.796$; Lateral Site: $p=.135$). Interestingly, no significant interactions involving the factor emotion were found in the ASD group (all $ps >.05$).

Follow-up analysis on the Emotion*Site interaction highlighted a main effect of emotion in the dorsal site ($F(2,74)=3.809$; $p\eta^2 =0.093$; $p=.026$) and post-hoc pairwise comparisons on the main effect of emotion highlighted enhanced responses for fearful compared to happy expressions ($p=.013$, all other $ps >.05$), showing general differences in SCx responses to fearful and happy expressions.

Task dependent group differences in somatosensory responses (mid latencies P100, N140)

P100: The main ANOVA highlighted the following significant interactions involving the between-factor group: Group*Task ($F(1, 36) = 4.608$; $p\eta^2 =0.113$; $p=.039$), Group*Task*Region ($F(1.43, 51.83) =4.252$; $p\eta^2 =0.105$, $p =.03$), Group*Task*Site ($F(1.38, 49.83) = 4.958$; $p\eta^2 =0.121$, $p =.02$). Conversely, main effects of group ($p=.066$) and task ($p=.647$) were not significant.

To understand the Group*Task*Region interaction three separate Group*Task ANOVAs were carried out for frontal, central and posterior regions. We found a significant Group*Task interaction specific for the frontal region ($F(1,36) =6.729$, $p\eta^2=.157$, $p=.014$). No other group or task effects were significant in the other regions (all $ps>.05$). We computed an independent sample t-test which highlighted a significantly enhanced positivity in the TD compared to ASD Group in the emotion

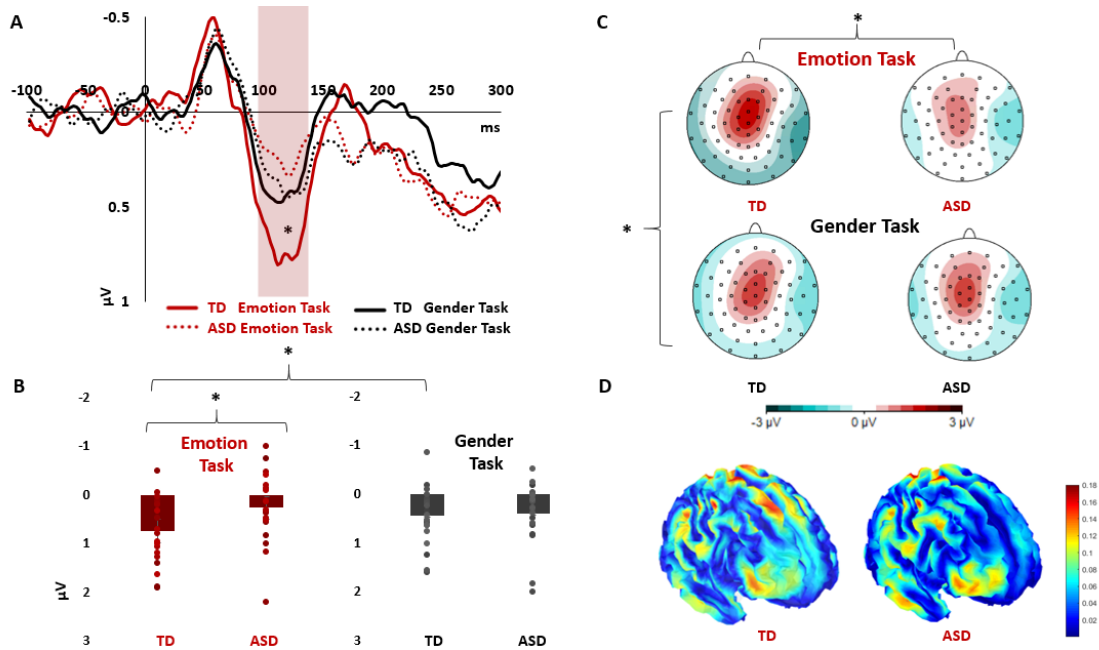


Figure 2.2. SEP P100 results. **A.** SEP P100 group differences in the frontal region (averaged activity of 6 electrodes, corresponding to electrodes Fc 1/2/3/4/5/6 of the 10/20 system), TD show enhanced positivity for emotion task compared to gender task ($p=.047$) and to Emotion Task in ASD ($p=.044$) **B.** Boxplots with individual data points of the P100 SEP amplitudes in the frontal region, in emotion and gender tasks, for the TD and ASD groups. **C.** Topographical maps of SEP P100 electrophysiological activity, highlighting increased positivity in fronto-parietal regions during emotion processing in TD but not ASD. **D.** Source reconstruction of the P100 SEP (VEP free) component highlights active voxels in Brodmann area 6 and primary and secondary somatosensory cortices. (* $p<.05$).

task ($t(36) = 2.054$, $p = .047$, Cohen's $D = .666$) but not in the gender task ($p = .823$) in the frontal region. Moreover, a paired sample T-test revealed a significantly increased positive response in the emotion task compared to the gender task in the TD ($t(18) = 2.166$, $p = .044$, Cohen's $D = .497$) but not the ASD Group ($p = .171$) in the frontal region. No effects involving group and task were found in the central and posterior regions (all $ps > .05$). These results are depicted in Figure 2.2.

To follow up the Group*Task*Site interaction three mixed repeated-measures ANOVAs for the dorsal, dorsolateral and lateral sites were carried out. This analysis revealed a significant Group*Task interaction specific for the dorsal site ($F(1,36) = 6.939$, $p\eta^2 = .162$, $p = .012$), where significant group differences, highlighted by in-

dependent sample t-tests, were found in the emotion task ($t(36) = 2.311$, $p = .027$, Cohen's $D = .750$) but not in Gender Task ($p = .777$). Task comparisons carried out by paired samples t-tests were not significant either in TD and ASD and no significant effects involving task and/or group were found in other sites (all $ps > .05$). We also computed two separate mixed repeated-measures ANOVAs for emotion and gender task, which revealed a main effect of group in the emotion task ($F(36, 1) = 6.51$, $p\eta^2 = .15$, $p = .015$). No main effect of group ($p = .395$) or interactions involving the factor group (all $ps > .05$) were found in the gender task. The main ANOVA also yielded an interaction with the within-factors task and emotion (Task*Emotion*Hemisphere*Site*Region ($F(5.52, 198.90) = 2.68$, $p\eta^2 = .069$, $p = .018$).

To explore general differences in emotion processing during emotion and gender task, we followed up this interaction computing two repeated-measures ANOVAs for the emotion and gender tasks, collapsing the between-factor group. Results revealed a significant Emotion*Site*Region interaction specific for the emotion task ($F(4.692, 173.588) = 2.600$, $p\eta^2 = .066$, $p = .030$), but further follow-up breaking by region and by site did not highlight any significant emotion effect (all $ps > .05$). No interactions or main effects involving the factor emotion were found in the gender task (all $ps > .05$).

N140: The analysis revealed a significant Group*Task*Emotion*Hemisphere interaction ($F(2, 72) = 4.06$; $p\eta^2 = 0.10$, $p = .021$). To follow-up this interaction, we computed two repeated measures ANOVAs for the TD and ASD groups including the factors task, emotion and hemisphere. In the TD, results revealed a significant Task*Emotion*Hemisphere interaction ($F(2, 36) = 6.596$; $p\eta^2 = 0.268$, $p = .004$), explained by a crossover interaction between task and emotion in the right hemisphere ($F(2, 36) = 3.302$; $p\eta^2 = 0.155$, $p = .048$). Further follow up on the Task*Emotion interaction, performed computing two separate repeated measures ANOVAs for emotion and gender tasks, did not show statistically significant differences between the three emotions (all $ps > .05$). In the ASD group, the repeated-measures ANOVA involving

the factors task, emotion and hemisphere didn't yield any significant interaction of main effect involving task or emotion (all p s $>.05$).

The main ANOVA also yielded a significant Task*Emotion*Hemisphere*Site*Region interaction ($F(8,288)=2.09$; $p\eta^2=0.05$, $p=.037$). To follow it up, we ran two repeated-measures ANOVAs for emotion and gender tasks separately. Results showed no significant interactions involving the factor emotion in the emotion task (all p s $>.05$). A significant Emotion*Hemisphere*Site*Region interaction ($F(8,296)=2.167$; $p\eta^2=0.055$, $p=.030$) was found in the gender task, however further follow-up analysis breaking the interaction by hemisphere, site and region did not show significant interactions involving the factor emotion (all p s $>.05$).

Linear relationships between personality traits and SEP amplitudes: We focused on the P100 component, where robust group differences were found. First, we ran correlations between participants' scores to Social Responsiveness Scale (SRS-2), Autism Quotient (AQ), Toronto Alexithymia Scale (TAS-20) and Multidimensional Assessment of Interoceptive Awareness (MAIA-2) and mean SEP amplitudes in all the clusters of electrodes where significant between-group differences were found (frontal SEP amplitudes (mean activity of 6 electrodes over frontal sensorimotor regions), mean SEP amplitudes (mean activity of 18 electrodes over sensorimotor regions), dorsal SEP amplitudes (mean activity of 6 electrodes over sensorimotor areas close to the midline)). Results of the correlations are reported in Tables 2.4 and 2.5.

Interestingly, autistic traits measured both by the Social Responsiveness Scale (SRS – 2) and the Autism Quotient (AQ) were highly correlated with SEP amplitudes evoked during the emotion task in all clusters of electrodes (all p s $<.006$). Conversely, correlation between SRS-2 and AQ scores and somatosensory activity evoked during

	SRS-2			AQ		
	r	p	n	r	p	n
<i>emotion frontal</i>	-.551	0.001**	34	-.518	0.001**	36
<i>emotion dorsal</i>	-.470	0.005**	34	-.479	0.003**	36
<i>emotion overall</i>	-.539	0.001**	34	-.528	0.001**	36
<i>gender frontal</i>	-0.288	0.098	34	-0.314	0.063	36
<i>gender dorsal</i>	-0.183	0.299	34	-0.241	0.157	36
<i>gender overall</i>	-0.301	0.084	34	-.361*	0.03*	36

Table 2.4. Correlations between autistic traits and P100 amplitudes in all participants. SRS-2: Social Responsiveness Scale; AQ: Autism Quotient; emotion/gender frontal: averaged somatosensory activity from the 6 electrodes placed over the frontal sensorimotor regions; emotion/gender dorsal: averaged somatosensory activity from the 6 electrodes placed over the dorsal sites, close to the midline; emotion/gender overall: averaged somatosensory activity from the 18 electrodes placed over fronto-parietal regions. (* $p < .05$; ** $p < .01$).

	TAS-20			MAIA-2		
	r	p	n	r	p	n
<i>emotion frontal</i>	-0.276	0.094	38	.417	0.009**	38
<i>emotion dorsal</i>	-0.27	0.102	38	.402	0.012*	38
<i>emotion overall</i>	-0.257	0.12	38	.403	0.012*	38
<i>gender frontal</i>	-0.253	0.126	38	0.152	0.361	38
<i>gender dorsal</i>	-0.241	0.146	38	0.095	0.571	38
<i>gender overall</i>	-.327*	0.045	38	0.153	0.36	38

Table 2.5. Correlations between alexithymia and interoception and P100 amplitudes in all participants. TAS-20: Toronto Alexithymia Scale; MAIA-2: Multidimensional Assessment of Interoceptive Awareness; emotion/gender frontal: averaged somatosensory activity from the 6 electrodes placed over the frontal sensorimotor regions; emotion/gender dorsal: averaged somatosensory activity from the 6 electrodes placed over the dorsal sites, close to the midline; emotion/gender overall: averaged somatosensory activity from the 18 electrodes placed over fronto-parietal regions. (* $p < .05$; ** $p < .01$).

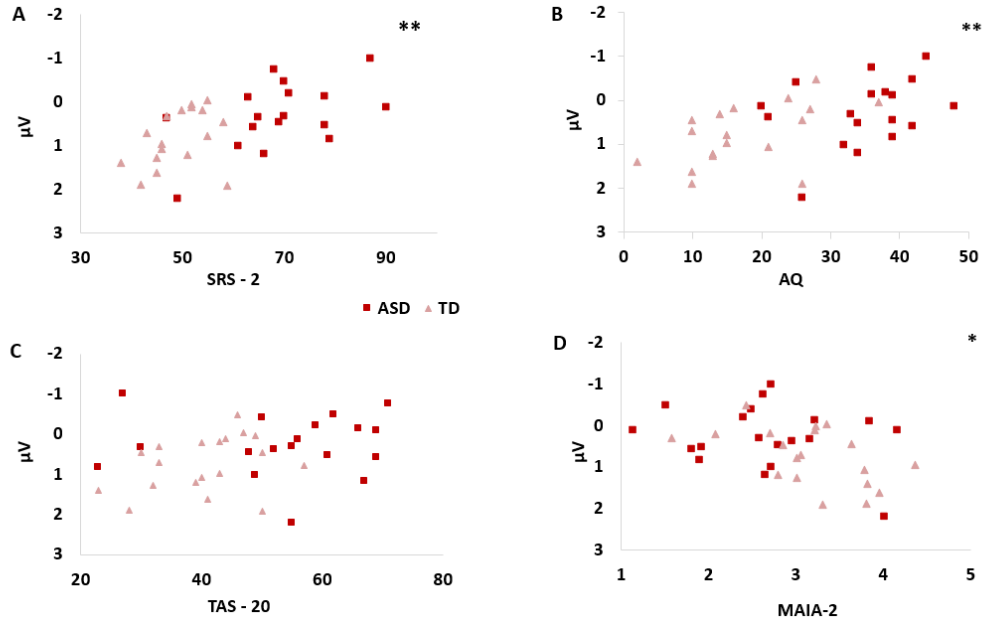


Figure 2.3. Correlations between personality traits and frontal SEP P100 amplitudes in emotion task. A. Social Responsiveness Scale (SRS-2), $**p=.001$; B. Autism Quotient (AQ), $**p=.001$; C. Toronto Alexithymia Scale (TAS-20), $p=.094$. D. Multidimensional Scale of Interoceptive Awareness (MAIA-2), $*p=.009$

the gender task was not significant in almost every electrode cluster. These results highlight a strong and persistent relationship between patterns of somatosensory responses evoked during the emotion discrimination and autistic traits. Interoceptive awareness was also significantly correlated with the activity evoked during the emotion task (all $ps < .015$) but not gender task (all $ps > .35$) in all cluster of electrodes. Alexithymia did not show a significant relationship with SEP amplitudes. For a graphical representation of these results, see Figures 2.3 and 2.4.

To further explore the relationship between clinical features of autism and somatosensory processing of emotional expressions, we ran the same analysis including the ASD group only. Results of the correlations confirmed the patterns observed in the whole sample of participants, showing significant correlations between individual scores to SRS-2 and AQ and SEP amplitudes specific for the emotion task (see Tables 2.6 and 2.7 for full results). Furthermore, the analysis confirmed that alexithymia was not significantly correlated with SEP amplitudes in any cluster and

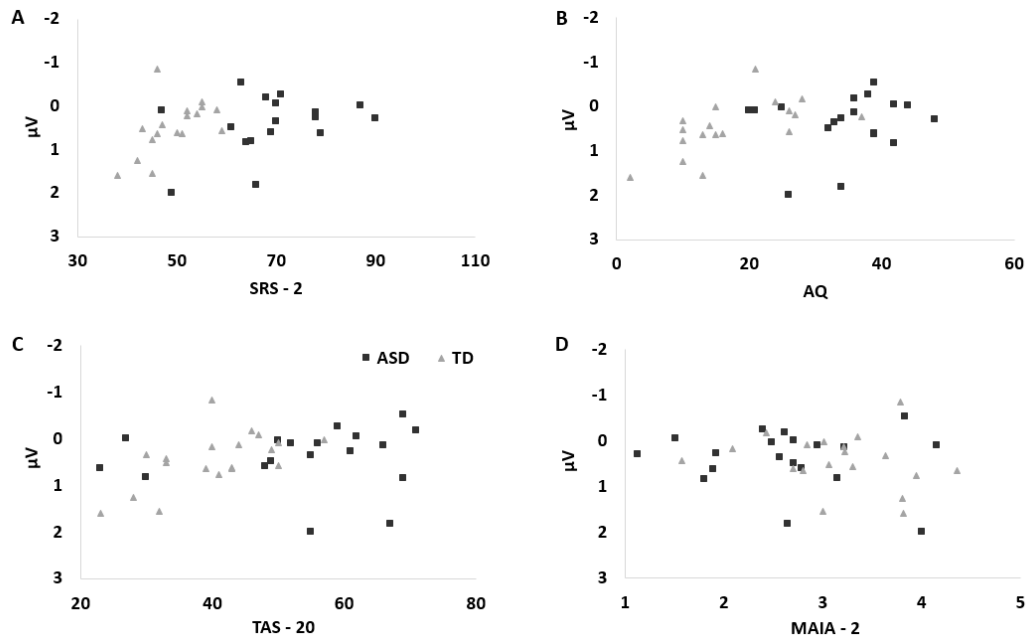


Figure 2.4. Correlations between personality traits and frontal SEP P100 amplitudes in gender task. **A.** SRS-2, $p=.098$; **B.** AQ, $p=.063$; **C.** TAS-20, $p=.152$; **D.** MAIA-2: $p=.361$)

task (all $ps > .25$). Interestingly, in the ASD group, interoceptive awareness was not significantly correlated with SEP amplitudes (all $ps > .07$).

In addition, we wanted to test if the individual scores to the personality questionnaires could significantly predict SEP amplitudes in the frontal region, where compelling patterns of group differences were observed. We ran multiple linear regressions using the backward method with SRS-2, AQ, TAS-20 and MAIA-2 as predictors of SEP P100 amplitudes evoked during the emotion and gender tasks. In the emotion task, the analysis yielded a highly significant model ($F(1,30) = 15.369$, $p=.000$, $R^2 = .339$; SEP amplitude decreased $0.036 \mu V$ for each $+1$ score). The model had AQ as a single predictor. This is explained by the highly significant correlations between questionnaires' scores (see Table 2.2), which generated collinearity between

	SRS-2			AQ		
	r	p	n	r	p	n
<i>emotion frontal</i>	-.517	0.034*	17	-0.313	0.207	18
<i>emotion dorsal</i>	-.513	0.035*	17	-0.394	0.105	18
<i>emotion overall</i>	-.622	0.008**	17	-.522	0.026*	18
<i>gender frontal</i>	-0.334	0.191	17	-0.155	0.539	18
<i>gender dorsal</i>	-0.24	0.353	17	-0.238	0.343	18
<i>gender overall</i>	-0.32	0.211	17	-0.263	0.292	18

Table 2.6. Correlations between autistic traits and P100 amplitudes in the ASD group. SRS-2: Social Responsiveness Scale; AQ: Autism Quotient; emotion/gender frontal: averaged somatosensory activity from the 6 electrodes placed over the frontal sensorimotor regions; emotion/gender dorsal: averaged somatosensory activity from the 6 electrodes placed over the dorsal sites, close to the midline; emotion/gender overall: averaged somatosensory activity from the 18 electrodes placed over fronto-parietal regions.
(*p<.05; **p<.01).

	TAS-20			MAIA-2		
	r	p	n	r	p	n
<i>emotion frontal</i>	-0.025	0.919	19	0.214	0.38	19
<i>emotion dorsal</i>	-0.206	0.397	19	0.381	0.107	19
<i>emotion overall</i>	-0.121	0.622	19	0.417	0.076	19
<i>gender frontal</i>	-0.091	0.71	19	0.113	0.644	19
<i>gender dorsal</i>	-0.268	0.268	19	0.297	0.216	19
<i>gender overall</i>	-0.241	0.32	19	0.294	0.222	19

Table 2.7. Correlations between alexithymia and interoception and P100 amplitudes in the ASD group. TAS-20: Toronto Alexithymia Scale; MAIA-2: Multi-dimensional Assessment of Interoceptive Awareness; emotion/gender frontal: averaged somatosensory activity from the 6 electrodes placed over the frontal sensorimotor regions; emotion/gender dorsal: averaged somatosensory activity from the 6 electrodes placed over the dorsal sites, close to the midline; emotion/gender overall: averaged somatosensory activity from the 18 electrodes placed over fronto-parietal regions.
(*p<.05; **p<.01).

predictors. In the gender task, the same model was not significant ($p=.051$).

We ran the same multiple linear regression on the ASD group, and the pattern observed in the whole sample was confirmed. We found a significant model for the emotion task $F(1,14) = 5.210$, $p=.039$, $R^2=.271$; SEP amplitude decreased $0.062 \mu V$ for each +1 score) with AQ as a single predictor. Again, this is explained by the highly significant correlation between questionnaires' scores in ASD (see Table 2.3). We ran another linear regression with the same predictors for the gender task, but also in this case the model was not significant ($p=.220$).

Source reconstruction. The best model for the TD group was the source reconstruction on 300 ms segment (log-evidence -1715.8, difference with the second best model = 311.9). The winning model for the ASD group was the source reconstruction on 200 ms (log evidence -1443.2, difference 60.2). Both models showed strong evidence compared to the others because difference in log evidence was > 50 (Ranlund et al., 2016).

P50: The main source of activity at 50 ms was localised in the right primary somatosensory cortex (S1) in both tasks for TD (coordinates: 46, -29, 54 for both tasks) and ASD (coordinates: emotion task: 42, -35, 58; gender task: 46, -31, 57).

N80: The primary source at 90 ms was located in right Brodmann Area (BA) 6 (coordinates: 12, -18, 71) for both groups and tasks. Active voxels were localised also in the right primary (S1) and secondary (S2) somatosensory cortices and in left BA6.

P100: For the TD group, the main source at 110 ms was localised in BA 6 (coordinates: 12, -18, 71 in both tasks) For the ASD group, the main source was localised in BA 6 (emotion task: 12, -18, 71; gender task: 14, -20, 69). Other active voxels were localised in the primary (S1) and secondary (S2) somatosensory cortices, right M1, left BA 6 and bilateral prefrontal areas (BA 46) for both tasks and groups. Brain maps from P100 source reconstruction of evoked activity during the emotion task can be visualised in Figure 2.2 D.

N140: In the TD group, for the emotion task the main source at 145 ms was localised in the right BA 6 (coordinates: 12, -18, 71), and for the gender task in BA 20 (coordinates 52, -14, -30). In the ASD group, for the emotion task the main source was localised in BA 6 (coordinates 60, -1, 22) and for the gender task in BA 20 (coordinates 52, -14, -30). Other active voxels were localised in the primary (S1) and secondary (S2) somatosensory cortices and the bilateral prefrontal cortex (BA 46) for both tasks and groups.

Amplitudes of Visual Evoked Potentials (VEP)

P120: results from the mixed repeated measures ANOVA showed the following significant interactions: Group*Emotion*Hemisphere*Electrode ($F(4,144)=3.613$; $p\eta^2=0.091$; $p=.008$), Task*Emotion*Hemisphere ($F(2,72) = 6.955$; $p\eta^2=0.161$; $p=.002$), Task*Emotion*Electrode ($F(2.90,104.25)=3.651$; $p\eta^2=0.092$, $p=.016$). We computed two separate repeated-measures ANOVAs for TD and ASD groups collapsing the factor task and we found a significant Emotion*Hemisphere*Electrode interaction ($F(4,72)=2.998$; $p\eta^2=0.023$; $p=.024$) in the TD group. No significant interactions were found in the ASD group. We computed two separate repeated-measures ANOVAs for left and right hemispheres only in TD and we found a significant Emotion*Electrode interaction ($F(2,72)=3.082$; $p\eta^2=0.146$, $p=.021$) in the right hemisphere. We computed three separate one-way ANOVAs for the three electrodes (O2, O10, PO10) but no main effects of emotion were found (all $ps >.05$). No significant interactions including the factor emotion were found in the left hemisphere (all $ps >.05$).

Moreover, we followed up the Task*Emotion*Hemisphere and Task*Emotion*Electrode interactions computing two mixed repeated-measures ANOVA for the emotion and gender task. Results highlighted significant Emotion*Hemisphere ($F(1.60,59.50)=5.316$; $p\eta^2=0.125$; $p=.012$) and Emotion*Electrode ($F(2.52,93.35) = 4.645$; $p\eta^2=0.112$; $p=.007$) interactions in the emotion task. We computed two repeated-measures ANOVAs breaking emotion task by hemisphere and we found a significant Emo-

tion*Electrode interaction in the Right Hemisphere ($F(2.71,100.31) = 4.707$; $p\eta^2 = 0.113$; $p = .005$). A significant main effect of Emotion was found in Electrode O2 ($F(2,72) = 3.841$; $p\eta^2 = 0.094$; $p = .026$) and post-hoc test revealed increased positivity for Happy expression compared to Fearful ($p = .022$). No significant interactions involving the factor Emotion were found in the Gender Task. These results suggesting increased sensitivity of the right occipital visual areas during early stages of emotion discrimination.

N170: We found these significant interactions: Task*Group ($F(1,36) = 4.76$; $p\eta^2 = 0.11$; $p = .04$), Task*Hemisphere*Electrode*Group ($F(2,72) = 3.988$; $p\eta^2 = 0.098$), Task*Emotion*Electrode ($F(3.41,123.07) = 3.02$; $p\eta^2 = 0.08$; $p = .02$), Hemisphere*Emotion ($F(2,72) = 5.75$; $p\eta^2 = 0.14$; $p = .005$), Electrode*Emotion ($F(2.90,104.62) = 8.48$; $p\eta^2 = 0.19$; $p = .000$), and a main effect of emotion ($F(2,72) = 21.90$; $p\eta^2 = 0.38$; $p = .000$). Follow-up analysis on the Task*Hemisphere*Electrode*Group (computed breaking for left and right hemispheres) revealed significant Task*Group interaction in the right hemisphere, electrodes P10 ($F(1,36) = 5.562$; $p\eta^2 = 0.134$; $p = .024$) and PO10 ($F(1,36) = 11.279$; $p\eta^2 = 0.239$; $p = .002$). Paired sample T-tests revealed significant task differences in ASD group in electrode P10 ($t(18) = 2.821$, $p = .011$, Cohen's $D = .647$) and PO10 ($t(18) = 3.373$, $p = .003$, Cohen's $D = .774$), both showing increased negativity for the gender task. No differences were found in the TD group and independent-sample T-tests did not show significant between-groups differences (all $ps > .05$). Moreover, we followed-up the Task*Group interaction computing two repeated-measures ANOVAs for TD and ASD groups comparing VEP amplitudes in emotion and gender tasks. We found significantly decreased negativity for emotion task compared to gender task in the ASD group ($F(1,18) = 7.162$; $p\eta^2 = 0.285$; $p = .015$). No significant differences were found in the TD group ($p = .541$). Moreover, results from mixed repeated-measures ANOVAs computed for emotion and gender tasks separately did not highlight significant group differences (all $ps > .05$). These results are depicted in Figure 2.5.

Moreover, to follow-up the Task*Emotion*Electrode interaction, we collapsed over groups and computed two repeated-measures ANOVAs for emotion and gender tasks.

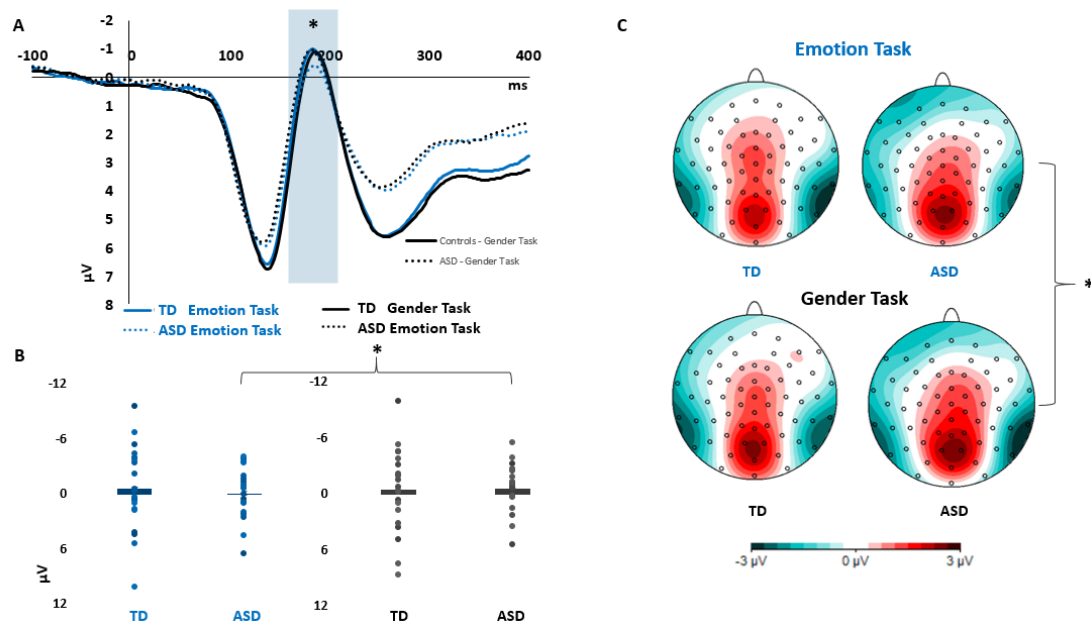


Figure 2.5. VEP N170 group differences. **A.** Reduced VEP amplitudes for emotion task compared to gender task in ASD ($*p=.015$) but not in TD ($p=.541$) (averaged activity of six occipital electrodes corresponding to electrodes O1/2, O9/10, PO9/10 of the 10/20 system.) **B.** Boxplots with individual data points of N170 VEP amplitudes in occipital areas, in emotion and gender tasks, for the TD and ASD groups. **C.** Topographical maps of VEP N170 electrophysiological activity, highlighting reduced negativity in occipital-temporal regions during emotion processing compared to gender processing in ASD but not TD.

Main effect of emotion was significant in emotion task ($F(2,72) = 14.217$; $p\eta^2 = 0.278$; $p < .001$) and gender task ($F(2,72) = 9.933$; $p\eta^2 = 0.216$; $p < .001$). Moreover we found a significant Electrode*Emotion interaction in the gender task ($F(2,72) = 6.597$; $p\eta^2 = 0.155$; $p < .001$). A significant main effect of emotion was found in all electrode positions: O1/2: $F(2,74) = 3.968$; $p\eta^2 = 0.097$ $p = .025$, Post-hoc: higher amplitude for neutral compared to fearful, $p = .040$; Electrodes O9/10: $F(2,74) = 8.892$; $p\eta^2 = 0.194$ $p < .001$, Post-hoc: increased negativity for fearful compared to neutral ($p = .001$) and happy ($p = .048$); electrodes PO9/10: $F(2,74) = 13.825$; $p\eta^2 = 0.272$, $p < .001$; post-hoc: increased negativity for fearful compared to neutral ($p < .001$) and happy ($p = .005$).

To explore the Hemisphere*Emotion interaction, we collapsed tasks, groups and electrodes and broke the ANOVA by hemisphere. Results highlighted a main effect of emotion in the left hemisphere ($F(2,74) = 14.431$; $p\eta^2 = 0.281$; $p = .000$, Post-hoc revealed increased negativity for fearful compared to neutral ($p = .000$) and happy ($p = .021$); marginally significant increased negativity for happy compared to neutral ($p = .050$). Main effect of emotion was found also in the right hemisphere ($F(2,74) = 23.429$; $p\eta^2 = 0.388$ $p = .000$) and post-hoc increased negativity for fearful compared to neutral ($p = .000$) and happy compared to neutral ($p = .000$). Finally, pairwise comparisons on main effect of emotion revealed increased negativity for fearful ($p = .000$) and happy ($p = .000$) expressions compared to neutral expressions.

P250: In this time window, we found no significant interactions or main effects involving the factor group. Results highlighted significant Task*Emotion ($F(2,72) = 4.87$; $p\eta^2 = 0.11$; $p = .01$), and Emotion*Electrode ($F(4,144) = 8.76$; $p\eta^2 = 0.19$; $p = .000$) interactions and a main effect of emotion ($F(2,72) = 3.30$; $p\eta^2 = 0.08$, $p = .04$). Follow up on the Task*Emotion interaction, performed breaking by task the main mixed repeated-measure ANOVA, revealed a main effect of emotion in the gender task ($F(2,74) = 3.921$; $p\eta^2 = 0.096$; $p = .024$). Post-hoc test did not reveal significant pairwise comparisons. Nevertheless, uncorrected post-hoc test highlighted significant reduced positivity for fearful compared to neutral ($p = .039$) and happy

(.022) expressions. Moreover, we ran a follow-up analysis on the Emotion*Electrode interaction computing three repeated-measures ANOVAs for the three electrode positions and we found a main effect of emotion in electrodes PO9/10 ($F(2,74)=7.341$; $p_{\eta^2}=0.166$, $p=.001$; post-hoc test highlighted a decreased positivity for fearful compared to neutral ($p=.003$) and happy ($p=.036$). Finally, post-hoc test on the main effect of emotion revealed a significantly increased positive amplitude for neutral compared to fearful ($p=.020$).

Correlations between personality Traits and VEP: Correlations were computed between SRS-2, AQ, TAS-20, MAIA-2 and the VEP N170 amplitudes, where significant group and task interactions were found. We collapsed 6 electrodes over occipital areas. Results highlighted that VEP amplitudes were not significantly correlated with any of the questionnaires (all $ps>.1$). We ran the same analysis on the ASD group only and we found a significant correlation between TAS – 20 and VEP amplitudes in emotion task ($N = 19$, $r = -.565$, $p=.012$) and gender task ($N = 19$, $r = -.528$, $p=.020$).

2.4 Discussion

The role of somatosensory activity system in re-enacting the somatic patterns associated with the observed emotional expressions is well-established in the typically developed population (Adolphs et al., 2000; Pitcher et al., 2008; Sel et al., 2014). Nevertheless, the hypothesis of reduced embodiment of emotional expressions in individuals with Autism Spectrum Disorder (ASD) is poorly investigated. In this study, we assessed the dynamics of the somatosensory activity during emotion processing over and above differences in visual responses in two groups of ASD and typically developing participants. By evoking task-irrelevant Somatosensory Evoked Potentials (SEP), we probed the state of the somatosensory system during a visual emotion discrimination task and a control gender task. Moreover, we dissoci-

ated somatosensory from visual activity by subtracting Visual Evoked Potentials (VEP) from SEP (Galvez-Pol, Calvo-Merino, & Forster, 2020), and compared pure somatosensory responses in ASD and TD during emotion and gender perception. We hypothesised that the two groups differently modulated their SEP in the emotion task but not in the gender task. Results were in line with our predictions and provided the first empirical evidence that autistic individuals show reduced activations of the somatosensory cortex during observation and discrimination of facial emotional expressions.

Our main finding concerns the significantly increased somatosensory responses during emotion processing in typically developed individuals compared to autistic individuals in the P100 SEP component, during the emotion discrimination task but not the control gender task. Group differences in somatosensory responses were systematically observed in the frontal sensorimotor region, in the overall evoked activity measured in electrodes placed over sensorimotor areas, and in the dorsal sites. Specifically, the ASD group showed reduced P100 amplitudes compared to the TD during emotion processing. Importantly, the observed group differences were specific for the emotion recognition task, revealing reduced embodiment of emotional expressions during emotion recognition in ASD. Moreover, in the TD group, but not in ASD, we observed significantly increased P100 amplitudes during emotion compared to gender recognition, suggesting stronger engagement of the somatosensory system during emotion compared to gender processing in the typical population, but not in autistic individuals.

Importantly, in behavioural emotion and gender recognition task, the ASD group showed overall decreased accuracy in catch trials compared to TD; however, these differences were not dependent from the task (i.e., ASD scored overall less accurate in behavioural emotion/gender recognition compared to TD). This suggests that the observed task-related group differences in somatosensory responses are unlikely to be explained by reduced attention or poor behavioural performance during emotion discrimination in ASD compared to TD.

Task-dependent group differences were also observed in the N140 SEP component. Here, we observed task-related modulations of SEP in typically developed individuals which were absent in ASD, suggesting persistently increased recruitment of the somatosensory system during emotion discrimination in typically developed participants but not in ASD. This effect was localised in the right hemisphere, consistently with previous literature (Adolphs et al., 2000; Pitcher et al., 2008). Conversely, in early stages of emotion processing, the two groups showed similar patterns of responses (P50) or emotions-related differences, which were not task-dependent (N80). Specifically, we showed how the somatosensory cortex is sensitive to different emotional expressions in early stages of emotion processing, consistently with previous results (Sel et al., 2014), which appeared to be enhanced in typically developing compared to autistic individuals in the N80 component, as shown by significant interactions involving the factor emotion in TD but not ASD group.

We provided further evidence on the relationship between autism and reduced recruitment of the somatosensory system during emotion discrimination in mid-latency stages of emotion processing by showing that SEP amplitudes in P100 could be predicted by autistic traits. In fact, the Social Responsiveness Scale (SRS-2) and Autism Quotient (AQ) scores, both measuring autistic traits, strongly correlated with P100 amplitudes in all clusters of electrodes where significant between-group differences were observed. Importantly, only SEP amplitudes evoked during the emotion task were significantly correlated with autistic traits.

The relationship between autistic traits and somatosensory activity during emotion processing was further confirmed by the multiple linear regressions. Here we observed that autistic traits and interoceptive awareness, but not alexithymia, were significant predictors of SEP amplitudes. The regression model was significant only for the emotion task, and SEP amplitudes were predicted both in the whole sample and in the ASD group. The choice to include TD individuals in the regression analysis was justified by recent studies showing that subclinical autistic traits in the general population are effectively detected by the SRS-2 and the AQ questionnaires, suggesting

that clinical and subclinical autistic traits may be conceived as a continuum (Bölte et al., 2011; Constantino & Todd, 2003, 2005; Ruzich et al., 2015).

Crucially, alexithymia traits (measured by TAS-20) were not associated to enhanced somatosensory responses, suggesting that reduced recruitment of the somatosensory system during emotion discrimination may be related to autism rather than alexithymia, which is often associated with ASD. This result suggests that not all facets of emotion-related processing difficulties observed in ASD can be attributed to co-occurring alexithymia as some have suggested (Bird & Cook, 2013; R. Cook et al., 2013). Interestingly, interoceptive awareness was correlated with emotional embodiment, which may be consistent with evidence suggesting a possible role of the insula in triggering emotion processing difficulties associated with autism (Ebisch et al., 2011; Silani et al., 2008). This pattern of findings contributes to a growing literature, which suggests that alexithymia and interoception may play distinct but interacting roles in the emotion processing difficulties associated with ASD (Gaigg et al., 2016; Garfinkel et al., 2016; Nicholson et al., 2018; Poquérusse et al., 2018). Source reconstruction on the SEP components of interest highlighted sources of activity in primary and secondary right somatosensory cortices and right BA6. This is consistent with evidence showing distributed cortical sources of SEP (Allison et al., 1996; Allison et al., 1992; Dowman & Darcey, 1994; Hämäläinen et al., 1990; Hari et al., 1984; Klingner et al., 2015; Klingner et al., 2011; Mauguière et al., 1997; Nakamura et al., 1998).

It is worth noticing that, according to recent accounts, atypical top-down modulations of sensorimotor (A. F. d. C. Hamilton, 2013) and sensory areas (J. Cook et al., 2012) could be implicated in reduced embodied simulation and atypical social perception in ASD. Therefore, it is possible that differential somatosensory responses in mid-latency components in ASD and TD (P100 and N140) are driven by atypical top-down modulations from frontal areas. This hypothesis is consistent with the notion that SEP amplitudes, especially mid-latency components (P100, N170) are modulated by high-order processes, for instance attention Desmedt and Tomberg,

1989; Forster and Eimer, 2005; Josiassen et al., 1982; Michie et al., 1987.

Overall, these patterns of responses reveal a decreased engagement of the somatosensory and sensorimotor systems, possibly triggered from top-down mechanisms modulating somatosensory responses, during emotion processing in ASD compared to typical participants. These results are in line with previous literature suggesting decreased vicarious representations of others' bodily states in ASD (Grèzes et al., 2009; Masson et al., 2019; Minio-Paluello et al., 2009).

Importantly, our results cannot be explained in terms of carry-over effects from atypical visual processing in ASD. Through subtractive methods (Galvez-Pol, Calvo-Merino, & Forster, 2020), we isolated somatosensory activity from visual evoked potentials and highlighted pure somatosensory responses over and above visual responses. Moreover, the analysis of VEP did not show the same patterns of between-group differences that we observed in SEP, therefore it is unlikely that reduced embodiment is driven by cascade effects of atypical visual responses. Instead, our results suggest a specific role of the somatosensory system in triggering atypical emotion processing in ASD. Indeed, in the visual N170 component, possibly arising concurrently to somatosensory processing (Pitcher et al., 2008), we observe task differences only in the ASD group, resulting in reduced responses during emotion recognition tasks compared to the gender task. This might underlie reduced responses in visual areas during emotion perception in ASD, as also suggested by previous studies (Kang et al., 2018; Martínez et al., 2019). Nevertheless, autistic traits were not significantly correlated with N170 amplitude. Conversely, N170 amplitude correlated with alexithymia in the ASD group in both tasks. These results may suggest a possible dissociation between atypical somatosensory and visual responses related to autistic and alexithymia traits in face processing, which should be systematically tested in future studies.

Our study provides novel data on atypical recruitment of the somatosensory system during emotion discrimination in ASD, suggesting reduced embodiment of the observed expressions independently from visual processing. These results offer a

novel perspective on the neural dynamics underlying emotion discrimination in ASD, consistent with a theoretical framework which proposes that difficulties of autistic individuals in the domain of social cognition are tied to reduced vicarious representations of others' bodily states.

Chapter 3

The relationship between somatosensory processing of emotions and interoception in ASD

3.1 Introduction

Experiencing emotions involves feeling the physiological patterns of visceral, somatic and motor changes associated with a certain affective state (A. Damasio & Carvalho, 2013; James, 1884). Sensing the corporeal changes associated with emotional states involves both the exteroceptive (i.e., proprioception) and interoceptive (visceral feelings and internal sensations) systems (Craig, 2003; Critchley & Garfinkel, 2017; Pace-Schott et al., 2019). These networks, underlying the conscious feeling of our own emotions, are also recruited during perception of others' emotions, with the function of re-enacting the somatic and visceral patterns associated with the observed emotional expression (Adolphs et al., 1996; Niedenthal, 2007). One of the most common measures of individual ability to consciously access their

inner corporeal feelings is the Heartbeat Counting Task (HCT) (Schandry, 1981), measuring interoceptive accuracy (Garfinkel et al., 2016; Schandry, 1981) (i.e., the objective accuracy of perceiving bodily signals (Christensen et al., 2017)). This task, first proposed by Shandry (Schandry, 1981), involves perceiving and silently counting heartbeats, without feeling the pulse, while the actual heartbeats are recorded through ECG, and it is nowadays commonly used to provide measures of interoceptive accuracy (Christensen et al., 2017; Garfinkel et al., 2016; Maister et al., 2017; Monti et al., 2020; Tsakiris et al., 2011; Villani et al., 2019), although alternative methods based on estimating heartbeat rate has recently been proposed (Legrand et al., 2021). Behavioural measures of Interoceptive Accuracy (IAcc) provided evidence for associations between levels of interoception, the quality of affective experience, and electrophysiological responses measured with EEG. For instance, it has been shown how people with higher interoceptive accuracy, measured with a heartbeat counting task, experience greater intensity of emotional experience and stronger P300 and slow wave, measured with EEG, after visual perception of emotional expressions (Herbert et al., 2007; Pollatos, Gramann, et al., 2007; Pollatos et al., 2005; Pollatos, Matthias, et al., 2007). Specifically, Herbert and colleagues (Herbert et al., 2007) showed that the P300, an ERP component sensitive to the affective valence of visual stimuli (Cuthbert et al., 2000; Keil et al., 2002; Keil et al., 2001), was stronger in good heartbeats perceivers compared to poor heartbeats perceivers for pleasant and unpleasant but not neutral pictures, and that P300 and slow wave amplitudes (550-900 ms) positively correlated with heartbeats perception scores. In a similar experiment, Pollatos and colleagues (Pollatos, Gramann, et al., 2007) confirmed the relationship between the reported intensity of emotional feelings, interoceptive accuracy in a heartbeat detection task, and P300 amplitude, and performed source reconstruction of the P300 ERP components, which revealed activation in the insula and somatosensory cortices, as well as in the anterior cingulate and prefrontal cortex. Another EEG experiment suggested that modulations of the P300 with relation to high IAcc could be a marker or better emotion regulation and re-appraisal (Füstös

et al., 2013).

Neuroimaging studies revealing activity in insular, somatomotor and cingulate cortices underlying heartbeats' detection (Critchley et al., 2004), suggest that the neural basis of interoception partly overlap with the circuits underlying self (A. R. Damasio, 1995) and others' (Adolphs et al., 1996) emotion processing. In particular, it has been shown that evaluating the inner states of the body and experiencing emotions rely on the same neural systems, in particular the right anterior insular cortex and ventromedial prefrontal cortex (Terasawa et al., 2013). The role of the somatosensory system in sensing emotional feelings (A. Damasio & Carvalho, 2013; A. R. Damasio et al., 2000) and physiological changes in the body (Bechara & Naqvi, 2004; Critchley et al., 2004; Khalsa, Rudrauf, & Tranel, 2009) has also been highlighted. Nevertheless, experiencing and discriminating between emotions requires both interoceptive and exteroceptive information (Craig, 2003), which rely on partly dissociable networks, primarily involving the insular cortex and the somatosensory cortex respectively (Farb et al., 2013).

Somatosensory activity can be modulated by combined exteroceptive and interoceptive signals. Indeed, by inducing a cardio-visual full bodily illusion (i.e., participants saw a virtual body flashing either synchronously or asynchronously with respect to their heartbeats) it has been shown that somatosensory evoked potentials (SEP) were modulated by the degree of self-identification with the virtual body (Heydrich et al., 2018). Notably, in a recent EEG experiment, Al and colleagues (2020) showed that Heartbeat Evoked Potentials (HEP), a neural marker reflecting cortical processing of visceral states, in particular associated to heartbeats, and mainly generated within the insula and the operculum (Park et al., 2018), followed by tactile stimulation, modulated the detection of tactile stimuli and the amplitude of SEP P50, N140 and P300 components (Park & Blanke, 2019), suggesting cortical integration of visceral and somatic information. Another study testing adolescents showed that the amplitude of fronto-central heartbeat evoked potentials during a heartbeat detection task, but not during a resting condition, was associated to increased interoceptive

accuracy (Mai et al., 2018), thus providing evidence for a role of cortical processing of cardiac-related activity in interoception. Structures identified as generators of the HEP are the anterior cingulate, the right insula, the prefrontal cortex and the left secondary somatosensory cortex Pollatos et al., 2005.

The past decade has been characterized by growing interest towards the hypothesis that ASD would be associated with reduced interoception (Garfinkel et al., 2016; Schauder et al., 2015), which has been sometimes suggested to arise as a consequence of co-morbidity between ASD and alexithymia (Bird & Cook, 2013; Shah, Catmur, et al., 2016). Difficulties in interoception have broader implications for poor emotion processing (Critchley & Garfinkel, 2017; Mulcahy et al., 2019; Shah et al., 2017) and empathy (Mul et al., 2018; Shah et al., 2017) in autistic individuals. The most influential proposal is that atypical interoception and poor awareness of self and others' emotions in ASD are associated to differences in how the insular cortex operates, compared to neurotypicals. For instance, it has been proposed that difficulties in understanding emotional feelings and in sensing the inner states of the body are both caused by altered intrinsic functional connectivity of anterior and posterior insula (Ebisch et al., 2011). Another fMRI experiment (Silani et al., 2008) investigated in two groups of autistic and typically developing individuals the relationship between activations in the Anterior Insula (AI) while observing emotional stimuli and reporting their feelings, and questionnaires measuring alexithymia and lack of empathy. Interestingly, results highlighted a positive association between AI activation during emotional stimuli perception and evaluation and empathy, and a negative association with alexithymia. Moreover, alexithymia and empathy were negatively correlated with each other.

Importantly, it has been proposed that interoceptive awareness occurs through two different pathways, one involving visceral afferents projecting to the insula, and another involving skin afferents projecting to the somatosensory cortex (Khalsa, Rudrauf, Feinstein, et al., 2009), in accord with other authors who previously suggested a the role for the somatosensory system in interoception (Bechara & Naqvi,

2004; Critchley et al., 2004). These observations are confirmed by recent empirical evidence showing a somatosensory pathway for perceiving 'artificial' heartbeats of an extracorporeal left-univentricular cardiac assist device (LVAD), non mediated by a visceral-vagal pathway, providing further evidence for a double pathway of interoception (Couto et al., 2014). Finally, recent evidence showed that physiological changes in the body have cascade effects for cortical processing of somatosensory (Al et al., 2020) and emotional (Garfinkel et al., 2014) stimuli, suggesting a tight link between bodily, affective and cognitive processes. Nevertheless, the possible role of the somatosensory system in triggering difficulties in interoception and its relation with emotion processing in ASD is poorly investigated.

The aim of this study is to explore whether there is an association between somatosensory processing of emotions, autistic traits, and interoception in individuals with and without ASD. We tested two matched groups of individuals with or without a diagnosis of ASD, who previously participated in experiment 1 (see Chapter 2), on a heartbeat counting task (Garfinkel et al., 2016; Schandry, 1981) to measure their interoceptive accuracy. In addition, we measured exteroceptive accuracy by adapting the HCT to tactile stimuli detection, which were delivered on participants' left index at a fixed pace. Finally, we self-paced a time counting task in which participants were asked to silently count seconds as a control measure. We first checked if individuals with and without autism exhibited different levels of interoceptive and exteroceptive accuracy, measured with the heartbeat detection task, and the adapted tactile detection task, and if levels of interoceptive and exteroceptive accuracy were associated to the strength of autistic traits. Then, we tested if there was a significant relationship between the amplitudes of somatosensory evoked potentials evoked during emotion processing (see Chapter 2), and interoceptive and exteroceptive accuracy.

3.2 Materials and methods

Participants. Twenty-two adult participants with a diagnosis of Autism Spectrum Disorder (ASD) and twenty-two Typically Developing (TD) adults matched for IQ, age and gender, who previously took part in the experiment described in Chapter 2, participated in the experiment. Data from two participants were not collected due to technical issues. The final sample was composed by 21 ASD (19 right handed, 1 female, mean age 40.47 ± 8.865) and 19 TD participants (19 right handed, 1 female, mean age 40.84 ± 12.249). All participants in the ASD group had a formal diagnosis of autism spectrum disorder from qualified professional clinicians based on the DSM criteria. To control for IQ we tested all our participants with a short version of the Weschler Adult Intelligence Scale (WAIS), and obtained a Verbal IQ (VIQ) and Performance IQ (PIQ) for each participant. Moreover, participants completed the adult self-report form of the Social Responsiveness Scale (SRS-2; (Constantino, 2002)), the Autism Spectrum Quotient (AQ; (Baron-Cohen et al., 2001b)), the Toronto Alexithymia Scale (TAS - 20; (Taylor et al., 2003)) and the Multidimensional Assessment for Interoceptive Awareness (MAIA - 2; (Mehling et al., 2018)). For a summary of test and questionnaire scores, see Table 2.1 in Chapter 2.

Experimental task. A Heartbeat Counting Task (HCT) was used to measure participants' Interoceptive Accuracy (IAcc) (Garfinkel et al., 2016; Schandry, 1981). In addition, Tactile Accuracy (TAcc) was measured through a Tactile taps Counting Task (TCT) and Time Accuracy (TimeAcc) as a control task were measured. The order of presentation of these tasks was counterbalanced across participants. During all tasks, participants sat in an electrically shielded chamber (Faraday's cage) in front of a monitor at a distance of 80 cm. The tasks were presented centrally on a black background using E-Prime software (Psychology Software Tools). Participants could communicate with the experimenter, who was sitting in a room next to the Faraday's cage, through an intercom. The experimenter could see the participants

through a webcam during the whole experimental session.

During the heartbeat counting task, the actual heartbeats of each participant were recorded through an electrode placed over the participants' chest, on the left. The ground electrode was placed over the right ear. Data was collected through a BrainAmp amplifier (BrainProducts) and processed in Brainvision Analyser.

Participants were asked to relax, focus on their inner feelings, and count their own heartbeats, without physically taking their pulse, during four time intervals of 25, 35, 45 and 100 s. The order of presentation of these intervals was counterbalanced across participants, who were not informed about their specific durations. Each trial started with a red fixation cross (1 s), which became green at the beginning of each counting session, and turned into red again at the end of the counting time (0.1 s). At the end of each counting session, participants were asked to report the number of heartbeats they perceived. Moreover, they were asked to rate confidence of their performance in the heartbeat counting task from 0 (not very confident) to 10 (extremely confident) and to report the body part they were paying attention to during the HCT. Each participant completed a training session before starting the experimental task, which consisted in a heartbeats counting session of 15 s, followed by questions on the number of counted heartbeats, the confidence level expressed in a value from 0 to 10, and the body part to which they paid attention during the HCT.

During the Tactile taps Counting Task (TCT), a mechanical stimulator was placed around the left index finger of participants. Tactile taps, which could be consciously detected from participants, were delivered using two 12 V solenoids driving a metal rod with a blunt conical tip that contacted with participants' skin when current passed through the solenoids. To mask sounds made by the tactile stimulators, we provided white noise through one loudspeaker placed 90 cm away from the participants' head and 25 cm to the left side of the participants' midline (65 dB), measured from the participants' head location with respect to the speakers). Tactile taps lasted 0.2 s each and were continuously delivered through E-Prime software

at a pace of 75 taps per minute, consistent with normal values of Heart Rate (HR) in adults (between 60 and 100 bpm according to the “Target Heart Rates Chart”, 2015).

We measured Tactile Accuracy (TAcc) by providing tactile taps on the left index finger of participants during four time intervals of 25, 35, 45 and 100 s and asking them to sit down, relax, and count the tactile stimuli they felt on their finger. The order of presentation of these intervals was counterbalanced across participants, who were not informed about their specific durations. Each trial started with a red fixation cross (1 s), which became green at the beginning of each counting session, and turned into red again at the end of the counting time (0.1 s). Participants completed a training session before starting the experimental task, which consisted in a tactile taps counting session of 15 s, followed by a question on the number of counted tactile taps.

Finally, we measured Time Accuracy (TimeAcc) simply asking our participants to sit down, relax and count seconds during the time interval defined by the green fixation crosses displayed on the screen, as in the other tasks, without using a watch. The task was repeated for four time intervals of 25, 35, 45 and 100 s. The order of presentation of these time intervals was counterbalanced across participants, who were not informed about their specific durations. Each trial started with a red fixation cross (1 s), which became green at the beginning of each counting session, and turned into red again at the end of the counting time (0.1 s). Participants completed a training session before starting the experimental task, which consisted in a time counting session of 15 s, followed by a question on the number of counted seconds. For a graphical depiction of the tasks, see Figure 3.1.

Data pre-processing. The ECG tracks were processed in BrainVision analyser software (BrainProducts). The data relative to each time interval was segmented through markers and the number of heartbeats from each participant and time window was extracted through an automatic algorithm (ECG Markers solution).

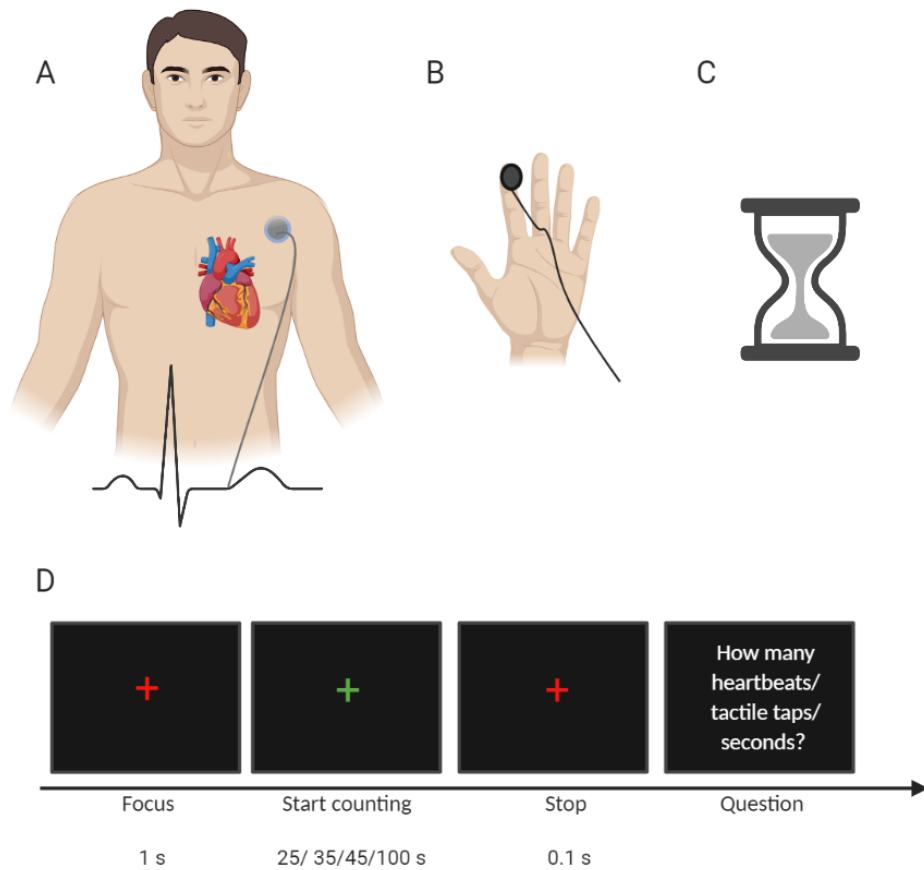


Figure 3.1. Experimental Task. **A.** The heartbeat counting task consisted in feeling the heartbeats, which were recorded through an electrode placed on the left side of the chest. **B.** During the tactile taps counting task, a mechanical tactile stimulator was used to delivered tactile taps on the left index finger. **C.** The control task consisted in counting seconds. **D.** Participants were instructed to count the heartbeats (or the taps or seconds), for the time the green fixation cross was displayed on the screen.

Accuracy scores were calculated for the three tasks, for each of the four trials separately, in Matlab 2019b. We employed a commonly used formula:

$$i_{acc} = 1 - \frac{(|nbeatsreal - nbeatsreported|)}{((nbeatsreal + nbeatsreported)/2)}$$

(Christensen et al., 2017)

which was adapted for the tactile taps counting task

$$t_{acc} = 1 - \frac{(|ntapsreal - ntapsreported|)}{((ntapsreal + ntapsreported)/2)}$$

and the time counting task:

$$time_{acc} = 1 - \frac{(|nsecondsreal - nsecondseported|)}{((nsecondsreal + nsecondsreported)/2)}$$

.

Statistical analysis

Interceptive accuracy: we computer linear mixed models in R (Winter, 2013) using the package LmerTest (Bates et al., 2015) to test accuracy scores, involving the fixed effects Group (TD, ASD), and Task (Heartbeat Counting Task, Tactile Counting Task, and Time Counting Task) and Duration (25, 35, 45, 100 s) and the interaction between factors, and a random effect of Duration (25, 35, 45, 100 s) as well as by-subject intercepts. Before running the test, assumptions of normality of residuals, homoscedasticity, linearity, and collinearity were tested. We chose to run this analysis because it is more robust to violations of assumptions of normality compared to a mixed repeated-measures ANOVA (Schielzeth et al., 2020) and therefore is often used to analyse datasets unsuitable for classic linear models (Casals et al., 2014). Moreover, it can be run on data with some missing observations. Significant effects are reported in type II anova via Satterthwaite’s degrees of freedom (Winter, 2013). We computed post-hoc tests on significant interactions and main effects correcting for multiple comparisons (Bonferroni) and using Kenward-Roger to correct degrees

of freedom.

Interoceptive accuracy and personality traits: we were interested in exploring whether participants' Interoceptive Accuracy was significantly related to their individual scores to questionnaires measuring autistic traits (Social Responsiveness Scale, SRS-2 and Autism Quotient, AQ), alexithymia (TAS-20) and interoceptive awareness (MAIA – 2). We did not exclude the outliers highlighted by visual inspection of the data (see Figure 3.2), because this would have represented excessive loss of information. In fact, very low scores in the heartbeat counting tasks can reflect severe impairments in interoception. Moreover, the data from all three tasks was negatively skewed, and had outliers. Therefore, we run non-parametric correlations (Spearman ρ), between individual scores of Interoceptive Accuracy (IAcc), Tactile Accuracy (TAcc) and Time Accuracy (TimeAcc) and personality traits measured with the Social Responsiveness Scale (SRS-2), the Autism Quotient (AQ), the Toronto Alexithymia Scale (TAS-20) and the Multidimensional Assessment of Interoceptive Awareness (MAIA-2).

Interoceptive accuracy and embodiment of emotional expressions: finally, we explored a relationship between Interoceptive Accuracy, calculated through the Heartbeat Counting Task (HCT), and exteroceptive accuracy, measured through the Tactile taps Counting Task (TCT) and the degree of somatosensory embodiment of observed emotional expressions, as measured in Experiment 1 (see Chapter 2). We focused on the P100 component, where significant group-differences in somatosensory emotion processing were found. First, we run non-parametric correlations, including the outliers (see Figure 3.2), between participants' accuracy in the three tasks (interoceptive accuracy, tactile accuracy, time accuracy) and SEP amplitudes in the frontal, dorsal, and fronto-parietal clusters. Then, to further explore the relationship between interoception and embodiment of emotions, we excluded the two outliers from the IAcc dataset and we run multiple linear regressions. We were driven by

the results of the correlation analysis to select our models' predictors.

3.3 Results

Interoceptive accuracy. Results from preliminary analysis through linear mixed model highlighted a significant interaction between Group and Task ($F(2, 407.45)$, $p = 0.002$, a main effect of Task ($F(2, 407.52) = 71.84$, $p = .000$; and a main effect of Group ($F(1, 37.95) = 4.52$; $p = .04$). No main effects or interactions involving the factor Duration were significant (all $ps > .05$).

We followed up the significant interaction involving the factors Task and Group by computing post-hoc tests corrected for multiple comparisons (Bonferroni) and adjusted degrees of freedom with the Kenward-Roger method. Results highlighted a significant difference between ASD and TD in interoceptive accuracy ($t(73.3) = 3.68$, $p = .006$) but not tactile or time accuracy (all $ps = 1.000$).

Results

Correlations between Interoceptive Accuracy and Personality Traits. We were interested in investigating whether interoceptive accuracy, tactile accuracy, and time accuracy were significantly related to personality traits, in particular autism, alexithymia, and interoceptive awareness. We computed these correlations on the whole sample of participants, treating autistic traits as a continuum, consistently with the correlation analysis ran in Experiment 1 (See Chapter 2). Results from non-parametric correlations (Spearman's ρ) between individual scores to the SRS-2, AQ, TAS-20 MAIA-2 questionnaires and interoceptive accuracy highlighted a significant relationship between interoceptive accuracy and autistic traits, measured with the Social Responsiveness Scale (SRS-2) ($\rho = -.350$, $p = .046$) and Autism Quotient (AQ) ($\rho = -.397$, $p = .017$). Moreover, there was a moderately significant correlation between the average of subscales of MAIA-2 and IAcc ($\rho = -.329$, $p = .050$). We run an additional analysis computing non-parametric correlations between IAcc and each subscale of the MAIA-2 questionnaire, and we found a significant correlation

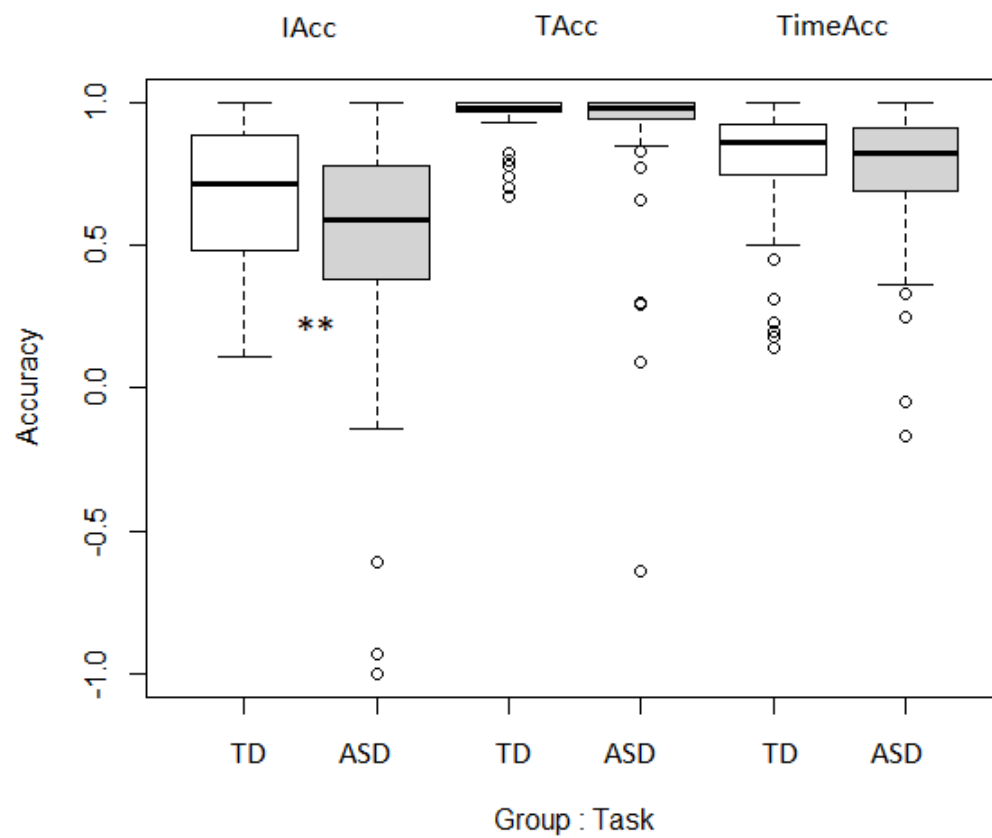


Figure 3.2. Results: interoceptive accuracy. The ASD group showed significantly reduced accuracy during the heartbeat counting task, but not the tactile or time counting task, compared to the TD group. (** $p < .01$)

between IAcc and the Not Worrying subscale ($\rho = -.376$, $p = .028$). Alexithymia was not significantly correlated with IAcc ($p = .232$)

Moreover, we found a significant correlation between tactile accuracy and autistic traits (SRS: $\rho = -.350$, $p = .046$) The other questionnaires were not significantly correlated with TAcc (AQ: $p = .057$; TAS – 20: $p = .333$; MAIA – 2, $p = .184$. Time accuracy was not correlated with any personality trait (all $p > .074$) and the three measures (IAcc, TAcc, TimeAcc) were not correlated to each other (all $p > .184$). For correlations between personality traits, see Tables 2.2 and 2.3 in Chapter 2.

Relationships between Interoceptive Accuracy and Embodiment of Emotional Expressions

Correlations: to explore the association between interoception and somatosensory embodiment of emotional expressions, we computed non-parametric correlations (Spearman's ρ) between P100 SEP amplitudes (See Chapter 2) and IAcc, TAcc, and TimeAcc. Results from this analysis showed a highly significant correlation between IAcc and SEP amplitudes in the frontal cluster evoked during the emotion task ($\rho = .493$, $p = .002$). Interestingly, IAcc was not correlated to SEP amplitudes evoked during the gender task ($p = .493$). The same pattern was observed in the dorsal sites, where IAcc correlated with SEP amplitudes in the emotion task ($\rho = .516$, $p = .002$) but not gender task ($p = .531$) and the overall activity measured in fronto-parietal regions during the emotion task ($\rho = .426$, $p = .010$) but not gender task ($p = .598$). Tactile accuracy was not significantly correlated with any of the SEP clusters (all $p > .1$). Time accuracy was also significantly correlated with SEP amplitudes in dorsal site ($\rho = .390$, $p = .016$) and overall activity ($\rho = .411$, $p = .010$, only in emotion task (all gender $p > .07$).

Although Spearman's ρ is robust against outliers, to confirm the robustness of our results, we also run parametric correlations (Pearson's r) between IAcc and SEP after excluding the two outliers. Importantly, there was a significant linear relationship between SEP amplitudes evoked during the emotion task and IAcc also

after excluding the outliers in all clusters (frontal: $r=.468$; $p=.005$; dorsal: $r=.494$, $p=.003$; overall: $r=.437$; $p=.01$). These results are depicted in Figures 3.3 and 3.4. Finally, to ensure these results were not triggered by visual effects, we also computed non-parametric correlations between VEP N170 amplitudes and IAcc, TAcc, and TimeAcc. Results showed non-significant correlations between VEP amplitudes evoked during emotion or gender tasks and accuracy in three counting tasks (all $p > .27$).

Linear regressions: we excluded the two outliers who scored $< -.09$ in the heartbeat counting task, and obtained a normally distributed IAcc dataset (tested with Shapiro Wilk's test for normality). Then, we run a multiple linear regression with the backward method in RStudio on the whole sample of participants, following the rationale of treating clinical and subclinical autistic traits as a continuum (Bölte et al., 2011), also adopted in Chapter 2. We added IAcc and autistic traits, measured with the SRS-2, and the interaction between these two factors as predictors, and frontal SEP amplitudes evoked during the emotion task as dependent variable. We chose these predictors because they were both strongly correlated with SEP amplitudes (see Figure 2.3 in Chapter 2 and 3.3 in the current Chapter). For the same reason, we run the same model adding AQ IAcc, and the interaction between AQ and IAcc, and then MAIA-2 and IAcc and the interaction between MAIA-2 and IAcc as predictors. We ran three separate models to avoid collinearity (see Table 2.2, Chapter 2). Moreover, we chose the frontal cluster, consistently with the regression analysis on SEP amplitudes and autistic traits ran in the previous study, because here crucial differences between neural responses of TD and ASD participants to emotional expressions were observed (see Figure 2.2 Chapter 2).

Results showed that all three regression models were significant. The first model ($F(2,27) = 7.362$, $p=.003$, $R^2=.353$) had SRS-2 ($p=.030$) and IAcc ($p=.029$) as significant predictors of SEP amplitudes evoked during the emotion task. The second model ($F(2,29) = 9.510$, $p=.001$, $R^2=.396$) also showed that both autistic traits (AQ,

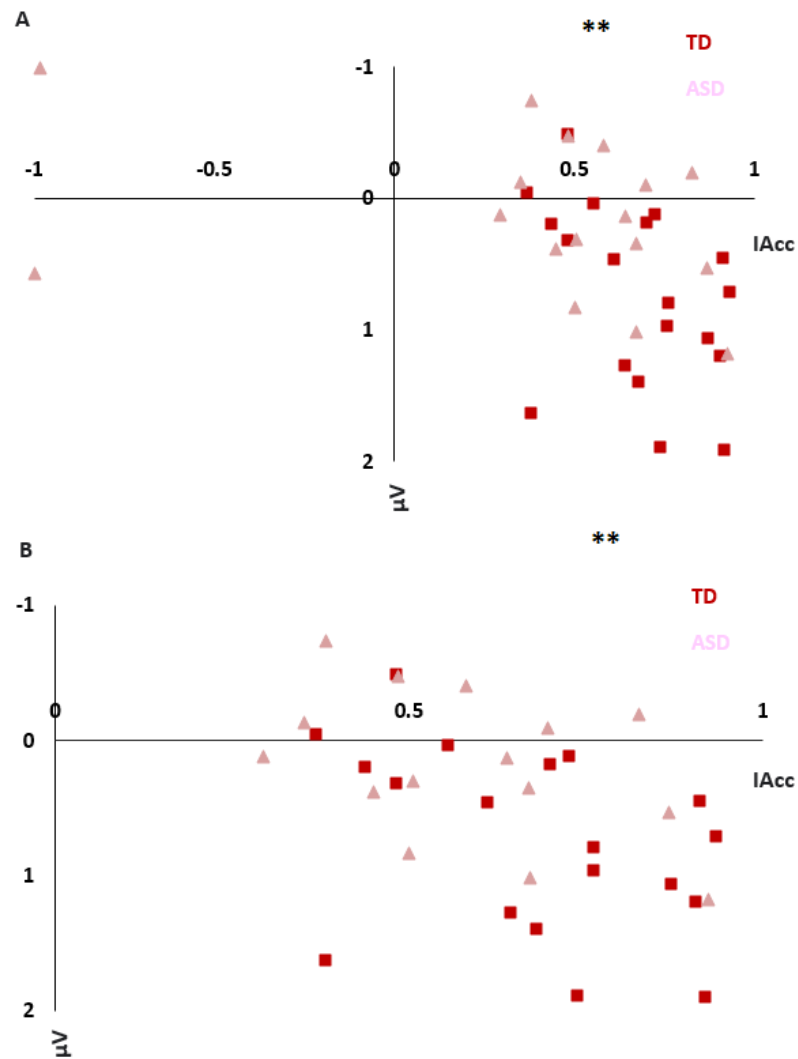


Figure 3.3. Correlations between IAcc and SEP amplitudes evoked during emotion task. A. Significant correlation between frontal SEP amplitudes in the emotion task and interoceptive accuracy including outliers and **B.** excluding outliers. (** $p < .01$)

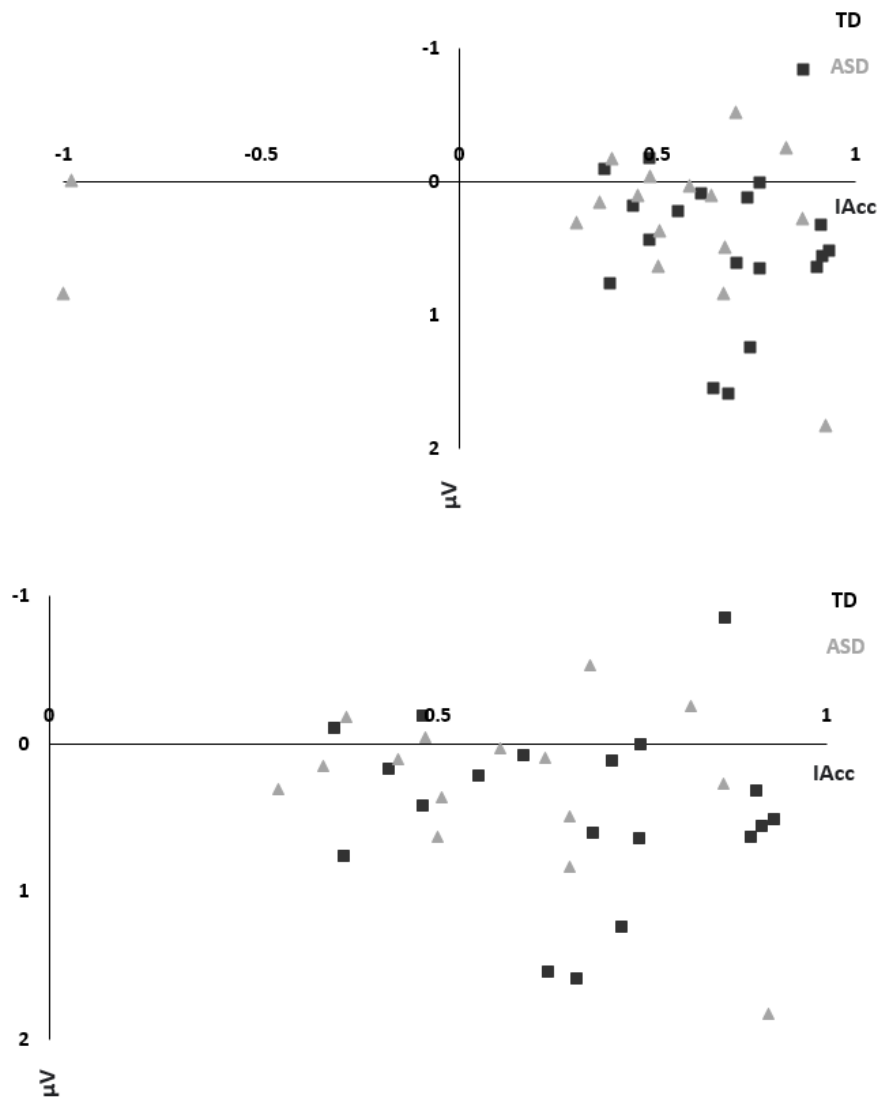


Figure 3.4. Correlations between IAcc and SEP amplitudes evoked during gender task. **A.** Non-significant correlation between frontal SEP amplitudes in the gender task and interoceptive accuracy including outliers and **B.** excluding outliers.

$p=.009$) and IAcc ($p=.040$) were significant predictors of SEP amplitudes evoked during the emotion task. Finally, a significant model ($F(1,33) = 8.976$, $p=.005$, $R^2=.291$) having only IAcc as significant predictor ($p=.005$) was found. In all cases, due to multicollinearity, models excluding the interaction between predictors were automatically selected through the backward method.

3.4 Discussion

The aim of this study was to explore the relationship between somatosensory processing of emotional expressions in individuals with or without ASD and their levels of interoceptive accuracy. Difficulties in the domain of interoception have been described in autistic individuals (Garfinkel et al., 2016). In addition to this, individuals with autism exhibit difficulties in integrating interoceptive and exteroceptive signals (Noel, Lytle, et al., 2018). We administered a heartbeat counting task and an adapted version of this task, where participants had to count tactile stimuli, to measure exteroceptive accuracy, and a control time counting task to our two groups of individuals with or without a diagnosis of ASD.

Our main finding concerns a strong and stable association between the degree of somatosensory embodiment during emotion perception, and participants' levels of interoceptive accuracy. The amplitude of P100 SEP component, which showed to be sensitive to emotion processing in TD, but not ASD individuals, was also significantly associated with interoception. Importantly, only somatosensory activity evoked during the emotion task showed to have a relationship with interoception, consistently with the hypothesis that the same neural systems are recruited for interoception and emotion processing (Critchley & Garfinkel, 2017). These results were confirmed by the multiple linear regressions, showing that models including interoceptive accuracy and the strength of autistic traits as predictors, measured by two different questionnaires, could significantly predict SEP amplitudes evoked during emotion processing. These results corroborate the hypothesis that the somatosensory system might be

involved in processing the physiological signals associated to emotional states, in accord with a two-pathway model of interoception (Khalsa, Rudrauf, Feinstein, et al., 2009). Moreover, they provide evidence of a possible disruption of somatosensory processing of emotional feelings and physiological signals in ASD.

Previous EEG experiments have shown how the amplitudes of late ERP components (P300 and slow wave) evoked by visual, emotionally salient, pictures, were significantly associated to participants' performance in a heartbeat detection task (Füstös et al., 2013; Herbert et al., 2007; Pollatos, Gramann, et al., 2007; Pollatos et al., 2005; Pollatos, Matthias, et al., 2007) and to the quality of their emotional experience. Moreover, source reconstruction of these ERP components highlighted active voxels in the insular and somatosensory cortices (Pollatos, Gramann, et al., 2007). However, to our knowledge, this is the first EEG study directly probing the association between somatosensory processing of emotional expressions and interoceptive accuracy in individuals with autism spectrum disorder. Moreover, through subtraction of visual evoked potentials from visual and somatosensory activity (see Chapter 2), we were able to disentangle somatosensory from visual processing of emotions (Galvez-Pol, Forster, et al., 2020; Sel et al., 2014). Interestingly, the role of the somatosensory system in emotion processing and its relationship with IAcc, over and above visual carryover effects, was confirmed by the fact that interoceptive accuracy was not significantly correlated with VEP N170 amplitudes.

Results also showed that participants with ASD scored lower in the heartbeat counting task, but not in the tactile counting task and the time counting task, compared to typically developing controls, consistently with previous results (Garfinkel et al., 2016) but contradicting others (Nicholson et al., 2018). Importantly, after running non-parametric correlations between autistic traits, measured with the SRS-2 and AQ scales, we found an association between autistic traits and IAcc. Interoceptive awareness, which is a multidimensional construct relative to the degree of attention, trust, and regulation towards inner bodily sensations (Mehling et al., 2018), was also associated to IAcc. Surprisingly, Alexithymia did not show a significant associations

with IAcc, contradicting the hypothesis that this condition would be at the core of interoceptive disturbances experienced by autistic individuals (Shah, Hall, et al., 2016). Interestingly, tactile accuracy was associated to autistic traits too, consistently with previous studies showing atypical sensory processing in ASD (Thye et al., 2018). Nevertheless, exteroceptive (tactile) accuracy did not show an association with emotion processing or with interoception, suggesting that differences in tactile processing may not be related to emotional feelings. Moreover, accuracy in the time counting task also correlated with somatosensory responses. Although we did not expect to find this association, we speculate this may have been triggered by attentive mechanisms modulating both SEP amplitudes and accuracy in counting seconds.

Future research will need to provide direct evidence of the state of activity of the somatosensory system during tasks involving interoception, such as the heartbeat counting task, in individuals with ASD, and its possible association to emotional feelings, to confirm these observations.

Chapter 4

Interpersonal motor interactions shape multisensory representations of the peripersonal space

4.1 Introduction

The present perspective review aims at proposing that interpersonal interactions may affect (sensorimotor) body and (multisensory) peripersonal space (PPS) representations. This perspective is grounded on two established piece of evidence regarding the plasticity of body and PPS representations, namely: 1) that synchronous visuo-tactile stimulation applied on ones' own body and a fake ("rubber" or virtual) body part can induce changes in body representations, leading to the incorporation (i.e., feeling of ownership, proprioceptive drift, self-location drift) of the rubber body part in one's own body representation (see Table 1); 2) that active tool use modulates the PPS by strengthening multisensory integration effects between visual (Iriki et al., 1996; Maravita et al., 2002) or auditory (Canzoneri et al., 2013; Galigani

et al., 2020; Galli et al., 2015) stimuli delivered near the tool and tactile stimulation applied on the body, respectively, thus leading to the incorporation of the tool in the representation of the body of the user (Farnè et al., 2007; Maravita & Iriki, 2004; Maravita et al., 2003; Maravita et al., 2002).

A relevant difference between the paradigms originally used to study the expansion of the PPS after tool use and the illusion of incorporating a rubber limb is that the first family of experiments implied the “active” use of a tool (however, see Galli et al., 2015; N. P. Holmes et al., 2004; N. P. Holmes and Spence, 2004) followed by measuring crossmodal congruency effects (CCE) (Spence et al., 2000; Spence et al., 2004) (see the section **Key Concepts** for a definition), while the second family of studies used “passive” visuo-tactile synchronous stimulations to induce subjective (ownership) or behavioural (proprioceptive drift, self-location drift) changes of body representation (Botvinick & Cohen, 1998; Pavani et al., 2000; Tsakiris & Haggard, 2005). Regarding the role of different sensory modalities in modulating body representations, it has been shown that not only visuo-tactile, but also visuo-interoceptive synchrony may facilitate incorporation of external body parts. For example, seeing a virtual hand (Suzuki et al., 2013), body (Aspell et al., 2013; Park et al., 2016; Park et al., 2018), or face (Sel et al., 2017 but see Porciello et al., 2016) pulsing in synchrony with participants’ heartbeat can increase their feeling of ownership towards it. As for the case of standard bodily illusions, the role of interoception (i.e., the inner sense of the physiological and visceral signals of the body, such as cardiac, respiratory, and gastric activity (Critchley & Harrison, 2013) in triggering changes in body representations and body ownership has recently been addressed using immersive virtual reality set-ups. Monti and colleagues (Monti et al., 2020), for example, showed that breathing in synchrony with a virtual body (vs asynchrony) induces sense of ownership and agency of the virtual body, and that these effects depend on individuals’ interoceptive ability to perceive respiratory and cardiac signals. Conversely, the role of interoception in inducing the rubber hand illusion is debated (Horváth et al., 2020). It has been proposed that individuals with stronger

interoceptive sensitivity are less likely to incorporate a rubber limb, suggesting stronger anchorage to own body in highly interoceptive individuals (Tsakiris et al., 2011). These results have been replicated during the enfacement illusion (Tajadura-Jiménez, Grehl, et al., 2012; Tajadura-Jiménez, Longo, et al., 2012), and led to the proposal that interoceptive bodily signals may underlie self–other distinctions in the context of social interactions (Palmer & Tsakiris, 2018).

Here, we propose that interpersonal motor interactions entail temporarily exploiting the neural mechanisms underlying both multisensory integration involved in bodily illusions and tool incorporation. This would be translated in dynamic changes of own body and PPS representations, in order to facilitate sensorimotor predictions and accordingly adjust our behaviour to our partner’s movements (Brozzoli et al., 2014). In fact, in the context of interpersonal interactions finalised to shared goals, i.e., joint action (Sebanz et al., 2006), individuals’ sensorimotor channels need to become spatio-temporally aligned to facilitate interpersonal coordination. We suggest that acting together with a partner triggers plastic reorganisation of individual’s body and PPS boundaries, based on this spatio-temporal alignment, to form a joint representation of the agents’ bodies and the surrounding space. The proposed mechanism is in agreement with ‘we mode’ (Gallotti & Frith, 2013), or Shared Action Space (SAS) (Pezzulo et al., 2013) models, proposing that interacting agents represent their individual actions together with aspects of the interactive scene, framing their movements, their representation of the space, and even their sense of the bodily self, in a co-constructed entity.

Consistently with this interpretation, and endorsing recent proposals supporting a Bayesian interpretation of body ownership (Samad et al., 2015), PPS (Noel, Blanke, & Serino, 2018; Noel et al., 2019), self (Apps & Tsakiris, 2014; Limanowski & Blankenburg, 2013), and action observation (J. M. Kilner et al., 2007a, 2007b), we propose that temporary reorganisations of body and PPS representations through “predictive” multisensory integration of events occurring in one’s own action space support predictions of other people’s behaviour and mutual adjustments during

motor interactions. Moreover, we suggest that this mechanism forms the basis for high-order mutual understanding, in particular the ability to infer the internal (i.e., motivational and intentional) causes of our partners' behaviour. Importantly, Bayesian models of body ownership, PPS, and observed actions understanding are also useful to describe the mechanisms supporting self–other distinction, which are fundamental for efficient interpersonal interactions (Fotopoulou & Tsakiris, 2017; Ishida et al., 2015).

To support our proposal, we first briefly introduce the concept of peripersonal space, describe its neural basis, and summarise studies providing evidence for a tight link between the PPS and body representations (Section 4.2). In Section 4.3, we review the literature concerning changes in the PPS during action execution. Then, we link the notion that motor processes have a role in shaping body and PPS representations to evidence of plastic modifications of the body schema and the PPS after ‘incorporating’ tools through their active use (Section 4.4). Section 4.5 is devoted to describing the core idea of the present perspective review, i.e., that the pairing of motor and multisensory signals during interpersonal interactions may result in the emergence of a joint PPS. Here, we describe initial evidence of how interpersonal interactions trigger the formation of joint body and PPS representations. In Section 4.6, we further develop this idea by proposing that interindividual sensorimotor interactions support higher-order forms of mutual understanding through the shaping of this shared PPS, based on multisensory integration (Brown & Brüne, 2012; Hoehl & Bertenthal, 2021; Meltzoff & Marshall, 2020; Nagai, 2019). This view is consistent with the idea that, during social interactions, understanding others' internal states stems from a sensorimotor representation of their behaviour (Candidi et al., 2012). In the last section (Section 4.7), we link our proposal to the evidence that individuals with Autism Spectrum Disorder (ASD) show differences in PPS representations compared to neurotypical individuals (Jp et al., 2020; Noel, Blanke, Serino, & Salomon, 2017; Noel, Paredes, et al., 2020).

Key Concepts

Rubber Hand Illusion (RHI)

A bodily illusion based on synchronous tactile stimulation of an unseen self-hand, and observed tactile stimulation of a rubber (Botvinick & Cohen, 1998; Pavani et al., 2000; Tsakiris & Haggard, 2005) or virtual (Sanchez-Vives et al., 2010) hand, placed in a congruent position with the real hand. This induces feeling of ownership of the fake hand and changes in where the real hand is perceived in the space (proprioceptive drift). Interestingly, the sense of ownership over a virtual hand in Virtual Reality (VR) can be induced by its mere observation in a first-person perspective, inducing visuo-proprioceptive congruency (Fusaro et al., 2019; Tieri et al., 2015).

Rubber Foot Illusion

A bodily illusion based on the same multisensory integration principles of the RHI, but based on synchronous visuo-tactile stimulation of a rubber/virtual foot and consequent incorporation of the external foot (Crea et al., 2015; Lenggenhager et al., 2015; Matsumoto et al., 2020).

Enfacement Illusion

An illusion based on multisensory integration of tactile stimuli felt on one's own face and synchronous observation of tactile stimulation delivered on another face. This illusion induces incorporation of the partner's face onto the person's identity representation (Cardini et al., 2013; Porciello et al., 2018; Sforza et al., 2010; Tsakiris, 2008).

Full Body Illusion

A bodily illusion tested in immersive virtual reality, based on multisensory integration of tactile and visual information between stimulation received on the body and observed on a virtual body, inducing relocation of the self onto the virtual body, as shown by subjective (sense of ownership) and objective (self-location drift) measures

(Aspell et al., 2009; Blanke & Metzinger, 2009; Lenggenhager et al., 2007; Noel, Pfeiffer, et al., 2015; Provenzano et al., 2020)). Interestingly, the sense of ownership over a virtual body in VR can be induced by its mere observation in a first-person perspective, inducing visuo-proprioceptive congruency (Fusaro et al., 2021; Slater et al., 2010).

Embreathment Illusion

A bodily illusion based on synchronous or asynchronous breathing with a virtual avatar in immersive virtual reality, mediated by multisensory integration of interoceptive and visual cues, showing incorporation, ownership, and sense of agency of the virtual body after congruent respiration (Monti et al., 2021; Monti et al., 2020).

Crossmodal Congruency Effect (CCE)

The difference in reaction time in detecting a tactile stimulus on a body spot (Spence et al., 2000; Spence et al., 2004) when visual (Maravita et al., 2002) or auditory stimuli (Canzoneri et al., 2012; Canzoneri et al., 2013; Galli et al., 2015) are presented on an incongruent location on the body.

Proprioceptive drift

A change of perceived hand location towards the rubber hand during the RHI (Tsakiris & Haggard, 2005).

Self-location drift

A shift of perceived full-body location towards the virtual body during the full-body illusion (Blanke & Metzinger, 2009).

4.2 Body representations and the PPS

Successfully interacting with the environment requires the online integration of sensorimotor information concerning one's own body posture and position (i.e., the body schema) with the events happening and the objects located in the space around the body (PPS) (Maravita et al., 2003; Rizzolatti et al., 1997; Roll et al., 2021; Spence et al., 2004). The body schema has been defined as a specific type of body representation encoding the current posture of the body and its extension in space, based on the integration of somatic, proprioceptive, and tactile sensory information, implicated in guiding action (Dijkerman & de Haan, 2007; Head & Holmes, 1911; Paillard, 1999; Preester & Knockaert, 2005). Given the strong functional relation between the body schema and the representation of the space around the body upon which individuals can operate (PPS), the neural resources dedicated to representing the PPS and the body schema are functionally (and anatomically) interconnected (see Cardinali, Brozzoli, and Farnè, 2009; di Pellegrino and Làdavas, 2015 for reviews). The notion of PPS is based on initial evidence of premotor and parietal bimodal visuo-tactile neurons responding to visual stimulation near the corresponding tactile receptive field in monkeys. These processes were later explored through multimodal (visuo-audio-tactile) integration of behavioural effects in (healthy and brain damaged) humans, and, more recently, by neuroimaging and brain stimulation studies in humans. Pioneering single-unit recording studies in monkeys described a class of multisensory, predominantly visual-tactile, neurons in premotor area 6 (Fogassi et al., 1999; M. Graziano et al., 1994; M. S. A. Graziano et al., 1997) parietal areas (Brodmann area 7b and the Ventral IntraParietal area (VIP)) (Avillac et al., 2007; Bremmer et al., 2001) and the putamen (M. S. A. Graziano & Gross, 1995). These studies showed that the visual receptive fields of visuo-tactile premotor neurons were anchored to the tactile receptive fields (i.e., visual receptive field would respond to stimuli appearing near the part that was touched, no matter their retinal projection) (M. Graziano et al., 1994). These cells remain active even when the visual stimulus

disappears (M. S. Graziano, 1997) and respond to visual stimuli presented near a fake hand placed in front of the monkey in anatomical congruency with their own hand (M. S. A. Graziano et al., 1999). The majority of 7b visuo-tactile neurons are mostly active for stimuli approaching the face, arm, hand, and trunk, and this region contains bimodal neurons of which the visual fields might be either dependent or independent from the position of their tactile receptive fields (M. S. A. Graziano & Gross, 1995). The VIP contains a majority of bimodal neurons responding to stimuli near the head and face (Colby et al., 1993; Duhamel et al., 1998). More recently, neuroimaging research on monkeys described an extended cortical network of occipital, parietal, premotor, and prefrontal areas, including somatosensory regions (Cléry, 2018; Guipponi et al., 2015, see Cléry and Hamed, 2018, playing a key role in the definition of peripersonal space and supporting spatio-temporal predictions of the impact time of external objects (Cléry et al., 2017).

In humans, behavioural and neuroimaging studies provided evidence of similar multisensory representations of the peripersonal space, which are mainly implemented in fronto-parietal cortical areas (Brozzoli, Gentile, Petkova, et al., 2011; Gentile et al., 2011; Makin et al., 2007; Sereno and Huang, 2006; Serino et al., 2011, reviewed in di Pellegrino and Làdavas, 2015; Serino, 2019). As in the case of monkeys, the human PPS is not a unique entity, and distinct neural systems selectively respond to events occurring in the space surrounding specific body parts (Cléry & Hamed, 2018). Similarly to the segregation of different body parts observed in monkeys, studies suggest the existence of specific neural representations of the peri-trunk space (Bernasconi et al., 2018), as well as the peri-face (Làdavas et al., 1998) and peri-hand (Brozzoli et al., 2012; Gentile et al., 2011), in humans, as confirmed by behavioural evidence (Serino, Noel, et al., 2015). Importantly, behavioural studies on the peri-hand space demonstrated that this region of space is sensitive to tool-use modulations (Farnè & Làdavas, 2000; Farnè et al., 2007).

In sum, since the PPS is organised in a body part-specific manner and it is affected by the position of the different body parts in space, body representations (i.e., the body

schema) and the PPS are thought to be tightly linked functionally and underpinned by similar fronto-parietal networks. Nevertheless, important distinctions between body representations (with particular relation to the body schema) and the PPS have been recently reviewed (Hunley & Lourenco, 2018).

4.3 The PPS is shaped by action planning and execution

Relevant for the present perspective is the relation between the PPS and action execution. Specifically, extensive literature has described how the brain devotes resources to integrating multisensory processing with motor programmes to build unified representations of actions and the space in which these are performed (see Brozzoli et al., 2014; Bufacchi and Iannetti, 2018; di Pellegrino and Làdavas, 2015 for reviews). For its role as a perception-to-action interface (Brozzoli, Makin, et al., 2011), the PPS has been recently proposed as an “action-value field”, i.e., a graded representation of the space according to event’s relevance for actions (Bufacchi & Iannetti, 2018; Noel & Serino, 2019). Coherently with this action-based model, representations of the PPS are sensitive to rapid recalibrations (Noel, Bertoni, et al., 2020), reflecting the functional role of the peripersonal space as a spatial framework to create or avoid contact between objects and the body. Both avoidance and approach functions have been proposed for the PPS, based on the evidence that fronto-parietal regions responded during bodily protection behaviours (Clery et al., 2015; M. S. A. Graziano & Cooke, 2006) as well as during goal-directed action (Rizzolatti et al., 1997), leading to the proposal of a dual model of the peripersonal space (see (de Vignemont & Iannetti, 2015) for a review).

For instance, it has been shown that, when an object enters the defensive peripersonal space (DPPS) around the face, it elicits a (subcortical) defensive response known as the hand-blink reflex (Fossataro et al., 2016; Sambo et al., 2011). This consists in an eye-blink elicited by the electrical stimulation of a hand, which is enhanced by

proximity of the stimulated hand to the face. Interestingly, this automatic hand-blink reflex is triggered not only when the stimulated hand is near the self-face, but also to another person's face, providing evidence for a shared substrate of self and others' maps of PPS (Fossataro et al., 2016). Importantly, this hand-blink reflex is modulated by the movement of the hand, so that the reflex is present when the hand which receives the tactile stimulation triggering the hand-blink reflex is moving toward the face, but it is absent when the hand occupies the same position but is moving away from the face (Bisio et al., 2017).

On the other hand, clear online dependency of the dimension of the PPS on the planning and execution of actions was established by showing that planning and executing actions trigger a dynamic reorganisation of the peripersonal space (Berger et al., 2019; Brozzoli et al., 2010; Brozzoli et al., 2009; Lohmann et al., 2019; Noel, Grivaz, et al., 2015; Patané et al., 2018). Brozzoli and colleagues (Brozzoli et al., 2010; Brozzoli et al., 2009; Patané et al., 2018) employed a visuo-tactile integration task to measure the degree of interference caused by visual distractors placed over a to-be-grasped object on the detection of spatially congruent or incongruent tactile stimuli delivered on participants' hands, during movement preparation and execution. These authors observed that the degree of interference between visual and tactile incongruent stimuli (CCE as defined in **Key concepts**) was stronger during action planning and movement execution compared to when the object was merely shown to individuals. The authors interpreted these results as the consequence of a dynamic reorganisation of the peripersonal space around the far object, when the object becomes the target of ones' own movement.

Remarkably, not only hand actions re-shape the PPS, but walking has also been shown to affect multisensory integration in the space surrounding the trunk (Noel, Grivaz, et al., 2015). Indeed, a study revealed that walking extended the behavioural effects of audio-tactile integration of stimuli perceived in the direction of locomotion, regardless of the coherence of the visual information (Noel, Grivaz, et al., 2015). Moreover, by combining reaching movements with walking toward the to-be-grasped

object, Berger and colleagues (Berger et al., 2019) were able to show higher CCE at movement's onset not only towards reaching targets, but also for walk-and-reach targets. However, these authors found that the PPS is not purely hand-centred with respect to orientation, such that when participants needed to change hand orientation to reach the object, the CCE decreased, and did not simply invert as expected.

All in all, the evidence shows that the PPS may be extended to external objects one is going to act upon, or the portion of space one is approaching. This literature bridges the role of action execution to the emergence of multisensory integration effects, normally occurring within the PPS, which were originally described after active tool use. We will review evidence concerning plastic reorganisations of the PPS after tool use in the next section.

4.4 Incorporating tools in the PPS

In the previous section, we introduced the concepts of PPS as a dynamic multi-sensory representation of the space around the body, shaped by the actions of an individual. Before moving to the core of our perspective review, we now describe how body and PPS representations are sensitive to plastic reorganisations entailing the 'incorporation' of tools in ones' own sensorimotor body representation. More in detail, we will suggest that the mechanisms supporting tool incorporation may share properties with those underlying the incorporation of the partner's body parts when individuals actively interact.

Experimental evidence has shown that the body schema (Cardinali, Frassinetti, et al., 2009) and the peripersonal space (Farnè and Làdavas, 2000, for reviews see di Pellegrino and Làdavas, 2015; Serino, 2019) can be temporarily remapped during active or passive interaction (Serino, Canzoneri, Marzolla, et al., 2015) with a tool. This phenomenon was originally observed in monkeys (Iriki et al., 1996) (for a review see Maravita and Iriki, 2004), and was later described in brain damaged

(Bonifazi et al., 2007; Farnè et al., 2007) and healthy humans (Biggio et al., 2020; Biggio et al., 2017; Cardinali, Frassinetti, et al., 2009; Forsberg et al., 2019; Galigani et al., 2020; Maravita et al., 2002). It has been suggested that modifications of the PPS underlying these effects depend on Hebbian plasticity (Bertoni et al., 2021; Magosso, Serino, et al., 2010), i.e., connectivity transformations driven by statistical associations of multisensory inputs from the environment. Plastic reorganisations of the PPS and the body schema after tool use are supported by evidence showing stronger CCE when a visual stimulus is presented near the used tool (Bonifazi et al., 2007; Farnè et al., 2007) or specifically next to the used part of the tool (N. P. Holmes et al., 2004), while a tactile stimulus is delivered on the participants' hand. Moreover, Cardinali and colleagues (Cardinali, Brozzoli, & Farnè, 2009) showed that tool use not only changes the multisensory integration effects near the object ("extending" the PPS), but that it also affects motor indexes related to the body schema (i.e., action execution), and to the somatosensory body representation (i.e., increase of the represented length of the arm), once again supporting the close relation between the PPS and sensorimotor body representations. Interestingly, in a recent study, Miller and colleagues found that the somatosensory cortex responds to stimuli located beyond the physical body, and showed how, when a hand-held tool was touched, vibrotactile stimuli triggered activity in the primary and secondary somatosensory cortices of the participants (Miller et al., 2019). Taken together, these results reveal how the body schema and the PPS can be temporarily extended in humans to incorporate external objects, which are useful needed to perform an action in the environment.

The similarities between the constructs of the PPS, the multisensory interface between the body and the space immediately surrounding it (Serino, 2019), and the body schema, a sensorimotor representation of the body finalised to action execution (Maravita et al., 2003), and their sharing of anatomical and functional properties, made researchers even question hypothesize a dissociation of the two constructs (Cardinali, Brozzoli, & Farnè, 2009). Nevertheless, by studying tool use aftereffects

or bodily illusions, several studies were able to partly disentangle the multisensory and sensorimotor representations underlying the PPS and different types of bodily representations. For instance, researchers aimed to understand whether the rubber hand illusion (based on multisensory integration) induces a change in the sensorimotor representations of the body (body schema). Kammers and colleagues (Kammers et al., 2009) showed that the RHI does not affect reaching execution (based on the body schema), suggesting that visuo-tactile-proprioceptive illusions do not translate to alterations in body representations used to move (i.e., the RHI may affect the ‘body image’ but not the ‘body schema’ (Preester & Knockaert, 2005). Conversely, a specific effect of tool use on the role of tactile information processing for motor control was studied by Cardinali and colleagues (Cardinali et al., 2011). These authors showed that motor localisation of tactile stimuli on one’s limb is affected after tool use as if the limb has extended, and that this effect is not observed in case the localisation follows a verbal indication. By studying a deafferented patient, these authors have also shown that processing proprioceptive information is a necessary condition to support body schema plastic changes after tool use (Cardinali et al., 2016). Similarly, pairing of motor efferent signals with perceived sensory consequences may also affect the rubber hand illusion, such as in the moving and virtual Rubber Hand illusions (Dummer et al., 2009; Ma & Hommel, 2015a, 2015b; Newport et al., 2010; Sanchez-Vives et al., 2010; Shibuya et al., 2018; Tsakiris et al., 2006).

The relation between the role of efferent motor and afferent sensory signals to the incorporation process has been recently cast in the perspective of Bayesian sensory filtering through predictive coding (Grechuta et al., 2019). This study showed that task-relevant distal cues could affect the sense of body ownership of a virtual hand during action execution, providing evidence that forward models of body ownership are formed not only through integration of internal (motor) and proximal (tactile and proprioceptive) cues, but also of distal (visual and auditory) ones, if they are informative of the action’s outcome (Grechuta et al., 2019).

This evidence reveals how the brain integrates sensory information from external and internal bodily cues during action execution, suggesting that generative models of body ownership are updated through upcoming information from multiple proximal (proprioceptive, tactile) and distal (visual, auditory) channels, when the agent pursues goal-oriented actions in the environment. Thus, we note that while synchronous visuo-tactile stimulations might be sufficient per se (see Serino, Canzoneri, Marzolla, et al., 2015) to extend the PPS over an object, it is likely that concurrent visual, tactile, proprioceptive, auditory, and motor information, paired in time during natural (transitive) tool use, underlie the incorporation of the tool in a user's PPS. Given the action-based (Berger et al., 2019; Brozzoli et al., 2010; Brozzoli et al., 2009; Bufacchi & Iannetti, 2018; Lohmann et al., 2019; Noel, Grivaz, et al., 2015) and predictive nature of the PPS (Clery et al., 2015; Cléry & Hamed, 2018), researchers have proposed the Bayesian framework as a useful model to interpret the emergence and structure of the PPS (Fossataro et al., 2020; Noel, Blanke, & Serino, 2018; Noel, Samad, et al., 2018), as in the case of self and body representations (Apps & Tsakiris, 2014; Hohwy & Paton, 2010; Limanowski & Blankenburg, 2013; Samad et al., 2015). Specifically, according to these proposals, the PPS would act as a multisensory coupling prior, sensitive to recalibrations driven by experience (Magosso, Serino, et al., 2010; Magosso, Ursino, et al., 2010; Noel, Bertoni, et al., 2020). Coherently with a predictive view of the PPS, it has been shown that forward models extend predictive mechanisms of multisensory integration, related to the body, to hand-held tools, such that self-touch reduces sensory perception either when performed with the hand or an incorporated tool (Kilteni & Ehrsson, 2017). This is explained by the fact that Bayesian priors inherently adapt to a dynamic environment in which sensory expectations are updated through experience, linking multisensory perception to action.

Expanding the idea of the PPS as a space where events may enter in contact with one's body (Clery et al., 2015) this evidence supports the idea that motor capabilities shape the way the brain dedicates multimodal processing of events that will enter

in contact with one's body. This makes the PPS the perfect candidate to support our ability to coordinate our behaviour with our interaction partner's actions. In fact, during interpersonal interactions, we need to predict which when and where the movements of our partner will generate events that we will feel on our body, whether we are directly touching the body of our partner, or whether we are using an object to interact. Consistently, predictive accounts of interpersonal interactions have already been proposed for these scenarios (Brown & Brüne, 2012; Frith et al., 2003).

The tight functional link between visuo-audio-tactile and proprioceptive integration and motor control leads to the idea that extensions of the body schema and the PPS (such as after active tool use) may contribute to support our ability to interact with others. The next section is dedicated to building the proposal that the multisensory integration underlying tool incorporation may be extended to the incorporation of a partner body part during interpersonal interactions. Indeed, during interpersonal interactions, visuo-tactile and auditory events are perceived as a function of one's own, but also other people's actions. In these cases, one's own sensory inflow co-occurs with the movements of a partner, thus establishing statistical associations between one's own motor command and the effects of the behaviour of a partner.

4.5 The PPS is modulated by motor interactions

Several researchers have suggested that our body and other people's bodies, and the space surrounding them, may be represented in a common framework (Brozzoli et al., 2014; Brozzoli et al., 2013). According to Gallagher, the idea of joint body representations has its philosophical roots in Merleau-Ponty's notion of intercorporeity (Gallagher, 2018). Merleau-Ponty considers intercorporeity to be a pre-reflective, relational phenomenon, which he defines as "an internal relation that makes the other person appear as the completion of the system" (Merleau-Ponty, 1968, p. 368). This concept is now relevant for cognitive neuroscientists interested in disclosing the

neurocognitive mechanisms underlying social interactions.

Thomas, Press, and Haggard investigated the existence of a shared representation of our own body and the other's body (and PPS), by investigating the degree of visuo-tactile integration between tactile stimuli delivered on the participants' body and observed visual stimuli appearing near a facing model's body (Thomas et al., 2006). Participants exhibited faster responses to tactile events on their own body after a visual event that was presented in the corresponding anatomical (e.g., left hand-left hand) location on the model's body, compared to a non-corresponding location. This shared representation of the body was expanded by a study investigating whether shared sensory experiences between two people, induced by the enfacement illusion, could trigger the remapping of one's own peripersonal space around the other's body (Maister et al., 2015). Crucially, results showed an increase in audio-tactile integration in the space close to the confederate's body after the shared experience, demonstrating a temporary remapping of one's own PPS around the confederate's body. Coherently with these behavioural effects, an fMRI study identified shared pattern of activity in the left ventral premotor cortex for processing events occurring in self and other people's peripersonal space, but also activations in the anterior cingulate cortex specific for processing information related to the space surrounding other people's bodies (Brozzoli et al., 2013).

Interestingly, the impact of sensory sharing on these shared body and PPS representations is modulated by higher-order factors such as the social context. In a series of experiments, by using an audio-tactile integration task, Teneggi and colleagues (Teneggi et al., 2013) described how individuals' peripersonal space is differently modulated by the presence of another individual or a mannequin. Then, they showed that the boundaries between self and the other's peripersonal spaces merged after playing an economic game with another person, but only if this person behaved cooperatively. These observations were corroborated by another study, showing that modulations of the peripersonal space in presence of others was modulated by people's perceived morality (Pellencin et al., 2018). These results revealed that PPS

representations are sensitive to top-down modulations related to social information, showing a link between low-level multisensory processing and high-level social cognition.

Shared multimodal body and space representations may be extremely relevant to support interpersonal interactions, where the movements and sensory events happening on a partner's body need to be integrated with one's own actions. Indeed, interacting successfully with others requires to predict the outcomes of other people's actions in order to facilitate mutual adjustments and motor coordination between partners (Braun et al., 2011; Pezzulo & Dindo, 2011). Previous studies showed how sensorimotor resonance may support action prediction not only in the context of action observation (J. M. Kilner et al., 2007b) but also during joint action, in order to facilitate interpersonal coordination (Sebanz et al., 2006). According to this hypothesis, individuals engaging in joint action would manage to understand and predict the actions of their partners and consequently adjust their behaviour by representing aspects of the interactive scene in a 'we-mode' (Gallotti & Frith, 2013). As Pezzulo and colleagues (Pezzulo et al., 2013) suggested, social interactions are embedded in a shared representation of the space, the 'Shared Action Spaces' (SAS), which supports crucial computations underlying interpersonal interactions. Specifically, they propose that, during joint actions, the mechanisms for sensorimotor transformations and multisensory integrations incorporate information relative to the co-actors and induce a recalibration of individual spatial representations onto a shared one, re-referenced on the dyade. Crucially, sensorimotor transformations in the SAS enable real-time coordination, because they enclose predictions about the partner's future actions.

In line with these accounts, we propose that plastic reorganisations of the body schema and the surrounding peripersonal space support interpersonal attunement between partners in the context of joint actions. This phenomenon would be supported by temporary reorganisations of individual bodily and spatial maps onto a shared representation, having implications beyond plastic reorganisation of the body

and PPS shaped by ‘tool use’ (i.e., incorporating the partner’s body in a shared self-other representation). For a graphical depiction, see Figure 4.2.

In the context of the emerging field of ‘two persons neuroscience’ (Hari et al., 2015; Hari & Kujala, 2009; Schilbach et al., 2013), interactive paradigms have been developed to investigate the neurocognitive mechanisms supporting dyadic or group interactions and these paradigms have been also used to study changes in body and PPS representations in social contexts. The first study that tested the effect of the presence of another person inside (or outside) participants’ PPS on individuals’ visuotactile CCE showed that multisensory integration is reduced while performing a tactile detection task when another individual was performing a complementary task within the participant’s PPS (Heed et al., 2010). More recently, evidence of the formation of a shared PPS (or an ‘entangled’ body schema, as the authors call it) after interpersonal interactions comes from a behavioural study, where two individuals had to synchronise their pulling of a rope to cut a candle (i.e., interpersonal visuo-motor and proprioceptive coupling) and were then tested for incongruent visuo-tactile stimulation effects on their partner’s hand (Soliman et al., 2015). Interestingly, the interaction increased the interference effect of incongruent visual stimuli occurring near the partners’ (used for the interaction) index or thumb finger on the detection of tactile stimuli on the participant’s (unused for the interaction) thumb or index finger indicating that individuals remapped the space around the partners’ body on their corresponding body part. This bodily entanglement was found especially in participants with high interdependent self-construal levels, suggesting that lower-level multisensory bounding is modulated by higher-order social representations of the self. To further investigate the effects of interpersonal sensorimotor sharing on individuals’ body schema, in two other experiments, Soliman and colleagues (Soliman et al., 2015) measured the degree of visuo-motor interference (that is, the automatic simulation of other’s movements during action execution) (J. Kilner et al., 2003) after the joint and the solo sawing conditions, asking their participants to execute a movement while observing the partner performing a dif-

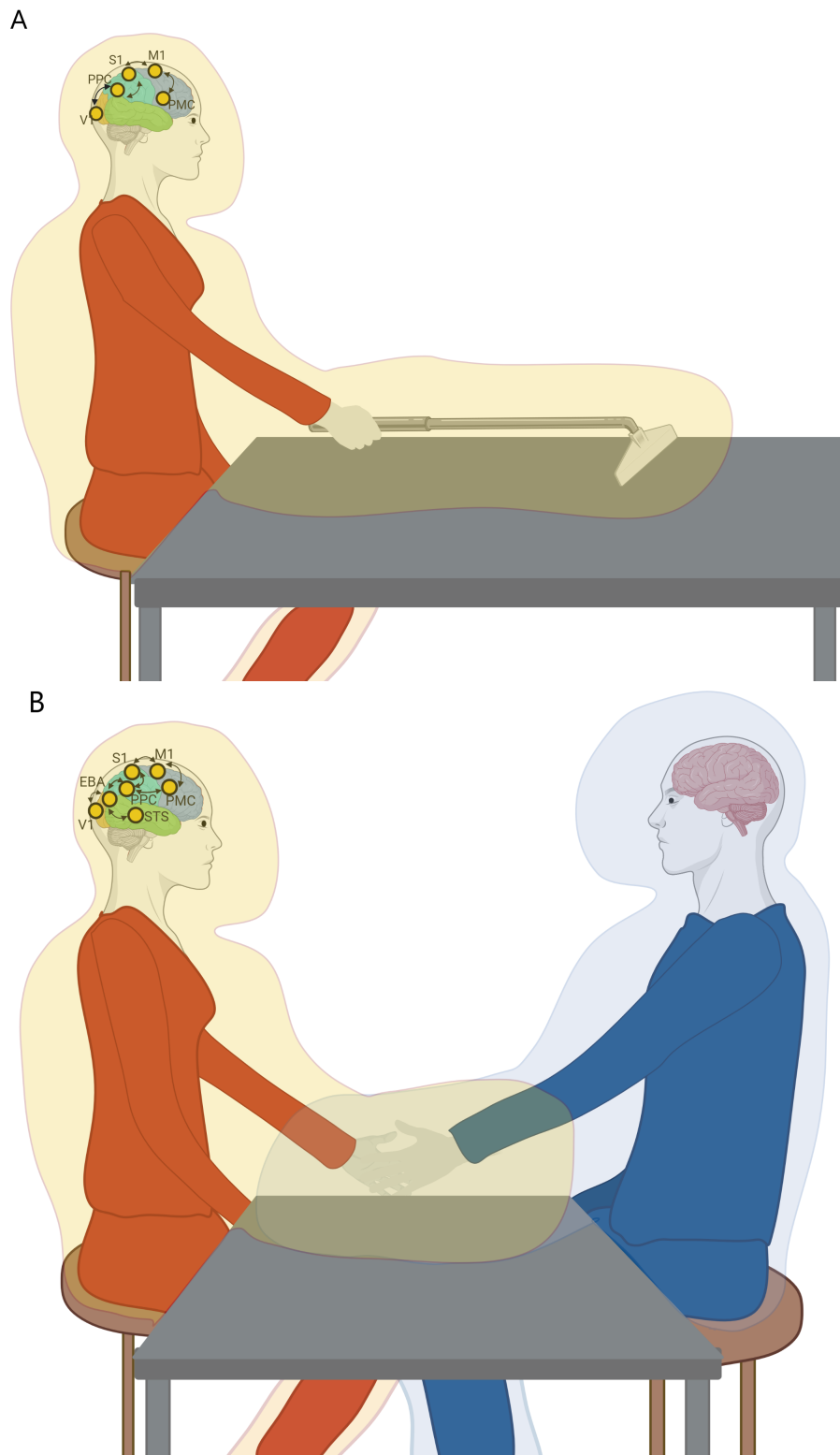


Figure 4.1. Plasticity of the PPS. **A.** Plastic changes in the peripersonal space (PPS) during tool-use and interpersonal motor interactions. **B.** Incorporation of a tool in own PPS during active tool use. Right panel: The same mechanism could underlie the incorporation of the partners' limb during motor interactions (i.e., handshake), to facilitate interpersonal coordination. The neural network involves feedforward and feed-back projections between visual (V1, Extrastriate Body Area (EBA), Superior Temporal Sulcus (STS)), somatosensory (S1), and motor (M1) areas, as well as multisensory areas involved in representing the PPS, i.e., the posterior parietal cortex (PPC) and premotor cortex (PMC). The orange/blue shadow represents the PPS expanded around the tool or partner (Created with Biorender.com).

ferent one. Participants' performance was more affected by the observation of an incongruent action after the joint sawing task compared to the solo control condition, suggesting that the interaction affected individuals' motor representations of the partner's movements. These results are in line with previous studies showing that visuo-motor interference effects automatically arise when participants coordinate their actions with a partner to perform complementary (incongruent) interactions (era; Candidi, Curioni, et al., 2015; Candidi et al., 2017; Candidi, Sacheli, & Aglioti, 2015; Era, Aglioti, & Candidi, 2020; Era, Aglioti, Mancusi, et al., 2020; Fini et al., 2020; Gandolfo et al., 2019; Sacheli, Candidi, Era, et al., 2015; Sacheli et al., 2012; Sacheli, Christensen, et al., 2015; Sacheli et al., 2013). Interestingly, these effects are present only in situations requiring predictions of the partner's action (Era, Aglioti, & Candidi, 2020; Sacheli, Christensen, et al., 2015), highlighting the link between motor simulation and action prediction during motor interactions (Aglioti et al., 2008; Candidi et al., 2014; Panasiti et al., 2017).

The results from Soliman and colleagues suggest that the effects of interpersonal coordination on plastic reorganisations of the body schema persist over the completion of the task. It is not clear whether this 'entanglement' effect (Soliman et al., 2015) (i.e., the persistence of a shared representation of the body schema beyond the completion of the interactive task) may facilitate long-lasting interpersonal coordination and social bonding (Wolf et al., 2016). Recent research showed that long-term experience with a tool stably modifies peripersonal space (Biggio et al., 2017) and modulates internal models of sensorimotor representations, which drive the tool-based action (Biggio et al., 2020). In interpersonal interactions, the long-lasting effects of interpersonal entrainment (Dell'Anna et al., 2018) on social behaviour have been discussed in a recent review (Cross et al., 2019), suggesting its role in promoting social bonding and prosocial behaviour.

Recently, CCE modulations have been used in the context of interpersonal paradigms that involve grasping, or observing a partner grasping, an object to study the role of the object's ownership in modulating individuals' PPS representation. Extending

previous studies on the role of reaching actions in shaping PPS (Brozzoli et al., 2010; Brozzoli et al., 2009; Lohmann et al., 2019), researchers have developed a paradigm where individuals act in turn with a partner on an object (Patané et al., 2020). They assessed changes in the PPS through a visuo-tactile task, while dyads of participants either grasped or observed a partner grasping an object, whose ownership was experimentally assigned to either one of the two partners (individual ownership), or to both partners (shared ownership). Interestingly, when ownership was assigned exclusively to one participant, a stronger CCE emerged when grasping one's own object and observing others grasping their own object. Instead, no modulations of CCE were found when grasping and observing to grasp an object that was not one's own. However, when ownership was equally assigned to the two participants, the CCE modulation emerged both when the action toward the shared object was executed or observed.

Another study has shown that the PPS is also sensitive to more abstract forms of interactions, such as music making. Participants showed plastic reorganisations of the PPS (i.e., audio-tactile congruency effect) after joint jazz performance (Dell'Anna et al., 2020). More specifically, the authors asked dyads of musicians to perform a jazz improvisation in a cooperative (correct harmony) or uncooperative (incorrect harmony) condition and tested plastic reorganisation of the peripersonal space through an audio-tactile integration task, by measuring reaction times to tactile stimuli on the subjects' right hand and auditory stimuli delivered at two different distances, next to the subject and next to the partner. Results showed an increase of reaction times to tactileauditory stimuli presented near the partners' body (indexing poor crossmodal integration) only following the uncooperative condition. The authors interpreted this result as a multisensory marker of withdrawal from an uncooperative partner.

These studies indicate that crossmodal integration mechanisms characterising the representation of the space surrounding our body may be modulated by sensory sharing and sensorimotor coupling during interactions with others, suggesting that

the emergence of interpersonal multisensory integration processes may support fundamental action predictions during joint actions. In this respect, we speculate that the left anterior intraparietal sulcus (aIPS), known to code for the goal of executed (Desmurget et al., 1999; Tunik et al., 2005) and observed actions (A. F. d. C. Hamilton, 2006), as well as to support the ability to perform interpersonal complementary motor interactions (Era, Aglioti, & Candidi, 2020; Era et al., 2018; Sacheli, Candidi, Era, et al., 2015; Sacheli et al., 2018) might be involved in integrating sensorimotor information of observed and executed actions. Crucially, the studies mentioned above highlighted a causal contribution of this region in supporting complementary motor interactions where individuals need to mediate incongruent visuo-motor information. Other studies have addressed the neural underpinnings of interpersonal coordination during the occurrence of unpredicted events, which represent another situation where sensory events need to be integrated with ones' own movements. Indeed, when interacting with others, we sometimes need to deal with their errors, which represent discrepancies between expected and executed actions. Thus, motor interactions necessarily require predicting and monitoring the interactor's actions. Electroencephalographic (EEG) studies highlighted the presence of specific fronto-central markers (in particular theta/alpha synchronisation) occurring when performing errors (Luu et al., 2004) or observing errors performed by one's own avatar in a first-person perspective (Pavone et al., 2016; Pezzetta et al., 2021; Pezzetta et al., 2018; Spinelli et al., 2018). Furthermore, recent studies using transcranial alternating current stimulation provided evidence for a causal role of midfrontal theta activity during conflict monitoring (Fusco et al., 2018), and a causal role of midfrontal and occipito-temporal theta activity (observed when participants are presented with stimuli depicting hands in EEG studies, (Moreau et al., 2019; Moreau, Pavone, et al., 2018) in a task where conflict is elicited by hand stimuli (Fusco et al., 2020). Importantly for the present review, a recent study showed that the same fronto-central electroencephalographic markers (in particular theta/alpha synchronisation) registered when performing or observing errors also emerge during motor interactions

(Moreau, Candidi, Era, Tieri, & Aglioti, 2018), when prediction and monitoring of the partner's action is needed (Vesper et al., 2010). It is relevant to note that the source of the registered theta/alpha activity included frontal and occipito-temporal regions (i.e., the Extrastiate Body Area) (Moreau et al., 2020), suggesting their putative role in integrating visual and motor information during motor interactions (Era et al., 2019). Taken together, these studies highlight a fundamental role of brain regions implicated in visuo-motor transformation, known to be linked to multisensory body and PPS representations (Serino, 2019), in supporting the ability to efficiently interact with others.

In this respect, Dumas and colleagues (Dumas et al., 2020) recently provided empirical evidence for a unified model of sensorimotor and high-order cognitive processes underlying interpersonal coordination. The authors investigated the behavioural and neural mechanisms underlying a human–avatar interaction, and found a link between sensorimotor representations and attribution of intentions at a behavioural and at a neural level. Specifically, behavioural results highlighted a correlation between sensorimotor performance and the correct attribution of intention, and whole-scalp connectivity analysis of EEG data highlighted that large-scale connectivity modulations were associated with both top-down (social cognition) and bottom-up (sensorimotor) aspects during live interactions.

In the next section, we will describe how unified models of sensorimotor/multisensory and high-order cognitive processes are well-captured by the predictive coding framework (K. Friston, 2005; Rao & Ballard, 1999), which may also account for the core mechanisms underlying interpersonal motor interactions (K. Friston & Frith, 2015; Pezzulo, 2013).

4.6 Predictive coding accounts of PPS and their possible role for interpersonal interactions

Predictive coding is a computational framework that allows to explain sensorimotor processes as the brain attempts to minimise prediction errors through the generation of internal representations of the hidden causes of sensory inflow, i.e., priors (K. Friston, 2003). When applied to the case of interpersonal interactions, it is plausible that the success of interactions rests on the accuracy of our models of the causes of other people's behaviour. Specifically, in this context, priors are conceivable as models of the internal (motivational, emotional, cognitive) causes of other people's behaviour, which are coupled to our sensory inflow through forward and backward connections (K. Friston, 2003; J. M. Kilner et al., 2007a, 2007b; Pezzulo et al., 2018). Predictive coding is a framework based on minimising prediction error through recurrent interactions among different levels of a neuronal hierarchical architecture. Specifically, each level of this hierarchy employs a generative model to produce a prediction in the lower level. The generative model is connected to the lower level through backward connections, in order to compare the higher-order prediction to the lower-level representation and generate a prediction error. This prediction error is then sent to the higher level, via forward connections, to adjust the neuronal representation of the causes of sensory information (prior). This reciprocal exchange of signals continues until the prediction error is minimised and the most likely cause of the input has been modelled (K. Friston, 2003, 2018; J. M. Kilner et al., 2007b)). Originally, predictive coding accounts of the mirror neuron system (MNS) provided a hierarchical and unified neurocognitive architecture of sensorimotor transformations (involving the STS, premotor, and parietal areas) to recognise other people's intentions and action's goals (J. M. Kilner et al., 2007a, 2007b). As the somatosensory system is now considered part of this simulative network (Keysers & Gazzola, 2009; Keysers et al., 2010), Ishida and colleagues proposed a predictive coding account of shared body representations that include parietal and insular regions, integrating

exteroceptive, proprioceptive, and interoceptive information to create shared, or distinct, bodily and affective representations (Ishida et al., 2015). Importantly, it has been proposed that interpersonal predictive coding may underlie interpersonal synchronisation between the interactive partners. This would be achieved through a mutual exchange of sensory signals, generating reciprocal predictions on the partner's behaviour, which is reflected in interpersonal synchrony between neuronal states (K. Friston & Frith, 2015).

More recently, the PPS has been conceptualised, and tested, as a prior for coupling visual and proprioceptive systems, allowing for the computation of the probability that visual and proprioceptive signals are associated with each other (Noel, Samad, et al., 2018). Through statistical learning of paired visual and proprioceptive information during action execution, this prior would be updated from incoming sensory information during adaptive PPS recalibrations (Noel, Bertoni, et al., 2020; Noel, Blanke, & Serino, 2018), including PPS expansions to external objects.

Indeed, in the context of interpersonal motor interactions, the brain is challenged with the need to integrate visual or auditory (i.e., distal) and tactile-proprioceptive (i.e., proximal) information from the two partners, while behaving to achieve goals. In case these events are synchronised in time and repeated over time, the brain may solve this challenge by generating a joint representation of the two agents' PPS, forming a prior, which enables predictions on the incoming sensory information generated not only from self-actions, but also from the partner's actions, within a unified model. This idea is reminiscent of the fact that sensory sharing may enlarge PPS (Maister et al., 2015) and that humans seem to code other people's PPS too (Brozzoli et al., 2013).

One way to realise sensorimotor sharing is to reuse one's own internal representations of "what it is like" to perform the action of our interactive partner (i.e., motor and somatic simulation). A recent study adopting an interactive paradigm explored how individual or shared predictive models enable compensatory movements while two partners lift a glass-like object from the partner's tray, either simultaneously

or sequentially, or from their own tray (Pezzulo et al., 2017). Results showed that participants' compensatory movements to balance the tray while the partner was lifting the glass were reduced when they were simultaneously lifting the partners' glass, compared to lifting each other's glasses sequentially. This evidence indicates that performing the action allowed participants to access sensorimotor information paired with the movement, which was used to predict and accordingly adjust for the effects of the other person's lifting. Moreover, the authors interpreted these results as evidence to support the hypothesis that co-actors did not combine two sets of forward models (one for self-movement and one for the other's movement) to predict the outcome of the joint action, but reused a bimanual model (i.e., a model which generates predictions on the outcome of their movement when they lifted the glass from their own tray) while performing simultaneous joint action, thus using a unified model to generate predictions on the synchronous lifting. Conversely, in the sequential condition, when lifting and balancing were performed in turns, the participants used two separate, unimanual models. The authors suggested that the bimanual model was more effective in making predictions on the outcome of the partners' lifting, compared to the unimanual model, because it formed a joint motor plan, where sensory information from self-movement was used to make predictions on the partners' movement. Crucially, this experiment provided the first evidence for an 'agent neutral' predictive model of joint action.

Interpersonal predictive coding could also play a role in the development of social skills during infancy. Recent computational views of typical and atypical predictive learning (Nagai, 2019; Philippsen & Nagai, 2020) propose that higher-order social functions develop from becoming able to master the laws of interpersonal sensorimotor coupling. Specifically, the authors suggested that predictive learning of sensorimotor signals plays a key role in early cognitive development, in particular in distinguishing the self from others, imitating gestures, understanding other people's actions, and sharing emotions. Importantly, these skills and the underlying neural systems develop through primary social interactions, which are grounded in senso-

rimotor mutual exchanges between the infant and caregiver (R. P. Hobson, 2008; Marshall & Meltzoff, 2015).

4.7 Plastic representations of the body and PPS in typical and atypical development

In the previous sections, we proposed that interpersonal motor interactions induce plastic reorganisations of body and PPS representations, and, on the basis of predictive coding accounts, we outlined how high-order social communication may be grounded in low-level, interpersonal embodied processing. Here, we aim at exploring how these processes may operate differently in individuals with atypical neurodevelopment (i.e., Autism Spectrum Disorder). Autism Spectrum Disorder (ASD) is a neurodevelopmental condition characterised by difficulties in social interaction and communication, as well as restricted interests and repetitive behaviours (Association, 2013). Differences in how individuals with autism process sensory and social information have been extensively shown, for instance in the domain of touch (Blakemore et al., 2006), vision (Simmons et al., 2009), auditory stimuli (O'Connor, 2012), as well as social stimuli, including faces (Adolphs et al., 2001; Dawson et al., 2005), gaze (Kliemann et al., 2012; Kylliäinen & Hietanen, 2006), biological motion (Freitag et al., 2008; Kaiser et al., 2010), emotional body language (Grèzes et al., 2009; Hubert et al., 2007), and speech prosody (Mulcahy et al., 2019).

Relevant for this work is that individuals with Autism Spectrum Disorder show reduced bodily illusions (Cascio et al., 2012; Mul et al., 2019) and smaller and more sharply defined PPS (Jp et al., 2020; Mul et al., 2019; Noel, Cascio, et al., 2017). In a recent experiment, Mul and colleagues (Mul et al., 2019) investigated autistic individuals' sensitivity to the full bodily illusion (FBI). Participants with ASD showed to be less susceptible to the FBI, as highlighted by lower scores in questionnaires of self-identification with the virtual body, and reduced changes in self-location. Moreover, ASD participants were also characterised by a smaller PPS. Interestingly,

the degree of identification with the virtual body was positively correlated with individuals' empathic traits. The authors interpreted the observed reduced plasticity of body and PPS boundaries as a marker of more pronounced self–other distinction. These results partly replicate previous findings showing delayed plastic modulations of body representations after the rubber hand illusion in children with ASD compared to Typically Developing (TD) children, and a significant association between reduced susceptibility to the RHI and lower empathy (Casio et al., 2012). Importantly, it has been shown that atypical multisensory integration in ASD encompasses interoceptive signals (Noel, Lytle, et al., 2018), having implications for empathy as well (Mul et al., 2018).

These differences in body and PPS plasticity may have important implication for difficulties in developing interpersonal motor coordination skills characterising ASD. For instance, Curioni and colleagues (Curioni et al., 2017) tested pairs of individuals with and without autism in a social coordination task, where participants engaged in a joint grasping task, where each participant was either in charge of performing a movement in accord with a received instruction (coordinating in time) or adapting to the partner's movement (coordinating in time and space). The results of this study highlighted that the strength of autistic traits negatively correlates with participants' ability to modulate their behaviour according to their role in the interaction, suggesting reduced disposition to attune with the partner in individuals with stronger autistic traits.

Initial evidence of the lack of plastic modulations of the PPS in a social context in autistic individuals is provided by a recent work by Noel and colleagues (Noel, Paredes, et al., 2020), who used EEG to investigate changes in the PPS induced by the presence of another individual in two groups of ASD and TD. Participants engaged in a tactile detection task while visual stimuli were presented in the near and far space in a social (the experimenter sat in front of them, at a distance of 150 cm) or non-social situation (they performed the task being alone in the room). In line with their hypothesis, electrophysiological markers of PPS remapping, reflecting changes

in neural activity underlying multisensory processing, were modulated by the social context in TD but not ASD individuals, confirming inflexibility of their PPS in the presence of others. Moreover, the authors proposed a biologically plausible neural network of the observed EEG responses, based on Hebbian plasticity, highlighting that the PPS rigidity in ASD would be based on changes in excitatory and inhibitory connections at the level of multimodal areas. More broadly, the authors interpret their findings in the framework of a Bayesian account and suggest an inflexible updating of priors in ASD.

Remarkably, a Bayesian account of autism have been previously proposed (Pellicano & Burr, 2012; Sevgi et al., 2019). Pellicano and Burr (Pellicano & Burr, 2012) first suggested that atypical sensory processing in autism might be explained in terms of weaker (hypo) Bayesian priors, i.e., when processing current sensory information, autistic individuals rely less on internal models based on previous sensory experience. This hypothesis provides an appropriate explanation for hypersensitivity to sensory information characterising autism (Baranek et al., 2007; Baron-Cohen et al., 2009; Green et al., 2018; Kern et al., 2006) having implications for social difficulties as well (Green et al., 2018; Hilton et al., 2010), although hyposensitivity to sensory stimuli has also been observed (Ward et al., 2017), see (Rogers & Ozonoff, 2005) for a review. This model was then reformulated within the predictive coding framework (K. J. Friston et al., 2013; Lawson et al., 2014; Van Boxtel & Lu, 2013; Van de Cruys et al., 2014)), providing a unified account of atypical sensory, cognitive, and social computations in ASD (Bolis & Schilbach, 2018)).

The Bayesian account of intersubjectivity recently proposed by Bolis and Schilbach (Bolis et al., 2017; Bolis & Schilbach, 2018) is of particular interest for the scope of this work. In particular, the authors propose that poor interpersonal coupling in social interactions in ASD compared to TD might be a result of different predictive styles across these populations. This proposal is grounded in the idea that social interactions are a key factor in the formation of consciousness and higherorder human psychological processes (Vygotsky, 1980). This idea also has many antecedents in

the domain of attachment during infant development, such as Bowlby's attachment theory (Bowlby, 1969, 1973, 1980), arguing that early interactions with the caregiver shape our cognitive and affective style in social interactions during further stages of development.

More recently, Fotopoulou and Tsakiris (Fotopoulou & Tsakiris, 2017) proposed that embodied interactions with other people in early infancy shape our capacity to distinguish the self and other, and contribute to building the bodily sense of self. In their account, feelings of body ownership may develop through early multisensory integration mechanisms, encompassing exteroceptive (i.e., visual, auditory), proprioceptive, and interoceptive signals (Fotopoulou & Tsakiris, 2017).

In accord with this idea, multisensory integration mechanism in infants have been described in a study showing that infants look preferentially at visual face stimuli being touched in synchrony with their own face and are able to discriminate visuo-tactile synchrony from visual-tactile asynchrony (Filippetti et al., 2013). According to Fotopoulou and Tsakiris' account, during parents-child interactions in early infancy, caregivers offer naturalistic "matching" between multisensory stimuli in an interactive frame, such as the experience of perceiving tickling and giggling at the same time. These experiences would underlie early mentalisation of one's own body, and differentiation with other people's bodies, structured as a Bayesian inference enabling self or other attribution of the sensory experience through statistical learning.

With relation to ASD, it has been proposed that early interactions between autistic toddlers and the social environment would be characterised by reduced innate orientation towards social stimuli (Dawson et al., 1998; Dawson, Toth, et al., 2004) during early stages of development, having cascade effects on the maturation of the so-called social brain. Specifically, this reduced engagement with the social environment may shape differently ASD sensory and social processing (R. P. Hobson & Hobson, 1993). Future research should investigate the role of early interpersonal sensorimotor interactions in shaping the mechanism of the underlying body and PPS

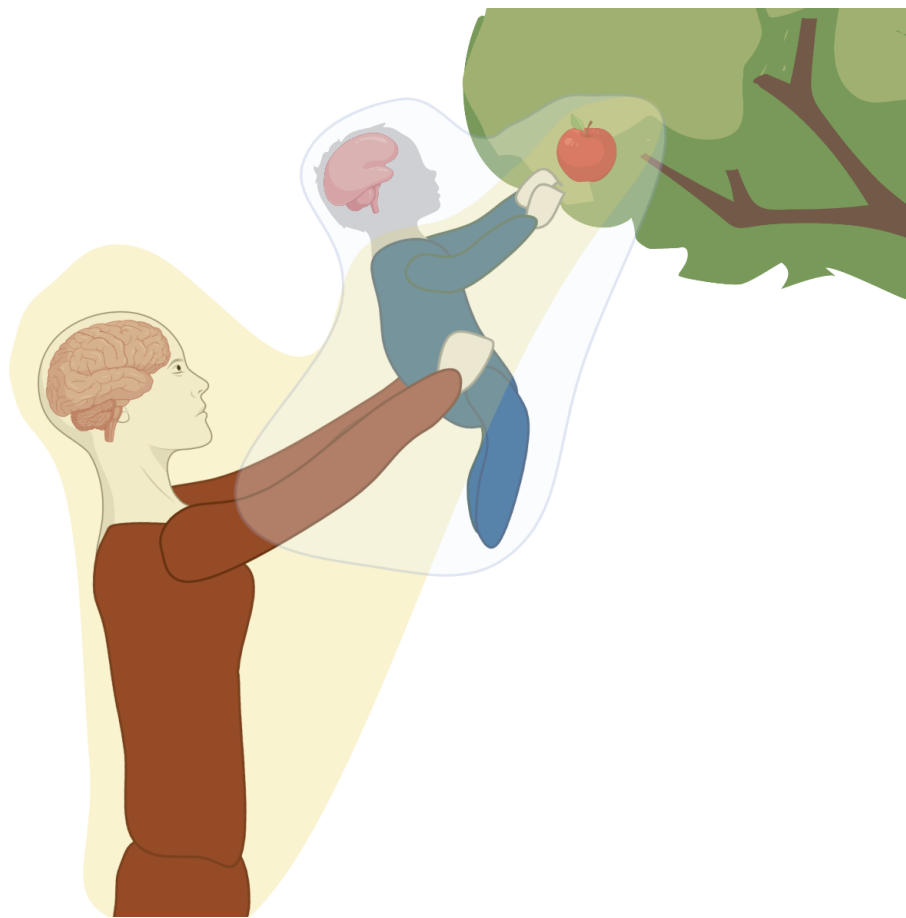


Figure 4.2. Early interactions shape embodied representations of self and others. The bodily sense of self in infants may develop through multisensory integration mechanisms occurring during interactions with the caregiver

representations in the typical population and neurodevelopmental and psychiatric conditions.

4.8 Conclusions

The main purpose of this work was to develop a conceptual framework for the hypothesis of a joint PPS, which would arise to facilitate interpersonal coordination during joint action. In particular, we proposed that this mechanism would have advantages for predicting and aligning with the partners' actions, with potential implications for inferring their high-order mental states. First, we described how multisensory representations of the body and PPS are modulated by actions, and showed how the body schema and the peripersonal space can be temporarily extended to incorporate tools, or other body parts, for instance during bodily illusions. We proposed the hypothesis of the formation of shared body and peripersonal space representations during interpersonal interaction and discussed findings suggesting the creation of an 'entangled' body schema and joint PPS, after two individuals engaged in a task which required interpersonal sensorimotor coordination. Then, we reviewed how body and PPS representations have been interpreted in the context of predictive coding frameworks, which may have important implications for mutual coordination during interpersonal interactions. Finally, we considered how this mechanism might operate differently in individuals with autism spectrum disorder, with relation to traditional and contemporary theories emphasising the role of early interactions in constructing embodied representations of self and others.

Future research will need to expand our knowledge of the neurophysiological, behavioural and computational mechanisms underlying plastic reorganisation of the PPS during and after joint action, linking multisensory and sensorimotor representations to feelings, intentions, and other high-order mental states, in typical and atypical development.

Chapter 5

Entangled body schema in joint action

5.1 Introduction

In the past decades, the idea that a turn from ‘individualism’ towards ‘interactionism’ (Gallotti & Frith, 2013) or ‘two-persons neuroscience’ (Hari & Kujala, 2009) would lead towards a better understanding of social cognition and its neural substrates has attracted the interest of the scientific community. Due to this ‘interactionist turn’, in the past years researchers have developed interactive paradigms suitable for investigating dyadic or group dynamics and their neural underpinnings (Candidi et al., 2017; Dumas et al., 2014; Era et al., 2018; Moreau et al., 2020; Sacheli, Candidi, Era, et al., 2015; Soliman et al., 2015).

Performing successful social interactions is grounded in the capacity of agents to co-represent the goal of the interaction, as well as a shared space through multisensory predictive mechanisms. According to Pezzulo and his colleagues (Pezzulo et al., 2013), in the context of social interactions, neurocognitive mechanisms for sensorimotor transformations and multisensory integration incorporate information relative to the co-actor. In the motor domain, Kilner and colleagues (J. M. Kilner et al., 2004) showed that motor activity could occur prior to observing someone else’s

action and suggested that this would enable people to anticipate others' actions. Further experiments involving interactive tasks showed that our ability to coordinate with a partner relies upon moment-to-moment prediction and integration of visual and motor information (Moreau, Candidi, Era, Tieri, & Aglioti, 2018; Sacheli et al., 2012). Nevertheless, the role of the body schema in the context of joint action is still poorly understood.

Interestingly, it has been suggested that shared bodily representations formed during interactions can be used as coordination tools (Pezzulo et al., 2011). In a recent study, Soliman and his colleagues (Soliman et al., 2015) proposed that coordinating with a partner in a joint action task is associated to the formation of a joint body schema, which persists also after having completed the interaction, generating a sort of interpersonal entanglement.

A body schema is a multisensory construct represented in a brain network including the primary somatosensory (S1), secondary somatosensory (S2) cortex, premotor cortex, and primary motor cortex (N. P. Holmes & Spence, 2004). Representations of the body in the brain are characterized by plasticity. It has been shown that the body schema can be extended to include noncorporeal objects (Berlucchi & Aglioti, 1997), for instance through the 'rubber hand illusion' (Botvinick & Cohen, 1998; Pavani et al., 2000; Tsakiris & Haggard, 2005), and the incorporation of tools to extend the body's reaching space (Iriki et al., 1996). Reorganizations of body schema also trigger a redefinition of the peripersonal space (PPS), defined as a multisensory representation of the space immediately surrounding our bodies (Rizzolatti et al., 1997), involving visual, somatosensory, and proprioceptive modalities (N. P. Holmes & Spence, 2004). For a more-in-depth dissertation on the properties of the body schema and the PPS, see Chapter 4.

While behavioural measures of plastic reorganisations of the body schema in interpersonal interactions have been previously addressed (Soliman et al., 2015), the neural dynamics associated with this phenomenon are still unexplored.

The aim of our study is to test whether engaging in a joint action requiring sensori-

motor coordination with a partner induces a re-organization of the body schema of the people involved in the interaction, and if this effect persists beyond the time of the online interaction. We expect that, to complete a joint task which entails interpersonal sensorimotor synchronisation (cutting a candle with a tight rope), participants will ‘incorporate’ the other person’s limb into their own body schema by remapping the other person’s hand onto the neural representation of their own. Moreover, we expect to observe ‘entanglement’, (Soliman et al., 2015) meaning this phenomenon will not be restricted to the period of time of the interactions, but it will be characterized by a longer-lasting plastic modification of the body schema of the two partners.

In order to test our hypothesis, we will measure the brain activity of participants with electroencephalography (EEG) after completing a joint action task which requires coordinating with a partner to achieve a common goal (i.e., cutting a candle with a rope). Specifically, we will test whether interacting with a partner (joint sawing task), compared to a solo (observation) condition, induces significant modulations of multisensory body representations. These changes will be measured through a tactile detection task involving congruent and incongruent visuo-tactile stimulation on self and other’s hands. We will deliver mechanical taps on either the thumb or the index finger, to evoke Somatosensory Evoked Potentials (SEP), while a visual stimulus appears next to the thumb or index of the partner. We will collect participants’ reactions time to the tactile stimuli. Moreover, we will record electrophysiological activity with EEG, to investigate modulations in somatosensory responses to tactile stimulations induced by interpersonal entanglement.

5.2 Materials and methods

Participants. We will recruit 26 participants, who will be tested in the Cognitive and Social Neuroscience Lab at the Department of Psychology and the IRCCS Santa Lucia in Rome. We extracted this number from a power analysis based on a previous

study (Sambo & Forster, 2009) investigating modulations of SEP amplitude when visual distractors/facilitators were presented in the peripersonal space or in the far space. The software MorePower 6.0.4. The following parameters were added to the power analysis: Power: .90; Partial Eta Squared: 0.32; F: 5.17; Repeated measured design: 2*2*2*3; effect of interest: 2*2 (see the section *Statistical analysis*).

Experimental task. Participants will engage in the task developed by Soliman (Soliman et al., 2015). The task involves the participant and the confederate sitting at a distance of 100 cm at the edge of a table, in a 90° position (see Figure 5.1). A paid intern will cover the role of the confederate during the whole experiment. A wooden candle-holder (constructed for the experiment) will be attached to the table midway between the two partners. The two participants will perform the task either in a joint or in a solo condition. Each condition will be repeated 5 times, for a total of 10 sawing sessions, and will last 5 minutes. Two tools will be used in sawing. Both consist of a 60-cm-long wire with a black handle at one end. For the joint-sawing tool, another black handle will be attached to the other end of the wire. For the solo condition, the second handle will be replaced by a plumb weight. In both conditions, the goal of the action will be to cut the candle in a fixed amount of time (5 minutes for each session). In order to match both visual and proprioceptive feedback in the joint and solo conditions, participants will be sitting in a 90° position and will be able to see what the other person is doing in both conditions. During the joint condition, the participant will perform the task with the right hand and the confederate with the left hand. During the solo condition, the participant will observe the confederate performing the task on its own with the left hand. Participant will perform 10 blocks, 5 for the joint condition and 5 for the solo condition, and the order of conditions will be counterbalanced across participants.

At the end of each sawing session (5 minutes), an Entangled Body Schema (EBS) measurement will be run. Here, a visuo-tactile integration task similar to the one

developed by Maravita and colleagues (Maravita et al., 2002, adapted by Soliman et al., 2015) will be adopted. Participants will be sitting in a 90° position, consistently with their location during the sawing task. Both participants will lean their left hands on a computer screen set in an horizontal position. Tactile stimulations will be provided to the participants' left hand with a mechanical stimulator (Heijo Electronics, Beckenham, UK; www.heijo.com). Participants' feet will be placed on a double pedal (left/right foot), which will be used to collect their responses

Before starting the experimental task, we will measure individual thresholds to detect tactile stimulation, and adjust the intensity of the mechanical taps consequently for each participant. More specifically, the individual threshold will be set to the lowest intensity of tactile stimulation consciously and unambiguously detected by the participant. Two mechanical tactile stimulators will be attached to the participants left thumb and index. Visual stimuli will be delivered next to the confederate hand, laying on the horizontal computer screen, through Eprime 2.0 software. The hand of the participant will lay next to the confederate's hand, on the same computer screen, in a 90° position. The beginning of each trial will be signaled by a white fixation cross, appearing between the confederate's thumb and index, in a centred position (see Figure 5.1). Participants will be instructed to observe the fixation cross, but ignore the visual distractors. The fixation cross will last $750 \text{ ms} \pm 250 \text{ ms}$ (we added a jitter to the fixation cross' duration to avoid habituation). At the end of this time, a visual stimulus (a red dot) will appear next to the confederate's index or thumb, and 50 ms after visual onset, a congruent/incongruent tactile stimulus will be delivered on the participant's left hand, either on the thumb or the index finger. This tactile stimulation will last 100 ms. Visual and tactile stimuli offset will occur simultaneously, after 150 ms from visual onset and 100 ms after tactile onset. Participants will be asked to respond by pressing a pedal as soon as they feel the tactile stimulus. They will be instructed to press the left pedal with their left foot when they feel the tactile stimulation on their index, and the right pedal with the right foot when they feel the tactile stimulation on their thumb.

Each session will begin with a training part, composed by 10 trials (5 congruent and 5 incongruent). Each experimental session will be composed by 40 trials (20 congruent and 20 incongruent), in a randomised order. Given that participants will engage in 5 sessions for each condition (joint/solo, total 10 sessions, counterbalanced order across participants), the total number of trials for the whole experiment will be 400 trials (10 sessions*40 trials). Of these 400 trials, 200 will follow the joint condition, and 200 the solo condition. Of each condition, 100 trials will be congruent (visual stimulus delivered on the thumb/index finger of the confederate, tactile stimulus delivered on the same (congruent) finger of the participant) and 100 incongruent (visual stimulus delivered on the thumb/index finger of the confederate, tactile stimulus delivered on the other (incongruent) finger of the participant), for a total number of 200 congruent and 200 incongruent trials

. During the experimental session (tactile detection task) EEG will be recorded and amplified by NeuroscanSynAmps System by using 64 tin electrodes embedded in a fabric cap (Electro-Cap International, Eaton, OH, USA).

Statistical analysis

Behavioural data analysis

Data relative to the inverse efficiency (the ratio between RT mean and accuracy mean, see Soliman et al., 2015) will be analysed through linear mixed models in the R Software. The purpose of this analysis is to validate the effectiveness of the experimental manipulation on participants' behaviour.

EEG data analysis

SEP amplitudes: the mean amplitudes of Somatosensory Evoked Potentials (SEP) for the P50, N80, P100 and N140 will be computed for each task (joint/solo) and condition (congruent/incongruent). We will analyse the EEG data through a Repeated Measures ANOVA, in a 2*2*2*3 design, involving the following factors: Task (Joint/Solo); Condition (Congruent/Incongruent); Hemisphere (Ipsilat-

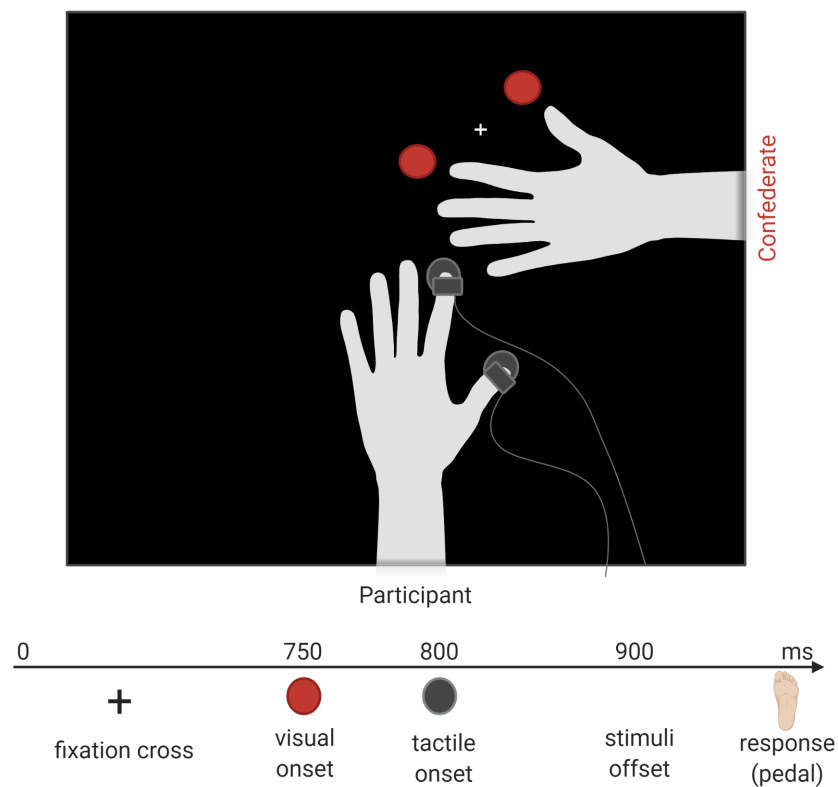


Figure 5.1. Experimental Task. The participant and the confederate will sit in a 90° position around a table during the sawing task and also during the tactile detection task. Each trial will start with a fixation cross of 750 ms \pm 250 ms, followed by a visual stimulus next to the thumb or index finger of the confederate's (used) hand. After 50 ms, a tactile stimulus will be delivered to the thumb or index of the participant's (unused) hand, for 100 ms. The participant will be instructed to press the pedal correspondent to the tactile stimulation (right: thumb; left: index) as soon as possible.

eral/Contralateral); Electrode cluster (Frontal, Central, Parietal).

Time-Frequency analysis: in addition to the ERP analysis, an exploratory time-frequency analysis will be carried out. Specifically, we will employ the Cluster Based Analysis implemented in the Fieldtrip toolbox.

5.3 Expected results

Behavioural results. We predict to replicate previous behavioural findings, showing stronger crossmodal congruency effect after the joint compared to the solo condition. Specifically, we expect to observe increased inverse efficiency in the incongruent (i.e., tactile stimulation occurring on the opposite finger of the confederate's finger where the visual stimulus was presented) compared to the congruent (tactile and visual stimuli delivered to the same finger) condition after the joint sawing task, compared to the solo (observation) task, as a consequence of the entangled body schema (Soliman et al., 2015).

EEG results. We predict to observe enhanced amplitudes of Somatosensory Evoked Potential during synchronous visual and tactile stimuli presentation as an index of increased visuo-tactile integration (Forsberg et al., 2019; Sambo and Forster, 2009), with stronger effects after the joint compared to the solo condition. Moreover, we expect to observe increased coupling in oscillatory activity across neural populations underlies visuo-tactile integration (Kanayama et al., 2021; Kanayama et al., 2012).

5.4 Discussion

Being in interaction with someone relies upon representations held collectively by both interactors rather than by each individual alone. Moreover, social interactions are often complex, dynamic and nonlinear (Froese & Paolo, 2010; Port & Gelder, 1995; Thelen & Smith, 1996), and therefore social cognition is fundamentally different

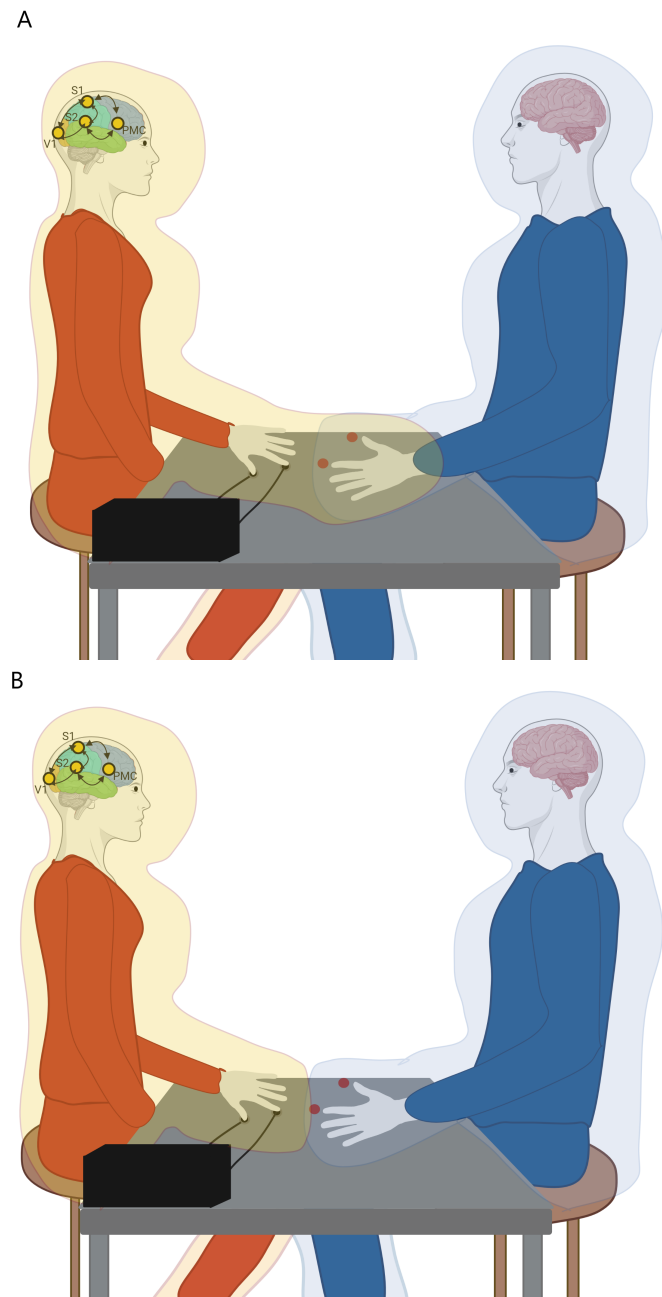


Figure 5.2. Modulations of visuo-tactile integration after joint action. We expect to observe stronger crossmodal congruency effect after the **A.** joint condition compared to **B.** the solo condition. This would reflect the formation of an entangled body schema (Soliman et al., 2015). This is a conceptual depiction of the expected results. In the experimental setting, participants will be sitting in a 90° position (see Figure 5.1), and not in front of each other.

when we are in interaction with others rather than merely observing them (Schilbach et al., 2013). For these reasons, proceedings in the field of social neuroscience requires a shift from studies on individual participants to those focusing on dyads.

Interactive paradigms has been used to study the mechanisms underlying joint attention, action observation, task sharing, action coordination and agency (Sebanz et al., 2006) as well as in pioneering experiments investigating the brain-behaviour dynamics of visuo-motor integration during social interaction (Dumas et al., 2010; Konvalinka et al., 2014; Ménoret et al., 2014; Naeem et al., 2012; Novembre et al., 2016; Tognoli et al., 2007). However, multisensory representations of body schema in interactive task are still unexplored.

Our project aimed at describing for the first time how the brain is capable of creating a temporally extended bodily representation, which is referenced on the dyad and could affect behaviour even after the joint task is completed. This could entail, for example, that, while dancing with a partner, we adjust our own body schema to coordinate, and that adjustment continues even when no longer dancing.

This could also lead to identify novel neural markers of entangled mental representations across individuals, and possibly open new perspectives in the field of distributed cognition and interbrain interconnectivity (Astolfi et al., 2010; Babiloni & Astolfi, 2014; Dumas et al., 2010; Konvalinka et al., 2014).

Moreover, understanding the dynamics underlying joint embodied representations could also have crucial implications for our understanding of typical and atypical neurodevelopment, where mother-child dyadic interaction has been shown to be crucial for the development of cognitive functions (R. P. Hobson, 2008; Johnson, 2001; Meltzoff, 2007). This would also lead to a better understanding of psychiatric conditions characterized by reduced capacity to ‘attune’ with others, such as autism spectrum disorder (Trevvarthen & Aitken, 2001).

Future developments of this experiment will be further investigating the neural dynamics underlying entangled body schema by simultaneously recording EEG from two participants during and after the task execution (hyperscanning). In this

case, it would be of particular interest to test whether we can observe significant differences in interbrain synchrony while participants engage in a joint condition (acting together upon a common goal) or a parallel condition (acting simultaneously but without pursuing a common goal). Moreover, we aim to test this experimental paradigm on individuals with Autism Spectrum Disorder, to explore whether we can observe reduced malleability of the body schema and the PPS during interpersonal interactions in people within the spectrum..

Chapter 6

General discussion and conclusions

6.1 General discussion

The aim of this thesis was to systematically examine the role of the somatosensory system in processing social information during passive observation of social stimuli and active engagement in interpersonal interactions. During the first stage of my PhD, carried out at the Cognitive Neuroscience Research Unit at City, University of London, I investigated through EEG the neural mechanisms underlying emotion perception and discrimination in individuals with and without autism spectrum disorder (Experiment 1). This experiment is contextualized in a theoretical framework proposing that emotions are essentially 'embodied', i.e., are implemented in specific patterns of physiological feelings and sensorimotor states, from which the conscious experience of emotions arise (Critchley & Nagai, 2012; A. Damasio & Carvalho, 2013; A. R. Damasio et al., 2000; James, 1884; Niedenthal et al., 2005). These somatomotor and visceral patterns can be re-enacted while observing others' expressions (Adolphs, 2002; A. I. Goldman & Sripada, 2005; Niedenthal, 2007), to facilitate the understanding of others' feelings.

Specifically, We hypothesized that ASD would be characterised by reduced em-

bodiment of the observed emotional expressions, compared to typically developing individuals. In Chapter 1, I described an EEG experiment based on a novel methodology based on delivering task-irrelevant tactile taps to participants during an emotion discrimination task and a control gender task in 50% of trials, then dissociating visual from somatosensory activity through subtraction (Galvez-Pol, Calvo-Merino, & Forster, 2020). In a previous study (Sel et al., 2014), this methodology provided evidence of modulations of SEP amplitudes during emotion discrimination, but not gender, in the neurotypical population, highlighting somatosensory processing of emotional expressions over and above visual carryover effects. The current study replicated this methodology on two groups of autistic and typically developing individuals, hypothesizing reduced somatosensory embodiment of emotional expressions (Pitcher et al., 2008) in the ASD group. Specifically, we were interested in testing whether the somatosensory cortex of the two groups of participants (ASD, TD) would respond differently during discrimination of emotional expressions, and if these differences were associated to personality traits, such as autism, alexithymia, and interoceptive awareness.

Our results were in line with our hypothesis. The ASD group showed reduced modulations of somatosensory evoked potentials during emotion processing, compared to the TD group, and these modulations were significantly associated to the strength of autistic traits and to interoceptive awareness. Importantly, these pattern of responses were independent from differences visual processing, showing other patterns of group differences, predominantly characterised by reduced responses over occipital areas in emotion compared to gender task in the ASD group. Moreover, through the subtraction of visual-only from visual-somatosensory evoked potentials (Sel et al., 2014; Sel et al., 2020) we ensured that the observed responses were not driven by visual carryover effects.

Importantly, our results suggested a tight link between somatosensory processing of emotional expressions, difficulties in interoception, and clinical and subclinical autistic traits, as highlighted by the significant linear regressions.

Chapter 2 is devoted to provide empirical evidence on the association between somatosensory processing of emotional expressions, interoceptive accuracy, and autistic traits. Experiment 2 provides compelling evidence for a relationship between somatosensory processing of emotional expression and interoceptive accuracy in individuals with and without autism spectrum disorder. This finding represents novel evidence for the current state of art, since most of empirical studies investigating the neural basis of impaired interoception in autism focused on the role of the insular cortex (Ebisch et al., 2014; Silani et al., 2008, see DuBois et al., 2016 for a review) neglecting the possible contributions of the somatosensory cortex in triggering these difficulties.

Importantly, these experiments highlighted that the strength of autistic traits was a significant predictor of reduced somatosensory processing of emotional expressions and of reduced interoceptive accuracy. Conversely, alexithymia, which has been proposed to be at the core of emotional and interoceptive difficulties in individuals with ASD (R. Cook et al., 2013; Mul et al., 2018; Shah, Hall, et al., 2016), was not associated with reduced somatosensory processing or interoceptive accuracy. Although disentangling the causes of emotional symptoms in ASD was not the main purpose of this thesis, this finding deserves attention and can enrich the current debate in the field.

In the second part of my PhD, I developed an interactive paradigm, based on the behavioural experiment of Soliman and colleagues (Soliman et al., 2015), with the purpose of investigating changes in body representations as a consequence of joint action (Chapter 5). Specifically, this paradigm aimed at probing somatosensory responses through mechanical stimulation delivered to the participant fingers, while a visual distractor appeared next to the confederate's fingers, after motor interactions or a solo (observation) condition. We hypothesized that engaging with a partner in a motor task would lead to the formation of an entangled body schema, compared to the solo condition. We planned to test our hypothesis exploiting mechanisms of visuo-tactile integration which effectively highlighted plasticity of the

body schema and the peripersonal space (PPS) after tool use (Cardinali, Frassinetti, et al., 2009; Farnè et al., 2007; Maravita et al., 2003; Maravita et al., 2002). In fact, it is known that mechanisms of multisensory integration are sensitive to the congruency/incongruency of stimuli presented in two different sensory domains (visual-tactile) within the PPS (crossmodal congruency effect (CCE), Spence et al., 2000; Spence et al., 2004). In this experiment, we wanted to test if interacting with a partner could modulate the strength of the CCE when a visual stimulus was delivered next to the confederate's hand, and a tactile stimulus was delivered to the participants' hand. This would reflect the incorporation of the partner's limb in the participants' body schema and PPS, as observed for tools (Iriki et al., 1996; Maravita et al., 2002). Moreover, we hypothesized to observe significantly different modulations of SEP amplitudes when a congruent/incongruent visual stimulation appeared next to the partner's hand after the joint condition, compared to the solo condition, as a neural marker of increased/decreased visuo-tactile integration within the PPS (Sambo & Forster, 2009).

I further developed this conceptual framework in Chapter 4, where I proposed a theoretical explanation of recent evidence showing plastic reorganisations of the PPS during interpersonal interactions. Specifically, I argued that predictive multisensory integration occurring in one's peripersonal space supports individuals' ability to efficiently interact with others, by integrating sensorimotor signals from the interactive partners to frame them in a shared representation of the PPS. Moreover, I suggest that PPS expansions after tool use and in interpersonal interactions may be contextualized in the predictive coding framework (J. M. Kilner et al., 2007b), and could have important implications for high-order cognitive processes. Finally, I suggested how these mechanisms might operate differently in individuals with Autism Spectrum Disorder, consistently with recent evidence suggesting rigidity of peripersonal space representations and difficulties in interpersonal coordination in individuals with autism. Moreover, I contextualised this proposal within developmental theories of typical and atypical neurodevelopment emphasizing the role of

embodied interactions during infancy in shaping our social skills.

6.2 Conclusions and future directions

Overall, these studies expand our knowledge of the role of the somatosensory system in low-level as well as high-order processes underlying our capacity to understand other individuals and effectively interact with them. A deeper investigation of these dynamics would have crucial implications for our understanding of typical and atypical neurodevelopment, where mother-child dyadic interaction has been shown to be essential for the development of cognitive functions (R. P. Hobson, 2008; Johnson, 2001; Meltzoff, 2007). The first empirical study leaves an open question on the structure of the neural system underlying the observed electrophysiological responses. In fact, source analysis highlighted distributed fronto-parietal areas involved in generating somatosensory evoked potentials during emotion and gender processing. Therefore, I am currently exploring through Dynamic Causal Modelling (K. Friston et al., 2003; Garrido et al., 2007) the computational architecture underlying between group differences in EEG responses, in particular bottom-up and top-down processes which may be responsible for the observed group-differences. Similar re-analysis of EEG data, aiming at modelling the neural architecture underlying differences in EEG responses in healthy and psychiatric populations, such as schizophrenia, has been previously performed (Ranlund et al., 2016). Consistently with this background, I am currently working on a model involving forward and backward connections between visual, somatosensory and frontal areas (see for instance Zeller et al., 2016), to propose a biologically plausible model of the neural system underlying somatosensory processing of emotional expression in autistic and typically developing individuals. Another future direction of the current work may be to run an additional study on somatosensory contributions to interoception in ASD and typically developing and its relationship with emotion processing, for instance investigating modulations of Heartbeat Evoked Potentials during emotion processing and its relation with

somatosensory activations.

Importantly, the next months will be dedicated to run the experiment described in Chapter 4, if the situation concerning social distancing will allow to start with the data collection. Moreover, it may be very interesting to further develop this line of research by testing differences in changes in body and PPS representations as a consequence of motor interactions in two groups of ASD and TD individuals. Finally, it may be of interest to investigate the role of interoception in modulating changes in body and PPS representations during interpersonal interactions in typically developing and autistic individuals.

More broadly, future research will have the role to systematically investigate the role of interpersonal interactions in shaping our somatosensory and visceral responses to social situations, during the whole course of typical and atypical development, and the possible cascade effects on high-order social cognition.

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