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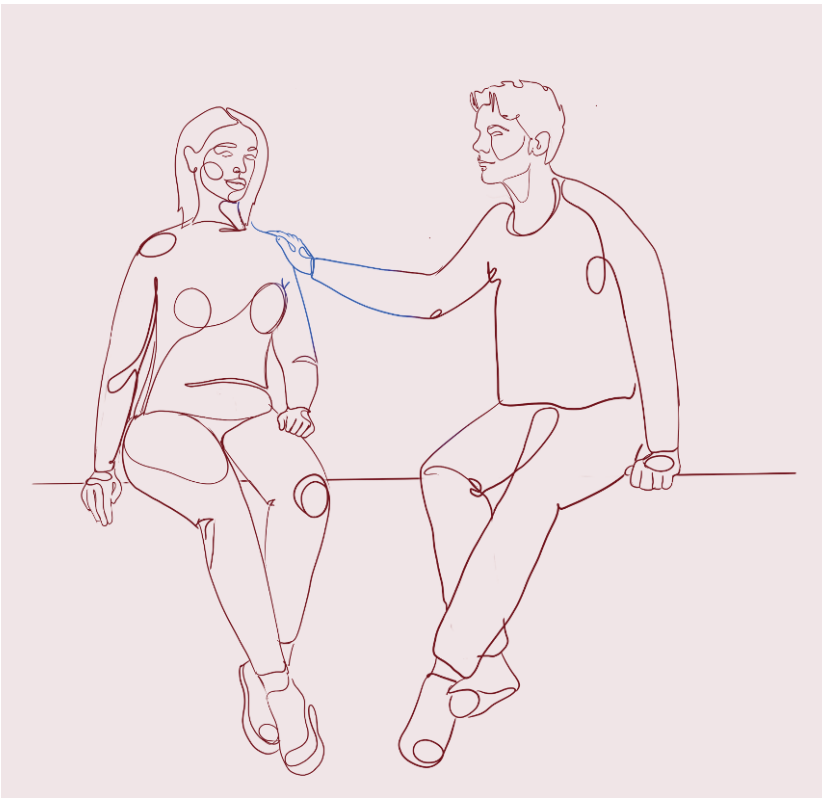
Touch and the body

First-hand and others' tactile experiences reveal the embodied nature of pleasant social touch

Manuel Mello



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The body is our general medium for having a world

Maurice Merleau-Ponty, Phenomenology of Perception

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1. General introduction

1.1. On touch, the body, and their relations

The sense of touch is an extremely fascinating sensory channel. This claim mainly stems from one specific reason: the affective meaning that touch can assume (Morrison et al., 2010). At its fundamental level, touch subserves the perception and processing of diverse tactile inputs – such as pressure and vibration, temperature, itch, pain, and proprioceptive stimuli – through the workings of specialized mechano-, thermo-, and chemo-receptors situated in the skin and joints (Mountcastle, 2005; Kandel et al., 2013; McGlone et al., 2014). For most of the sense of touch's scientific history, researchers have focused on the discriminative functions of touch (McGlone et al., 2014). When a tactile stimulus reaches the skin, as the result of a passive stimulation or an active effort of interacting with an object, the transduction of the mechanic input leads to the activation of rapidly conducting large myelinated (Aβ) afferents that transmit the signal along the dorsal column in the spinal cord and through the geniculate nucleus to the cerebral cortex (Kandel et al., 2013). The primary role of this fast-conducting tactile system is to "detect, discriminate, and identify external stimuli with a view to ultimately making rapid decisions to guide subsequent behavior" (McGlone et al., 2014, p. 737). While of paramount importance, we are certainly not here to discuss the wonders of discriminative touch.

Along with discriminative touch, it is today acknowledged the existence of a second tactile system, whose function is strictly related to the emotional life of individuals. Affective touch, what this system is called, relies physiologically on the role of unmyelinated signal-transmitting fibres, defined C-tactile (CT), whose conduction speed are in the range 0.5–2 m/s, as opposed to the more heavily myelinated Aβ fibres, and whose characteristics have been widely described within the interoceptive functions (Craig, 2002; Olausson et al., 2010). While the discovery of this type of fibres in cats traces back to the work by Zotterman (1939), it was only recently that CT afferents were reported in human's arms and legs (Vallbo et al., 1999). In fact, these afferents are mostly found in hairy, as opposed to glabrous, areas of the skin and maximally respond to gentle stroking touch, uncovering a first link between the anatomical properties of these fibres and their importance in interoceptive and affective touch functioning (McGlone et al., 2014). Löken and colleagues (2009) demonstrated the relationship between stroking speed and firing rate to be different between CT and Aβ fibres, with the former showing a U-shaped relationship between brushing velocity and mean firing rate with highest activity occurring between 1 and 10 cm/s. Importantly, subjective pleasantness of brush stroking (measured on a visual analogue scale) showed a similar inverted U-shaped function with 1 to 10 cm/s being rated as most pleasant (Löken et al., 2009; McGlone et al., 2104). The effect that the findings just described had on sparking new research on socio-affective touch is immeasurable, and I will try and provide a general picture of the importance of social touch in human and other species' life in the next section.

1.1.1. On social touch

I challenge you to think back to a moment where a tactile stimulation you experienced and originating from another person did not elicit even a minimal emotional reaction. According to the "skin as a social organ" hypothesis (Morrison et al., 2010), the sense of touch represents an extremely important facet constituting the world of social interactions – and how could we disagree. A shake of hands, a casual pat on the back, consolatory, as well as painful touch all have loaded meanings that transcend mere tactile perception (Gallace and Spence, 2010; Morrison et al., 2010; McGlone et al., 2014). The discovery of CT afferents boosted the research on pleasant touch, as it was shown that gentle stroking of the skin, especially when originating from another close individual, is associated with several positive outcomes, such as reduced stress, formation of social bonds, and the communication of positive emotions in humans and other species (Hertenstein et al., 2009; Dunbar, 2010; Gallace and Spence, 2010; Morrison et al., 2010; Cascio et al., 2019). – It has been shown that interpersonal touch with a stranger may have positive consequences too. In the classic study by Crusco and Wetzel (1984), waitresses of a restaurant were instructed to casually touch customers either on the hand, on the shoulder, or not touch them at all as they were returning the bill change. The authors found that the tipping rate of both male and female customers was higher in both touching conditions compared with the baseline no-touch condition, and they labelled this phenomenon the "Midas touch" effect (Crusco and Wetzel, 1984). Guéguen and Fischer-Lokou (2003) reported that bus drivers were more likely to give passengers a free ride if the request came with a casual touch than if it did not (Guéguen and Fischer-Lokou, 2003). Other studies, preceding and following the ones described, also demonstrated a link between interpersonal touch from a stranger and consequent positive outcomes (e.g., Fisher et al., 1976; Guéguen, 2004; Erceau and Guéguen, 2007; Joule and Guéguen, 2007).

However, the physiology of CT afferents aside, the socio-affective value of touches such as a caress ranges from extreme pleasantness (e.g., erotic, or consolatory feelings) to extreme unpleasantness (e.g., pain, disgust) depending on factors such as the age, ethnicity, sex, and sexual orientation of both the toucher and receiver, as well as factors related to the context of the tactile stimulation (Gallace and

Spence, 2010; Morrison et al., 2010; Gliga et al., 2019; Saarinen et al., 2021). For instance, the evaluation of interpersonal touch highly depends upon the touched body location within specific social contexts and/or existing emotional bonds between toucher and receiver. Suvilehto and colleagues (2015) reported relevant results on touch allowability between individuals. Utilizing an online painting task, the authors found that the total area of the body wherein people were allowed to touch the participants linearly depended on the emotional bond between toucher and receiver. For instance, partners of a romantic relationship were those that were allowed to touch basically throughout the whole body, whereas strangers were only allowed to touch areas deemed as social, such as arms and hands (with a wide range of touchability levels for parents and other relatives; Suvilehto et al., 2015). These findings demonstrate that social touch interactions and how they are perceived highly depend on the degree of familiarity and emotional bond between toucher and receiver (Suvilehto et al., 2015; Saarinen et al., 2021).

1.1.2. On social touch and human development

Social touch interactions in adulthood are scaffolded on the myriad of tactile exchanges we experience during peri-natal life, infancy, and childhood (Cascio et al., 2019). In fact, there is general consensus that interpersonal touch crucially shapes human and other species' development (Dunbar, 2010; Cascio et al., 2019; Jablonski, 2021). Touch is the first sense to develop, and during pre- and post-natal developmental periods, tactile combined with proprioceptive and vestibular stimulations (such as gentle stroking of the mother's abdomen or maternal carrying and holding) represent highly rewarding and soothing experiences that are thought to prepare the new-born to respond to social reward. Social touch, especially with the caregiver, is also extremely essential during infancy and childhood. Experimental works (e.g., Feldman et al., 2010) suggest that gentle touch between infant and caregiver has stress-reducing and analgesic effects, both short-term and long-lasting. Moreover, childhood is the developmental period in which social touch experiences extend to others beyond the caregiver, with immense repercussions on the development of the child's social life. Finally, adolescence is characterized by tactile experiences permeating the spheres of romanticism and sexuality (Cascio et al., 2019).

The importance of social touch during neural, individual, and social development is clear in cases where a deprivation or a disruption of tactile inputs during infancy has developmental consequences throughout the lifespan in both the sensory and social interaction domains (Cascio et al., 2019). One paradigmatic case of this possible scenario is autism spectrum disorder (ASD). ASD is a developmental disorder characterized by difficulties in social communication and interactions and restricted/repetitive behaviour. Sensory processing impairments and subsequent aberrant reactions to sensory stimuli, including tactile ones, are typical of ASD, such that the latest version of the Diagnostic and Statistical Manual of Mental Disorders (DSM-5) includes "hyper- and hypo-reactivity to sensory input or unusual interests in sensory aspects of the environment" as diagnostic criteria of ASD (American Psychiatric Association, 2013). Many studies, including first-hand accounts, parental reports, and clinical observations, have documented that most individuals with ASD are hypo-sensitive and/or hyper-sensitive to tactile stimuli (Kadlaskar et al., 2019). Tellingly, different tactile responsiveness patterns (such as hypo- and hyper-reactivity) have been associated with levels of communicative and social impairments in ASD (Hilton et al., 2010; Foss-Feig et al., 2012). Recent work on socio-affective touch in ASD provides specific support to the idea that not only basic tactile processing is somewhat disrupted in ASD, leading to long-term social impairments (Kadlaskar et al., 2019), but that the processing and understanding of socio-affective touch is impaired too in this clinical population. For instance, Cascio and colleagues (2016) investigated defensive responses of neurotypical (NT) children and children with ASD to unpleasant, pleasant, and social touch (touch delivered by an experimenter, as opposed to textures for the first two conditions). They reported that children with ASD showed significantly more defensiveness responses to touch compared with NT children and that this difference was more accentuated in the case of social touch. Moreover, within the ASD group, defensive responses to social touch on forearm and perioral areas highly correlated with social impairments (Cascio et al., 2016). Finally, there is evidence that the socio-affective processing of pleasant and social touch at the neural level is anomalous in children and adults with ASD (Kaiser et al., 2016; Peled-Avron et al., 2017; Masson et al., 2019).

1.1.3. On body representations that are shaped by and shape touch

Serino and Haggard (2010) put forward a model that describes the interrelations between the body and the sense of touch. First and foremost, "touch is inevitably body-referenced in the sense that the receptor surface, the skin, itself forms part of the body" (Serino and Haggard, 2010, p. 233). Tactile stimuli are initially processed by mechanoreceptors in the skin, which transmit the signal through the spinal cord to the primary somatosensory area (SI) in the cerebral cortex, where topographically organized representations of the body exist (somatosensory homunculus; Penfield and Boldrey, 1937). Thus, touches on specific regions of the body activate localized brain regions that process these sensory stimuli and, conversely, the stimulation of specific neural populations in SI (and thus the activation of the corresponding body part representation) results in tactile perceptions localized in specific body areas (Pathway 1 in Serino and Haggard, 2010). The tactile stimuli thus processed in SI are further elaborated by higher-order brain regions, such as the secondary somatosensory cortex, or SII. SII also retains a somatotopic organization (Ruben et al., 2001) and the neurons constituting it seem to process tactile information in relation to the state of the body itself, highly contributing to the formation of mental body representations (MBRs; Berlucchi and Aglioti, 2010; Serino and Haggard, 2010) (Pathway 2 in Serino and Haggard, 2010). The hypothesis that tactile information contributes to the formation of MBRs is supported by evidence stemming from studies on the rubber hand illusion (RHI, Botvinick and Cohen, 1998). These studies show that the illusory ownership of a fake hand – in other words, the formation of a mental representation of it that is incorporated into one's own body – highly depends on correlated tactile and visual inputs (e.g., Tsakiris and Haggard, 2005; Costantini and Haggard, 2007). In turn, MBRs exert a top-down influence on primary levels of tactile processing (Pathway 3 in Serino and Haggard, 2010). For instance, the visual enhancement of touch effect demonstrates that visual information pertaining the body enhances tactile acuity and facilitates tactile processing (e.g., Kennett et al., 2001; Serino et al., 2007; Serino and Haggard, 2010). Finally, cognitive representations of the body (MBRs) can influence how a primary tactile sensation is interpreted (Pathway 4 in Serino and Haggard, 2010). That is, "exteroceptive tactile perception depends on, and implicitly includes, information from MBRs. In this sense, tactile perceptions are always referenced to the body, even if the content of the perception is an external object" (Serino and Haggard, 2010, p. 233).

1.2. On the embodied nature of the (social) mind

"The brain is just like a computer; it filters in sensory information from the environment, elaborates it thanks to the functioning of a central processor (the mind), and produces an output in the form of motor behaviour" – I'm sure these exact words were spelled out at least once by a cognitive scientist in the 1950s. But this fictitious person was definitely leaving out of the picture a crucial aspect of cognition: the fact that any given mental process is tightly linked to the workings of the body. Within the classical cognitivism (CC) account, in fact, cognition is separable from the physical body, and its interactions with the environment, and the body is seen as a mere hardware enacting the commands dictated by the mind (the software). However, any given mental act unfolds within an experiencing and acting body, and the idea that all cognitive functions – including socially oriented ones – are deeply rooted in perception and action recently gained much deserved attention thanks to the embodied cognition (EC) perspective (Wilson, 2002; Gallagher, 2006; Goldman and de Vignemont, 2009; Shapiro, 2014).

On a more superficial level, body anatomy and body activity (such as posture and actions) have a causal role on (social) cognition. For instance, if we assume a specific posture or a specific facial expression, our mood or temporary emotional reactions may be affected (Wilson, 2002; Goldman and de Vignemont, 2009; Körner et al., 2015). On a more intricate level, body representations, characterized by a specific content and/or a specific format, also have a causal role on mental processes, including those having a social nature – e.g., when the automatic re-enactment of "first-hand" body representations allows us to understand others' feelings and sensations (see next section) (Wilson, 2002; Goldman and de Vignemont, 2009; Serino and Haggard, 2009; Körner et al., 2015). For instance, behaviour imitation, joint action, emotional contagion, empathy, mindreading, and language understanding all seem to possess crucial embodied features (Gallagher, 2006; Goldman and de Vignemont, 2009). See Wilson, 2002 and Goldman and de Vignemont, 2009 for thorough descriptions of the embodied cognition account.

1.2.1. On embodied simulation

Humans are endowed with the ability to understand others' feelings, which helps them to efficiently navigate the social world (Decety and Jackson, 2004; Gallese et al., 2044; de Vignemont and Singer, 2006; Keysers and Gazzola, 2009). When witnessing others' emotions and sensations, people may share the target feeling on two levels. On one hand, affective sharing allows the observer to evaluate the valence of the observed affect, whereas on the other, sensorimotor resonance permits to share its sensory and motor consequences (Keysers and Gazzola, 2009; Keysers et al., 2010; Gallese and Sinigaglia, 2011; Betti and Aglioti, 2016). Working together, these processes ultimately allow individuals to grasp what another person is experiencing in its totality.

Within the much broader EC perspective, the theory of embodied simulation provides an interesting theoretical framework for these phenomena. This account postulates that the understanding of others' emotions and sensations relies on the automatic and unconscious activation of individual embodied representations associated with the very same event (Gallese, 2005; Keysers and Gazzola, 2009; Gallese and Sinigaglia, 2011; Gallese and Ebisch, 2013). For instance, the first-hand experience of pain is characterized by an ensemble of bodily sensations, sensorimotor reactions, and conscious affect (Iannetti and Mouraux, 2010) that is automatically re-enacted when witnessing someone else in pain, thus aiding the understanding of others' feelings in painful situations. A specific prediction of this theory is that the same neural structures involved in our own experiences also underlie the automatic understanding of the emotions and sensations of other individuals (defined as vicarious activation; for an extensive review of pain empathy studies see Betti and Aglioti, 2016). Mirror neurons systems, discovered in monkeys in the 1990s (Di Pellegrino et al., 1992), fuelled the development of this view, providing a possible neural correlate for emotional and sensorimotor sharing phenomena (Keysers and Gazzola, 2006). This was demonstrated utilizing various neuroscientific techniques, including functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS). A pivotal study investigating the neural correlates of empathy for pain was run by Singer and colleagues (2004). The authors reported that harmful stimulations (electric shocks) delivered on participants' hands elicited brain activations (as measured via fMRI) that were very similar to those yielded by the same stimuli delivered to participants' romantic partners. Here, it was systematically shown, for the first time, that first-hand pain and empathy for pain shared neural activation in insular and cingulate cortices, brain areas known to underlie various aspects of affective processing (Singer et al., 2004). In another seminal work by Avenanti and colleagues (2005), the observation of others' tactile pain elicited an enhancement of somatotopic corticospinal inhibition induced via the application TMS over sensorimotor areas. This modulation was thought to represent the mapping of others' somatic experiences in one's own sensorimotor system (sensorimotor resonance; Avenanti et al., 2005). Many more studies followed, which provided support to the shared representations account (Morrison et al., 2004; Botvinick et al., 2005; Jackson et al., 2005; Morrison and Downing, 2007; Lamm et al., 2011; Betti and Aglioti, 2016).

1.2.1.1. On the embodied simulation of touch

Recent evidence has extended the shared embodied representations hypothesis to neutral and pleasant touch observation and scholars have postulated that people come to understand others' tactile experiences through the implementation of cognitive and somatic representations that are also involved in the first-hand perception of similar somatic events (Keysers et al., 2010; Peled-Avron and Woolley, 2022). This hypothesis has been initially supported by fMRI studies showing overlapping brain activation for personal and observed neutral and pleasant touch, which included higher-order and limbic areas but, importantly, also sensorimotor brain regions (such as premotor areas, SI, SII, posterior insula, inferior frontal gyrus) (Blakemore et al., 2005; Ebisch et al., 2011; Morrison et al., 2011; Schaefer et al., 2012; Lamm et al., 2015). Crucial evidence in this sense stems also from electrophysiology and neural stimulation studies, which have highlighted the sensorimotor resonance mechanisms at play and, consequently, the recruitment of the sensorimotor system when observing others' neutral and pleasant touch experiences (Wood et al., 2010; Bolognini et al., 2013; Peled-Avron et al., 2016, 2019; Schirmer et al., 2019).

1.3. On the aims of this thesis

The aim of the present thesis is to characterize pleasant social touch as an embodied phenomenon, critically depending on the many ways we perceive and interact with our own body and grounded in somato-motor representations of the self (Wilson, 2002; Gallagher, 2006; Goldman and de Vignemont, 2009; Shapiro, 2014). Perhaps, the sense of touch represents the best instance of embodied phenomenon: there is no touch without a body, and there is no body (and self) without touch (Serino and Haggard, 2010; de Haan and Dijkerman, 2020). Tactile interactions throughout the lifespan generate an ensemble of somatic sensations, conscious and unconscious feelings, and sensorimotor correlates forming embodied mental representations that shape intrapersonal and interpersonal processes (Serino and Haggard, 2010; Gallese and Ebisch, 2013; de Haan and Dijkerman, 2020).

Touch is the first sense to develop (Gallace and Spence, 2010; Cascio et al., 2019) and the impact of interpersonal touch on post-natal development is conspicuous (Bales et al., 2019; Gliga et al., 2019; Cascio et al., 2019). Mother-infant tactile interactions represent a main force driving healthy neural and social development, ensuring secure attachment, fostering the formation of emotional bonds, and setting the stage for the associative learning of social reward. Importantly, these initial interpersonal touch experiences provide the scaffolding for later social exchanges, such as those occurring during adolescence and adulthood (Cascio et al., 2019). Evidence suggests that socio-affective touch processing might be compromised in ASD (Cascio et al., 2016, 2019), with the roots of this impairment deep into basic sensory processing difficulties and its consequences leading to long-term complex social disabilities (Foss-Feig et al., 2012; Lundqvist, 2015; Kadlaskar et al., 2019). In the first work constituting this thesis – Chapter 2 –, we investigate how social touch preferences are differentially affected by various social contexts and specific body locations in typically developing and autistic adults.

But how does the *perception* of and the *sense of ownership* for our bodies affect social touch experiences? Chapter 3 deals with this interesting topic. It is framed within the perspective that the ensemble of feelings and perceptions constituting body ownership can be dramatically modified by brain damage and body ownership illusions (Maister et al., 2015). Studies have shown that illusory ownership over a virtual body can affect people's perceptions and behaviour, as well as their implicit attitudes, depending on conspicuous features of the virtual body they are embodying (Maister et al., 2015). In the study constituting Chapter 3, we utilize immersive virtual reality and the full-body illusion (Maselli and Slater, 2013) to investigate how the perception of social touch is affected by owning an opposite-sex virtual body.

Chapter 4 serves as a connection between first-hand embodied experiences – including tactile ones – and empathy for others' feelings and sensations. It examines the new emerging topic of positive empathy – of which empathy for pleasant touch is a special case – by comparing it to the much more beaten and fruitful field of empathy for pain (Betti and Aglioti, 2016). Here, we argue that embodied simulation mechanisms, at the basis of emotional sharing and widely accredited as concerns negative empathy, are likewise at play during the perception and understanding of others' positive emotions (Morelli, Sacchet, and Zaki, 2015) and sensations like pleasant touch (Keysers et al., 2010). Thus, the review presented in Chapter 4 serves the purpose of facilitating the passage from first-hand tactile experiences (Chapter 2 and 3) to tactile events that occur to others (Chapter 5).

Based on these premises, we examine the role of sensorimotor mechanisms in the observation of pleasant social touch in Chapter 5. In the study constituting this chapter, we postulate that the activation of sensorimotor representations when observing other's touch results in a generalized motor activation in the self that eventually leads to a motor facilitation effect when carrying out a simple motor task. This hypothesis is mainly based on previous studies on empathy for pain showing indeed motor facilitation following the observation of others' pain (Morrison et al., 2007a, 2007b; Galang et al., 2017, 2021).

Finally, we propose a research project aimed at examining the relation between positive empathy and prosocial behaviour in Chapter 6. Positive empathy is a rather emerging topic in social neuroscience (Morelli et al., 2015) and, while a huge amount of work has been dedicated to exploring the prosocial consequences of empathizing with others' negative emotions, still very little is known on how sharing others' positive emotions and sensations might foster prosociality (Telle and Pfister, 2016). Within this frame, the study proposed in Chapter 6 is specifically aimed at demonstrating a link between empathy for pleasant touch and prosocial behaviour.

2. Social touch experiences of neurotypical people and people on the autism spectrum are differentially affected by social context and body location

2.1. Introduction

In humans and other social species, social encounters are pervaded with tactile interactions. While allogrooming is certainly the most common type of interpersonal touch among non-human species, the complexity of human touch is apparent in everyday life (Dunbar, 2010; Gallace and Spence, 2010; Morrison et al., 2010; Jablonski, 2021). A shake of hands, a casual pat on the back, consolatory, as well as hurtful touch all have loaded meanings that transcend mere tactile perception (Gallace and Spence, 2010; McGlone et al., 2014). In fact, it is accepted to reduce the functions of touch in *discriminative*, which allows us to perceive and process the physical features of objects, and *affective*, which involves the ability to extract emotional and social meanings from a tactile event (McGlone et al., 2007, 2014).

In the psychology and neuroscience literature, different meanings have been attached to the concept of social touch. Some authors adopt a definition based on the sensory features of a target touch, such as velocity, temperature, and pressure, that make it pleasant (Löken et al., 2009). In other works, social touch includes all those tactile events that convey information about the toucher's intentions and feelings (Gliga et al., 2019; Saarinen et al., 2021). In fact, touch constitutes a powerful non-verbal communication channel through which we convey and understand a variety of emotions (Hertenstein et al., 2006, 2009). The affective value of social touches such as a caress ranges from extreme pleasantness (e.g., erotic, or consolatory feelings) to extreme unpleasantness (e.g., pain, disgust) and factors such as the age, ethnicity, gender, and sexual orientation of both the toucher and receiver, as well as factors related to the context of the tactile stimulation, have all been found to affect how touch is perceived (Gallace and Spence, 2010; Morrison et al., 2010; Gliga et al., 2019). While non-mutually exclusive, the two accounts described above focus on different aspects of social touch. Here, we refer to social touch as any interpersonal tactile experience with a social and/or affective meaning, thus approaching the second definition.

The richness of adult tactile life, with its manifold influences, is deeply rooted in the touch experiences that characterize our peri-natal, infancy and, adolescence periods (Cascio et al., 2019). There is general consensus that interpersonal touch highly shapes human and other species' development (Dunbar, 2010; Cascio et al., 2019; Gliga et al., 2021; Jablonski, 2021). Touch is the first sense to develop, and during pre- and post-natal developmental periods, tactile combined with proprioceptive and vestibular stimulations (such as gentle stroking of the mother's abdomen or maternal carrying and holding) represent highly rewarding and soothing experiences that are thought to prepare the new-born to respond to social reward. Social touch, especially with the caregiver, is also extremely essential during infancy and childhood. Experimental works (e.g., Feldman et al., 2010) suggest that gentle touch between infant and caregiver has stress-reducing and analgesic effects, both short- and long-term. Moreover, childhood is the developmental period in which social touch experiences extend to others beyond the caregiver, with immense repercussions on the development of the child's social life. Finally, adolescence is characterized by tactile experiences permeating the spheres of romanticism and sexuality (Cascio et al., 2019).

Social touch experiences are so important during neural and social development that a deprivation or a disruption of these types of inputs during infancy may have developmental consequences throughout the lifespan in both the sensory and social interaction domains (Cascio et al., 2019). One paradigmatic case of the interrelation between social touch disruption and disordered development is autism spectrum disorder (ASD). ASD is a developmental disorder characterized by impairments in social communication and interactions and restricted and repetitive behaviour. Sensory problems together with aberrant reactions to sensory stimuli, including tactile ones, are pervasive in ASD, such that the latest version of the Diagnostic and Statistical Manual of Mental Disorders (DSM-5) includes "hyper- and hypo-reactivity to sensory input or unusual interests in sensory aspects of the environment" as diagnostic criteria of ASD (American Psychiatric Association, 2013). In fact, many studies, including first-hand accounts, parental reports, and clinical observations, have documented that most individuals with ASD are hypo-sensitive and/or hyper-sensitive to tactile stimuli (Kadlaskar et al., 2019). Furthermore, different tactile responsiveness patterns (such as hypo- and hyper-reactivity and sensory seeking) have been associated with levels of communicative and social impairments in ASD (Hilton et al., 2010; Foss-Feig et al., 2012). This evidence suggests that basic tactile processing is disrupted in ASD, leading eventually to dysfunctional reactivity and long-term social impairments (Kadlaskar et al., 2019). Recent work on social touch in ASD provides more specific support to this scenario. For instance, Cascio and colleagues (2016) investigated defensive responses of neurotypical (NT) children and children with ASD to unpleasant, pleasant, and social touch (touch delivered by an experimenter, as opposed to textures for the first two conditions). They reported that children with ASD showed significantly more defensiveness responses to touch compared with NT children and that this difference was more accentuated in the case of pleasant materials and social touch. Moreover, within the ASD group, defensive responses to social touch on forearm and perioral areas highly correlated with social impairments (Cascio et al., 2016). Finally, there is evidence that the socio-affective processing of pleasant and social touch at the neural level is anomalous in children and adults with ASD (Kaiser et al., 2016; Peled-Avron et al., 2017; Masson et al., 2019).

In the present study, we build on available evidence on the disfunctions of social touch in ASD to examine differences in interpersonal tactile experiences between NT and ASD adults. More specifically, we were interested in feelings of appropriateness, pleasantness, and erogeneity elicited by daily tactile interactions. Previous studies suggest that the perception of a touch in terms of these individual experiences highly depends on social context, emotional bonds between humans, and body location (Gallace and Spence, 2010; Morrison et al., 2010; Suvilehto et al., 2015; Fusaro et al., 2021; Mello et al., 2021). To examine this, we employed an online painting task in which the participants had to rate how appropriate/inappropriate, pleasant/unpleasant, and erogenous/non-erogenous they would consider a touch in a certain social context and over their whole body. We hypothesized that ASD people would experience less appropriateness, pleasantness, and erogeneity in situations characterized by higher social and affective meaning, such as intimate and friendly contexts (as compared to professional ones). Furthermore, we expected these differences to pertain body areas that commonly elicit these sensations in specific social contexts, such as groin, chest, lower back (considered intimate areas) in intimate scenarios and hands and arms in friendly situations. Finally, we had participants complete a series of questionnaires related to the spheres of social touch perception, alexithymia, and social anxiety to investigate the relationship between social touch experiences and these individual dispositions.

2.2. Materials and methods

2.2.1. Participants

Participants included sixty-four adults with a formal diagnosis of ASD according to the DSM-5 criteria (AUT; 32 females; mean age = 35.95 years, *SD* = 10.55, range = 18-62 years) with no intellectual disability [ID; Intelligence Quotient (IQ) mean percentile = 83.61, SD = 27.76, range = 4–100] and sixty-four neurotypical adults (32 females; mean age = 35.79 years, *SD* = 10.99; range = 18-63 years) with no ID (IQ mean percentile = 92.36, SD = 11.91, range = 34–100), no neuro-psychiatric diagnosis and no first degree relatives with an ASD diagnosis. AUT and NT groups were participant-wise matched for biological sex and group-wise matched for age and IQ (Mann-Whitney U/W = 1980, p-value = 0.74). IQ was measured via the Raven's Standard Progressive Matrices (SPM) or via the Wechsler Intelligence Scales (WAIS-R or WAIS IV). Table A1 in Appendix A summarizes participants' gender identity and sexual orientation demographics.

AUT participants were required to provide a copy of their diagnostic assessment, which was carried out by an experienced clinician in ASD. To measure participants' autistic traits, they completed the Social Responsiveness Scale-Second Edition (SRS-2; Constantino and Gruber, 2012) and the Autism-spectrum Quotient (AQ; Baron-Cohen et al., 2001) self-report questionnaires. AUT and NT groups differed in their mean SRS-2 total T score (W = 3925.5, p-value < 0.001; AUT = 33.39 ± 6.73, NT = 16.39 ± 5.49) and mean total AQ score (W = 3945, p-value < 0.001; AUT = 71.66 ± 8.95, NT = 51.61 ± 7.32). For the SRS-2, 6% of AUT and 80% of NT had a total T score ≤ 59, which is considered as not associated with an ASD diagnosis (Constantino and Gruber, 2012). For the AQ, 9% of AUT and 87% of NT scored outside the Broad Autism Phenotype (BAP) (AQ ≤ 22), 9% of AUT and 11% of NT scored within the BAP (22 > AQ < 29), 31% of AUT and 1% of NT scored within the Medium Autism Phenotype (MAP, 28 > AQ < 35), 50% of AUT and 0% of NT scored within the Narrow Autism Phenotype (NAP, AQ ≥ 35) (Wheelwright et al., 2010).

The sample size was estimated using MorePower 6.0 Software, which indicated that, for a mixed design (3-level within-subjects factor * 2-level between-subjects factor), a sample of 80 participants (40 per group) was sufficient to identify a medium effect (0.06 eta^2) with at least 80% power. However, we adjusted the sample size considering the availability of participants with ASD, and consequently increased the sample size to 128 participants (64 per group).

The experimental protocol was approved by the ethics committee of the IRCCS Santa Lucia Foundation and followed the ethical standards of the 2013 Declaration of Helsinki. All participants gave their informed consent to take part in the study and were naïve to the purposes of the research.

2.2.2. General procedures

The study was run online. The primary task consisted of a painting task aimed at exploring participants' social touch experiences in different interpersonal contexts. The painting task was devised by Dr. J. Sulik as an open-source experimental tool (jsPsych plug-in; https://osf.io/5wpa2/) and modified by us according to our needs. Three interpersonal scenarios were chosen to represent an intimate, a friendly, and a professional situation wherein the participants had to imagine that touches were delivered to them by another person (see Table A2 for more information on the social scenarios). After having read the description of a scenario, participants were presented with two silhouettes representing the front and the back of their own body and were asked to rate how erogenous, pleasant, and appropriate they would consider a touch delivered by another person in that specific situation. The ratings were made by colouring the silhouettes. The colour palette ranged from yellow to blue with grey in the middle. Shades of yellow represented different levels of erogeneity, pleasantness, and appropriateness, whereas shades of blue represented different levels of non-erogeneity, unpleasantness, and inappropriateness. The central part of the palette (grey colour) represented a neutral feeling. Each participant completed the painting task for each combination of interpersonal scenario/feeling. Participants were asked to colour the silhouettes in their entirety. The part of instructions that concerned the other person in the scenario was adapted to participants' sexual orientation. Figure 2.1 shows an example of a painting trial.

The second part of the study consisted of the completion of various questionnaires, i.e.: the AQ (Baron-Cohen et al., 2001); The SRS-2 (Constantino and Gruber, 2012); the Social Touch Questionnaire (STQ, Wilhelm et al., 2001); the Toronto Alexithymia Scale (TAS-20, Bagby et al., 1994); the Adolescent/Adult Sensory Profile

(AASP, Brown and Dunn, 2002); and the Liebowitz Social Anxiety Scale (LSAS, Liebowitz, 1987).

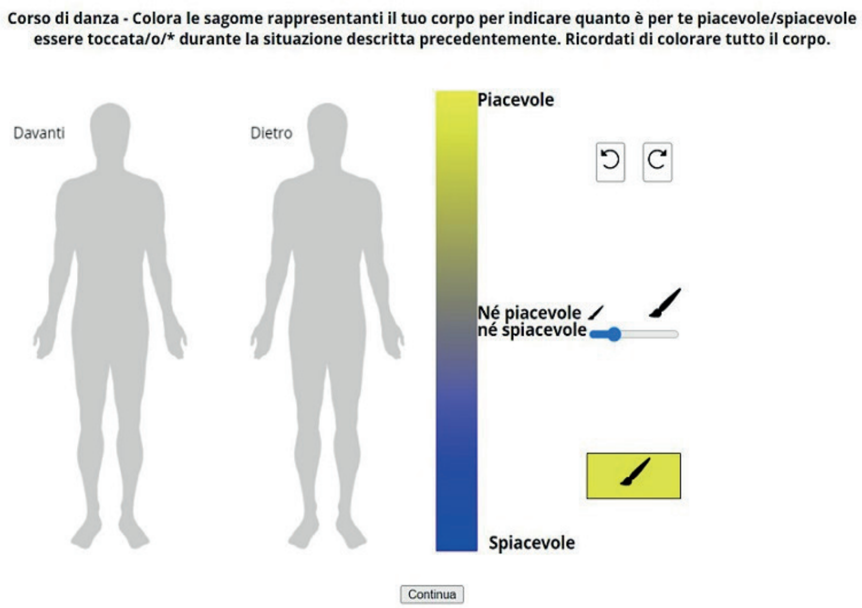


Fig. 2.1. An example of experimental trial. *English translation of Italian text:* "Dance course – Colour the silhouettes representing your body to indicate how pleasant/unpleasant you consider being touched during the scenario previously described. Remember to colour the silhouettes in their entirety". *Next to the silhouettes:* "Front/Back". *Next to the colour bar:* "Pleasant/Neither pleasant nor unpleasant/Unpleasant".

2.2.3. Questionnaires

2.2.3.1 AQ. The AQ (Baron-Cohen et al., 2001) is a 50-item self-report questionnaire measuring autistic traits across five domains: communication, social skills, attention switching, imagination, and attention to detail. The respondent rates how strongly they agree or disagree with each statement, using a four-point scale. Total score ranges from 0 to 50 and scores above 31 are indicative of autism.
2.2.3.2 SRS-2. The SRS-2 (Constantino and Gruber, 2012) is a 65-item rating scale measuring deficits in social behaviour associated with ASD. The questionnaire's subscales tap into the domains of social awareness, social cognition, social communication, social motivation, and restricted interests and repetitive behaviours.
2.2.3.3 STQ. The STQ (Wilhelm et al., 2001) is a 20-item questionnaires devised to test a variety of affects and attitudes towards social touch. Higher scores at this questionnaire represent a stronger aversion to social touch.
2.2.3.4 TAS-20. The TAS-20 (Bagby et al., 1994) is a 20-item self-report questionnaire with three subscales each tapping a component of alexithymia: difficulty identifying feelings, difficulty describing feelings, and externally oriented thinking. Total scores range between 20 and 100, with higher scores indicating more alexithymic traits. Alexithymia seems highly prevalent in people on the autistic spectrum compared to the general population, and it seems to play a role in autism emotion recognition skills and empathic responses.

2.2.3.5 AASP. The AASP (Brown and Dunn, 2002) is a 60-item self-report questionnaire evaluating responses to daily sensory experiences across various sensory modalities, including touch. The touch processing subscale of the AASP is a subscale consisting of 13 items measuring the frequency of responses to various sensory experiences. Higher scores indicate that individuals display more unusual responses to tactile stimuli, both under- and over-responsiveness.
2.2.3.6 LSAS. The LSAS (Liebowitz, 1987) is a 24-item questionnaire devised to assess the range of social interactions and performance situations that individuals with social phobia may fear or avoid. It consists of two subscales that tap into social interaction and performance situations. Higher scores at the LSAS indicate a higher probability of social anxiety disorder.

2.2.2. Data pre-processing and analysis

Data were pre-processed using Python (modules: pandas, json, collections, PIL, drawSvg, numpy). First, subject-wise painting choices were re-created offline by applying a pink background to individual strokes in each trial (combination interpersonal scenario/rating). Silhouette masks (representing front and back sections) were then overlaid to this initial image and pixels outside the masks were discarded. Lastly, body areas masks were applied to the previously masked image in order to obtain mean ratings per body area to be used in the analysis steps (see Fig. 2.2 for a graphical overview of these pre-processing steps). The body areas were 14 and included: face, shoulders (front), shoulders (back), chest, belly, hands, arms, groin, legs, feet, back of head, back (upper), back (lower), lower back. Mean ratings were obtained via image processing of the different body areas. Specifically, colour information was extracted for each pixel within a body area and the G component of each colour in the RGB dimension was divided by 255 (e.g., #0303fc == [3 3 252] RGB → pixel value = 3/255). The G component was chosen because the values that are obtained by dividing it by 255 form an informative distribution of data (ranging between 0 and 1) reflecting the participants' chosen colour (and relative feeling concerning social touch). Pixel values within a body area were then averaged. Thus, we obtained mean ratings for each body area that could range between 0 (0/255) and 1 (255/255). Although the participants were asked to colour the whole silhouettes, a portion of them did not do so. To avoid unnecessary loss of data, body areas containing more than 33% of uncoloured pixels were eliminated from the subject-wise data files (coded as NAs). When the amount of uncoloured pixels in a certain body area did not exceed the 33% of the total, these uncoloured pixels were assigned a value of 0.5. Groups did not significantly differ in the average number of body areas excluded – tested with a two-sample Mann-Whitney U test (Erogeneity: $W = 2111$, p-value = 0.73; AUT mean = 0.63 ± 1.35; NT mean = 0.55 ± 1.37. Pleasantness: $W = 2046$, p-value = 0.99; AUT mean = 0.27 ± 0.53; NT mean = 0.58 ± 1.48. Appropriateness: $W = 1992$, p-value = 0.77; AUT mean = 0.56 ± 1.24; NT mean = 0.79 ± 1.47). Likewise, groups did not significantly differ in the average proportion (per area) of uncoloured pixels that were assigned a value of 0.5 (Erogeneity: $W = 2018$, p-value = 0.88; AUT mean = 0.05 ± 0.08; NT mean = 0.05 ± 0.09. Pleasantness: $W = 1879$, p-value = 0.42; AUT mean = 0.03 ± 0.03; NT mean = 0.05 ± 0.09. Appropriateness: $W = 1971$, p-value

= 0.71; AUT mean = 0.05 ± 0.09; NT mean = 0.06 ± 0.10). For each participant, nine data files were generated containing mean ratings per body area: friendly scenario-erogeneity/pleasantness/appropriateness; intimate scenario-erogeneity/pleasantness/appropriateness; professional scenario-erogeneity/pleasantness/appropriateness.

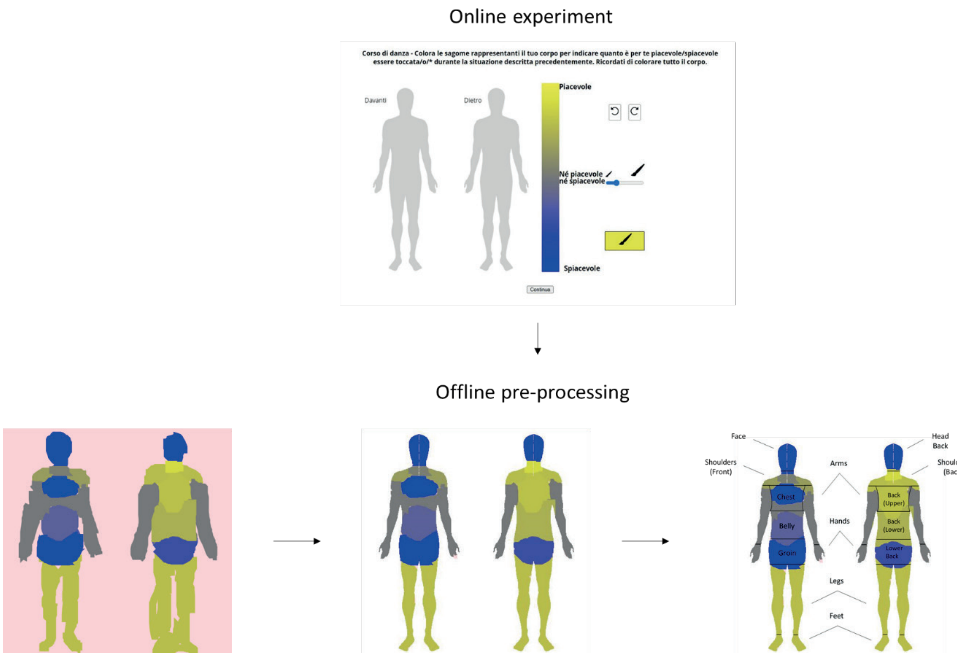


Fig. 2.2. Graphical overview of the data pre-processing steps.

Data analysis was carried out in RStudio (R Core Team, 2021). As our dependent variables (ratings of erogeneity, pleasantness, and appropriateness) were bounded between 0 and 1, we decided to linearly model them by assuming they followed a beta distribution (e.g., Verkuilen and Smithson, 2012; see Fig. A1 for graphs showing the distributions of the ratings in our sample). We did this by utilizing the glmmTMB() function from the glmmTMB package (Brooks et al., 2017), which allows to define the distribution of the outcome as belonging to the beta family, and efficiently deals with dependency in the data (within-subjects factors) and missing data. Goodness-of-fit $R^2_{conditional}$ measurements for models with erogeneity, pleasantness, and appropriateness ratings as outcome variable were, respectively, $R2_{conditional} = 1.016$, $R^2_{conditional} = 1.267$, and $R2_{conditional} = 1.659$ – however, note that this measurement is only partially reliable in the case of a beta generalized linear model (a proper goodness-of-fit measure for this case is not yet available). See also Appendix A for more information on this. For each of the ratings, planned comparisons were set for the *Scenario* and *Body area* factors using contrast coding before running the main analyses. According to our hypotheses, stated in the Introduction section, non-orthogonal contrasts were set for the *Scenario* factor comparing both the intimate and the friendly scenarios to the professional one; for the *Body area* factor, deviation coding was chosen instead (each body area was compared to the grand average of all the areas). When relevant, and especially for interaction effects, specific comparisons between conditions were examined using post hoc tests [False discovery rate (FDR)-corrected]. Post hoc tests were performed using the lsmeans() function from the lsmeans package (Lenth, 2017).

2.3. Results

2.3.1. Questionnaires

We tested between-group differences at each questionnaire by implementing two-sample Mann-Whitney U test with a significance level set at $p < 0.05$.

2.2.3.1 AQ. The AUT and NT groups differed at the AQ questionnaire: W = 3945, p-value < 0.001, with the AUT group scoring higher than the NT group (AUT mean score = 33.39 ± 6.73; NT mean score = 16.39 ± 5.49).

2.3.1.2 SRS-2. The AUT and NT groups differed at the SRS-2 questionnaire: W = 3925.5, p-value < 0.001, with the AUT group scoring higher than the NT group (AUT: mean score = 71.66 ± 8.95; NT: mean score = 51.61 ± 7.32).

2.3.1.3 STQ. The AUT and NT groups differed at the STQ questionnaire: W = 3427, p-value < 0.001, with the AUT group scoring higher than the NT group (AUT: mean score = 45.41 ± 12.26; NT: mean score = 30.19 ± 10.14).

2.3.1.4 TAS-20. The AUT and NT groups differed at the TAS-20 questionnaire: W = 3333.5, p-value < 0.001, with the AUT group scoring higher than the NT group (AUT: mean score = 57.25 ± 10.88; NT: mean score = 43.25 ± 10.75).

2.3.1.5 LSAS. The AUT and NT groups differed at the tactile subscale of the AASP questionnaire: W = 3440.5, p-value < 0.001, with the AUT group scoring higher than the NT group (AUT: mean score = 67.76 ± 23.54; NT: mean score = 37.91 ± 19.21).

2.3.1.6 AASP (tactile subscale). The AUT and NT groups differed at the tactile sub-scale of the AASP questionnaire: W = 2865, p-value < 0.001, with the AUT group scoring higher than the NT group (AUT: mean score = 37.59 ± 5.84; NT: mean score = 33.47 ± 5.44).

2.3.2. Social touch questionnaires

Below, we report the results of the analyses carried out on the painting task data.

2.3.2.1 Erogeneity feeling. Figure 2.3 graphically summarizes the results concerning the erogeneity ratings. These descriptive illustrations were created by averaging the individual images for each group and scenario separately.

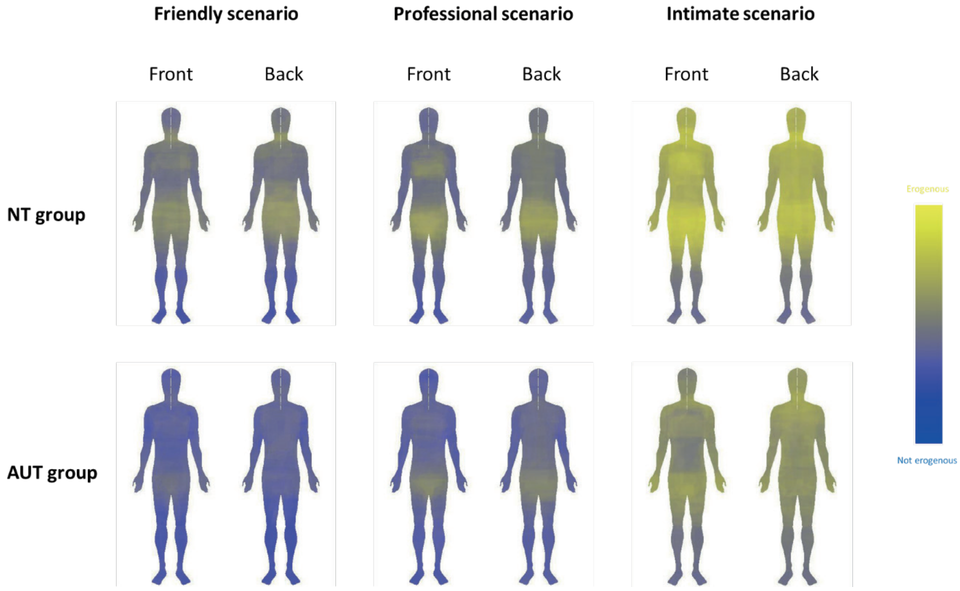


Fig. 2.3. By-group and by-scenario whole-body erogeneity images averaged across subjects.

Overall, touch was considered as more erogenous by the NT group compared to the AUT group (main effect of Group: $\chi^2(1) = 7.29$, p-value = 0.007). We found a main effect of Body area ($\chi^2(13) = 180.68$, p-value < 0.001): arms (z-value = -2.49, p-value = 0.01; mean = 0.47 ± 0.02), back (lower) (z-value = 2.26, p-value = 0.02; mean = 0.54 ± 0.02), feet (z-value = -10.02, p-value < 0.001; mean = 0.37 ± 0.02), groin (z-value = 5.66, p-value < 0.001; mean = 0.58 ± 0.02), legs (z-value = -4.4, p-value < 0.001; mean = 0.45 ± 0.02), lower back (z-value = 4.95, p-value < 0.001; mean = 0.57 ± 0.02), and shoulders (back) (z-value = 2.22, p-value = 0.02; mean = 0.53 ± 0.02) significantly differed from the grand average (0.51). The main effect of Scenario ($\chi^2(2) = 648.51$, p-value < 0.001) was explained by the intimate (z-value = 21.25, p-value < 0.001; mean = 0.65 ± 0.01) and friendly (z-value = -2.94, p-value = 0.003; mean = 0.42 ± 0.02) scenarios both differing from the professional one (mean = 0.45 ± 0.02). We found two interaction effects: the factor Group interacted with Body area ($\chi^2(13) = 27.02$, p-value = 0.01) and Scenario ($\chi^2(2) = 9.76$, p-value = 0.007). As concerns the first interaction, FDR-corrected post-hoc tests revealed that back (lower) (t-ratio = -2.44, p-value = 0.03), belly (t-ratio = -2.80, p-value = 0.01), chest (t-ratio = -2.76, p-value = 0.01), face (t-ratio = -2.51, p-value = 0.03), groin (t-ratio = -3.27, p-value = 0.004), lower back (t-ratio = -3.53, p-value = 0.002), and shoulders (front) (t-ratio = -2.44, p-value = 0.03) significantly differed between the two groups with the ratings being higher for the NT group in each case (see Appendix A for relevant descriptive statistics). Finally, AUT and NT groups differed in the erogeneity experienced within the intimate (t-ratio = -2.37, p-value = 0.02) and friendly (t-ratio = -3.24, p-value = 0.002) scenarios, with higher ratings for the NT group, but not within the professional one (t-ratio = -1.88, p-value = 0.06).

2.3.2.2 Pleasantness feeling. Figure 2.4 graphically summarizes the results concerning the pleasantness ratings.

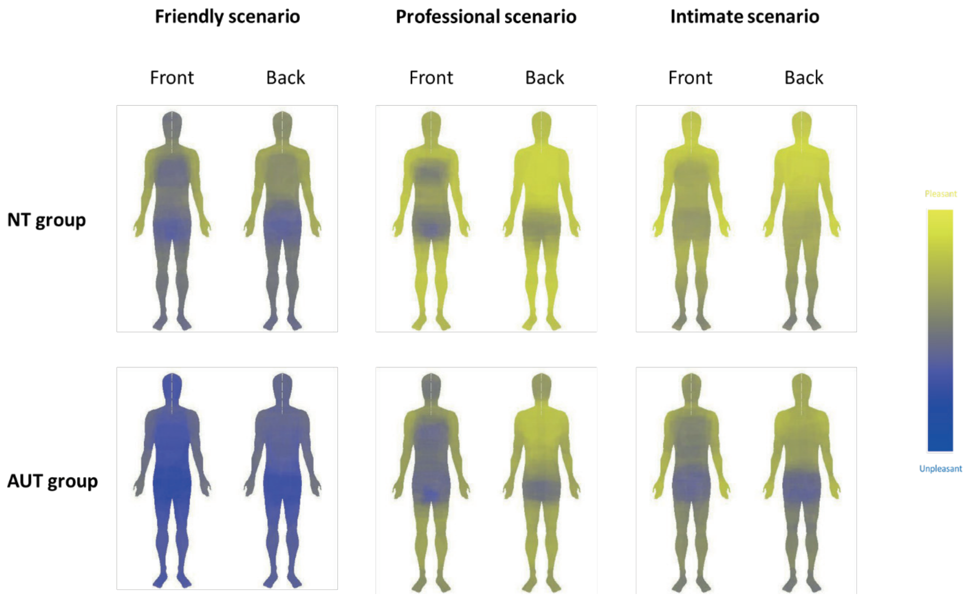


Fig. 2.4. By-group and by-scenario whole-body pleasantness images averaged across subjects.

Overall, touch was considered as more pleasant by the NT group compared to the AUT group (main effect of Group: $\chi^2(1) = 19.15$, p-value = 0.007). The main effect of Body area ($\chi^2(13) = 364.92$, p-value < 0.001) was explained by arms (z-value = 4.80, p-value < 0.001; mean = 0.66 ± 0.02), back (upper) (z-value = 6.10, p-value < 0.001; mean = 0.67 ± 0.02), belly (z-value = -6.00, p-value < 0.001; mean = 0.51 ± 0.02), chest (z-value = -4.71, p-value < 0.001; mean = 0.53 ± 0.02), feet (z-value = -3.96, p-value < 0.001; mean = 0.54 ± 0.02), groin (z-value = -9.83, p-value < 0.001; mean = 0.46 ± 0.02), hands (z-value = 6.97, p-value < 0.001; mean = 0.68 ± 0.02), back of head (z-value = 4.29, p-value < 0.001; mean = 0.65 ± 0.02), lower back (z-value = -6.68, p-value < 0.001; mean = 0.51 ± 0.02), shoulders (back) (z-value = 7.79, p-value < 0.001; mean = 0.69 ± 0.02), and shoulders (front) (z-value = 2.18, p-value = 0.02; mean = 0.62 ± 0.02) significantly differing from the grand average (0.59). The main effect of Scenario ($\chi^2(2) = 834.06$, p-value < 0.001) was explained by the friendly scenario (z-value = -25.98, p-value = 0.003; mean = 0.44 ± 0.02) differing in pleasantness ratings from the professional one (mean = 0.67 ± 0.01). We found two interaction effects: the factor Scenario interacted with Body area ($\chi^2(26) = 91.61$, p-value < 0.001) and Group ($\chi^2(2) = 17.10$, p-value < 0.001). Table A6 summarizes the significant differences in pleasantness for specific areas between different scenarios (FDR-corrected post-hoc tests). AUT and NT groups differed in the pleasantness experienced within intimate (t-ratio = -3.82, p-value < 0.001), friendly (t-ratio = -5.37, p-value < 0.001), and professional scenarios (t-ratio = -3.38, p-value = 0.001), with lower ratings for the ASD group in each condition.

2.3.2.3 Appropriateness feeling. Figure 2.5 graphically summarizes the results concerning the appropriateness ratings.

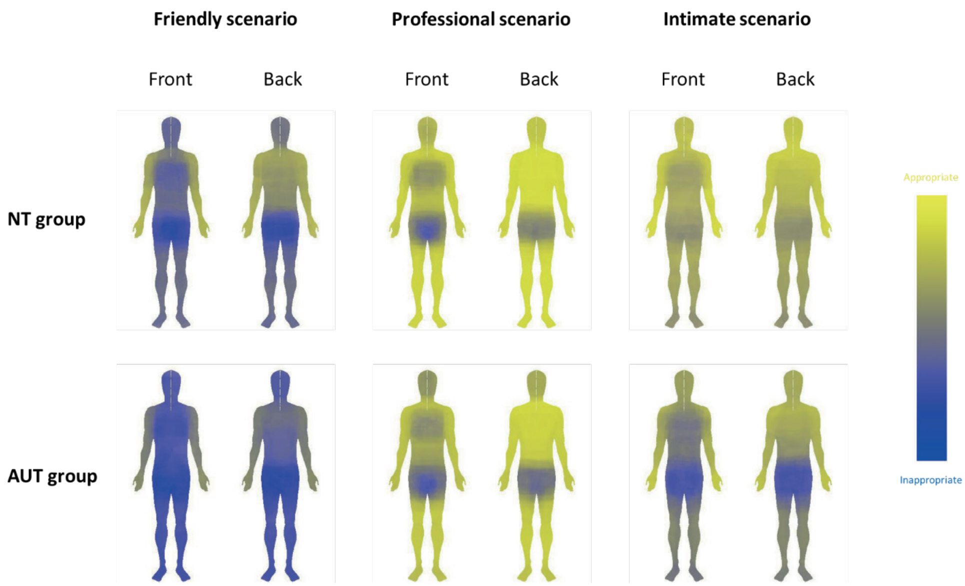


Fig. 2.5. By-group and by-scenario whole-body appropriateness images averaged across subjects.

Overall, touch was considered as more appropriate by the NT group compared to the AUT group (main effect of Group: $\chi^2(1) = 14.13$, p-value < 0.001). We found a main effect of Body area ($\chi^2(13) = 515.21$, p-value < 0.001) whereby arms (z-value = 7.06, p-value < 0.001; mean = 0.69 ± 0.02), back (upper) (z-value = 6.67, p-value < 0.001; mean = 0.68 ± 0.02), belly (z-value = -4.53, p-value < 0.001; mean = 0.53 ± 0.02), chest (z-value = -4.39, p-value < 0.001; mean = 0.53 ± 0.02), groin (z-value = -12.65, p-value < 0.001; mean = 0.41 ± 0.02), hands (z-value = 8.96, p-value < 0.001; mean = 0.71 ± 0.02), back of head (z-value = 3.09, p-value = 0.002; mean = 0.63 ± 0.02), lower back (z-value = -11.41, p-value < 0.001; mean = 0.43 ± 0.02), shoulders (back) (z-value = 8.38, p-value < 0.001; mean = 0.70 ± 0.02), and shoulders (front) (z-value = 2.28, p-value = 0.02; mean = 0.63 ± 0.02) significantly differed from the grand average (0.59). The main effect of Scenario ($\chi^2(2) = 1055.26$, p-value < 0.001) was explained by the friendly (z-value = -32.54, p-value < 0.001; mean = 0.42 ± 0.01) and intimate (z-value = -8.62, p-value < 0.001; mean = 0.65 ± 0.01) scenarios both differing in appropriateness ratings from the professional one (mean = 0.72 ± 0.01). We found two 2-way interaction effects whereby the factor Scenario interacted with Body area ($\chi^2(26) = 107.82$, p-value < 0.001) and Group ($\chi^2(2) = 35.78$, p-value < 0.001). Table A7 summarizes the significant differences in appropriateness for specific areas between different scenarios (FDR-corrected post-hoc tests). AUT and NT groups differed in the appropriateness experienced within the intimate (t-ratio = -4.51, p-value < 0.001) and friendly (t-ratio = -4.79, p-value < 0.001) scenarios, with higher ratings for the NT group, but not within the professional one (t-ratio = -1.53, p-value = 0.13). Finally, we found a 3-way interaction effect ($\chi^2(26) = 41.95$, p = 0.02). Table 2.1 summarizes the significant findings obtained by running FDR-corrected post-hoc tests (by-group and by-scenario differences for each area).

		AUT vs NT **Friendly scenario** t-ratio, p-value	AUT vs NT **Intimate scenario** t-ratio, p-value	AUT vs NT **Professional scenario** t-ratio, p-value
Appropriate-ness	Arms	**-3.27, 0.002**	-1.79, 0.10	-0.38, 0.75
	Back (lower)	**-3.28, 0.002**	**-3.25, 0.002**	-0.74, 0.52
	Back (upper)	**-3.83, < 0.001**	-1.47, 0.18	-0.44, 0.71
	Back of head	**-2.90, 0.006**	-1.94, 0.07	-1.58, 0.15
	Belly	**-2.28, 0.03**	**-3.36, 0.001**	-0.86, 0.45
	Chest	**-2.52, 0.01**	**-2.43, 0.02**	-0.21, 0.86
	Face	-1.81, 0.09	**-2.19, 0.04**	-1.41, 0.20
	Feet	**-2.57, 0.01**	-1.39, 0.20	-0.91, 0.42
	Groin	-0.70, 0.55	**-4.94, < 0.001**	-1.04, 0.35
	Hands	**-3.09, 0.003**	**-2.90, 0.005**	-0.65, 0.56
	Legs	**-2.47, 0.02**	**-2.53, 0.01**	-0.72, 0.53
	Lower back	-1.01, 0.37	**-5.08, < 0.001**	-1.75, 0.11
	Shoulders (front)	**-3.51, < 0.001**	-2.09, 0.05	-0.74, 0.52
	Shoulders (back)	**-3.64, < 0.001**	-1.52, 0.17	-0.23, 0.85

Tab. 2.1. Between-group significant differences for specific body locations and social contexts. Obtained implementing FDR-corrected post-hoc tests.

2.3.2.4 AQ models. Besides group differences in social touch experiences, we were also interested in examining whether participants' autistic traits (AUT and NT groups combined) would predict scores at the three rating scales (erogeneity, pleasantness, and appropriateness). To explore this, we ran linear models replacing the factorial predictor *Group* with the continuous predictor *AQ*, which represents the individual scores at the AQ questionnaire (Baron-Cohen et al., 2001). We hypothesized that higher AQ scores would predict lower ratings at each of the three feeling scales. Trend analyses with AQ as continuous predictor were performed using the emtrends() function from the emmeans() package (Lenth, 2020).

Erogeneity. Higher AQ scores significantly predicted lower erogeneity ratings ($\chi^2(1)$ = 7.72, p-value = 0.005). Furthermore, AQ interacted with both Body area ($\chi^2(1)$ = 23.52, p-value = 0.03) and Scenario ($\chi^2(1)$ = 32.91, p-value < 0.001). Trend analyses revealed that higher AQ predicted lower erogeneity for belly (t-ratio = -3.08, p-value = 0.04), chest (t-ratio = -3.36, p-value = 0.03), groin (t-ratio = -3.21, p-value = 0.04), and lower back (t-ratio = -3.71, p-value = 0.01) compared to feet. Finally, higher AQ predicted lower erogeneity for friendly (t-ratio = -5.71, p-value < 0.001) and intimate (t-ratio = -3.34, p-value = 0.001) scenarios compared to the professional one, and for the friendly compared to the intimate scenario (t-ratio = -2.26, p-value = 0.02).

Pleasantness. Higher AQ scores significantly predicted lower pleasantness ratings ($\chi^2(1)$ = 24.42, p-value < 0.001). AQ interacted with Scenario ($\chi^2(1)$ = 25.47, p-value < 0.001): higher AQ predicted lower erogeneity for friendly (t-ratio = -5.04, p-value < 0.001) and intimate (t-ratio = -2.85, p-value = 0.006) scenarios compared to the professional one, and for the friendly compared to the intimate scenario (t-ratio = -2.19, p-value = 0.02).

Appropriateness. Finally, higher AQ scores significantly predicted lower appropriateness ratings ($\chi^2(1)$ = 12.46, p-value < 0.001). AQ interacted with Scenario ($\chi^2(1)$ = 53.79, p-value < 0.001): higher AQ predicted lower erogeneity for friendly (t-ratio = -6.41, p-value < 0.001) and intimate (t-ratio = -6.33, p-value < 0.001) scenarios compared to the professional one, while the trends did not differ for the friendly compared to the intimate scenario (t-ratio = -0.05, p-value = 0.95). See Appendix A for more information on the trend analyses carried out.

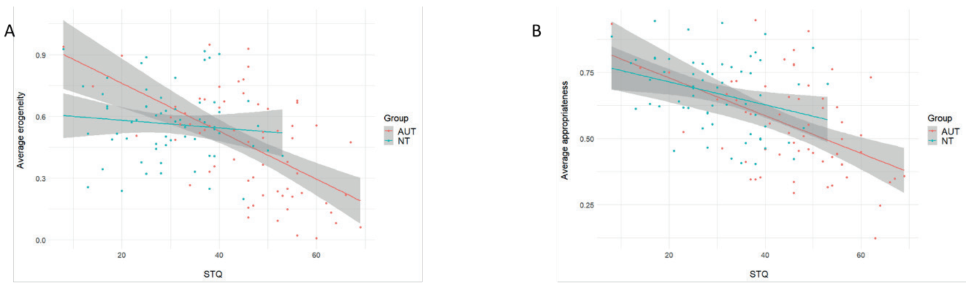
2.3.2.5 Mediation analyses. The co-occurrence of ASD with alexithymia and social anxiety is highly prevalent (Bejerot et al., 2014; Gaigg et al., 2018; Poquérusse et al., 2018; Spain et al., 2018; Kinnaird et al., 2019). Moreover, a recent study reported a strong positive association between autistic traits and social touch aversion as measured via the STQ (Ujiie and Takahashi, 2022) – also replicated in the present study (see Appendix A). As these factors could partly explain our results on the modulation of social touch preferences by AQ scores, we decided to run a series of mediation analyses investigating the direct and mediated effects (by alexithymia, social anxiety, and social touch avoidance) of AQ on social touch experiences. Three parallel mediation analyses were run for each social touch rating scale with AQ as predictor and TAS-20, LSAS, and STQ as mediators [using the sem() function from the lavaan package (Rosseel, 2012)]. We used bootstrapping (1000 samples) to estimate standard errors and confidence intervals.

Erogeneity. The effect of AQ on erogeneity ratings was fully mediated by individual scores at the STQ questionnaire (indirect effect: estimate = -0.008, z-value = -3.84, p-value < 0.001; direct effect: estimate = 0.001, z-value = 0.52, p-value = 0.60; total effect: estimate = -0.005, z-value = -2.84, p-value = 0.005). The effect of AQ on erogeneity ratings was not mediated by TAS (indirect effect: estimate = 0.001, z-value = 0.39, p-value = 0.69) nor LSAS (indirect effect: estimate = 0.001, z-value = 0.61, p-value = 0.54) scores.

Pleasantness. The effect of AQ on pleasantness ratings was fully mediated by STQ (indirect effect: estimate = -0.008, z-value = -5.16, p-value < 0.001; direct effect: estimate = 0.000, z-value = 0.02, p-value = 0.98; total effect: estimate = -0.008, z-value = -5.63, p-value < 0.001). The effect of AQ on pleasantness ratings was not mediated by TAS (indirect effect: estimate = 0.001, z-value = 0.73, p-value = 0.46) nor LSAS (indirect effect: estimate = -0.001, z-value = -0.72, p-value = 0.47) scores.

Appropriateness. The effect of AQ on appropriateness ratings was fully mediated by STQ (indirect effect: estimate = -0.005, z-value = -3.46, p-value = 0.001; direct effect: estimate = 0.001, z-value = 0.35, p-value = 0.73; total effect: estimate = -0.005, z-value = 3-90, p-value < 0.001) and LSAS (indirect effect: estimate = -0.003, z-value = -1.99, p-value = 0.04; direct effect: estimate = 0.001, z-value = 0.35, p-value = 0.73; total effect: estimate = -0.005, z-value = 3-90, p-value < 0.001), but it was not mediated by TAS (indirect effect: estimate = 0.002, z-value = 1.95, p-value = 0.05). See Appendix A for more information on the mediation analyses.

2.3.2.6 Correlation analyses. In this section, we will explore the associations between social touch preferences and individual dispositions regarding social touch aversion, tactile sensory processing, alexithymia, and social anxiety in the two experimental groups. We used Spearman's rank correlation and FDR correction to account for multiple comparisons. We found that average erogeneity (mediated across body locations and social scenarios) negatively correlated with social touch aversion in the AUT group (STQ; ϱ = -0.58, p-value < 0.001) but not in the NT group (STQ; ϱ = -0.08, p-value = 0.52) (Fig. 2.6A). Average erogeneity was not associated with social anxiety (LSAS; AUT: ϱ = -0.06, p-value = 0.59; NT: ϱ = -0.11, p-value = 0.41), alexithymia (TAS; AUT: ϱ = -0.09, p-value = 0.51; NT: ϱ = 0.12, p-value = 0.41), or sensory processing (AASP-Tactile; AUT: ϱ = -0.19, p-value = 0.17; NT: ϱ = 0.11, p-value = 0.41). Average appropriateness was negatively correlated with social touch avoidance in the AUT group (ϱ = -0.54, p-value < 0.001) and in the NT group (ϱ = -0.29, p-value = 0.03) (Fig. 2.6B). We found a negative association between average appropriateness and social anxiety in the NT group (ϱ = -0.41, p-value = 0.002) but not in the AUT group (ϱ = -0.14, p-value = 0.31). Alexithymia (AUT: ϱ = 0.07, p-value = 0.59; NT: ϱ = 0.07, p-value = 0.57) and sensory processing (AUT: ϱ = -0.05, p-value = 0.69; NT: ϱ = 0.12, p-value = 0.39) did not correlate with average appropriateness. Finally, average pleasantness negatively correlated with social touch avoidance in both groups (AUT: ϱ = -0.58, p-value < 0.001; NT: ϱ = -0.38, p-value = 0.005) (Fig. 2.6C). Average pleasantness also negatively correlated with social anxiety in the NT group (ϱ = -0.30, p-value = 0.03) but not in the AUT group (ϱ = -0.17, p-value = 0.21). Alexithymia (AUT: ϱ = -0.06, p-value = 0.62; NT: ϱ = -0.001, p-value = 0.99) and sensory processing (AUT: ϱ = -0.19, p-value = 0.17; NT: ϱ = 0.08, p-value = 0.60) did not correlate with average pleasantness.



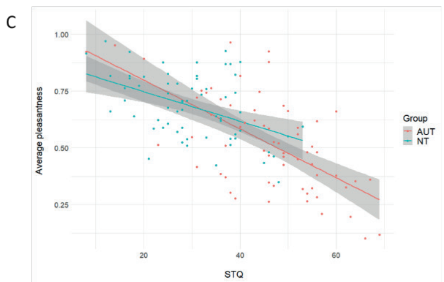


Fig. 2.6. Correlations between erogeneity, appropriateness, and pleasantness ratings with social touch aversion (STQ) in the two experimental groups.

2.4. Discussion

In the present study, we investigated daily social touch experiences in a sample of NT and ASD adult individuals. As hypothesised, we report that ASD individuals consider touch in social interactions as less appropriate, less pleasant, and less erogenous than NT controls, and that interpersonal contexts and body areas to whom it is generally attached a higher socio-affective meaning are those that more clearly differentiate between groups. Below we discuss these findings in light of the relevant literature.

Social touch is an essential feature of human (and other species) interactions, representing an important communication channel (Hertenstein et al., 2009; Kirsch et al., 2018) and fostering the formation of social bonds and secure attachment during infancy (Dunbar, 2010; Cascio et al., 2019; Gliga et al., 2019). A recent focus on the essential role of interpersonal touch during neural and social development has brought about evidence that positive experiences associated with social touch are fundamental contributors to healthy developmental trajectories (Bales et al., 2018; Cascio et al., 2019; Gliga et al., 2019). ASD is a developmental condition characterized by complex social communication and interaction impairments and recent evidence connects these difficulties to social touch processing (American Psychiatric Association, 2013). In fact, the well-known tactile processing disfunctions – hypo- and hyper-sensitiveness (Mikkelsen et al., 2018) – seem to extend to the socio-affective dimension of touch in this clinical population (Cascio et al., 2016, 2019; Kaiser et al). In one of the first studies specifically investigating social touch in ASD, Cascio and colleagues (2016) reported higher defensiveness reactions to social touch (touch delivered by an experimenter) in ASD compared to NT children. Moreover, greater defensive reactions for touch on forearm and perioral areas highly correlated with social impairment in the ASD sample (Cascio et al., 2016). In a recent work, Ujiie and Takahashi (2022) utilized self-report questionnaires to investigate the association between autistic traits, social touch aversion, and hypo/hyper-sensitivity in a Japanese sample. The authors reported that levels of social touch aversion positively correlated with autistic traits and levels of hypersensitivity while negatively correlating with levels of hyposensitivity.

However, still little is known on how adults with ASD experience daily interpersonal tactile interactions. In the present study, we provide new evidence in support of a difference in social touch processing between ASD and NT adults. In fact, across social scenarios and independently from the specific body area, our ASD participants rated touch as less appropriate, less pleasant, and less erogenous compared to our NT participants. Few studies on socio-affective touch in ASD have examined, along with behavioural (Cascio et al., 2008, 2016) and neural responses to touch (Kaiser et al., 2016; Masson et al., 2019), the perceived pleasantness arising from tactile inputs. These studies have generally reported a lower pleasantness sensation for affective touch in ASD compared to NT children/adults. For instance, Cascio and colleagues (2016) found that defensive responses to touch negatively correlated with individual perceived pleasantness in children with ASD (Cascio et al., 2016). Masson and colleagues (2019), in a study on the neural correlates of observed affective touch, found a group difference in the perceived pleasantness of positive tactile interactions, with ASD individuals reporting lower pleasantness than NT individuals

(Masson et al., 2019). On the other hand, the appropriateness and erogeneity sensations associated with social touch have been seldomly analysed in ASD, with the available evidence and insights arising indirectly from studies on hypo- and hypersensitiveness to touch (Mikkelsen et al., 2018). A recent series of studies on interpersonal touch run by our research group has shed light on the feelings of appropriateness, pleasantness, and erogeneity for touch in NT adults (Fusaro et al., 2021; Lisi et al., in preparation; Mello et al., 2022). From these studies, a clear picture has emerged that the pleasantness, appropriateness, and erogeneity of interpersonal touch highly depend on touched body area, demographic factors such as sex and sexual orientation, and contextual factors. For instance, touches delivered by a stranger in intimate areas (e.g., groin and chest), are deemed as highly erogenous but not appropriate (Fusaro et al., 2021; Mello et al., 2022). In the present study, using a self-report task, we provide new findings on the ensemble of feelings elicited by interpersonal touch, and we show that levels of appropriateness, pleasantness, and erogeneity for touch are lower in the ASD compared with the NT group.

To expand on the body location, Fusaro and colleagues (2021) and Mello and colleagues (2022) investigated the reactivity to social touch in an ecological manner by utilizing immersive virtual reality and virtual touch (i.e., the touches were not actually delivered to the participants but only "seen" on their virtual body). In these studies, chest and groin regions, representing together intimate areas, were associated with higher feelings of erogeneity and pleasantness – when touches were delivered by an avatar matching participants' sexual orientation – and with lower appropriateness compared with neutral (knee and feet) and social (hands and head) body areas. On the other hand, body regions regarded as social were associated with high appropriateness and pleasantness compared with neutral areas and with low erogeneity compared with intimate areas (Fusaro et al., 2021; Mello et al., 2022). In the present study, the self-report task we implemented allowed us to examine these interpersonal touch feelings considering the participants' whole body. We found that a set of areas consisting of the lower part of the back, belly, chest, face, groin, and lower back significantly differentiated between groups in terms of experienced erogeneity, with the ASD group reporting on average less erogeneity for these body areas. These regions included the areas examined by Fusaro and colleagues (2021) and Mello and colleagues (2022) and other body areas generally deemed as intimate and able to elicit erogenous sensations when touched (Dorros et al., 2008; Turnbull et al., 2014; Nummenmaa et al., 2016; Fusaro et al., 2021; Mello et al., 2022). On the other hand, while ASD participants experienced less pleasantness overall, the two groups did not differ in pleasantness ratings when considering specific body areas. It has to be noted that, while some studies have found differences between ASD and NT groups in pleasantness for affective touch (e.g., Cascio et al., 2016; Masson et al., 2019), other works have failed to do so, even when testing touch on different body locations (e.g., Kaiser et al., 2016). Moreover, the nature of our task was essentially different from those of previous studies, as we tested daily social touch preferences utilizing a self-report measure – as opposed to actual (or observed) touch in psychophysics and neuroimaging studies. To discuss body location differences in appropriateness between ASD and NT individuals we need first to consider the results concerning group differences in social touch for different social context.

To our knowledge, the present study is the first attempt at systematically investigating feelings of pleasantness, appropriateness, and erogeneity for social touch experienced by individuals with ASD within different interpersonal contexts. Social touch experiences highly depend on contextual factors (Gallace and Spence, 2010; Saarinen et al., 2021). Suvilehto and colleagues (2015) reported results on touch allowability (close to our appropriateness scale) that are interesting for our discussion. Utilizing a similar paradigm that our own, i.e., an online painting task, the authors found that the total area of the body wherein people were allowed to touch the participants linearly depended on the emotional bond between toucher and receiver. For instance, partners of a romantic relationship were those that were allowed to touch basically throughout the whole body, whereas strangers were only allowed to touch areas deemed as social, such as arms and hands (with a wide range of touchability levels for parents and other relatives; Suvilehto et al., 2015). These findings demonstrate that touch preferences highly depend on the degree of familiarity and emotional bond between toucher and receiver (Suvilehto et al., 2015; Saarinen et al., 2021). In addition, touch behaviour is characterized by different patterns in public vs. non-public settings (Gladney and Barker, 1979; Major et al., 1990), with the majority of touches occurring in private settings, especially in intimate body areas (Saarinen et al., 2021). Finally, a peculiar circumstance in which touch is delivered by a stranger but in a neutral/appropriate fashion is within professional settings (e.g., therapists, doctors, masseuse/masseurs). It has been shown that, in these occasions, touch is generally considered appropriate and may have psychophysiological benefits (Nilsen and Vrana, 1998; Vrana and Rollock, 1998; Saarinen et al., 2021). It is however currently unexplored whether (and how) individuals with ASD differ in social touch processing in different social scenarios. In the present study, we found as expected that lower feelings of appropriateness and erogeneity for touch in ASD compared with NT individuals were typical of friendly and intimate scenarios but not of the professional one, thus confirming that the processing of tactile events in circumstances that have an intrinsic socio-affective meaning differs in this clinical population. On the other hand, experienced pleasantness was lower for ASD individuals in all social scenarios, including the professional one.

We discussed how the appropriateness of touch is fundamentally dependent on body location and emotional bond/social context by looking at the study by Suvilehto and colleagues (2015). Here we provide new evidence showing that the experienced inappropriateness for touches in certain body locations within specific social contexts is accentuated in ASD. Again, the results concern interpersonal situations – friendly and intimate scenarios – characterized by a direct socio-affective importance, with the significance of a touch in a specific body area highly depending on contextual factors. We report, in fact, that touch in all areas except face, groin, and lower back – considered intimate areas (Nummenmaa et al., 2016) – within the friendly scenario was rated as more inappropriate by the ASD group compared with the NT group. On the other hand, and coherent with the nature of the intimate scenario, the two groups only differed when touch in this scenario pertained intimate areas like belly, chest, lower back, and groin. Finally, as hypothesized, no group differences were found for the professional scenario where touch is expected to be neutral and/or appropriate (Saarinen et al., 2021).

Several studies on socio-affective touch, especially those interested in the neural correlates underlying this phenomenon, have examined the relation between touch processing and autistic traits in NT samples (Voos et al., 2013; Scheele et al., 2014; Peled-Avron et al., 2017; Haggarty et al., 2020; Ujiie and Takahashi, 2022). For instance, Ujiie and Takahashi (2022) found that levels of social touch aversion positively correlated with autistic traits and levels of hypersensitivity while negatively correlating with levels of hyposensitivity in a large Japanese sample. On the other hand, neurophysiology and neuroimaging studies have reported that diminished or altered brain responses to social touch were linearly associated with the degree of participants' autistic traits (Voos et al., 2013; Scheele et al., 2014; Peled-Avron et al., 2017; Haggarty et al., 2020). The current study clarifies the interrelation between social touch preferences and individual autistic traits. By utilizing the degree of autistic traits – in AUT and NT groups combined – as predictor of social touch ratings, we were able to demonstrate that lower appropriateness, pleasantness, and erogeneity for touch were predicted by higher scores at the AQ questionnaire. Furthermore, this relation was specific for friendly and intimate scenarios compared with the professional scenario and for body locations deemed intimate when considering the erogeneity feeling. Our results thus complement previous studies reporting an association between autistic traits and altered social touch processing (Voos et al., 2013; Scheele et al., 2014; Peled-Avron et al., 2017; Haggarty et al., 2020; Ujiie and Takahashi, 2022), while also providing new important evidence on this relationship at the daily level. However, these findings have to be taken carefully, as mediation analyses showed that the relations between autistic traits and social touch preferences were fully mediated by levels of social touch avoidance (as measured by the STQ) as well as by social anxiety (LSAS) in the case of appropriateness feelings.

Finally, we found that social touch experiences highly correlated with social touch aversion. With stronger relationships in the ASD group, we report that the higher the trait social touch aversion the lower the reported appropriateness, pleasantness, and erogeneity feelings for interpersonal touch. In particular, the erogeneity feeling was the one that mostly differentiated between the two groups, as no significant correlation was found between touch aversion and erogeneity for touch in the control group. Several studies have found a strong relation between autistic traits and social touch aversion as measured via the STQ (e.g., see Voos et al., 2013; Peled-Avron et al., 2017, Ujiie and Takahashi, 2022 for some examples), which was also replicated in the present study (see Appendix A for results on correlations between questionnaires). Coherently, we show that the association between autism and social touch aversion extends to the feelings of appropriateness, pleasantness, and erogeneity for daily interpersonal touch. Furthermore, appropriateness and pleasantness were found to correlate with social anxiety in the control group, in line with evidence showing a strong association between anxiety and social touch aversion (e.g., Wilhelm et al., 2001), but not in the ASD group.

2.5. Conclusions

In this study, we built on previous evidence showing an impairment of socio-affective touch processing in autism (Cascio et al., 2016, 2019) to examine social touch preferences in ASD and typically developing adults. Our paradigm, involving an online painting task, allowed to us to investigate this in relation to two critical factors affecting interpersonal touch, namely social context and body location. We found, as expected, that interpersonal contexts characterized by an intrinsic social meaning – i.e., friendly and intimate situations – differentially influenced self-reports of erogeneity, pleasantness, and appropriateness of touch in AUT compared with NT individuals, with lower ratings for the former group in each case. Expectedly, within these scenarios, specific body locations – such as intimate areas within the intimate scenario – were also associated with lower ratings in the ASD group. Moreover, in the total sample (AUT and NT combined), autistic traits predicted lower erogeneity, pleasantness, and appropriateness – but this relation was fully mediated by social touch aversion.

Our findings provide newer support to the hypothesis that social touch is dysfunctional in ASD and pave the way for future studies aimed at investigating specific aspects of daily social touch in autism. For instance, future studies may want to separately address the topics of social and intimate touch in ASD by exploring the relations between body locations and different social contexts, using a similar task to the one we implemented or utilizing high ecological techniques, such as virtual reality (Parsons et al., 2015). An important extension of these works – and of our findings in general – would be to relate daily social touch preferences to long-term social communication and interaction problems that are typical of ASD, which could bridge the gap between the already apparent connection between basic tactile processing and social impairments in autism (Foss-Feig et al., 2012; Kadlaskar et al., 2019). Finally, our findings might represent the starting point for targeted interventions to the spheres of social and intimate touch in ASD (Cullen et al., 2005).

Appendix A – Supplementary material for Chapter 2

Sub n°	Age	Group	Sex	Gender	Sexual orientation
1	38	AUT	M	M	Heterosexual
2	29	AUT	M	M	Heterosexual
3	32	AUT	M	M	Heterosexual
4	19	AUT	M	Non-B	Heterosexual
5	35	AUT	F	F	Bisexual
6	47	AUT	M	M	Homosexual
7	24	AUT	M	M	Heterosexual
8	32	AUT	M	M	Heterosexual
9	35	AUT	M	M	Heterosexual
10	30	AUT	M	M	Heterosexual
11	19	AUT	M	M	Heterosexual
12	30	AUT	F	F	Bisexual
13	30	AUT	M	M	Heterosexual
14	48	AUT	M	M	Heterosexual
15	18	AUT	M	M	Heterosexual
16	40	AUT	F	F	Heterosexual
17	49	AUT	F	F	Heterosexual
18	52	AUT	F	F	Heterosexual
19	18	AUT	F	F	Bisexual
20	47	AUT	F	M	Heterosexual
21	43	AUT	F	F	Bisexual
22	34	AUT	F	F	Heterosexual
23	57	AUT	F	Non-B	Bisexual
24	45	AUT	F	Non-B	Heterosexual
25	55	AUT	F	F	Bisexual
26	31	AUT	F	F	Bisexual
27	36	AUT	F	F	Heterosexual
28	40	AUT	F	F	Heterosexual
29	39	AUT	F	F	Homosexual
30	23	AUT	M	M	Heterosexual
31	42	AUT	F	F	Heterosexual
32	43	AUT	F	F	Heterosexual

33	37	AUT	F	F	Homosexual
34	25	AUT	M	M	Heterosexual
35	38	AUT	F	F	Bisexual
36	33	AUT	F	Non-B	Bisexual
37	22	AUT	F	F	Heterosexual
38	23	AUT	M	M	Heterosexual
39	24	AUT	M	M	Heterosexual
40	25	AUT	M	M	Heterosexual
41	25	AUT	M	M	Heterosexual
42	26	AUT	M	Non-B	Heterosexual
43	29	AUT	M	M	Heterosexual
44	28	AUT	M	M	Heterosexual
45	33	AUT	M	M	Bisexual
46	34	AUT	M	M	Heterosexual
47	35	AUT	M	M	Heterosexual
48	35	AUT	M	M	Heterosexual
49	37	AUT	M	Non-B	Heterosexual
50	41	AUT	M	M	Heterosexual
51	44	AUT	M	M	Heterosexual
52	55	AUT	M	M	Heterosexual
53	57	AUT	M	M	Bisexual
54	22	AUT	F	F	Heterosexual
55	29	AUT	F	F	Heterosexual
56	32	AUT	F	F	Heterosexual
57	36	AUT	F	F	Bisexual
58	41	AUT	F	F	Heterosexual
59	49	AUT	M	F	Heterosexual
60	37	AUT	F	F	Heterosexual
61	44	AUT	F	F	Heterosexual
62	34	AUT	F	F	Bisexual
63	49	AUT	F	F	Heterosexual
64	62	AUT	F	F	Bisexual
65	41	NT	F	F	Heterosexual
66	28	NT	M	M	Homosexual
67	28	NT	M	M	Heterosexual
68	26	NT	M	M	Homosexual
69	43	NT	F	Non-B	Heterosexual
70	45	NT	F	F	Heterosexual
71	23	NT	F	F	Heterosexual

72	30	NT	F	F	Heterosexual
73	25	NT	M	M	Heterosexual
74	28	NT	F	F	Heterosexual
75	44	NT	M	M	Heterosexual
76	37	NT	M	M	Heterosexual
77	44	NT	F	F	Heterosexual
78	32	NT	M	M	Heterosexual
79	63	NT	F	F	Homosexual
80	47	NT	M	M	Heterosexual
81	33	NT	M	Non-B	Heterosexual
82	50	NT	M	M	Heterosexual
83	43	NT	F	F	Heterosexual
84	35	NT	M	M	Heterosexual
85	38	NT	F	F	Heterosexual
86	21	NT	M	M	Bisexual
87	40	NT	M	M	Heterosexual
88	31	NT	M	M	Heterosexual
89	33	NT	M	M	Heterosexual
90	37	NT	F	F	Bisexual
91	33	NT	M	M	Heterosexual
92	47	NT	F	F	Heterosexual
93	18	NT	M	Non-B	Homosexual
94	30	NT	M	M	Heterosexual
95	38	NT	M	M	Homosexual
96	50	NT	M	M	Homosexual
97	41	NT	F	F	Heterosexual
98	39	NT	M	M	Heterosexual
99	33	NT	M	M	Heterosexual
100	49	NT	F	F	Heterosexual
101	32	NT	F	F	Heterosexual
102	53	NT	F	F	Heterosexual
103	53	NT	M	M	Heterosexual
104	60	NT	M	M	Heterosexual
105	27	NT	M	M	Heterosexual
106	60	NT	F	F	Homosexual
107	26	NT	M	M	Heterosexual
108	21	NT	M	M	Heterosexual
109	51	NT	F	Non-B	Heterosexual
110	31	NT	M	M	Heterosexual

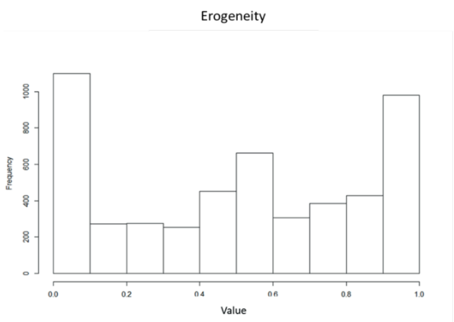
111	39	NT	F	F	Heterosexual
112	19	NT	M	M	Heterosexual
113	35	NT	F	F	Heterosexual
114	29	NT	F	F	Heterosexual
115	30	NT	F	F	Heterosexual
116	31	NT	F	F	Heterosexual
117	45	NT	F	F	Heterosexual
118	21	NT	M	M	Heterosexual
119	40	NT	F	F	Heterosexual
120	20	NT	M	M	Heterosexual
121	25	NT	F	F	Bisexual
122	41	NT	F	F	Heterosexual
123	29	NT	F	F	Heterosexual
124	20	NT	M	M	Homosexual
125	29	NT	F	F	Heterosexual
126	20	NT	F	F	Bisexual
127	30	NT	F	F	Heterosexual
128	51	NT	F	F	Heterosexual

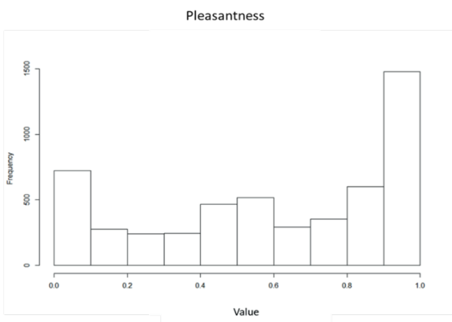
Tab. A1. Age, sex, gender, and sexual orientation demographics of our sample.

Scenario	Italian (example)	English
Friendly	È una domenica pomeriggio di primavera. Sei andata a fare un pic-nic in riva al lago con una ragazza che ti piace. Vi conoscete da poco e senti che l'interesse e l'attrazione sono corrisposte. Dopo aver mangiato rimanete sedute in riva al lago a parlare dei vostri interessi ed a scherzare. Non c'è nessuno oltre a voi. Ti senti a tuo agio e sei emozionata di essere con lei.	It's a spring Sunday afternoon. You went for a picnic by the lake with a girl you like. You have known each other for a bit and feel that interest and attraction are reciprocal. After having eaten, you sit by the lake to talk about your interests. You are having fun. There is no one around besides you two. You feel comfortable and are excited to be with her.
Intimate	È un venerdì pomeriggio di fine estate. Sei andata al secondo incontro di un corso di danza moderna. Sei contenta di partecipare a questo corso che porterà alla creazione di	It's a Friday afternoon in late summer. You went to the second meeting of a modern dance class. You are happy to participate in this course that will lead to the creation of a group

	una coreografia di gruppo. Sei motivata a conoscere meglio gli altri partecipanti al corso. Arrivata alla palestra trovi ad aspettare una delle ragazze che partecipa al corso ed inizi a parlarci per conoscerla meglio, sembra simpatica.	choreography. You are motivated to get to know the other course participants better. Arrived at the gym, you meet one of the girls who participates in the course, and you start talking to her to get to know her better; she seems nice.
Professional	È un venerdì pomeriggio di inizio estate. Sei andata al secondo appuntamento con una fisioterapista che fa dei massaggi che ti hanno detto essere molto efficaci. La fisioterapista ti ha fatto una buona impressione e sei motivata a fare il ciclo di massaggi perché pensi ti saranno utili. Dopo alcune domande inziali, ti sdrai sul lettino per iniziare la seduta di massaggi.	It's a Friday afternoon in early summer. You went on the second meeting with a physiotherapist who does massages that you were told were very effective. The physiotherapist has made a good impression on you, and you are motivated to do the massage cycle because you think they will be useful to you. After a few initial questions, you lie down on the bed to start the massage session.

Tab. A2. Social scenarios utilized in the painting task. Gender and sexual orientation information of the protagonists differed according to participants' demographic characteristics.





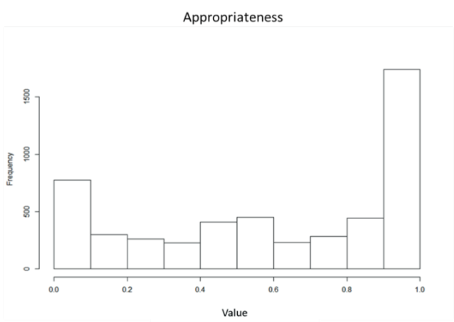


Fig. A1. Distribution of appropriateness, erogeneity, and pleasantness ratings. The data are bounded between 0 and 1 and approximate a beta distribution.

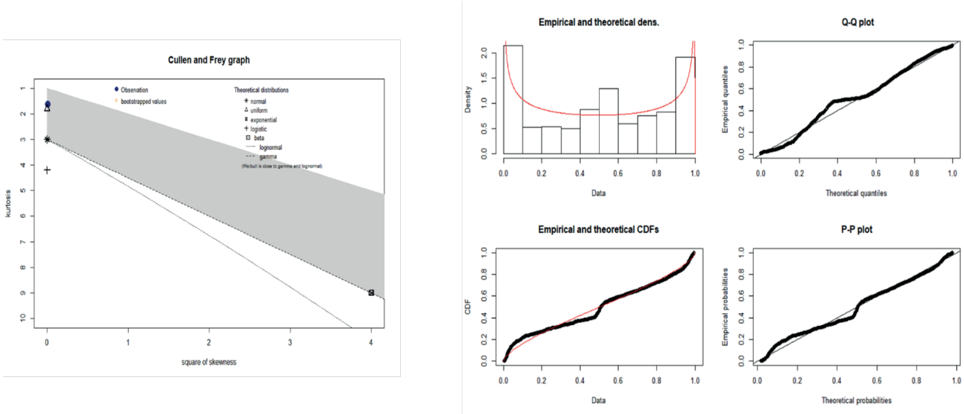


Fig. A2. Descriptive parameters of empirical distribution of erogeneity data and approximate fit to a beta distribution.

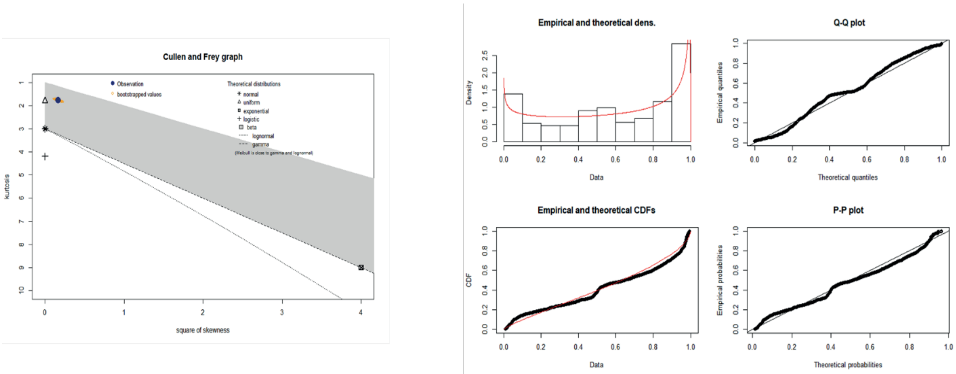


Fig. A3. Descriptive parameters of empirical distribution of pleasantness data and approximate fit to a beta distribution.

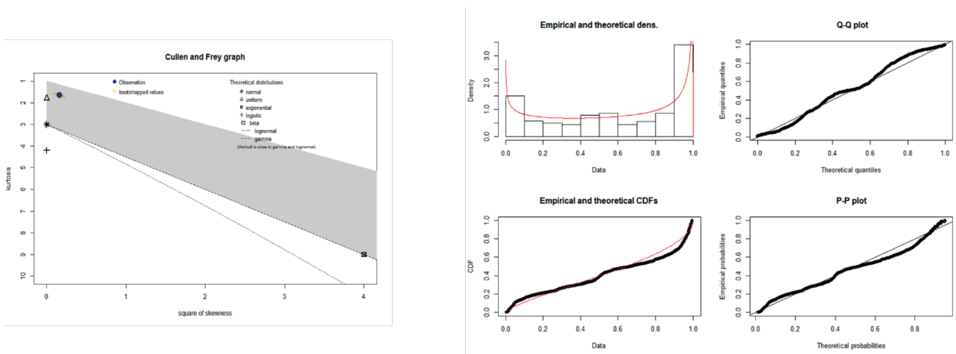


Figure A4: Descriptive parameters of empirical distribution of appropriateness data and approximate fit to a beta distribution.

	Autistic group Friendly (mean ± SE)	Intimate (mean ± SE)	Professional (mean ± SE)	Neurotypical group Friendly (mean ± SE)	Intimate (mean ± SE)	Professional (mean ± SE)
Arms	0.49 ± 0.039	0.69 ± 0.033	0.78 ± 0.027	0.67 ± 0.034	0.77 ± 0.028	0.79 ± 0.025
Back (lower)	0.33 ± 0.034	0.52 ± 0.038	0.73 ± 0.031	0.51 ± 0.039	0.69 ± 0.033	0.76 ± 0.028
Back (upper)	0.41 ± 0.037	0.68 ± 0.033	0.80 ± 0.025	0.41 ± 0.037	0.75 ± 0.029	0.82 ± 0.023
Back of head	0.35 ± 0.034	0.68 ± 0.033	0.72 ± 0.032	0.51 ± 0.040	0.77 ± 0.028	0.78 ± 0.027
Belly	0.29 ± 0.033	0.48 ± 0.038	0.64 ± 0.035	0.41 ± 0.037	0.66 ± 0.036	0.68 ± 0.033
Chest	0.30 ± 0.034	0.54 ± 0.038	0.64 ± 0.036	0.43 ± 0.037	0.66 ± 0.035	0.64 ± 0.034
Face	0.33 ± 0.035	0.65 ± 0.034	0.65 ± 0.035	0.43 ± 0.037	0.75 ± 0.030	0.72 ± 0.032
Feet	0.31 ± 0.033	0.51 ± 0.039	0.76 ± 0.029	0.45 ± 0.039	0.55 ± 0.038	0.80 ± 0.025
Groin	0.24 ± 0.029	0.36 ± 0.036	0.45 ± 0.039	0.27 ± 0.031	0.64 ± 0.037	0.50 ± 0.038
Hands	0.55 ± 0.038	0.77 ± 0.028	0.76 ± 0.029	0.72 ± 0.032	0.80 ± 0.026	0.78 ± 0.027
Legs	0.30 ± 0.033	0.52 ± 0.039	0.74 ± 0.030	0.43 ± 0.038	0.66 ± 0.036	0.77 ± 0.027
Lower back	0.25 ± 0.029	0.35 ± 0.036	0.49 ± 0.040	0.29 ± 0.033	0.62 ± 0.036	0.59 ± 0.038
Shoulders (front)	0.35 ± 0.036	0.63 ± 0.036	0.73 ± 0.031	0.55 ± 0.038	0.73 ± 0.031	0.76 ± 0.028
Shoulder (back)	0.46 ± 0.037	0.72 ± 0.031	0.81 ± 0.024	0.65 ± 0.036	0.79 ± 0.026	0.82 ± 0.023

Tab. A3. Estimated means and SEs for the appropriateness rating.

	Autistic group Friendly (mean ± SE)	Intimate (mean ± SE)	Professional (mean ± SE)	Neurotypical group Friendly (mean ± SE)	Intimate (mean ± SE)	Professional (mean ± SE)

Arms	0.35 ± 0.039	0.59 ± 0.042	0.38 ± 0.040	0.46 ± 0.042	0.64 ± 0.039	0.44 ± 0.041
Back (lower)	0.39 ± 0.040	0.61 ± 0.041	0.45 ± 0.041	0.53 ± 0.043	0.72 ± 0.035	0.53 ± 0.042
Back (upper)	0.39 ± 0.040	0.63 ± 0.041	0.43 ± 0.041	0.48 ± 0.042	0.69 ± 0.036	0.50 ± 0.041
Back of head	0.39 ± 0.040	0.65 ± 0.039	0.41 ± 0.040	0.52 ± 0.042	0.72 ± 0.035	0.49 ± 0.042
Belly	0.35 ± 0.038	0.56 ± 0.042	0.41 ± 0.041	0.50 ± 0.042	0.71 ± 0.035	0.50 ± 0.041
Chest	0.36 ± 0.039	0.58 ± 0.042	0.42 ± 0.042	0.49 ± 0.042	0.72 ± 0.034	0.52 ± 0.042
Face	0.35 ± 0.039	0.58 ± 0.042	0.37 ± 0.039	0.48 ± 0.043	0.72 ± 0.035	0.44 ± 0.041
Feet	0.29 ± 0.036	0.45 ± 0.043	0.33 ± 0.038	0.33 ± 0.037	0.44 ± 0.043	0.36 ± 0.040
Groin	0.39 ± 0.041	0.63 ± 0.039	0.49 ± 0.042	0.57 ± 0.042	0.78 ± 0.030	0.61 ± 0.041
Hands	0.39 ± 0.040	0.66 ± 0.039	0.39 ± 0.040	0.50 ± 0.043	0.67 ± 0.038	0.45 ± 0.042
Legs	0.31 ± 0.037	0.55 ± 0.043	0.39 ± 0.040	0.42 ± 0.041	0.58 ± 0.042	0.44 ± 0.042
Lower back	0.37 ± 0.040	0.61 ± 0.041	0.51 ± 0.042	0.58 ± 0.042	0.76 ± 0.032	0.63 ± 0.039
Shoulders (front)	0.37 ± 0.039	0.61 ± 0.041	0.39 ± 0.041	0.51 ± 0.042	0.72 ± 0.034	0.48 ± 0.041
Shoulder (back)	0.39 ± 0.040	0.66 ± 0.039	0.43 ± 0.041	0.52 ± 0.042	0.72 ± 0.034	0.51 ± 0.042

Tab. A4. Estimated means and SEs for the erogeneity rating.

		Autistic group			**Neurotypical group**	
	Friendly	**Intimate**	**Professional**	**Friendly**	**Intimate**	**Professional**

	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)
Arms	0.41 ± 0.038	0.68 ± 0.035	0.68 ± 0.035	0.66 ± 0.036	0.77 ± 0.029	0.77 ± 0.029
Back (lower)	0.35 ± 0.035	0.59 ± 0.038	0.67 ± 0.034	0.52 ± 0.039	0.73 ± 0.031	0.77 ± 0.028
Back (upper)	0.37 ± 0.037	0.68 ± 0.034	0.76 ± 0.029	0.59 ± 0.038	0.79 ± 0.027	0.82 ± 0.024
Back of head	0.40 ± 0.037	0.67 ± 0.034	0.67 ± 0.035	0.59 ± 0.038	0.79 ± 0.027	0.77 ± 0.029
Belly	0.30 ± 0.033	0.52 ± 0.039	0.50 ± 0.039	0.49 ± 0.039	0.67 ± 0.035	0.62 ± 0.037
Chest	0.33 ± 0.034	0.57 ± 0.037	0.50 ± 0.040	0.49 ± 0.039	0.70 ± 0.033	0.61 ± 0.037
Face	0.34 ± 0.035	0.62 ± 0.037	0.54 ± 0.039	0.51 ± 0.039	0.78 ± 0.028	0.69 ± 0.034
Feet	0.34 ± 0.036	0.54 ± 0.040	0.61 ± 0.038	0.45 ± 0.039	0.56 ± 0.039	0.75 ± 0.031
Groin	0.26 ± 0.031	0.47 ± 0.038	0.46 ± 0.039	0.41 ± 0.038	0.63 ± 0.037	0.54 ± 0.039
Hands	0.45 ± 0.040	0.75 ± 0.031	0.66 ± 0.036	0.69 ± 0.035	0.81 ± 0.026	0.78 ± 0.029
Legs	0.33 ± 0.035	0.57 ± 0.039	0.65 ± 0.036	0.48 ± 0.039	0.65 ± 0.036	0.75 ± 0.030
Lower back	0.31 ± 0.033	0.45 ± 0.038	0.54 ± 0.038	0.41 ± 0.038	0.68 ± 0.034	0.65 ± 0.035
Shoulders (front)	0.38 ± 0.036	0.65 ± 0.035	0.63 ± 0.036	0.59 ± 0.038	0.77 ± 0.028	0.73 ± 0.032
Shoulder (back)	0.41 ± 0.038	0.72 ± 0.032	0.77 ± 0.029	0.64 ± 0.037	0.80 ± 0.026	0.82 ± 0.025

Tab. A5. Estimated means and SEs for the pleasantness rating.

		Friendly vs Intimate t-ratio, p-value	**Friendly vs Professional** t-ratio, p-value	**Intimate vs Professional** t-ratio, p-value
Pleasantness	Arms	**-6.26, < 0.001**	**-6.29, < 0.001**	-0.08, 0.95
	Back (lower)	**-7.48, < 0.001**	**-9.54, < 0.001**	**-2.13, 0.04**
	Back (upper)	**-8.47, < 0.001**	**-10.48, < 0.001**	**-2.16, 0.04**
	Back of head	**-8.14, < 0.001**	**-7.55, < 0.001**	0.51, 0.65
	Belly	**-6.51, < 0.001**	**-5.19, < 0.001**	1.31, 0.22

	Chest	**-7.39, < 0.001**	**-4.60, < 0.001**	**2.74, 0.009**
	Face	**-9.10, < 0.001**	**-6.04, < 0.001**	**3.15, 0.002**
	Feet	**-4.71, < 0.001**	**-9.01, < 0.001**	**-4.32, < 0.001**
	Groin	**-6.93, < 0.001**	**-5.28, < 0.001**	1.63, 0.12
	Hands	**-7.02, < 0.001**	**-4.86, < 0.001**	**2.18, 0.03**
	Legs	**-6.43, < 0.001**	**-9.47, < 0.001**	**-3.10, 0.003**
	Lower back	**-6.62, < 0.001**	**-7.66, < 0.001**	-1.06, 0.33
	Shoulders (front)	**-7.66, < 0.001**	**-6.52, < 0.001**	-1.08, 0.32
	Shoulders (back)	**-8.24, < 0.001**	**-9.37, < 0.001**	-1.27, 0.24

Tab. A6. Between-scenarios differences in pleasantness for specific body locations.

		Friendly vs Intimate t-ratio, p-value	**Friendly vs Professional** t-ratio, p-value	**Intimate vs Professional** t-ratio, p-value
Appropriate-ness	Arms	**-4.79, < 0.001**	**-7.00, < 0.001**	**-2.16, 0.03**
	Back (lower)	**-5.72, < 0.001**	**-10.28, < 0.001**	**-4.63, < 0.001**
	Back (upper)	**-6.34, < 0.001**	**-10.18, < 0.001**	**-3.85, < 0.001**
	Back of head	**-9.59, < 0.001**	**-10.17, < 0.001**	-0.66, 0.54
	Belly	**-6.69, < 0.001**	**-9.58, < 0.001**	**-2.84, 0.006**
	Chest	**-7.16, < 0.001**	**-8.46, < 0.001**	-1.24, 0.24
	Face	**-9.95, < 0.001**	**-9.37, < 0.001**	0.66, 0.54
	Feet	**-5.29, < 0.001**	**-12.95, < 0.001**	**-7.62, < 0.001**
	Groin	**-7.74, < 0.001**	**-6.99, < 0.001**	0.74, 0.59
	Hands	**-5.28, < 0.001**	**-4.77, < 0.001**	0.58, 0.59
	Legs	**-6.77, < 0.001**	**-12.27, < 0.001**	**-5.48, < 0.001**
	Lower back	**-6.75, < 0.001**	**-8.23, < 0.001**	-1.61, 0.13
	Shoulders (front)	**-7.28, < 0.001**	**-9.58, < 0.001**	**-2.18, 0.03**
	Shoulders (back)	**-6.76, < 0.001**	**-9.39, < 0.001**	**-2.60, 0.01**

Tab. A7. Between-scenarios differences in appropriateness for specific body locations.

Correlation analysis – questionnaires. We ran correlations between pairs of questionnaires using Spearman's rank correlation and FDR correction to account for multiple comparisons. The AQ positively correlated with the SRS-2 ($\varrho = 0.80$, p-value < 0.001), the LSAS ($\varrho = 0.61$, p-value < 0.001), the TAS-20 ($\varrho = 0.57$, p-value < 0.001), the AASP-tactile ($\varrho = 0.45$, p-value < 0.001), and the STQ ($\varrho = 0.71$, p-value < 0.001); the SRS-2 positively correlated with the LSAS ($\varrho = 0.69$, p-value < 0.001), the TAS-20 ($\varrho = 0.61$, p-value < 0.001), the AASP-tactile ($\varrho = 0.48$, p-value < 0.001), and the STQ ($\varrho = 0.66$, p-value < 0.001); the LSAS positively correlated with the TAS-20 ($\varrho = 0.57$, p-value < 0.001), the AASP-tactile ($\varrho = 0.44$, p-value < 0.001), and the STQ ($\varrho = 0.65$, p-value < 0.001); the TAS positively correlated with the AASP-tactile ($\varrho = 0.40$, p-value < 0.001), and the STQ ($\varrho = 0.42$, p-value < 0.001); the AASP-tactile positively correlated with the STQ ($\varrho = 0.48$, p-value < 0.001) (see Fig. 3 for a graphical representation of the correlation matrix).

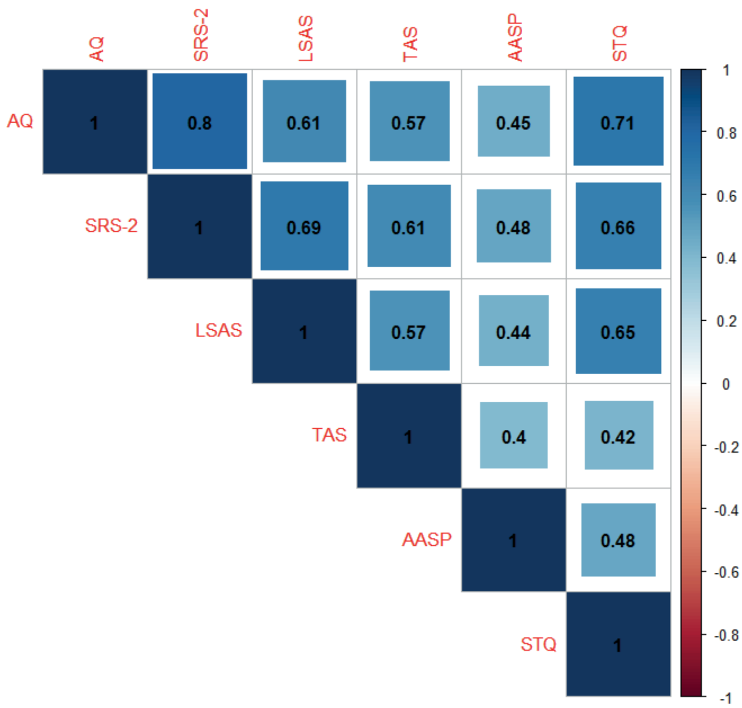


Fig. A5. Graphical representation of the pairwise correlation matrix.

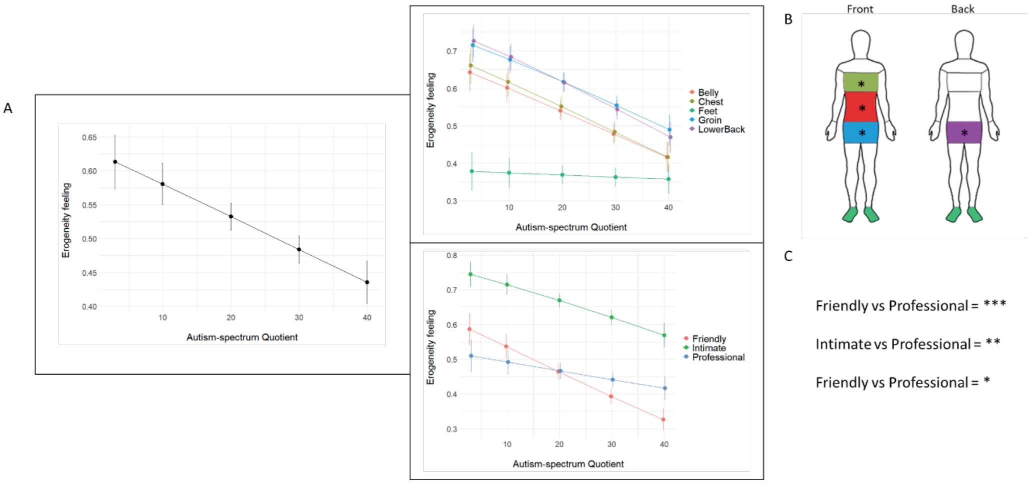


Fig. A6. Significant results concerning the erogeneity rating modelling it with AQ as continuous predictor.

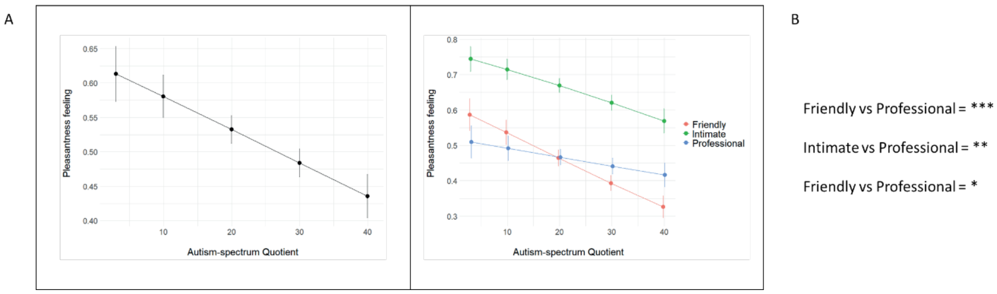


Fig. A7. Significant results concerning the pleasantness rating modelling it with AQ as continuous predictor.

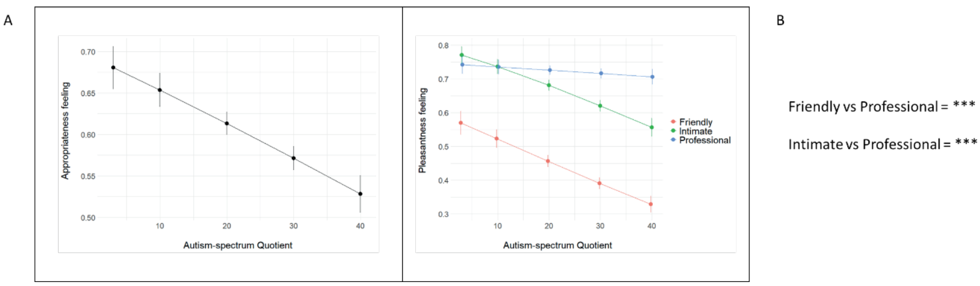
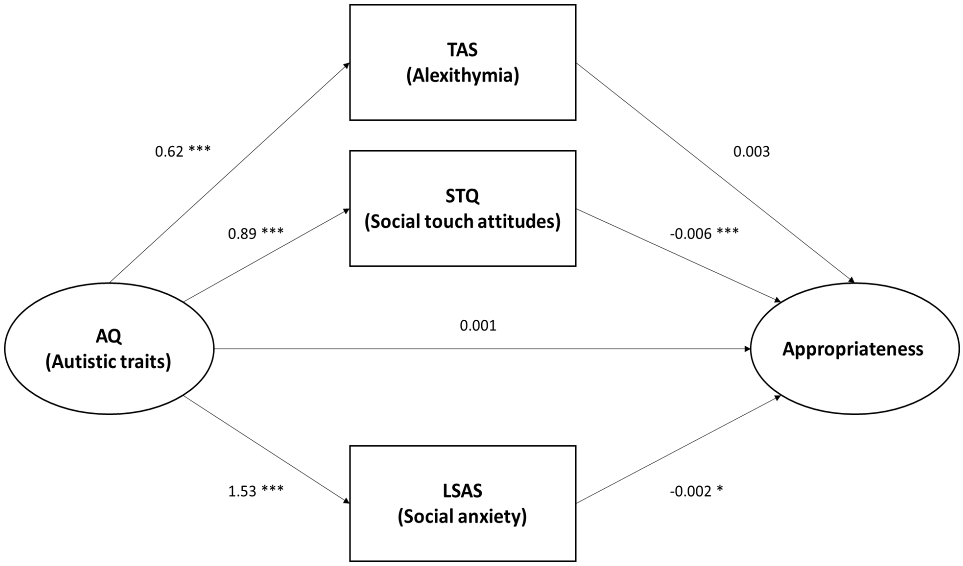


Fig. A8. Significant results concerning the appropriateness rating modelling it with AQ as continuous predictor.



Figu. A9. Mediation analysis graph for the appropriateness rating.

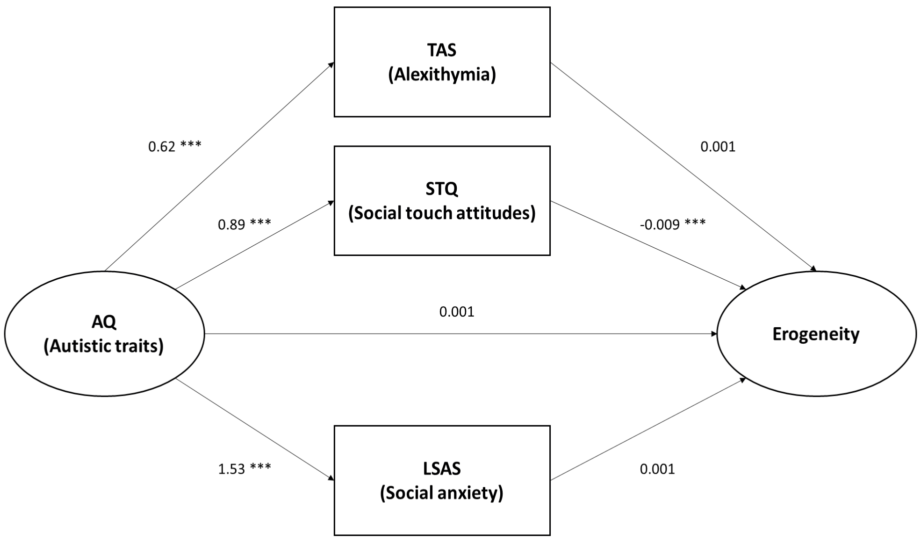


Figure A10: Mediation analysis graph for the appropriateness rating.

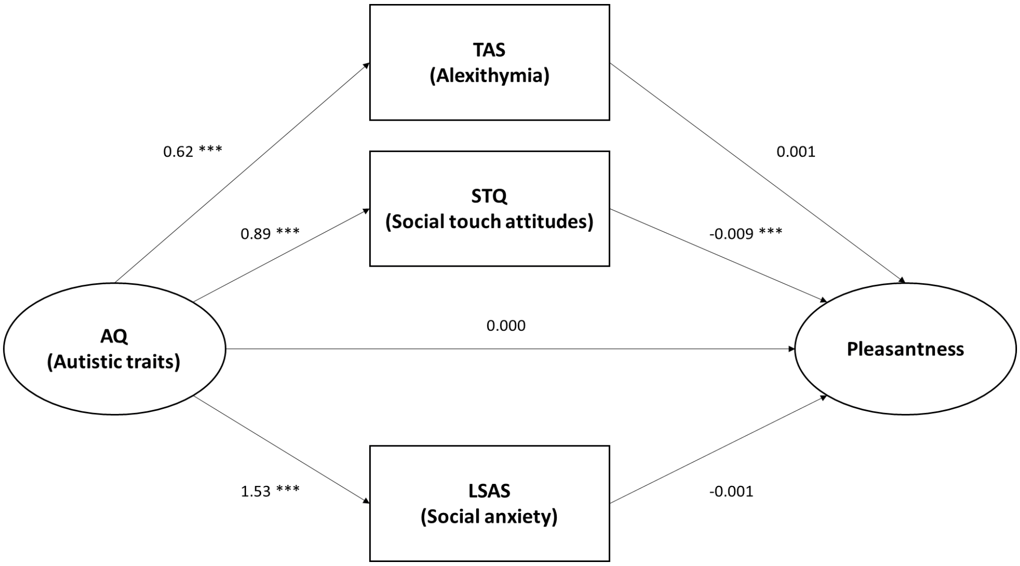
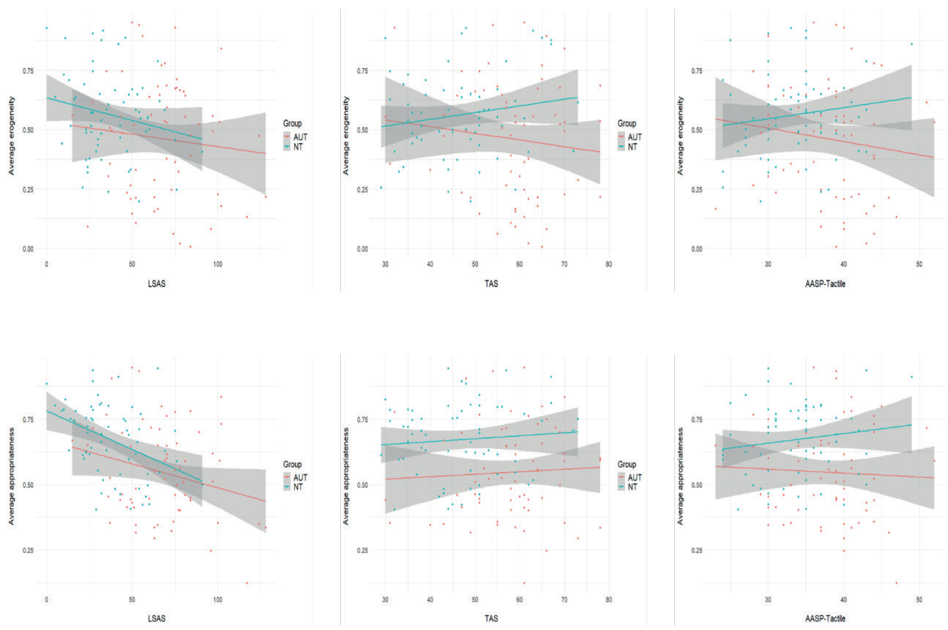


Fig. A11. Mediation analysis graph for the appropriateness rating.

Correlation analyses between social touch preferences (appropriateness, pleasantness, erogeneity) and questionnaires.



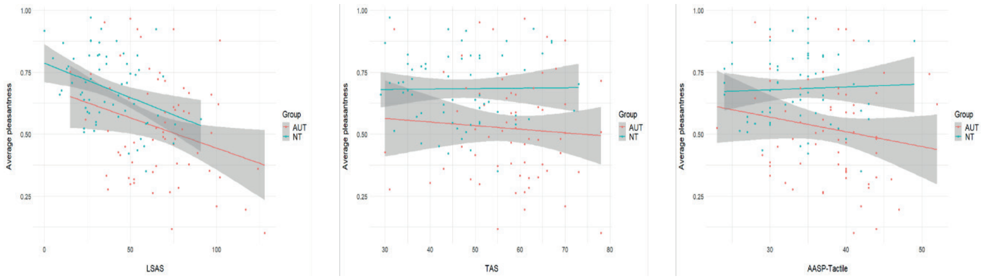


Fig. A12. *From top to bottom:* Correlation between erogeneity and social anxiety (LSAS), alexithymia (TAS), and tactile processing (AASP-Tactile). Correlation between appropriateness and social anxiety (LSAS), alexithymia (TAS), and tactile processing (AASP-Tactile). Correlation between pleasantness and social anxiety (LSAS), alexithymia (TAS), and tactile processing (AASP-Tactile).

3. Wearing same- and opposite-sex virtual bodies and seeing them caressed in intimate areas

3.1. Introduction

The ensemble of feelings, representations, and beliefs concerning the notion that the body and its parts belong to the "self" is referred to as body ownership (BO), an essential pillar of corporeal awareness (Berlucchi and Aglioti, 2010). Intuitively, we think of BO as a stable mental construct. However, fast and profound BO changes are observed in brain-damaged patients who deny that their contralesional limb belongs to them (Vallar and Ronchi, 2009; Moro et al., 2016; Blanke et al., 2004), as well as in healthy people who report the illusion of owning a physical (e.g., a rubber hand) or virtual limb as a consequence of synchronous visuo-tactile stimuli of the artificial and real body (Botvinick and Cohen, 1998; Sanchez-Vives et al., 2010; Kilteni et al., 2012; Pyasik et al. 2020). Immersive virtual reality (IVR) has proven to be an invaluable tool for exploiting full-body illusion paradigms, wherein a person's real body is replaced with a virtual one and an illusory feeling of BO over the virtual body (VB) is created (the body swap illusion; Kilteni et al., 2015; Petkova and Ehrsson, 2008). Studies indicate that mere observation of a VB from a first-person perspective (1PP, i.e., aligned with and spatially matching one's own real body) is sufficient to induce illusory BO (Slater et al., 2010; Pavone et al., 2016; Fusco et al., 2020; Monti et al., 2020; Keenaghan et al., 2020). Recent IVR studies have shown that illusory BO can affect people's perceptions and behaviour as well as their implicit attitudes, depending on conspicuous features of the VB (Maister et al., 2015) such as ethnicity (Peck et al., 2013), age (Banakou et al., 2013), shape (Van Der Hoort et al., 2011), size (Preston and Ehrsson, 2014; Provenzano et al., 2020), and sex (Slater et al., 2010; Peck et al., 2020).

It is relevant to the present study that even passive observation of painful or pleasant stimuli delivered to one's own VB may trigger vicarious sensations congruent with the observed stimuli (Fusaro et al., 2016, 2019, 2021). Fusaro and colleagues (2016, 2019), for example, reported that the observation of a virtual caress on an embodied virtual hand induced subjective feeling of vicarious touch, which were accompanied by changes in physiological reactivity (i.e., heart rate and skin conductance). The affective value of social touches such as a caress ranges from extreme pleasantness (e.g., erotic, or consolatory feelings) to extreme unpleasantness (e.g., pain, disgust). Moreover, the age, ethnicity, and gender of both the toucher and receiver—as well as factors related to the context of the tactile stimulation—have all been found to affect how touch is perceived (Gallace and Spence, 2010; Morrison et al., 2010). Tellingly, a recent extension of "virtual touch" studies (Fusaro et al., 2016, 2019) highlighted different patterns of behavioural and physiological responses to virtual caresses in heterosexual and homosexual participants, supporting that gender and sexual orientation (SO) play an important role in touch-mediated interactions (Fusaro et al., 2021).

What remains unknown is whether the pattern of behavioural and physiological reactivity to a same-sex vs. opposite-sex toucher is different based on whether one's own VB is or is not coherent with one's own sex. The topic of sex-related body swaps has recently gained momentum (Slater and Sanchez-Vives, 2014) after several virtual reality studies demonstrated that wearing opposite-sex VBs may reduce gender biases and/or enhance empathy and perspective-taking abilities (Peck et al., 2018; Seinfeld et al., 2018; Neyret et al., 2020; de Borst et al., 2020; Tacikowski et al., 2020). Here, in two different IVR experiments, heterosexual men (Experiment 1) and women (Experiment 2) embodied same-sex or opposite-sex avatars (i.e., swapping sexual appearance) and then observed virtual caresses delivered by a male or female avatar on different parts of their VB (Fig. 1; Movie S1). These body regions were defined as neutral (e.g., knee), social (e.g., hand), or intimate (e.g., pelvis) on the basis of an ad hoc survey reported in Fusaro and colleagues' study (21). Behavioural ratings were collected for each observed caress using visual analogue scales (VASs; Table 1). Physiological reactivity was recorded throughout the experiments in the form of galvanic skin response (GSR) and electrocardiogram (ECG). We predicted that embodying an opposite-sex VB would change heterosexual people's feelings and physiological reactivity by shifting them towards what was expected for their embodied VB. Specifically, if the body swap illusion works as predicted when heterosexual people embody an opposite-sex VB, we would expect increased feelings of pleasantness and erogeneity in response to same-sex intimate touch (i.e., men being virtually caressed by a male avatar and women being virtually caressed by a female avatar) when wearing an opposite-sex VB. Moreover, significant differences in physiological reactivity depending on the type of embodied VB are expected.

3.2. Materials and methods

3.2.1. Participants

A total of 21 healthy heterosexual men (average age = 26.53, *SD* = 3.92; range 18–36; Experiment 1) and 21 healthy heterosexual women (average age = 26.53, SD = 3.92; range 18–36; Experiment 2) participated in the study. Prior to being recruited for the experiment, participants rated their SO via a 0-to-100 Kinsey scale (Kinsey et al., 2003) ranging from "exclusively heterosexual" to "exclusively homosexual", with "bisexual" in the middle of the VAS scale (mean ± SD for male sample = 6.76 ± 8.91;

mean ± SD for female sample = 8.62 ± 8.25). We divided the VAS range into the Kinsey scale's 7 categories: 0-14.28 = exclusively heterosexual; 14.28-28.57 = predominantly heterosexual, only incidentally homosexual; 28.57-42.85 = predominantly heterosexual, but more than incidentally homosexual; 42.85- 57.14 = equally heterosexual and homosexual; 57.14-71.42 = predominantly homosexual but more than incidentally heterosexual; 71.42-85.71 = predominantly homosexual, only incidentally heterosexual; 85.71-100 = exclusively homosexual. The cut-off to be included in our sample was 28.57. The sample size was chosen based on our previous work (Fusaro et al., 2021), where sample size estimations were performed using MorePower 6.0 software. The experimental protocol was approved by the ethics committee of the IRCCS Santa Lucia Foundation and followed the ethical standards of the 2013 Declaration of Helsinki. All participants gave their written informed consent to take part in the study and were naïve to the purposes of the research.

3.2.2. General procedures

All participants laid down on a beach chair placed in the laboratory room and wore a head-mounted display (HMD) through which they observed from 1PP a VB in underwear that substituted for their own body (see Appendix B for a more detailed description of experimental stimuli and setup). In two different sessions, separated by a few days, participants embodied either a same-sex or an opposite-sex VB by means of a passive observation approach in 1PP, which has been described as a sufficient and necessary condition for inducing BO over a virtual avatar (Fig. 3.1; Movie S1; Slater et al., 2010; Pavone et al., 2016; Fusco et al., 2020; Monti et al., 2020; Keenaghan et al., 2020). Embodiment type order was randomized across participants. The exclusion of a non-human embodiment control condition was motivated by creating a balance between the costs (e.g., participant fatigue) and the benefits (e.g., maximal control of any relevant variable) associated with the development of experimental designs. The paradigm used in the present study did rely on evidence that we consider solid and that highlights some of the conditions that are necessary to obtain embodiment in IVR (e.g., Pavone et al., 2016; Monti et al., 2020). Each session consisted of two blocks during which participants observed virtual caresses delivered by either a female or male avatar. Thus, no actual touch was delivered to the participants. This is an important detail because the embodiment achieved by mere vision of a mannequin body is reduced with respect to a condition in which touch to participants' own, unseen body is added (Carey et al, 2019). The body parts touched by the avatar included the foot, knee, pelvis, chest, head, and hand. Four trials per body area were included in each block, with two delivered by the other avatar standing on the right side of the VB and the remainder two delivered by the other avatar standing on the left side of the VB. Thus, one block consisted of 24 touches in total. The six body areas were categorized as "neutral" (foot and knee), "social" (head and hand), or "intimate" (chest and pelvis). This categorization was based on a survey previously run by our research group (Fusaro et al., 2021). During the first minute, participants merely observed their VB aligned with their physical body. The experimental design included three experimental factors: embodiment type (whether the VB belonged to the same or the opposite sex), the sex of the touching avatar (male or female), and body area (neutral, social, or intimate).

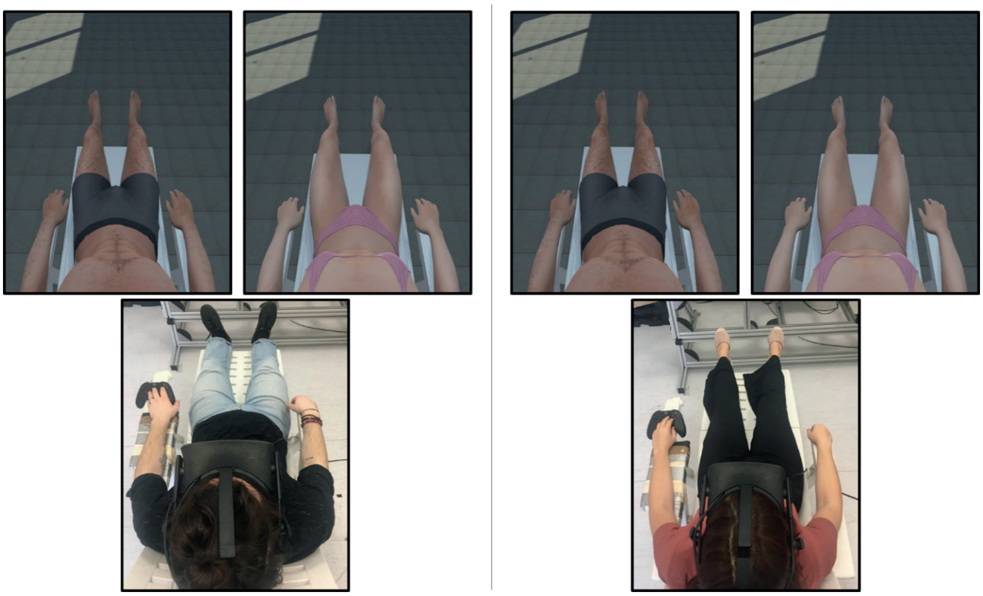


Fig. 3.1. Participants laid down on a beach chair and, through an HMD, saw from a first-person perspective a VB in underwear that replaced their own body. Left panel: depending on the experimental session, men embodied either a male (same-sex) or a female (opposite-sex) VB. Right panel: depending on the experimental session, women embodied either a male (opposite-sex) or a female (same-sex) VB.

Each caress lasted approximately 3 s and had a velocity of approximately 3 cm/s, regarded as the main feature of pleasant affective touch (Löken et al., 2009). After each caress was delivered, participants kept observing their own VB for 7000 ± 500 ms. At the end of the trial, they were presented with four VASs through which they provided ratings (moving a joystick-controlled cursor) about their touch-evoked experiences (Table 1). Moreover, at the end of each block, participants were asked to rate their feelings of virtual embodiment (ownership, identification, comfortableness) over the VB as well as vicarious touch in response to different VAS statements and questions (Table 1). For both in-session and end-of-block VASs, scores ranged from 0 to 100, where 0 meant absence of the feeling (e.g., no ownership, not pleasant, not erogenous) and 100 corresponded to a very strong feeling. Therefore, a score of 50 represented a feeling of intermediate strength (e.g., of ownership, pleasantness) and not a given degree of uncertainty. Prior to the beginning of the experiment, participants were given precise written instructions that, for each VAS, a score of 0 meant absence of the feeling, a score of 100 corresponded to a very strong feeling and a score of 50 to an intermediate feeling, and that they could choose any value between the two extreme points. At the end of each session (i.e., after the main experimental task), participants were asked to complete a gender-potency implicit association test (IAT, Greenwald et al., 1998; Rudman et al., 2001) and an online version of the ambivalent sexism inventory (ASI, Glick and Fiske, 1996; Italian validation: Manganelli Rattazzi et al., 2008; for further details on IAT and ASI analyses and results, see Appendix B, Additional results.

Category	Question/Statement
Appropriateness	How appropriate was the touch?
Arousal	How arousing was the touch?
Pleasantness	How pleasant was the touch?
Erogeneity	How erogenous was the touch?
Ownership	"It seemed like I was watching my body"
	"It seemed like the virtual body was my body"
(Ownership) Control	"It seemed like I had more than one body"
	"It seemed like I did not have my body anymore"
Vicarious touch	"It seemed like I was feeling the touches on my body"
Comfortableness	"How comfortable did you feel in the virtual body?"
Identification	"To what extent did you identify yourself with the body you observed in 1PP?"

Tab. 1. In-session and end-of-block VAS questions and statements. Scores ranged from 0 to 100, where 0 meant that the caress was not appropriate, not pleasant, not arousing, and not erogenous. A score of 100 meant that the caress was extremely appropriate, pleasant, arousing, and erogenous. As for end-of-block questions and statements, a score of 0 meant the absence of feelings of ownership, vicarious touch, identification, or comfortableness with the virtual body seen in 1PP, while a score of 100 meant corresponding very strong feelings.

3.2.3. Physiological recordings and pre-processing

SCR and ECG were used as measures of physiological reactivity to virtual social and intimate touch. An ADInstruments PowerLab 8/35 device was used as a signal amplifier along with the ML116 GSR Amplifier (providing a 75 Hz AC excitation with low constant voltage of 22 mVrms) with specific GSR sensors consisting of two bipolar finger electrodes. The sensors were applied on the distal phalanx of the index and middle fingers of the right hand, and the signal was sampled at 1 KHz. For the ECG, two electrodes (DORMO pre-gelled electrodes, 50 mm) were placed on the back of each hand, and the reference was placed on the left ankle. Signals were sampled at 1 kHz and filtered using a 30 Hz low-pass filter. Data were recorded using the LabChart 7 software (ADInstruments, Inc.).

Inter-beat intervals were computed and then converted into heart rate (HR) in beats per minute (bpm) using LabChart. Data were reduced offline in 1 s bins. HR changes contingent upon observation of virtual caresses were computed as differential values between 3 s after a virtual caress was delivered and 2 s of baseline before the appearance of the touching avatar. Raw skin conductance data were extracted from LabChart as .txt files and entered in MATLAB for analysis. The Ledalab toolbox was used to run a discrete decomposition analysis through which we separated phasic from tonic activity. The pre-processing steps included down-sampling, smoothing, and Butterworth filtering of the raw data. Event-related SCR was averaged across 6 s after a virtual caress was delivered (Fusaro et al., 2016) and transformed using square root transformation. Responses below 0.1 μS were discarded.

3.2.4. Data analysis

We performed a linear mixed-effects analysis using the scores for each of the four in-session VAS questions and end-of-block statements (ownership, comfortableness, identification, and vicarious touch) as outcome and the interactions among all our experimental factors (embodiment type, touching avatar, and body area) as predictors. Moreover, linear mixed-effects analyses were run with baselined HR in bpm and SCR in μS as outcome. The fitted models included by-subject intercepts, as well as by-subject slopes for the effects of embodiment type, touching avatar, and body area (when doing so did not produce model overfitting, in which case model complexity was reduced). For the in-session VAS questions and physiological measures, non-orthogonal planned comparisons for the body area factor were performed. Specifically, the social and intimate levels were both compared separately to the neutral level. When relevant, specific comparisons between conditions were examined using post hoc tests (Bonferroni-corrected, or Tukey-corrected for trend analyses). Statistical modelling was carried out in R using the function lmer() from the lme4 package (Bates et al., 2007). Model complexity was gradually increased by inserting fixed effects and their interactions to check for the model that best fitted the data. The different models were compared using the anova() function from the stats package in R (R Core Team, 2019). AIC, BIC, and Chi-square statistics informed us on which model best fitted the data compared to the previous ones in the hierarchy. Graphical inspection of model residuals and fitted vs. predicted values revealed that normality of model residuals, homoscedasticity and linearity assumptions were met for all the statistical models. Post hoc tests were performed using the lsmeans() function from the lsmeans package (Lenth, 2017). Trend analyses on physiological measures were performed using the emtrends() function from the emmeans() package (Lenth, 2020). Model effect sizes were computed using the r.squaredGLMM() function from the MuMIn package (Barton, 2020).

3.3. Results

3.3.1. Experiment 1. Only heterosexual male participants

3.3.1.1 Feelings of embodiment and vicarious touch. Participants' virtual embodiment was evaluated through a series of questions and statements related to their feelings of ownership, identification, and comfortableness regarding the VBs. One statement specifically assessed vicarious feelings for virtual touches (see Methods and Table 1). We found a significant effect of embodiment type (same-sex versus opposite-sex VB) on ownership ratings (estimate = 6.91; t-value = -2.3, $p = 0.02$; $R^2_{conditional} = 0.66$). This was explained by the higher ownership ratings when embodying a same-sex male VB (59.15 ± 4.66) compared to an opposite-sex female VB (52.23 ± 4.66). No other main effects or interactions were significant. Additionally, men identified with a male VB more than a female VB (estimate = -14.02; t-value = -2.26, $p = 0.04$; $R^2_{conditional} = 0.38$) (Fig. 3.2A), while feeling equally comfortable in both conditions (estimate = -3.13; t-value = -0.87, $p = 0.39$). Female avatar touch was found to generate stronger vicarious tactile feelings ($M = 48.28$, $SE = 4.51$) than male avatar touch ($M = 40.94$, $SE = 5.27$).

3.3.1.2 Pleasantness of touch. Overall, participants (all men) rated female avatar touch as more pleasant ($M = 49.35$, $SE = 2.93$) than male avatar touch ($M = 37.14$, $SE = 2.69$; estimate = -12.93; t-value = -4.92, $p < 0.001$). The embodiment of participants (all men) in a female VB produced a significant increase in the reported pleasantness of caresses on intimate areas from a male avatar (estimate = 13.97; t-value = 4.89; $p < 0.001$; $R^2_{conditional} = 0.60$; Fig. 3.2B). Direct comparison between specific conditions (Bonferroni-corrected) revealed that pleasantness ratings for intimate touch from a male avatar differed significantly between the same-sex and opposite-sex conditions (estimate = -12.16; t-ratio = -4.56, $p = 0.003$). This comparison specifically informs us of the degree of change in attitudes that depends on embodying an opposite-sex VB. Specifically, caresses on intimate areas from a male avatar were rated as more pleasant during opposite-sex embodiment (wearing a female VB; 40.16 ± 3.71) than during same-sex embodiment (wearing a male VB; 28 ± 3.49)

3.3.1.3 Erogeneity of touch. Intimate touch was rated as more erogenous ($M = 38.63$, $SE = 4.13$) than neutral touch ($M = 25$, $SE = 3.18$) (estimate = 15.58; t-value = 4.55; $p < 0.001$). The embodiment of participants (all men) in a female VB produced a significant increase in the erogeneity of caresses on intimate areas from a male avatar compared to neutral touch (estimate = 16.33; t-value = 4.78; $p < 0.001$, $R^2_{conditional} = 0.68$; Fig. 3.2B). No such difference was found when participants embodied a male VB. As with pleasantness ratings, post hoc tests showed that erogeneity ratings for intimate touch from a male avatar differed significantly between the same-sex and opposite-sex conditions (estimate = -28.72, $SE = 3.29$; t-ratio = -8.74, $p < 0.001$). Specifically, erogeneity for caresses on intimate areas delivered by a male avatar was rated 11.6 ± 4.17 during same-sex embodiment, while it was rated 40.32 ± 4 during opposite-sex embodiment.

3.3.1.4 Correlation analyses. The results presented above suggest, as expected, that the levels of pleasantness and erogeneity that heterosexual men experience for vicarious touch depend on the VB they are embodying. To provide additional evidence supporting the relationship between embodying a VB and vicarious touch sensation, we ran correlation analyses between the ownership scores and VAS ratings of pleasantness and erogeneity. For each dimension, we computed an index wherein ratings of neutral caresses were subtracted from ratings for caresses on intimate and social areas (intimate minus neutral index, social minus neutral index). Bonferroni correction for multiple comparisons returned a p-value of 0.003 (p-value of 0.05/16, as hypotheses were tested on two different dimensions [pleasantness and erogeneity], two indexes, and four conditions, namely male toucher/same-sex embodiment, female toucher/same-sex embodiment, male toucher/opposite-sex embodiment, and female toucher/opposite-sex embodiment). We found two significant positive correlations between erogeneity ratings for caresses on intimate areas (intimate minus neutral index) and ownership scores. The first (Spearman' $\varrho = 0.46$, $p < 0.001$) refers to the condition in which male participants embodying a male VB were caressed by a female avatar. Specifically, the more ownership that participants felt over the male VB, the greater their reported erogenous sensation for caresses on intimate areas from a female virtual avatar. The second correlation result (Spearman' $\varrho = 0.5$, $p < 0.001$) suggests that the more ownership that male participants felt over the female VB (sex-related body swap), the greater their erogenous sensation for intimate same-sex touch (caresses delivered by male avatars; Fig. 3.2C).

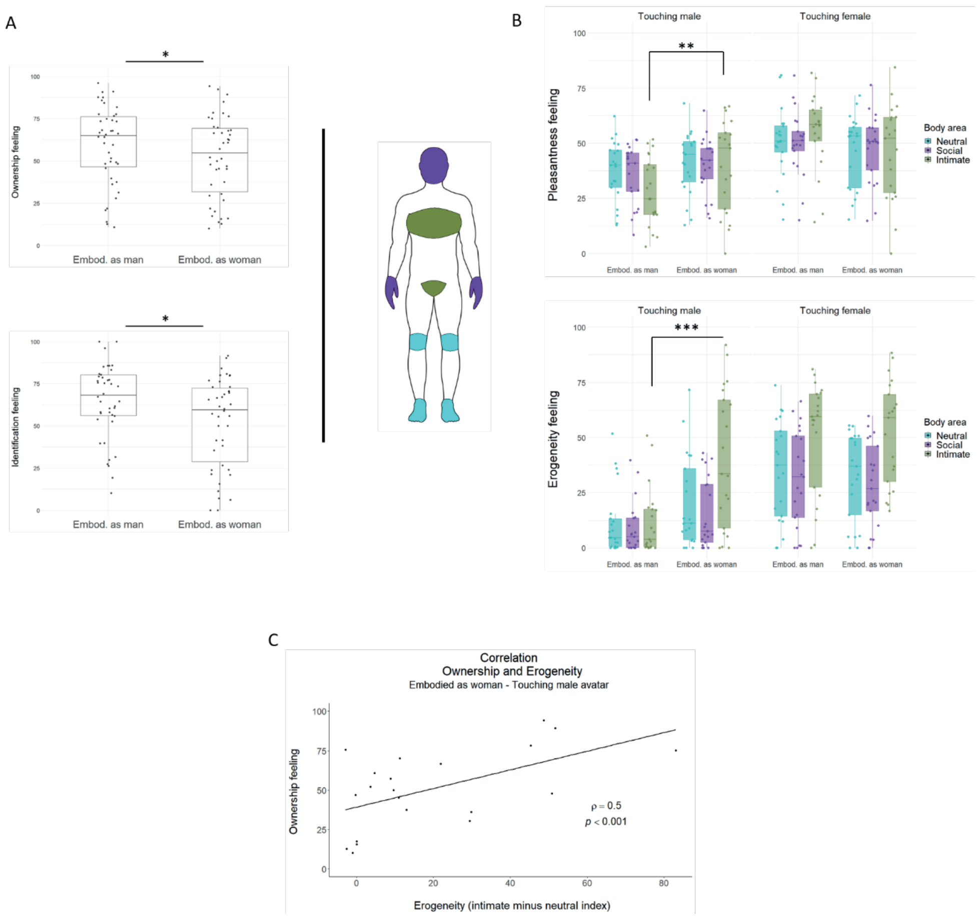


Fig. 3.2. Main behavioural results for Experiment 1 (all men). (A): Box plots showing that men felt more ownership towards and identified more with a same-sex (male) than an opposite-sex (female) VB. (B) Pleasantness and erogeneity ratings provided by Experiment 1 participants (all men). (C) Scatter plots of correlation analysis (Spearman's rho) between ownership and erogeneity scores. The more ownership that men felt over the opposite-sex VB, the higher their ratings of erogeneity for same-sex intimate touch. Notes: Error bars represent mean SEs. Black lines indicate significant direct comparisons. * = significant at < 0.05; ** = significant at < 0.01; *** = significant at < 0.001.

Due to space limitations, the main findings related to the appropriateness and arousing power VASs are reported in the Appendix B. This choice was motivated by the fact that appropriateness and arousal were less influenced by participants' embodiment in same-sex vs. opposite-sex avatars, which is related to our main hypothesis. The same is true for Experiment 2.

3.3.1.5 Physiological reactivity. Regarding the heart rate measurement, caresses on intimate body areas—independent of which avatar delivered them or whether participants embodied a male or female avatar—produced a heart rate deceleration (with respect to the baseline) compared to neutral caresses (estimate = -0.75; *t*-value = -2.16, $p = 0.03$; $R^2_{conditional} = 0.11$).

The analyses of skin conductance reactivity yielded a main effect of embodiment type (estimate = -0.07; *t*-value = -2.89, $p = 0.003$; $R^2_{conditional} = 0.31$). Participants' skin conductance response (SCR) was found to be higher in same-sex VB conditions ($M = 0.82$ µS, $SE = 0.08$) compared to opposite-sex VB conditions ($M = 0.75$ µS, $SE = 0.08$). We also found a significant main effect of the touching avatar (estimate = -0.05; *t*-value = -2.1, $p = 0.03$). More specifically, when heterosexual male participants were touched virtually by a female avatar, the average SCR was higher ($M = 0.81$ µS, $SE = 0.08$) than when they were touched by a male avatar ($M = 0.75$ µS, SE = 0.08).

To investigate the possibility that participants' physiological activation influenced their behavioural ratings, different statistical models were fitted with baselined HR and SCR as predictors of both erogeneity and pleasantness scores.
Trend analyses on baselined HR revealed that higher erogeneity scores were predicted by lower HR when men were virtually caressed by a male avatar and embodied an opposite-sex VB, compared to a same-sex VB (Fig. 3.3A; estimate = 0.57; *t*-ratio = 2.91, $p = 0.01$). Furthermore, trend analyses on SCR revealed that higher erogeneity scores were predicted by higher SCR when men were caressed by a male touching avatar and embodied an opposite-sex VB, compared to when they embodied a same-sex VB (Fig. 3.3B; estimate = -4.10, $SE = 0.71$; *t*-ratio = -5.77, $p < 0.001$).
As concerns pleasantness ratings, we found that higher pleasantness scores were predicted by higher SCR when men were caressed in intimate areas by a male touching avatar and embodied an opposite-sex VB, compared to when they embodied a same-sex VB (Fig 3.3C; estimate = -3.39; *t*-ratio = -3.89, $p = 0.005$).

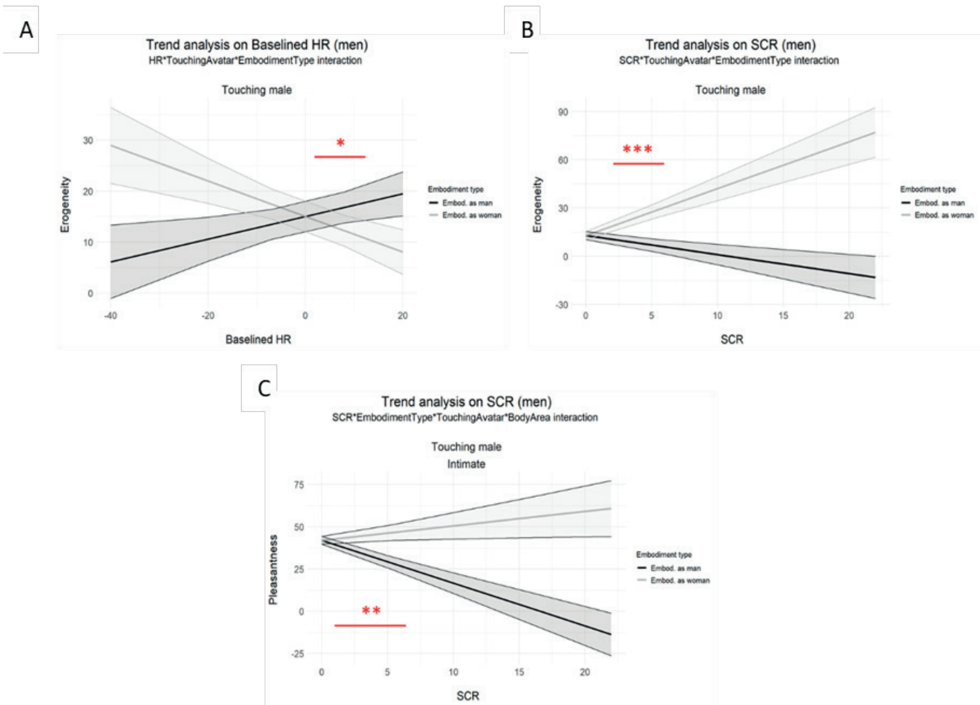


Fig. 3.3. For erogeneity ratings as outcome, (A) HR trends and (B) SCR trends differed depending on the touching avatar's sex and the type of embodiment. (C): For pleasantness ratings as outcome, SCR trends differed depending on the touching avatar's sex, the type of embodiment, and the caressed body area.

Notes: Error bars represent mean SEs. Red lines indicate significant post hoc comparisons. * = significant at < 0.05; ** = significant at < 0.01; *** = significant at < 0.001.

3.3.1.6 Gender-potency IAT. We hypothesized that the implicit gender-potency bias would be reduced by embodying an opposite-sex VB. The strength of the association that sees men as powerful and women as weak (D1 score) was significantly different from zero in men (mean D1 = 0.38; t = 7.43, $p < 0.001$). This means that men were quicker to associate male first names with power-related words and female first names with weakness-related words, compared to the opposite. IAT D1 scores did not differ across the two embodiment conditions (estimate = 0.02; t = 0.32, p = 0.75). Correlation analyses were run between IAT D scores (averaged across the two sessions) and two measures taken as indexes of behaviour change in IVR, i.e., ownership scores during the opposite-sex conditions and erogeneity scores for same-sex touch in intimate areas during opposite-sex conditions (intimate minus neutral index). We found no significant correlations between these measures.

3.3.1.7 ASI. Three participants did not complete this online questionnaire. An average ASI score for men was obtained by mediating across individual ASI scores. This score was compared with a sample normative mean from the Italian validation of the ASI questionnaire (ASI mean for men = 2.34; Manganelli Rattazzi et al., 2008). A one-sample t test showed a significant difference between our sample mean and the normative mean taken as comparison (t value = -2.93, p = 0.009). Specifically, men in our sample showed, on average, lower explicit ambivalent sexism (mean = 1.65) than did the normative sample (mean = 2.34). Moreover, this process was repeated with the hostile sexism (HS) and benevolent sexism (BS) ASI subscales (Glick and Fiske, 1996). Both HS and BS scores in our sample (HS mean = 1.76; BS mean = 1.53) were significantly lower than the respective normative means (HS normative mean = 2.46, t value = -2.44, p = 0.02; BS normative mean = 2.23, t value = -2.62, p = 0.01). Correlation analyses were run between the ASI, as well as its HS and BS subscales, and the same ownership and erogeneity scores used with the IAT D1 values. We found no significant correlations between these measures.

3.3.2. Experiment 2. Only heterosexual female participants

3.3.2.1 Embodiment and vicarious touch feelings. We found a main effect of embodiment type on ownership scores When embodying a same-sex body, women rated their BO as higher—on average, 58.87 ± 5.6 compared to 36.55 ± 5.6 in opposite-sex conditions (estimate = -22.33; t-value = -5.25, $p < 0.0001$; $R^2_{\text{conditional}} = 0.83$). Additionally, women identified more with and felt more comfortable in the female VB than the male VB (Fig. 3.4A; identification: estimate = -12.95, t-value = -3.25, $p = 0.001$; $R^2_{\text{conditional}} = 0.62$; comfortableness: estimate = 9.32, t-value = -2.37, $p = 0.02$; $R^2_{\text{conditional}} = 0.6$). We found no significant effects concerning feelings about vicarious touch in women, suggesting that women's vicarious sensations did not differ across conditions.

3.3.2.3 Erogeneity of touch. Overall, caresses from male avatars were rated as more erogenous (M = 26.22, SE = 4.09) than those from female avatars (M = 24.28, SE = 3.91). Compared to wearing a same-sex avatar, women's body swap (wearing a male VB) led to increased ratings of erogeneity for caresses from a female avatar on intimate areas and decreased ratings of erogeneity for caresses from a male avatar on intimate areas (estimate = -9.4, t-value = -3.18, p = 0.001; R2conditional = 0.74; Fig. 3.4B). However, direct comparisons between conditions did not show relevant differences. In particular, ratings of erogeneity for caresses on intimate areas delivered by a female avatar (estimate = -10.24; t ratio = -3.35, p = 0.07) or a male avatar (estimate = 6.57; t ratio = 2.14, p = 0.59) did not significantly differ across embodiment conditions (same-sex vs. opposite-sex embodiment).

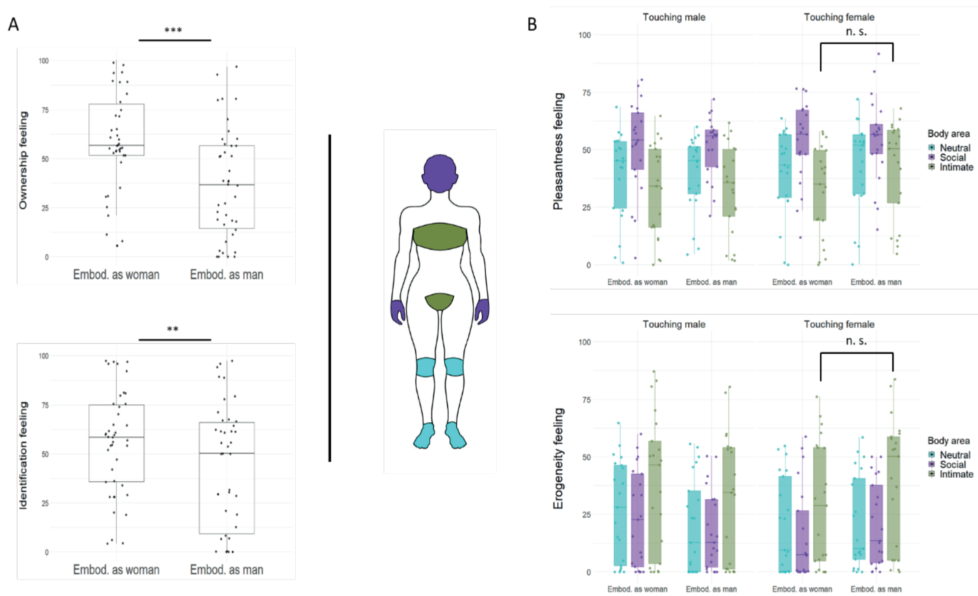


Fig. 3.4. Main behavioural results for Experiment 2 (all women). **(A)**: Box plots showing that women felt more ownership over and identified more with a same-sex (female) than an opposite-sex (male) VB. **(B)** Pleasantness and erogeneity ratings provided by Experiment 2 participants (all women). *Notes:* Error bars represent mean SEs. Black lines indicate significant (and nonsignificant) direct comparisons. ** = significant at < 0.01; *** = significant at < 0.001; n. s. = not significant.

3.3.2.4 Correlation analyses. The same criteria as those used in Experiment 1 were adopted for correlation analyses in Experiment 2. We found a significant negative correlation (Spearman' ϱ = -0.38, p = 0.002) between pleasantness scores for caresses on intimate areas and ownership scores. This correlation was specific to the condition in which women were caressed by a female avatar and embodied a same-sex VB; that is, female participants who reported higher ownership towards a female VB rated caresses on intimate areas by a female avatar as less pleasant.

3.3.2.5 Physiological reactivity. We did not find any significant effect with regard to the heart rate measure (see Appendix B for means and standard errors for each experimental condition).

Concerning SCR, caresses delivered by female avatars elicited a higher SCR (M = 0.82, SE = 0.1 μS) than caresses delivered by male avatars (M = 0.65, SE = 0.1 μS). Moreover, caresses on intimate areas (M = 0.75, SE = 0.1 μS) and social areas

($M = 0.76$, $SE = 0.1$ μS) elicited a stronger SCR than caresses on neutral areas ($M = 0.69$, $SE = 0.1$ μS). Finally, women's embodiment in a male VB (body swap) increased their SCR to female touching avatars (estimate = -0.13; *t*-value = -2.56, p = 0.01; $R^2_{\text{conditional}} = 0.41$).

As for experiment 1, statistical models were fitted with physiological measures as predictors of women's behavioural ratings. We found a significant interaction between SCR, embodiment type and touching avatar for erogeneity scores as outcome (estimate = -3.17; *t*-value = -4.69, $p < 0.001$; $R^2_{\text{conditional}} = 0.74$). Trend analyses revealed that higher erogeneity scores were predicted by higher SCR when women were caressed by a female touching avatar and embodied an opposite-sex VB, compared to when they embodied a same-sex VB (estimate = -1.44; *t*-ratio = -3.30, $p = 0.005$).

3.3.2.6 IAT. One participant was excluded from these analyses for reasons relating to technical problems during the task. D1 scores in women were not significantly different from zero (mean D1 = 0.01; t = 0.21, p = 0.83). IAT D scores did not differ across the two embodiment conditions (estimate = 0.07; t = 0.9, $p = 0.38$). Same correlation analyses as in experiment 1 were run for women. We found no significant correlations between these measures.

3.3.2.7 ASI. One participant did not complete this online questionnaire. A one-sample t test performed on mean ASI score from our sample showed that women expressed lower explicit ambivalent sexism (mean = 1.61) than did the normative sample (mean = 2.08). Furthermore, HS and BS scores in our sample (HS mean = 1.45; BS mean = 1.78) tended to be lower than the respective normative means (HS normative mean = 1.90, t value = -1.97, $p = 0.06$, not significant; BS normative mean = 2.25, t value = -2.60, $p = 0.01$). Same correlation analyses as in experiment 1 were run for women. We found no significant correlations between these measures.

3.3.3. Across studies comparisons

We decided to focus on separate experimental effects in men and women for several reasons. First, men and women were tested at two different times. Second, and more importantly, we conceived the study as a two-experiment one because we thought that focusing on men and women separately can better shed light on the effects of sex-related body swap on interpersonal touch preferences in both sexes. Third, we did not have any specific hypothesis concerning sex differences in sex-related body swap. In other words, we preferred parsimony over complexity, as the addition of a fourth factor in our experimental design would have made some results uninterpretable. However, across-studies differences in behavioural and physiological reactivity to virtual caresses were analysed through a between-subjects analysis, the results of which are described in detail in the Appendix B. Here, we report the main findings. The embodiment of women in an opposite-sex body was found to decrease the illusion of being touched on their own body (vicarious touch VAS), both for caresses delivered by male and female avatars. In contrast, when men embodied a female body, caresses delivered by a male avatar produced a stronger illusion of being touched on their own body, compared to same-sex conditions (estimate = 18.74; *t*-

value = 2.13, $p = 0.03$). As outlined above, the significant direct comparison of different subjective ratings concerning same-sex intimate touch when wearing a same-sex compared to an opposite-sex VB indicates that the consequences of the sex-related body swap illusion are stronger in men than in women. This was true for both pleasantness and erogeneity ratings. In line with this, we found that a between-subjects examination of these two VAS ratings yielded four-way interactions, which are explained by the stronger feelings of pleasantness (estimate = 19.85; t-value = 4.83, $p < 0.001$; $R^2_{\text{conditional}} = 0.63$) and erogeneity (estimate = 25.72; t-value = 5.7, $p < 0.001$; $R^2_{\text{conditional}} = 0.71$) for same-sex intimate touch (compared to neutral) in men while embodying an opposite-sex VB. Furthermore, the difference in ownership ratings between same- and opposite-sex conditions was stronger in women than in men (estimate = 15.48; t-value = 3.52, $p < 0.001$; $R^2_{\text{conditional}} = 0.72$), suggesting that men were more prone to embody an opposite-sex VB. A between-subjects analysis was run on gender-potency IAT D scores and Ambivalent Sexism Inventory (ASI) scores. The difference between men and women in gender-potency stereotypes was statistically significant (estimate = 0.39; $t = 3.98$, $p < 0.001$). Men had a stronger gender-potency bias than women (men: mean D score ± SD = 0.37 ± 0.06; women: mean D score ± SD = 0.01 ± 0.05). No differences between men and women were found in explicit sexist attitudes (ASI: $t = -0.11$, $p = 0.9$; HS: $t = -0.86$, $p = 0.39$; BS: $t = 0.78$, $p = 0.44$). Finally, while higher SCR was found in women when they were caressed by a female touching avatar, compared to a male one (estimate = 0.11; t-value = 3.14, $p = 0.001$), no such difference was observed in men.

2.4. Discussion

3.4.1 Wearing an opposite-sex virtual body

Capitalizing on the transformational power of IVR (Monti and Aglioti, 2018), we explored the behavioural and physiological consequences of embodying a same-sex or an opposite-sex VB and observing it being caressed on different regions by male and female avatars. First, we found that, in both men and women, the feeling of BO over the VB was higher when its sex matched the participant's. Despite this, ratings of illusory BO for an opposite-sex VB were not null, thus providing a frame in which to interpret the reactivity to intimate touch when embodying different types of VBs. Men appear to be more susceptible to the sex-related body swap illusion than women in terms of feelings of BO, comfortableness, and identification. Importantly, a comparison of men's and women's BO scores—reported in Appendix B, Between-subjects analysis, and Fig. B2—showed that women experienced significantly less ownership than men in the opposite-sex VB wearing condition.

Previous studies indicate that IVR users can experience faithful reproductions or replacements of their own body through which they can interact with virtual social environments. Bodily perception and representation can be easily manipulated by inducing in participants the feeling of "owning" a body different than the one they usually experience (i.e., their own body), as has been shown for avatars belonging to different demographic groups (Slater et al., 2010; Peck et al., 2013; Banakou et al., 2013; Peck et al., 2020; Tacikowski et al., 2020). The explicit and implicit attitudes and behaviour of people undergoing this illusion of BO have been found to be affected by such a body swap in a way that is coherent with the new body they are experiencing (Maister et al., 2015; Slater and Sanchez-Vives, 2014). Recent studies investigating sex-related body swaps are highly relevant for our purposes—i.e., the embodiment of men and women in opposite-sex VBs and its consequences for sex and gender biases and sex-related behaviours. In a pivotal example, Slater and colleagues (2010) reported that men could embody a female-appearing avatar and react behaviourally and physiologically to a threatening stimulation as if the VB were their own, provided that the embodiment happened in 1PP. More focused studies have recently examined the effects of sex-related body swaps on stereotype threat (Peck et al., 2018, 2020), working memory (Peck et al., 2020), gender violence and sexual harassment (Seinfeld et al., 2018; Neyret et al., 2020; de Borst et al., 2020), and gender identity (Tacikowski et al., 2020). Tacikowski and colleagues (2020) recently demonstrated that successful (and strong) sex-related body swap illusions are associated, in both women and men, with an online update of gender identity aspects. Specifically, wearing an opposite-sex VB: induced a modification of subjective feelings of femininity (women felt less feminine) and masculinity (men felt less masculine); balanced the strength of implicit associations between both genders and the self; updated gender-related stereotypes about one's own personality. The studies summarized above provide crucial evidence in support of the hypothesis that wearing an opposite-sex VB may be associated with behavioural changes coherent with the specific features of the embodied avatar (sex, in this case) and the cognitive representations and behaviours that are linked to them.

3.4.2 Vicarious feelings

Vicarious tactile sensations have been reported in healthy people observing pictures (Schirmer et al., 2015) and videos (Morrison et al., 2011; Walker et al., 2017), as well as in people observing representations of their own and others' VBs (Fusaro et al., 2016, 2019, 2021). Our IVR paradigm extends previous knowledge by investigating vicarious feelings elicited by caresses on a same-sex or opposite-sex VB seen from 1PP and thus perceived as one's own. Recent work from our research group shows that it is possible to simulate a virtual environment in which participants experience virtual caresses on several body parts from different virtual characters. The results reflect individuals' common reactions to real-life touch exchanges (Fusaro et al., 2021). Here, we expand on these findings by showing how sex-related body swaps can modulate the vicarious feeling of being touched on different regions of one's own VB.

3.4.3 Vicarious reactivity to virtual touches on a virtual body that is sexually congruent or incongruent with the participant's real body

Our present results show that vicarious feelings of touch in heterosexual men were higher when they were caressed by a female avatar. Heterosexual women, on the other hand, did not show any difference in vicarious feelings based on the sex of the touching avatar. Analyses of pleasantness and erogeneity ratings revealed that overall, both sexes preferred cross-sex touch in terms of the feeling of erogeneity elicited by vicarious touch on intimate areas. Additionally, correlation analyses showed that these feelings were stronger when ownership for the same-sex VB was higher. Our results are also coherent with theories suggesting that women engage more frequently in touch-mediated interactions and are more willing to be touched by members of both sexes, even strangers (as in our study), provided that the touch does not have sexual connotations (Stier and Hall, 1984; Russo et al., 2019; see also Appendix B, Additional results for results on the appropriateness of virtual caresses). Physiology results parallel the behavioural ones, supporting the notion that the simulation of social interactions in virtual environments may elicit body activation coherent with that experienced during real-life events. Heart rate deceleration (HRD), interpreted as a cardiac function reduction associated with attentional shift contingent upon the processing of an arousing event (Bradley et al., 2001), was found in men for virtual caresses on intimate areas. When asked to rate their feelings of arousal related to the virtual caresses, men considered virtual caress on intimate areas more arousing than caresses on neutral areas (see Appendix B, Additional results for analyses of the arousal elicited by virtual caresses). Similarly, SCR is considered a measure of sympathetic nervous system involvement related to the processing of arousing stimuli, regardless of their valence (Bradley et al., 2001). While men showed a higher SCR for caresses from a female touching avatar, coherent with the relevance of cross-sex touch in this demographic group, women experienced a higher SCR for both social and intimate touch (compared to neutral touch), paralleling behavioural results on the pleasantness of caresses.

An important result of our study is related to how experiencing an opposite-sex VB in 1PP affects vicarious tactile feelings. For both men and women, we predicted that embodying an opposite-sex VB would shift participants' preferences for touch-mediated interactions towards those of the opposite sex. This is indeed what we found. Heterosexual men rated caresses on intimate body areas from a touching male avatar as more pleasant and more erogenous when they embodied a female body. This change was stronger for the vicarious feeling of erogeneity. Moreover, heterosexual women rated caresses from a female touching avatar in intimate areas as more pleasant and more erogenous when they embodied a male VB. As such, despite the fact that participants in both studies felt greater ownership over a same-sex VB, experiencing an opposite-sex VB was found to elicit changes in explicit reactions to same-sex virtual caresses. It is worth noting that, although our results might stem from merely witnessing a preferred (cross-sex) erogenous scenario during the opposite-sex embodiment conditions, correlation analyses support the hypothesis that it was in fact the experience of owning an opposite-sex body that shaped participants' choices. Especially for men, we observed a significant positive correlation between erogeneity and BO scores for the condition in which they embodied a female body and were virtually touched on intimate areas by a male touching avatar (Fig. 3.2C). Tellingly, our results indicate that participants' physiological activation differently predicts behavioural outcomes (ratings at VAS scales) and suggest that implicit physiological reactivity may underlie full-body illusions in IVR, discriminate between different virtual scenarios, and predict how people behave in such circumstances. In our case, a decrease in HR and an increase in SCR – two correlates of enhanced processing of arousing stimuli (Bradley et al., 2001) – were associated with increments in erogeneity and pleasantness ratings when heterosexual men and women were caressed by a same-sex toucher and embodied an opposite-sex VB, which further supports the effectiveness of our sex-related body swap illusion.

It is worth noting that virtual touches on the pelvis and on the chest (only in women) were delivered on clothes, while all the other touches were delivered directly on the avatar's skin. However, we believe this should not be a concern when examining vicarious feelings for observed pleasant touch. For instance, in Walker and colleagues (2017)'s study, the observation of pleasant touch on the back of an individual wearing a shirt was considered more pleasant when delivered at the CT velocity (compared to other velocities), similar to pleasant touch on the arm (on naked skin). We acknowledge, however, that future studies should be devised to specifically address this point.

Interpersonal touch preferences, especially those concerning intimate touch, are tightly linked to people's SO (Gallace and Spence, 2010). Our results provide novel insights on the association between SO and tactile preferences and on the moderation effect that body ownership/perception plays on the latter two. We cannot yet speculate on a specific psychological mechanism being at play during the observed changes in tactile preferences – e.g., a temporary modification of gender identity (Tacikowski et al., 2020). It is highly likely, though, that owning an opposite-sex VB leads to an update in high-order cognitive representations of one's own body, which in turn may temporarily affect gender identity, SO, and, ultimately, interpersonal touch preferences (Maister et al., 2015). Anne Fausto-Sterling has recently put forward a theory of gender, sex, and sexual orientation that is solidly based on the embodied cognition account and can provide further theoretical support for our results (Fausto-Sterling, 2019). According to the author, personal and interpersonal experiences, within and with the body, are inextricably intertwined with the development and the expression of gender, sex, and sexual orientation in the child/adolescent. It follows that a modification of bodily features associated with these psychological representations, feelings, and experiences may have consequences as those we observed in our study.

Our results also suggest that, despite their implicit gender bias, men may be more susceptible to our sex-related body swap illusion (details on across-studies analyses of VAS ratings are provided in Appendix B, Between-subjects analysis), at least concerning its effect on touch-mediated interaction. Of note, women seem to be more willing to be touched by members of both sexes, even strangers (as in our study), provided that the touch does not have sexual connotations (Fusaro et al., 2021; present study). However, we do not believe that this could be a viable overall explanation of our results, as the effects observed in our study are strictly related to the swap of one's own sex in IVR. While the difference between gender-potency IAT scores speaks in favour of a higher bias in men, no across-sample differences in explicit sexist attitudes were observed. Concerning this apparent difference between men's and women's susceptibility to our sex-related body swap illusion, recent evidence suggests that sex differences in body perception processes may be relevant to understanding some of our results (Aleong and Paus, 2010; Burke et al., 2019). While heterosexual men seem to be more sensitive to self-related information about the opposite sex's bodies, heterosexual women are particularly sensitive to their own bodies (Burke et al., 2019). Patterns of brain activation in response to information related to one's own body also differ across sexes: Women seem to engage in complex cognitive-emotional processing more often than men, with activation reported in the amygdala and prefrontal areas (Kurosaki et al., 2006). Thus, it may be possible that the higher emotional sensitivity to one's own body demonstrated by women—which is likely based on paying greater attention to bodily signals (such as interoceptive signals)—could interfere with the illusion of owning an opposite-sex VB or at least weaken the consequences of such body swap. Interestingly, the processing of information related to bodies of the opposite sex has been associated with the deactivation of the right temporoparietal junction (rTPJ) in women, a brain region that has previously been linked to perspective-taking abilities (Decety and Lamm, 2007; Wang et al., 2016).

3.5. Conclusions and future directions

By capitalizing on IVR, we were able to investigate how heterosexual men and women reacted at subjective and physiological levels to the experience of wearing a same- or opposite-sex VB and seeing it touched on intimate areas by a male or female avatar. IVR allowed us to both create "impossible" scenarios, i.e., swapping people's sex, and to overcome ethical barriers associated with real intimate touch. While embodying a same-sex VB gave rise to heterosexual-like responses as expected, embodying an opposite-sex VB changed these responses as though the human participants were in the position of their embodied avatar. Both heterosexual men and heterosexual women rated same-sex touch on intimate areas as more pleasant and erogenous when they embodied an opposite-sex VB. Interestingly, this change of perspective had stronger effects in men, who also demonstrated stronger feelings of ownership over an opposite-sex VB. While future work is needed to further qualify this finding, we submit that it may be relevant for the current debate fuelled by IVR studies (26, 27) on domestic violence and sexual harassment perpetrated by men against women. It may be interesting, for example, to explore whether VR-mediated physical transformations may help misogynistic men to take on women's physical and mental perspectives. Finally, our study may have important translational implications by inspiring, for example, VR-based support for transgender people during their surgical and hormonal transitions as well as applications in which training, rehabilitation, or simply a promotion of social skills is sought, such as empathy and perspective-taking in people who may lack such skills.

Appendix B – Supplementary material for Chapter 3

Experimental stimuli and setup. The virtual scenario was designed using 3DS Max 2017 (Autodesk, Inc.) and implemented in Unity game engine software v5.3. The virtual avatars were created using Iclone 7 (https://www.reallusion.com/iclone/) and implemented in Unity. The scenario was presented by means of Oculus Rift (HMD, www.oculus.com). In order to realize naturalistic movements, we used the Xsense motion capture suits (https://www.xsens.com/) to record the kinematics of a real actor who gently caressed, with the right hand, different body parts of an actor seated on a beach chair. Actor's kinematics were transferred on the virtual avatar's bones by means of Motion Builder 2015 (Autodesk, Inc.) and rendered in Unity. This way, participants observed the same naturalistic kinematics implemented on the virtual character. Moreover, a customized C# script in Unity was realized ad hoc to connect an Xbox controller to a cursor that could be moved to rate along VAS questions specific features of the virtual stimuli.

Forza (strength)	**Debolezza (weakness)**	**Uomo (man)**	**Donna (woman)**
Potenza (power)	Timidezza (shyness)	Paolo	Anna
Dominio (supremacy)	Paura (fear)	Pietro	Maria
Conquista (conquest)	Fragilità (fragility)	Davide	Giulia
Autorità (authority)	Sconfitta (defeat)	Antonio	Emilia
Coraggio (courage)	Timore (dread)	Giovanni	Rebecca

Tab. B1. Words used within the gender-potency IAT task.

Experiment 1 (men)
Additional results

(Ownership) Control statements. We obtained an "ownership control score" per block per participant, by averaging the ratings provided at the two control VAS statements. As expected, we did not find a significant effect of the "Embodiment" factor on the control score (Estimate = -0.09; t value = -0.03; Pr(>|t|) = 0.97). Moreover, no significant main effect of the "Touching avatar" factor (Estimate = -5.25; t value = -1.65; Pr(>|t|) = 0.1) of the Embodiment*Touching avatar interaction (Estimate = 4.94; t value = 1.1; Pr(>|t|) = 0.28) were found.

Appropriateness of touch. The multilevel linear regression ran on men's subjective ratings at the "Appropriateness" VAS yielded main effects of Body area and Touching avatar, and three different 2-way interactions. The main effect of Touching avatar has model Estimate of -13.58 (with Error = 2.24), t value of -6.05, and probability Pr(>|t|) < 0.0001. Overall, caresses delivered by female avatars were rated by men as more appropriate (M = 45.06, SE = 3.05, 95% Cl = [39.08, 51.04]), compared to male touch (M = 34.18, SE = 2.74, 95% Cl = [28.81, 39.55]). The main effect of Body area, for the Intimate Vs Neutral areas contrast, has model Estimate of -10.44 (with Error = 2.91), t value of -3.58, and probability Pr(>|t|) of 0.001. Intimate touch was rated as strongly inappropriate (M = 25.97, SE = 3.12, 95% Cl = [19.86, 32.09]), compared to neutral one (M = 43.88, SE = 3.54, 95% Cl = [36.94, 50.81]). The main effect of Body area, for the Social Vs Neutral areas contrast, has model Estimate of 6.29 (with Error = 2.66), t value of 2.36, and probability Pr(>|t|) of 0.02. Social touch was rated as slightly more appropriate (M = 49.03, SE = 2.61, 95% CLs = low: 43.92 – up: 54.16), compared to neutral one (M = 43.88, SE = 3.54, 95% Cl = [36.94, 50.81]). The Embodiment*Touching avatar interaction has model Estimate of 6.6 (with Error = 2.4), t value of 2.75, and probability Pr(>|t|) of 0.006. Appropriateness for caresses delivered by male and female avatars - independently from which body area was caressed - was found to be modulated by the type of embodiment our participants went through. Specifically, while the appropriateness felt towards a touching male avatar during same-sex embodiment was of 31.76 ± 2.83 (95% Cl = [26.21, 37.31]), during opposite-sex conditions - i.e., men embodying a female body - this appropriateness feeling went up to 36.60 ± 2.89 (95% Cl = [30.92, 42.28]). At the same time, appropriateness felt towards a touching female avatar was of 46.94 ± 3.14 (95% Cl = [40.78, 53.1]) during same-sex conditions, compared to 43.18 ± 3.18 (95% Cl = [36.93, 49.44]) during opposite-sex ones. Overall, the difference in ratings existing between touching male and female avatars was reduced when participants embodied a female avatar. The Embodiment*Body area interaction, for the Intimate Vs Neutral areas contrast, has model Estimate of -13.07 (with Error = 2.4), t value of -5.44, and probability Pr(>|t|) < 0.0001. This strong interaction effect tells us that embodying a female avatar significantly reduces the appropriateness for caresses on intimate body areas compared to neutral ones, while there is no such decrement when social areas are considered. Specifically, appropriateness for caresses on intimate body areas during same-sex embodiment was of 29.09 ± 3.21 (95% Cl = [22.78, 35.39]), compared to 22.86 ± 3.28 (95% Cl = [16.42, 29.29]) during opposite-sex embodiment. The Touching avatar*Body area interaction, for the Intimate Vs Neutral areas contrast, has model Estimate of -6.2 (with Error = 2.4), t value of -2.58, and probability Pr(>|t|) of 0.009. As one would expect for heterosexual men, this interaction shows that a touching male avatar is rated as less appropriate than a female one when considering each of the body areas. Specifically, what the significant contrast tells us is that, while the reduction in appropriateness produced by a male avatar touching social areas compared to neutral areas is a negligible one, we have a significant decrease in appropriateness for intimate areas compared to neutral ones.

Arousal produced by touch. The multilevel linear regression ran on men's subjective ratings at the "Arousal" VAS yielded a main effect for the "Body area" factor, as well as two 2-way interactions. The main effect of Body area, for the Intimate Vs Neutral areas contrast, has model Estimate of 7.74 (with Error = 2.56), t value of 3.02, and probability Pr(>|t|) of 0.004. As one would expect, caresses on intimate areas were rated, on average, as more arousing (M = 64.78, SE = 3.82, 95% Cl = [57.29, 72.27]) than caresses on neutral areas (M = 54.39, SE = 3.41, 95% Cl = [47.71, 61.07]). The Embodiment*Touching avatar interaction has model Estimate of -2.95 (with Error = 1.33), t value of -2.21, and probability Pr(>|t|) of 0.02. While no difference is found for female touch between same-sex and opposite-sex embodiment conditions, men rated male touch as being less arousing when they embodied a female avatar (M = 56.79, SE = 3.89, 95% Cl = [49.15, 64.42]) compared to same-sex conditions (M = 59.73, SE = 3.96, 95% Cl = [51.97, 67.49]). The Embodiment*Body area interaction, for the Intimate Vs Neutral areas contrast, has model Estimate of 4.57 (with Error = 1.63), t value of 2.8, and probability Pr(>|t|) of 0.005. While the embodiment of a female virtual agent was found to reduce the arousal felt for neutral touch (same-sex = 56.21 ± 3.64, 95% Cl = [49.07, 63.35]; opposite-sex = 52.57 ± 3.52, 95% Cl = [45.66, 59.49]), this did not hold true for caresses on intimate areas (same-sex = 64.31 ± 3.87, 95% Cl = [56.73, 71.89]; opposite-sex = 65.24 ± 4.09, 95% Cl = [57.23, 73.26]).

Correlation analyses. We ran further correlation analyses to provide additional evidence that the ownership and control scores in fact reflected two different constructs, one measuring the ownership feeling of participants over a virtual body, the other not related to this sensation. If this is the case, then the two scores should correlate negatively, or at least not correlate positively. Moreover, we were interested in checking if, and in which circumstances, the feeling of ownership correlated with the vicarious feeling of touch. We predicted that stronger feeling of ownership would be associated with stronger feeling of vicarious touch, at least when embodying a same-sex virtual body. As expected, we found strong negative correlations between ownership and control scores in all conditions (all rs > -0.7 and all ps < 0.001), except in the one where men embodied an opposite-sex virtual body and were caressed by a female touching avatar (r = -0.08, p = 0.7) (Fig. B1). Furthermore, we found positive correlations between ownership scores and vicarious touch scores during the two same-sex virtual body conditions (male touching avatar: r = 0.48, p = 0.03; female touching avatar: r = 0.58, p = 0.005).

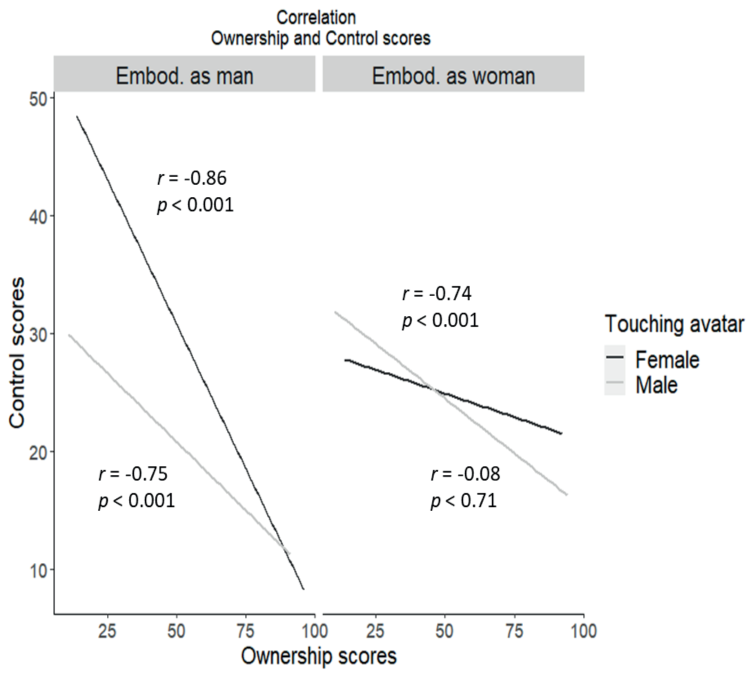


Fig. B1. Exp 1 (only men). Correlations between ownership scores and control scores. Rs are > -0.7 and ps < 0.001 for all conditions, except in the opposite-sex virtual body-female touching avatar one (r = -0.08, p < 0.7).

Descriptive statistics

		Male toucher (mean ± SE)	Female toucher (mean ± SE)
Ownership score	Same-sex emb	55.68 ± 5.09	62.43 ± 5.09
	Opposite-sex emb	50.9 ± 5.09	53.56 ± 5.09
Vicarious touch	Same-sex emb	39.2 ± 5.54	52.17 ± 4.67
	Opposite-sex emb	42.69 ± 5.73	44.38 ± 5.17
Comfortableness	Same-sex emb	65.36 ± 4.65	68 ± 4.23
	Opposite-sex emb	62.15 ± 5.19	64.87 ± 4.8
Identification	Same-sex emb	64.16 ± 5.19	66.12 ± 4.61
	Opposite-sex emb	52.2 ± 6.02	52.1 ± 5.28

Tab. B2. Exp 1 (only men): Means and standard errors (SEs) of each end-of-the-block statement [derived from model estimates using the *effect()* function from the effects package in R (Fox and Weisberg, 2019)] for each condition.

		Male toucher			Female toucher		
		Neutral (mean ± SE)	Social (mean ± SE)	Intimate (mean ± SE)	Neutral (mean ± SE)	Social (mean ± SE)	Intimate (mean ± SE)
Appropriateness	Same-sex emb	34.76 ± 3.43	40.26 ± 3.19	20.28 ± 3.18	48.33 ± 4-03	54.62 ± 2.86	37.9 ± 3.62
	Opposite-sex emb	43.72 ± 3.6	47.76 ± 3-11	18.36 ± 3.25	48.7 ± 4.17	53.52 ± 2.76	27.36 ± 3.67
Pleasantness	Same-sex emb	37.34 ± 3.23	35.73 ± 3.34	27 ± 3.49	50.28 ± 3.22	50.07 ± 2	55.06 ± 3.52
	Opposite-sex emb	41.34 ± 3.15	40.31 ± 2.99	40.16 ± 3.71	47.12 ± 3.72	47.48 ± 3.28	46.11 ± 4.24
Arousal	Same-sex emb	56.84 ± 4.18	57.41 ± 4.09	64.94 ± 4.18	55.58 ± 3.25	56.16 ± 3.06	63.68 ± 3.73

	Opposite-sex emb	51.73 ± 4.01	54.23 ± 3.93	64.4 ± 4.32	53.42 ± 3.2	55.92 ± 3.02	66.09 ± 4-02
Erogeneity	Same-sex emb	11.71 ± 3.53	8.9 ± 3.15	11.6 ± 4.17	35.25 ± 4.12	31.23 ± 3.77	50.83 ± 4.48
	Opposite-sex emb	20.5 ± 3.78	15.64 ± 3.63	40.32 ± 4	32.58 ± 4.17	28.48 ± 4.01	51.76 ± 5.13

Tab. B3. Exp 1 (only men): Means and SEs of each in-session question for each condition.

			Male toucher			Female toucher	
		Neutral (mean ± SE)	Social (mean ± SE)	Intimate (mean ± SE)	Neutral (mean ± SE)	Social (mean ± SE)	Intimate (mean ± SE)
Baselined heart rate (bpm)	Same-sex emb	-0.5 ± 0.54	-1.32 ± 0.54	-1.41 ± 0.54	-1.4 ± 0.54	-1.2 ± 0.54	-1.87 ± 0.54
	Opposite-sex emb	-1.13 ± 0.54	-0.5 ± 0.54	-1.82 ± 0.54	-0.96 ± 0.54	-0.94 ± 0.54	-1.75 ± 0.54
Skin conductance response (μS)	Same-sex emb	0.75 ± 0.09	0.83 ± 0.09	0.83 ± 0.09	0.83 ± 0.09	0.83 ± 0.09	0.86 ± 0.09
	Opposite-sex emb	0.72 ± 0.09	0.69 ± 0.09	0.73 ± 0.09	0.75 ± 0.09	0.79 ± 0.09	0.81 ± 0.09

Tab. B4. Exp 1 (only men): Means and SEs for the physiological measures for each condition.

Experiment 2 (women)
Additional results

Appropriateness of touch. The multilevel linear regression ran on women's subjective ratings at the "Appropriateness" VAS yielded main effects of Body area and Touching avatar, and two different 2-way interactions. The main effect of Touching avatar has model Estimate of -4.55 (with Error = 2.23), t value of -2.03, and probability Pr(>|t|) < 0.0001. Overall, caresses delivered by female avatars were rated by women as more appropriate (M = 40.17, SE = 3.93, 95% Cl = [32.45, 47.88]), compared to male touch (M = 36.57, SE = 3.54, 95% Cl = [29.62, 43.52]). The main effect of Body area, for the Intimate Vs Neutral areas contrast, has model Estimate of -26.99 (with Error = 3.89), t value of -6.93, and probability Pr(>|t|) < 0.0001. Intimate touch was rated as strongly inappropriate (M = 20.40, SE = 3.82, 95% Cl = [12.9, 27.91]), compared to neutral one (M = 40.04, SE = 4.47, 95% Cl = [31.27, 48.82]). The main effect of Body area, for the Social Vs Neutral areas contrast, has model Estimate of 17.71 (with Error = 3.56), t value of 4.98, and probability Pr(>|t|) < 0.0001. Social touch was rated as more appropriate (M = 54.69, SE = 4.3, 95% Cl = [46.25, 63.13]) than neutral touch (M = 40.04, SE = 4.47, 95% Cl = [31.27, 48.82]). The Embodiment*Body area interaction, for the Intimate Vs Neutral areas contrast, has model Estimate of 12.35 (with Error = 2.53), t value of 4.87, and probability Pr(>|t|) < 0.0001. While embodying a male body did not have any effect on neutral touch, the same embodiment condition increased the appropriateness women felt for caresses on intimate areas, independently of the sex of the avatar touching. Specifically, caresses on intimate areas during same-sex conditions were rated at 15.38 ± 4.03 (95% Cl = [7.48, 23.28]), compared to 25.44 ± 3.98 (95% Cl = [17.63, 33.26]) for caresses on intimate areas during opposite-sex conditions. The Touching avatar*Body area interaction, for the Intimate Vs Neutral areas contrast, has model Estimate of 5.43 (with Error = 2.53), t value of 2.14, and probability Pr(>|t|) of 0.03. The Touching avatar*Body area interaction, for the Social Vs Neutral areas contrast, has model Estimate of -5.15 (with Error = 2.53), t value of -2.58, and probability Pr(>|t|) of 0.04. These results tell us that whereas caresses on intimate areas were rated as very little appropriate by women independently of the touching avatar, we see a small reduction in appropriateness both for social and neutral areas when a male touching avatar was involved.

Arousal produced by touch. The multilevel linear regression ran on women's subjective ratings at the "Arousal" VAS yielded a main effect for the "Body area" factor. The main effect of Body area, for the Intimate Vs Neutral areas contrast, has model Estimate of 5.73 (with Error = 2.19), t value of 2.61, and probability Pr(>|t|) of 0.01. The main effect of Body area, for the Social Vs Neutral areas contrast, has model Estimate of 5.62 (with Error = 2.30), t value of 2.44, and probability Pr(>|t|) of 0.01. Women rated caresses on both intimate (M = 51.64, SE = 3.93, 95% Cl = [43.94, 59.35]) and social areas (M = 46.03, SE = 3.5, 95% Cl = [39.17, 52.9]) as more arousing than caresses on neutral areas (M = 49.89, SE = 3.45, 95% Cl = [43.13, 56.65]).

Correlation analyses. As in study 1, we ran further correlation analyses to provide additional evidence that the ownership and control scores in fact reflected two different constructs. Moreover, we ran correlations analyses between the ownership scores and the vicarious touch scores. We found no significant correlations between ownership and control scores. Instead, we found a strong positive correlation between ownership scores and vicarious touch scores during the same-sex virtual body condition in which women were caressed by a male touching avatar (r = 0.88, p < 0.001). Thus, the more ownership women felt for a female virtual body, the more vicarious touch feeling they experienced when caressed by a male touching avatar.

Descriptive statistics

	Male toucher (mean ± SE)	Female toucher (mean ± SE)

Ownership score	Same-sex emb	59.3 ± 5.88	58.45 ± 5.88
	Opposite-sex emb	32.27 ± 5.88	40.82 ± 5.88
Vicarious touch	Same-sex emb	54.24 ± 4.87	51.62 ± 5.18
	Opposite-sex emb	41.03 ± 5.31	45.88 ± 5
Comfortableness	Same-sex emb	54.18 ± 6.11	58.75 ± 6.11
	Opposite-sex emb	45.71 ± 6.11	48.57 ± 6.11
Identification	Same-sex emb	56.73 ± 6.29	55.12 ± 6.29
	Opposite-sex emb	42.37 ± 6.29	43.57 ± 6.29

Tab. B5. Exp 1 (only women): Means and SEs of each end-of-the-block statement for each condition.

			Male toucher			Female toucher	
		Neutral (mean ± SE)	Social (mean ± SE)	Intimate (mean ± SE)	Neutral (mean ± SE)	Social (mean ± SE)	Intimate (mean ± SE)
Appropriateness	Same-sex emb	37.38 ± 4.77	49.95 ± 4.5	15.82 ± 4.01	41.93 ± 5.96	59.64 ± 5.03	14.94 ± 4.24
	Opposite-sex emb	39.52 ± 4.52	52.63 ± 4.21	24.2 ± 4.04	41.34 ± 4.69	56.53 ± 4.64	26.68 ± 4.23
Pleasantness	Same-sex emb	39.97 ± 4.57	51.9 ± 3.39	32.29 ± 4.42	40.37 ± 4.06	53.42 ± 3.21	32.08 ± 3.78
	Opposite-sex emb	39.91 ± 3.6	51.44 ± 3.16	32.87 ± 3.74	43.52 ± 3.6	54.32 ± 3.63	41.76 ± 3.64
Arousal	Same-sex emb	48.67 ± 4.39	53.3 ± 4.01	56.29 ± 4.65	46.19 ± 3.9	51.81 ± 3.78	51.92 ± 4.24
	Opposite-sex emb	47.05 ± 4.38	47.68 ± 4.39	48.66 ± 4.77	42.24 ± 4.03	44.39 ± 4.32	49.7 ± 4.5
Erogeneity	Same-sex emb	26.67 ± 4.83	23.21 ± 4.44	37.96 ± 5.97	20.23 ± 4.65	15.62 ± 4.18	28.87 ± 5.17
	Opposite-sex emb	20.31 ± 4.01	17.72 ± 3.53	31.3 ± 5.79	21.28 ± 4.49	20.52 ± 3.99	39.11 ± 5.51

Tab. B6. Exp 1 (only women): Means and SEs of each in-session question for each condition.

			Male toucher			Female toucher	
		Neutral (mean ± SE)	Social (mean ± SE)	Intimate (mean ± SE)	Neutral (mean ± SE)	Social (mean ± SE)	Intimate (mean ± SE)
Baselined Heart Rate (bpm)	Same-sex emb	-1.15 ± 0.42	-0.93 ± 0.42	-1.03 ± 0.42	-0.74 ± 0.42	-1.19 ± 0.42	-1.13 ± 0.42
	Opposite-sex emb	-1.37 ± 0.42	-1.87 ± 0.42	-0.97 ± 0.42	-1.11 ± 0.42	-1.18 ± 0.42	-1.6 ± 0.42
Skin conductance response (μS)	Same-sex emb	0.63 ± 0.1	0.67 ± 0.1	0.71 ± 0.1	0.75 ± 0.1	0.84 ± 0.1	0.74 ± 0.1
	Opposite-sex emb	0.6 ± 0.1	0.65 ± 0.1	0.64 ± 0.1	0.77 ± 0.1	0.89 ± 0.1	0.93 ± 0.1

Tab. B7. Exp 1 (only women): Means and SEs for the physiological measures for each condition.

Between-subjects analysis results

In the main text, we focused on separate experimental effects in men and women for several reasons. First, men and women were tested at two different times. Second, and more importantly, we conceived the study as a two-experiment one because we thought that focusing on men and women separately can better shed light on the effects of sex-related body swap on interpersonal touch preferences in both sexes. Third, we did not have any specific hypothesis concerning sex differences in sex-related body swap. In other words, we preferred parsimony over complexity, as the addition of a fourth factor in our experimental design would have made some results uninterpretable. However, since we believe that across-sex differences are important to explore, we report below the main results of a between-subjects analysis. Only findings in which the between-subjects factor "Participants' sex" had a role are described.

Ownership statements. We found an interaction effect of Embodiment*Participants' sex, which has model Estimate of 15.48 (with Error = 4.39), t value of 3.52, and probability Pr(>|t|) of 0.0005. This strong interaction effect tells us that women are more sensitive to changes in their virtual body, as embodying an opposite-sex body was found to strongly decrease the feeling of ownership over it. This is in contrast with what happens for men, who still show a robust ownership feeling over an embodied female avatar (Fig. B2). This is coherent with the strength of shifts in ratings when embodying an opposite-sex virtual agent found for men (see results study 1).

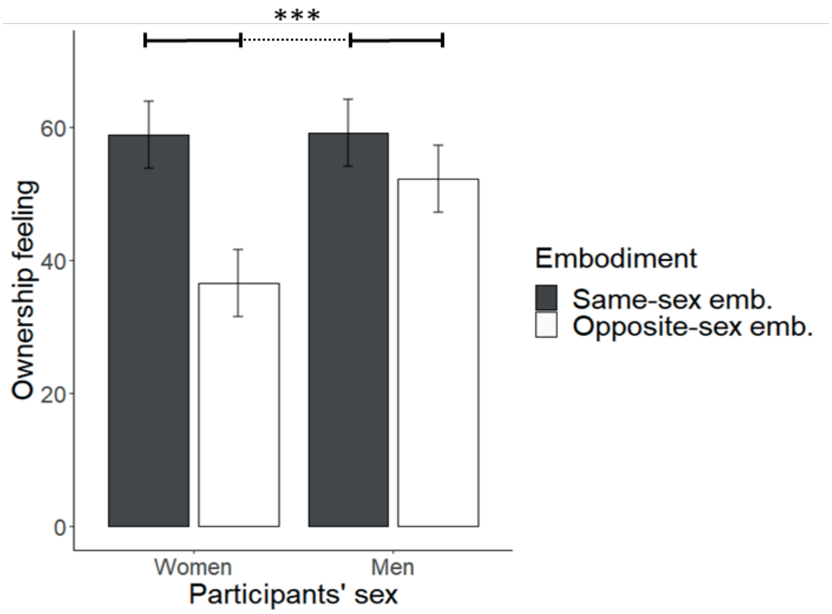


Fig. B2: Exp 1 and exp 2 comparisons. The difference between ownership felt for a same-sex virtual body compared to an opposite-sex virtual body is stronger in women than in men.

Vicarious touch statement. We found an interaction effect of Embodiment*Touching avatar*Participants' sex, which has model Estimate of 18.74 (with Error = 8.78), t value of 2.13, and probability Pr(>|t|) of 0.03. The embodiment of women in an opposite-sex body was found to decrease the illusion of being touched on their own body, both for caresses delivered by male and female avatars. In contrast, when men embodied a female body, caresses delivered by a male avatar produced a stronger illusion of being touched on their own body, compared to same-sex conditions.

Comfortableness statement. We found a main effect of the "Participants' sex" factor, which has model Estimate of 13.3 (with Error = 6.61), t value of 2.01, and probability Pr(>|t|) of 0.05. Overall, men felt more comfortable than women.

Appropriateness of touch. The multilevel linear regression ran on participants' subjective ratings at the "Appropriateness" VAS yielded a 4-way interaction. The Embodiment*Touching avatar*Body area*Participants' sex interaction, for the Intimate Vs Neutral areas contrast, has model Estimate of 10.43 (with Error = 4.94), t value of 2.11, and probability Pr(>|t|) of 0.03. While when analysing separately men's and women's data we do not find any 3-way interaction, the between-subjects analysis showed a 3-way interaction that is modulated by the between factor Participants' sex – thus a 4-way interaction. This effect (Pr(>|t|) of 0.03) only concerns caresses on intimate areas and tells us that, when men embody an opposite-sex body (a female virtual agent), caresses delivered by a female avatar are rated as less appropriate, compared to when a same-sex avatar is embodied. The same effect is not present for women, which explains the influence of the between factor Participants' sex on the analysis.

Pleasantness of touch. The multilevel linear regression ran on participants' subjective ratings at the "Pleasantness" VAS yielded a 4-way interaction. The Embodiment*Touching avatar*Body area*Participants' sex interaction, for the Intimate Vs Neutral areas contrast, has model Estimate of 19.85 (with Error = 4.11), t value of 4.83, and probability Pr(>|t|) < 0.0001. This strong effect pinpoints once again the robust change in ratings that characterizes men. Even though we see an increase in pleasantness ratings for women when they embody an opposite-sex body and are touched by a female avatar in intimate areas, it is when we look at men's ratings that we find the most interesting results. Indeed, when embodying a female body, their ratings were found to both decrease as concerns intimate female touch, compared to same-sex conditions, and to increase as concerns intimate male touch, still compared to same-sex conditions.

Arousal produced by touch. The multilevel linear regression ran on participants' subjective ratings at the "Arousal" VAS yielded a 3-way interaction. The Embodiment* Body area*Participants' sex interaction, for the Intimate Vs Neutral areas contrast, has model Estimate of 6.70 (with Error = 2.29), t value of 2.92, and probability Pr(>|t|) of 0.003. While the embodiment of an opposite-sex body was found to reduce arousal for caresses on all body areas for women, men rated caresses on intimate areas as being more arousing when embodying a female body. Opposite-sex conditions had the effect of decreasing the arousal for caresses on neutral body areas, but not decreasing the arousal for caresses on intimate areas, which created a difference in ratings between these two body areas that is wider compared to same-sex conditions.

Erogeneity of touch. The multilevel linear regression ran on participants' subjective ratings at the "Erogeneity" VAS yielded a 4-way interaction. The Embodiment*Touching avatar*Body area*Participants' sex interaction, for the Intimate Vs Neutral areas contrast, has model Estimate of 25.72 (SE = 4.51), t value of 5.7, and probability Pr(>|t|) < 0.0001. The robust effect found for this interaction represents the strong shift in ratings found for men when they embodied a female body and were touched by a male avatar in intimate areas. Indeed, ratings for this condition increased from 11.6 ± 5.15 (95% Cl = [1.5, 21.69]) for same-sex conditions to 40.32 ± 5.41 (95% Cl = [29.71, 50.93]) for opposite-sex ones. Even though for women we also see a similar effect on ratings prompted by the embodiment of an opposite-sex body, such effect is not as strong as the one found in men.

Heart Rate. The analyses yielded an interaction effect of Embodiment*Touching avatar*Body area*Participants' sex, and specifically for the Social Vs Neutral areas contrast, which has model Estimate of 0.35 (with Error = 0.14), t value of 2.53, and probability Pr(>|t|) of 0.01.

Skin conductance response. The analyses yielded an interaction effect of Touching avatar* Participants' sex, which has model Estimate of 0.11 (with Error = 0.03), t value of 3.14, and probability Pr(>|t|) of 0.001. We also found an interaction effect of Embodiment*Participants' sex, which has model Estimate of -0.1 (with Error = 0.03), t value of -2.72, and probability Pr(>|t|) of 0.006.

IAT. A between-subjects analysis was run on gender-potency IAT D scores. The difference between men and women in gender-potency stereotype was statistically significant (model Estimate = 0.39; t = 3.98, Pr(>|t|) < 0.001). Men were found to have a stronger gender-potency bias compared to women (men: mean D score = 0.37 ± 0.06; women: mean D score = 0.01 ± 0.05). Additional correlation analyses were run between IAT D scores (averaged across the two sessions) and two measures taken as indexes of behaviour change in IVR, i.e., ownership scores during the opposite-sex conditions and erogeneity scores for same-sex touch in intimate areas during opposite-sex conditions. Thus, Bonferroni correction returned a p value of 0.025 (two comparisons). We found a significant positive correlation between D scores and ownership scores ($r = 0.43$, $p = 0.004$). The correlation between D values and erogeneity scores was not significant ($r = 0.05$, $p = 0.76$).

ASI. As concerns our sample, no differences between men and women were found relating to their explicit sexist attitudes (ASI: t = -0.11, $p = 0.9$; HS: t = -0.86, $p = 0.39$; BS: t = 0.78, $p = 0.44$). Correlation analyses were run between the ASI, as well as its HS BS subscales, and the same ownership and erogeneity scores used with the IAT D values. None of the correlations resulted significant.

References

1. Greenwald, A. G., McGhee, D. E., and Schwartz, J. L. (1998). Measuring individual differences in implicit cognition: the implicit association test. Journal of Personality and Social Psychology, 74(6), 1464.
2. Rudman, L. A., Greenwald, A. G., and McGhee, D. E. (2001). Implicit self-concept and evaluative implicit gender stereotypes: Self and ingroup share desirable traits. Personality and Social Psychology Bulletin, 27(9), 1164-1178.
3. Glick, P., and Fiske, S. T. (1996). The ambivalent sexism inventory: Differentiating hostile and benevolent sexism. *Journal of personality and social psychology*, *70*(3), 491.
4. Manganelli Rattazzi, A. M., Volpato, C., and Canova, L. (2008). L'atteggiamento ambivalente verso donne e uomini. Un contributo alla validazione delle scale ASI e AMI. Giornale Italiano di Psicologia, 35(1), 217-246.

4. Intermezzo: The interpersonal sharing of negative and positive emotions

4.1. Introduction

There is little doubt that human social functioning vastly relies on understanding conspecifics' emotions. Whether one is involved in a face-to-face social interaction, is observing, or even imagining another displaying a specific emotion, the interpersonal sharing of that state allows its recognition and understanding (Preston and de Waal, 2002; de Vignemont and Singer, 2006; Decety, 2009; Zaki and Ochsner, 2012; Betti and Aglioti, 2016). We need not look much back in our individual past to bring to light a time when a stranger, a friend, or even a relative did not show what according to us would have been the right emotional reaction to our feelings. Disappointment probably arose. And the implications of disrupted mechanisms of interpersonal sharing of emotions are even more apparent in people suffering from neurological and psychiatric disorders who show such a deficit (Hillis, 2014).

The past few decades have witnessed a growth in scientific inquiries on this theme, especially in social sciences. This originated not only from a pure interest in comprehending what makes us a well-functioning social species, but also in examining the behavioural consequences of sharing others' emotions, and how this might be applied for societal reasons (Decety, 2009). So far, much of the work has focused on one specific construct, that is empathy. Despite this, a lack of consensus on a definition of empathy still haunts the field. Indeed, as it has been extensively discussed elsewhere (Batson, 2009), scholars have used the term empathy to refer to quite different things, from the pure imitation of others' emotional expressions (emotional contagion) to the practice of "putting oneself into someone else's shoes" (perspective-taking) (Batson, 2009). According to an influential and widely accepted view, put forward by de Vignemont and Singer (2006), an interpersonal reaction to someone displaying an emotion can be properly defined as empathy when i) the reaction itself consists of being in an emotional state, ii) which is isomorphic to the one just observed (or imagined), and iii) is accompanied by the awareness that the other person is the source of this reaction (de Vignemont and Singer, 2006). Despite being rather strict, this definition of empathy enables differentiations from related, although different, concepts. Distinguishing between empathy and related constructs is the aim of the first section of this review. Evidently, a straightforward answer to the question "What is empathy?" cannot be provided yet. Despite this, by relying on the state-of-the art literature about cognitive mechanisms and neural underpinnings of the interpersonal emotional reactivity, we hope to tackle some of the main issues about this fascinating topic.

In spite of the increased attention that has been paid to the investigation of empathy, progresses in the field are still held back by at least two factors: i) the focus on empathy for negatively-valenced events; ii) the detachment of emotional processing from its outcomes, i.e., behavioural reactions to the observation of others' emotions, such as helping behaviours. Although the study of empathy has mainly focused on the subjective perception of others' negative feelings, and specifically pain (Betti and Aglioti, 2016), the spectrum of emotions an individual can empathize with ranges from extreme negativity/unpleasantness (e.g., pain, sadness) to extreme positivity/pleasantness (happiness, erogeneity) (Fan et al., 2011; Bernhardt and Singer, 2012; Morelli et al., 2015). Moreover, complex scenarios may fall outside this negativity/positivity spectrum, such as empathizing with anxiety (Prehn-Kristensen et al., 2009; Shu et al., 2017). Tellingly, what emerged from early inquiries clearly speaks in favour of a separability of negative empathy and positive empathy constructs, the latter defined as the process of understanding and vicariously sharing an observed positive emotion (Morelli et al., 2015). Thus, the second and third section of this review will focus on the main insights on empathy coming from investigations about sharing targets' negative emotions (and specifically pain) and the main features characterizing the sharing of others' positive emotions, respectively.

4.2. Empathy and related concepts

The term empathy has ancient roots. It derives from the Greek word ἐμπάθεια (empatheia) and was coined by Titchener (1909) following Lipps (1903)'s interpretation of the German word "Einfühlung", which literally translates to "feeling into". First utilizations of the word empathy trace back to works on aesthetics. Gradually, the concept was introduced to psychological and social sciences, paving the way for contemporary investigations on its cognitive and neural mechanisms (Singer and Lamm, 2009). The construct of empathy is thus a relatively recent one. While several features of empathic processes have been examined and described thoroughly, many more questions on the topic await an answer. It does not surprise, then, that a shared unique definition of empathy is still missing. Batson (2009) summarizes this carefully: there might be up to eight different ways in which scholars have used the term empathy, often, but not always, as a function of the field it was applied to (Batson, 2009).

One way to tackle the problem is to focus on what empathy is not, rather than on what it is. According to Preston and de Waal (2002), and their Russian doll model, empathy is not emotional contagion, but it derives from it. These authors postulate that perception-action coupling mechanisms are at the core of emotional contagion processes, which allow animals, humans included, to share conspecifics' emotional states. Emotional contagion happens when an individual's sensorimotor, physiological, and affective state is the result of unconsciously mimicking the emotional state of another. Awareness of the cues eliciting this contagion, as well as self-other distinction, are not typical of this state. One clear example of emotional contagion is when a child starts crying because she heard another child doing the same (de Waal and Preston, 2017; Prochazkova and Kret, 2017). Built on emotional contagion mechanisms are more complex forms of empathic abilities, such as empathic concern and perspective-taking. Thus, not only emotional contagion might represent a phylogenetical thread linking other animals to humans, but also an ontogenetical one linking young humans to adults (Preston and de Waal, 2002; de Waal and Preston, 2017). Importantly, it has been suggested that the main difference between emotional contagion and empathy *tout court* lies in that one is characterized by awareness of the cues eliciting the response and by self-other distinction (empathy), while the other is not (emotional contagion) (de Vignemont and Singer, 2006; Prochazkova and Kret, 2017).

Empathy is also different from compassion (Singer and Klimecki, 2014). If we define empathy as a vicarious response to someone displaying an emotion, also referred to as affective empathy ("feeling with" the other, de Vignemont and Singer, 2006), then compassion differentiate from it in that the latter does not entail sharing that specific emotional state – it is, in other words, not isomorphic to it. Compassion is characterized by feelings of warmth and concern for the other in need (showing a negative emotion) ("feeling for" the other, de Vignemont and Singer, 2006; Singer and Klimecki, 2014). As these features have been associated with empathic concern as well, the two concepts are often used interchangeably (Singer and Klimecki, 2014). Importantly, in taxonomies based on the distinction between self-oriented versus other-oriented reactivity to others' emotions, a fundamental differentiation exits between responses of empathic distress and responses of empathic concern to a conspecific's emotional state. While empathic concern is, as said, "feeling for" the other, empathic distress refers to the self-oriented aversive reaction to someone else's distress, which is often associated with individuals' withdrawal from the stimulus triggering the excessive negative feelings (for self-protection reasons). Just as empathic concern, an empathic distress reaction is thought to be congruent with another's emotion, but not isomorphic to it (de Vignemont and Singer, 2006; Singer and Klimecki, 2014).

Finally, affective empathy differs from higher-order cognitive functions like perspective-taking and mentalizing. These functions have been often enclosed within the cognitive empathy construct, which in fact refers to the ability of understanding others' emotional states through the engagement of "cold" mental processes. Specifically, complex social scenarios may require that people represent others' mental states in order to understand the causes and consequences of their emotional behaviour. Thus, cognitive empathy is not associated with the sharing of others' emotions, but rather with a cognitive understanding of them (Shamay-Tsoory et al., 2009). As high-order and recent-developed processes, cognitive empathy and related constructs are thought to be limited to human beings (de Waal and Preston, 2017). It is worth noting that, while some authors prefer to discuss affective empathy and cognitive empathy as dissociable constructs based on specific evidence (Shamay-Tsoory et al., 2009), it is often the case that these two processes work in concert in order for an observer to better understand complex social situations (Zaki and Ochsner, 2009). Indeed, much of the evidence supporting the dissociation between the two concepts derives from studies using paradigms specifically employed to tease apart one mechanism or the other. In contrast, the implementation of more naturalistic tasks (ones resembling life-like situations) might shed light on the intertwined nature of the two processes for understanding conspecifics' emotions (Zaki and Ochsner, 2009).

In this review, we will focus on the affective empathy construct.

4.3. How it all started: Empathy for pain

The examination of the cognitive and neural mechanisms underlying empathy began with one specific model, that is empathy for pain (Singer et al., 2004; Betti and Aglioti, 2016). This is not surprising, giving that pain experiences are extremely salient, not only when they interest oneself, but also when the object of the painful experience in another, be it a familiar person or a stranger. Moreover, in an environment typical of social species, pain perception represents an important social signalling system underlying self-related actions, such as avoidance, or other-related actions, such as helping behaviours (de Waal and Preston, 2017; Riečanský and Lamm, 2019). Additionally, cortical networks involved in processing noxious stimuli, which include somatosensory, limbic, frontal, and parietal areas – often defined together as "pain matrix", are well understood (Iannetti and Moureaux, 2010; Legrain et al., 2011). This paved the way for studies aimed at investigating the neural correlates underlying the observation of painful stimulations on others (see Betti and Aglioti, 2016, for a recent comprehensive review).

Since its early stages, the study of cognitive and neural mechanisms of empathy for pain has benefitted from the ideas put forward within a new theory of social cognition, which postulates that humans come to understand others' minds through mental representation sharing. In a nutshell, observing others' actions and feelings would elicit activation in certain brain areas that are also involved in the processing of the first-hand experience of that same action or emotion (shared circuits). This similarity between first-person and third-person brain representations (also defined as vicarious activation) would help people interpret others' behaviour and feelings (Gallese et al., 2004; Keysers and Gazzola, 2006). Mirror neurons systems (MNS), discovered in monkeys in the 1990s (Di Pellegrino et al., 1992), fuelled the development of this view, providing a possible neural correlate for emotional sharing phenomena (Keysers and Gazzola, 2006). Within this scenario, empathy for pain studies rapidly set out to demonstrate that the perception of others' pain would be indeed associated with cerebral activation typical of the first-hand experience of pain. Importantly, increased blood oxygenation levels contingent to first-hand pain have been reported in somatosensory areas (S1 and S2) and posterior insula (PI), whose activation represents sensory-discriminative processing of the perceived stimulus, and in brain areas related to the motivational and affective aspects of the experience, such as anterior insula (AI) and dorsal anterior cingulate cortex (dACC). Importantly, these areas were found to correlate with participants' subjective reports of perceived unpleasantness (Bernhardt and Singer, 2012; Betti and Aglioti, 2016). As we will see below, these brain areas are involved in the perception of others' pain.

4.3.1. Sharing affective and sensorimotor pain

A pivotal study investigating the neural correlates of empathy for pain was run by Singer and colleagues (2004). The authors reported that harmful stimulations (electric shocks) delivered on participants' hands elicited brain activations that were very similar to those yielded by the same stimuli delivered to participants' romantic partners. These activations included AI, dACC, brain stem and cerebellum (Singer et al., 2004). Thus, it was systematically shown, for the first time, that first-hand pain and empathy for pain shared neural activation in insular and cingulate cortices. Many more studies followed, which provided support to the shared representations account (Morrison et al., 2004; Botvinick et al., 2005; Jackson et al., 2005; Morrison and Downing, 2007; Lamm et al., 2011; Betti and Aglioti, 2016). Moreover, recent meta-analytical evidence has strengthened these findings: activation in AI and anterior medial cingulate cortex (aMCC)/dACC was consistently reported across nine studies of empathy for pain. Importantly, this pattern of brain activation arose no matter what the paradigm used to induce the empathic feelings (Lamm et al., 2011). Indeed, two types of paradigms have been mainly used to elicit empathy for pain: in one, participants are shown pictures or videos of body parts being harmfully stimulated – defined as picture-based paradigms in Lamm et al., 2011; in the other, abstract cues anticipate if the painful stimulus will be delivered on another person or on the participant herself – labelled cue-based paradigms in Lamm et al., 2011. The fact that activation in AI and dACC has been observed in both scenarios suggests that these brain areas might be generally involved in extracting the affective meaning of an event and mapping it onto oneself when the painful stimulation is observed, thus facilitating the understanding of its consequences (Lamm et al., 2011; Betti and Aglioti, 2016). Coherently, the same brain areas are considered part of a brain network involved in representing self- and other-related affective states, a function that might be crucial for decision-making and emotional regulation (Craig, 2009; Singer et al., 2009).

The differences between the two types of paradigms used for the investigation of empathy for pain highlight another aspect of the neural processing of others' suffering. Not only, in fact, people seem to share others' affective state related to the harmful stimulation, but also their sensorimotor activation (Bernhardt and Singer, 2012; Betti and Aglioti, 2016). Several studies have demonstrated that observing others' pain elicits cortical and muscular activity that is often reported for the first-hand experience of pain (Avenanti et al., 2005; Avenanti et al., 2006; Bufalari et al., 2007; Cheng et al., 2008; Betti and Aglioti, 2016). Brain regions shown to be sensitive to sensorimotor aspects of pain in others are mainly somatosensory areas S1 and S2, motor cortices, and posterior sections of insula (PI), the latter being involved in sensorimotor integration and motor control. Tellingly, activity in these cortical regions often correlate with reported pain intensity and other sensory-discriminative aspects (e.g., location of the stimulus on the body) (Lamm et al., 2011; Bernhardt and Singer, 2012; Betti and Aglioti, 2016). Importantly, this pattern of brain activations has been mostly observed contingent to the observation of body parts being harmed, as it happens within picture-based paradigms. Thus, passively watching hands, arms, or feet being painfully stimulated might elicit an automatic mapping of the sensorimotor features of others' pain onto one's own body representations, just as it might happen for the affective component of pain. Alternatively, as similar, although weaker, activation in somatosensory areas has been observed for non-painful stimulation of body parts, the involvement of S1 and S2 might represent a non-specific processing of body-related stimuli, which is nonetheless heightened when painful outcomes come into play (Lamm et al., 2011; Betti and Aglioti, 2016).

It is important to note, however, that similar activations within brain macro areas does not necessarily mean that shared representations are at play, during the observation of others' emotions, at the neuronal level. And this is obviously complicated by the fact that brain regions are involved in more than one cognitive function (Betti and Aglioti, 2016). As micro-level investigations, such as intracranial electroencephalography (iEEG), in humans are often not possible, and classic neuroimaging approaches are characterized by poor spatial resolution, one interesting way to understand the degree to which shared representations are involved in empathy is to use multivariate pattern analysis (MVPA) on neuroimaging data. This technique offers the possibility to analyse in more detail brain activity arising within local cortical systems (Haxby, 2012). For instance, using MVPA, Corradi-Dell'Acqua and colleagues (2011) observed that felt and seen pain activated similar local regions within bilateral AI and MCC, thus providing stronger evidence for the shared representations hypothesis, at least as concerns the affective component of pain empathy (Corradi-Dell'Acqua et al., 2011).

4.3.2. Beyond localization: Neural networks mediating empathy for pain

Localization approaches, which mainly rely on functional magnetic resonance imaging (fMRI), have provided invaluable insights on the neural mechanisms underlying different brain functions. However, brain operations rely not only on functional specialization, the fact that every brain region is responsible for carrying out specific cognitive tasks, but also largely on functional integration. Integration of information happens within local and global neural circuits, and it is at the basis of every cognitive and emotional function. In other words, every cerebral region is dependent on its functional and anatomical connections with other parts of the brain. Thus, examining spatial and temporal covariation in the functioning of two or more brain regions might shed light on how cognition emerges within intertwined neural pathways (Betti and Aglioti, 2016).

As concerns empathy for pain, AI and ACC do not only take on empathy-related functions. In fact, different subregions of ACC and AI are involved in several other motor, sensory, cognitive, and emotional functions (Bush et al., 2000; Craig, 2002; Craig, 2009; Singer et al., 2009). According to recent models based on network approaches to neural functioning, these areas might in fact be part of a more general saliency network (Menon and Uddin, 2010; Barrett and Satpute, 2013). Thus, although fundamental, findings based on brain activation maps contingent to the observation of others' pain are stuck at the level of a modular view of brain activity, while adopting a network approach can better shed light on the large-scale interactions that characterize brain functioning in the domain of pain empathy (Betti and Aglioti, 2016). For instance, Zaki and colleagues (2007) reported different patterns of brain connectivity associated with felt and seen painful stimulations. In particular, perceiving others in pain elicited stronger functional connectivity between AI and ACC and medial prefrontal cortex (MPFC), while during first-hand pain AI was more strongly connected with brain areas linked to top-down control of pain perception, such as the periaqueductal grey (PAG). While this finding confirms that overlapping brain regions are involved in first-hand and observed pain, it also supports that self-other distinction is grounded in qualitatively different connectivity patterns (Zaki et al., 2007).

One influential view holds that functional communication between brain areas might happen via oscillatory neural activity (Varela et al., 2001). Importantly, research techniques characterized by high temporal resolution, such as electroencephalography (EEG) and magnetoencephalography (MEG), provide a crucial resource for understanding temporal dynamics underlying emotional sharing within specific cortical networks (Betti and Aglioti, 2016). Using MEG, Aglioti's group demonstrated a peculiar synchronization over sensorimotor areas in the gamma band frequencies (30-90 Hz) during the observation of others' pain, but not during other-related neutral stimulations. Moreover, this gamma-band synchronization strongly correlated with subjective feelings of intensity and unpleasantness for the seen pain stimulations (Betti et al., 2009). Interestingly, neural processing mediated by gamma-band oscillations has been observed contingent to the subjective experience of first-hand pain (Gross et al., 2007; Valentina et al., 2013).

Lastly, recent evidence suggests that our ability to empathize with others' pain might be somehow related to the intrinsic activity shown by human brains at rest. Indeed, task-independent functional connectivity between ventromedial prefrontal cortex (vPFC) and ACC was found to correlate with dispositional empathy for others' pain (Otti et al., 2010) (see Betti and Aglioti, 2016, for a comprehensive review on the role of resting-state activity in empathy for pain).

To summarize, despite the incredible amount of research that has been conducted on the neural correlates of pain empathy, it has become clear that, in order to fully understand how the interpersonal sharing of emotions happens, the integration of both localization and network-based approaches is essential, as each provides unique insights into the distributed and interactive nature of emotional experiences in the human brain.

4.3.3. Modulation of empathy for pain

Although affective empathy might be a developmental outcome of the automatic sharing of others' emotions, such as emotional contagion (Preston and de Waal, 2002; de Waal and Preston, 2017), it is clear that empathic feelings do not spread uncontrollably from the observed to the observer (de Vignemont and Singer, 2006).

Several factors have been found to modulate empathy for pain. Here we summarize the main ones, which may relate to either the empathizer or to the relationship between the empathizer and the object of the empathic feelings.

First, differences in empathic abilities between sexes have been observed, which might be dependent on evolutionary factors associated with caregiving needs. In fact, women show higher affective sharing during empathy for pain tasks; moreover, they score better in emotional recognition tasks and engage more often in prosocial behaviour (Christov-Moore et al., 2014).

Empathic abilities examined during experimental studies mainly concern the state in which the observer finds herself in because of the task she undertook. On the other hand, trait empathy refers to a relatively stable aspect of one's personality that indicate the degree to which an individual is prone to empathize with others. Some studies have found that trait empathy, as measured through questionnaires – the most used of which is the interpersonal reactivity index (IRI; Davis, 1983), correlates with activation in AI and ACC during empathy for pain tasks (Singer et al., 2004, 2006; Jabbi et al., 2007; Bernhardt and Singer, 2012).

Another personality trait related to empathic abilities is alexithymia, i.e., the inability to identify and describe one's own and others' emotions (Tesio et al., 2019). Bird and colleagues (2010), for example, observed that activation in AI during an empathy for pain task was highly modulated by alexithymia levels in both neurotypical and people on the autism spectrum (the latter group shows higher levels of alexithymia) (Bird et al., 2010).

Lastly, the physical state in which people are before observing others' suffering also matters. For example, first-hand experience of pain, as induced through laser evoked potentials (LEPs), was found to reduce concomitant empathic feelings for others' pain (Valeriani et al., 2008).

The outcomes of sharing others' pain are also affected by features related to the relationship between the empathizer and the person who the empathic feelings are directed to. One paradigmatic case was reported by Singer and colleagues (2006), who observed that the expected neural reactivity to others' pain, i.e., activation in AI and ACC, was reduced when the object of the empathic feelings was a person that had previously behaved unfairly during an economic game. This reduction was particularly strong in men, who also showed activation in reward-related brain regions (such as nucleus accumbens) that additionally correlated with feelings of revenge (Singer et al., 2006).

If temporary features of the other person matter, stable ones are also relevant for a "successful" empathic reaction to pain in others. Avenanti and colleagues (2010), for instance, demonstrated that sensorimotor reactivity to hands being pinpricked by a needle was reduced in both white and black people, who showed an implicit ingroup preference, when the body parts belonged to outgroup members. Interestingly, this did not happen for violet hands, suggesting an ethnicity-based modulation of empathy for pain (Avenanti et al., 2010). Other studies have confirmed the modulation exerted on empathy for pain by outgroup biases (Azavedo et al., 2013; Riečanský et al., 2015). As we shall see farther in this review, this is one of the main reasons why authors have suggested that empathy might not be a proper feeling on which to base one's own moral actions (Bloom, 2016; Bloom, 2017).

But if affective empathy is modulated by several dispositional and contextual factors, when does this modulation happen? According to de Vignemont and Singer (2006), there are two possible scenarios: in one, defined as late appraisal model, an empathic reaction is always generated contingent to the sight of others in pain. Parallelly, dispositional and contextual information is processed, which can affect the outcome of sharing others' suffering in one direction or the other. On the other hand, the early appraisal model is characterized by an initial evaluation of the emotional cue in light of prior personal and contextual information. An empathic response is thus not always elicited, but instead constrained by specific co-occurring variables (de Vignemont and Singer, 2006). Mainly using EEG, a technique equipped with high temporal resolution, many studies set out to investigate at which point in time an empathic response to others' pain would take place (Coll, 2018). In a now-seminal study, Fan and Han (2008) presented participants with real pictures or cartoons depicting hands in painful or neutral situations and asked them to either judge the intensity of the pain experienced or to count the number of hands in the pictures. They reported an early effect of pain in the N1 and N2 components, which was not dependent on the nature of the task (pain perception or counting), and a later effect in the P3 component, which was modulated by task requirements (Fan and Han, 2008). These results support the view of a late appraisal model of empathy for pain, and they have been confirmed by studies implementing both time domain and time-frequency domain analyses on EEG data (e.g., Fabi and Leuthold, 2017).

4.3.4. Empathy for other negative emotions

Although not consistently, empathy for other negative emotions has been also investigated. Interestingly, brain activity associated with the affective sharing of others' pain – AI and ACC/MCC – has been reported contingent to the observation of others' disgust (Wicker et al., 2003; Jabbi et al., 2007; Jabbi et al., 2008), anxiety (Prehn-Kristensen, 2009; Morelli et al., 2014; Shu et al., 2017), and social pain/exclusion (Masten et al., 2011; Meyer et al., 2013). This suggests that midline brain regions might hold a central role not only in empathic feelings for others' suffering, but in all those circumstances in which the understanding of others' emotional states happens through vicarious sharing. A recent meta-analysis, conducted by Fan and colleagues (2011), seems to suggest that this might indeed be the case, as similar activation patterns in AI and ACC were reported for empathic feelings across different domains, including empathy for positive emotions (although most of the studies included in this meta-analysis were pain empathy studies) (Fan et al., 2011). Alternatively, as the same brain regions might also be part of a more general saliency network (Menon and Uddin, 2010; Barrett and Satpute, 2013), midline brain regions could be generally involved in computing valence-independent salient affective cues. This is also supported by the fact that activity in AI and ACC was not reported for the observation of neutral touch on others (Blakemore et al., 2005; Ebisch et al., 2008). More studies are needed to shed light on the differences and similarities in sharing various affective states.

Below we focus on an often-neglected topic: sharing others' positive emotions.

4.4. Positive empathy

Positive empathy refers to the process of vicariously sharing and understanding an observed or imagined positive emotion (Morelli et al., 2015). As we have discussed so far, the investigations on empathy have mainly focused on the interpersonal sharing of others' negative states, and specifically pain (Betti and Aglioti, 2016). However, it is becoming increasingly clear that empathizing with positive emotions expressed by another person benefits not only the recipient of the empathic feelings, but also the empathizer herself (Morelli et al., 2015; Telle and Pfister, 2016). In this section, we will describe the main features characterizing the interpersonal sharing of others' positive emotions. Moreover, we will summarize early evidence showing that positive empathy might be dependent on cognitive and neural mechanisms of experience sharing, akin to what happens in the case of negative empathy in general, and pain empathy specifically (Morelli et al., 2015; Betti and Aglioti, 2016). It is worth noting that, being an extremely recent construct, positive empathy shares theoretical features with other concepts (Morelli et al., 2015). This is clear when one acknowledges the different terms that have been associated with the sharing of others' positive emotions or outcomes, such as vicarious reward (Mobbs et al., 2009; Morelli, Sacchet, and Zaki, 2015; Morelli et al., 2018), empathic joy (Smith et al., 1989; Batson et al., 1991), and empathic happiness (Light et al., 2015).

Empathy for positive emotions, characterized by vicarious reactivity to an observed or imagined positive feeling, clearly differs from the negative counterpart, in that the target emotion the observer empathizes with has positive valence and not negative valence (Andreychik and Migliaccio, 2015; Morelli et al., 2015; Andreychik and Lewis, 2017). Interestingly, both children/adolescents and adults were found to experience positive empathy at a similar or even higher level than empathy for negative emotions (Telle and Pfister, 2016). Coherently, it has been argued that people might be more motivated to empathize with positive emotions, compared to negative ones, in that doing so involves low costs but high benefits – the experience of positive affect – which might be highly rewarding (Duan, 2000; Telle and Pfister, 2016). At the brain level, empathizing with a positive emotion was found to yield activation in brain regions associated with positive affect and reward, such as ventromedial prefrontal cortex (vmPFC) (Haber and Knutson, 2010; Bhanji and Delgado, 2014; Fareri and Delgado, 2014; Berridge and Kringelbach, 2015); contrariwise, as already described, activation in brain regions associated with negative affect, such as AI and dACC, underlies empathy for negative emotions and pain (Morelli et al., 2014) (see below for a detailed description of the neural underpinnings of positive empathy). Although different in their essence, these two empathy constructs (as measured through questionnaires) were found to positively correlate at both trait and daily levels; moreover, they share activation within the medial and dorsomedial prefrontal cortices (m/dmPFC), brain areas associated with mentalizing, and within the septal area (SA), linked to prosocial behaviour (Morelli et al., 2014; Morelli et al., 2015).

In what is probably the first work systematically addressing the birth of a new topic, Morelli and colleagues (2015) clearly define the differences between positive empathy and other related concepts (Morelli et al., 2015). For instance, positive empathy is different from general positive affect, as the former only occurs when individuals experience others' positive affect and/or outcome and then share their affective state. "More broadly, general positive affect can occur when individuals personally experience positive outcomes, whereas positive empathy only occurs when individuals vicariously experience positive emotion" (Morelli et al., 2015, p. 60). Warm glow and positive empathy differ for a crucial reason: while positive empathy represents an altruistic motivation with the aim of increasing others' positive emotions, warm glow is an egoistic motivation aimed at increasing one's own positive affect. Lastly, whereas perceived positive empathy focuses on the discloser of a certain positive emotion, and on how much the observer empathizes with it from the discloser's point of view, positive empathy focuses on what the empathizer experiences (Morelli et al., 2015).

4.4.1. Neural underpinnings of positive empathy

First evidence originating from studies investigating the neural correlates of positive empathy suggests that the shared representations model can be also applied to the interpersonal sharing of others' positive emotions. A pivotal study, in this sense, is that of Jabbi and colleagues (2007), who set out to investigate the role of anterior insula and frontal operculum, which they jointly refer to as IFO, in processing not only food-related negative emotions (disgust) but also food-related pleasant feelings. Generally, both the observation of disgusted facial expressions and the experience of disgust activate the IFO (Wicker et al., 2003; Jabbi et al., 2007). Moreover, this brain region is involved in taste perception (Small, 2010) and in the sensing of one's own visceral feelings (Craig, 2002; Craig, 2009). Importantly, in this study the authors found that activity in the IFO was not only associated with the perception of food-related negative emotions (facial expressions of disgust) but also with food-related pleased facial expressions. Additionally, this activity was positively correlated with scores at the personal distress (PD) and FS (fantasy) subscales of the IRI. The authors thus suggested that "human bilateral IFO may constitute a critical component of the neural mechanism that allows the mapping of the bodily states of others onto our own inner states and thereby facilitate our understanding of the social environment and ultimately survival" (Jabbi et al., 2007).

In an interesting work, Morelli and colleagues (2014) set out to address three limitations of previous studies on empathy, the first two deriving from the focus of previous investigations on empathy for pain: i) the lack of comparison of different emotions within the same study; ii) the implementation of de-contextualized tasks (mostly picture presentation), which can affect the empathic mechanism engaged during the experimental tasks; iii) and the fact that few studies have addressed how neural activity during empathy tasks relates to subsequent prosocial behaviour. In order to address these limitations, the authors asked their participants to empathize with three different emotions while being scanned: pain, anxiety, and happiness. Painful stimuli were chosen as an example of context-independent emotion, whereas anxiety and happiness as an instance of context-dependent emotions. The results showed that empathizing with pain and anxiety activated areas associated with negative affect and known to be involved in empathic feelings, i.e., dACC and AI, whereas empathizing with happiness activated the vmPFC, previously linked to subjective positive affect, pleasure, and reward (Haber and Knutson, 2010; Bhanji and Delgado, 2014; Fareri and Delgado, 2014; Berridge and Kringelbach, 2015). Moreover, mirror system-related regions (intraparietal lobule, IPL, and posterior inferior frontal gyrus, pIFG) were activated during empathy for pain, a context-independent emotion, whereas mentalizing-related areas (m/dmPFC) were activated during empathy for context-dependent anxiety and happiness. Additionally, the septal area, a brain region previously linked to several prosocial tendencies and behaviours in humans (Moll et al., 2006; Moll et al., 2011), was activated across all conditions and was found to predict daily helping behaviour (Morelli et al, 2014).

A concept highly related to positive empathy is that of vicarious reward. Specifically, the latter refers to the behavioural and neural consequences of witnessing another person receiving a positive outcome, such as winning a sum of money, eating delicious food, or receiving a pleasant caress. Although often the two terms conceptually coincide, we can generally think of vicarious reward as a special case of positive empathy (Morelli et al., 2015; Morelli, Sacchet, and Zaki, 2015; Morelli et al., 2018). A seminal work on this topic is that of Mobbs and colleagues (2009), who explored the role of perceived similarity in reward-related reactivity to others' fortunes. The results showed that observing a socially desirable (SD) other winning money on a card game was associated with activation in the ventral striatum (VS), a brain area that was activated by the participants themselves winning and that is known to be involved in the personal experience of reward (Haber and Knutson, 2010; Bhanji and Delgado, 2014; Fareri and Delgado, 2014). Importantly, subjective scores defining the perceived similarity between the participants and the SD other positively correlated with activation in vmPFC and ACC, as well as with connectivity between ACC and VS during the SD other win conditions (Mobbs et al., 2009).

A recent meta-analysis, conducted by Morelli and colleagues (Morelli, Sacchet, and Zaki, 2015), confirms that personal and vicarious reward share common brain activations. Specifically, both experiencing first-hand rewarding outcomes and observing these on another person activates, among the others, vmPFC, mPFC, bilateral amygdala, AI, and dACC. On the other hand, whereas personal reward selectively activates the nucleus accumbens (NAcc), activity in dorsomedial prefrontal cortex (dmPFC) and posterior superior temporal sulcus (pSTS), involved in representing others' beliefs and intentions, is only reported contingent to witnessing others' positive outcomes (Morelli, Sacchet, and Zaki, 2015).

The implicit processing of positive empathy/vicarious reward has been also investigated. Combining continuous flash suppression (CFS; Tsuchiya and Koch, 2005) and affective misattribution procedure (AMP; Payne et al., 2005), Chiesa and colleagues (2017) evaluated the effect that observed pleasant (a caress) and unpleasant (a slap) tactile stimuli would have on the processing of neutral non-salient pictures. Beyond showing that the likeability for the neutral stimuli was higher when these were preceded by subliminal positive stimuli and lower when preceded by subliminal negative stimuli, the authors observed different brain activity patterns according to the different conditions. Indeed, the unconscious processing of other's pain activated the PFC and the ACC, while no significant activation was found for the AI. On the other hand, the unconscious processing of pleasant touch was associated with increased activity in S1, but not in vmPFC. This suggests that vmPFC could be selectively involved in the conscious evaluations of the hedonic quality of a stimulus (Chiesa et al., 2017).

4.4.2. A special case: Empathy for pleasant touch

Pleasant touch represents a highly rewarding outcome, helping the formation of emotional bonds, and possibly setting the stage for the associative learning of social reward (Cascio et al., 2019). Moreover, socio-affective touch constitutes a preferred sensory channel through which we communicate a variety of negative and positive emotions (Hertenstein et al., 2006, 2009; Kirsch et al., 2018). Thus, empathizing with others' pleasant touch has a great potential of informing us about individuals' experiences within social interactions (Morrison et al., 2010).

Recent evidence has extended the shared embodied representations hypothesis to neutral and pleasant touch observation and scholars have postulated that people come to under-stand others' tactile experiences through the implementation of cognitive and somatic representations that are also involved in the first-hand perception of similar somatic events (Keysers et al., 2010; Peled-Avron and Woolley, 2022). This hypothesis has been initially supported by fMRI studies showing overlapping brain activation for personal and observed neutral and pleasant touch, which included higher-order and limbic areas but, importantly, also sensorimotor brain regions (such as premotor areas, SI, SII, posterior insula, inferior frontal gyrus) (Blakemore et al., 2005; Ebisch et al., 2011; Morrison et al., 2011; Schaefer et al., 2012; Lamm et al., 2015). Crucial evidence in this sense stems also from electrophysiology and neural stimulation studies, which have highlight-ed the sensorimotor resonance mechanisms at play and, consequently, the recruitment of the sensorimotor system when observing others' neutral and pleasant touch experiences (Wood et al., 2010; Bolognini et al., 2013; Peled-Avron et al., 2016, 2019; Schirmer et al., 2019).

Coherently with the shared representations hypothesis of vicarious reward, Lamm and colleagues (2015) investigated if, and in what extent, the observation of different affective states would be associated with activity in segregated brain regions. If the understanding of others' affective states relies on the activation of the same representations involved in the first-hand experience of that state, then different brain networks should be engaged when empathizing with different emotions. Unpleasant and pleasant visuo-tactile stimuli were the objects participants empathized with during this study. The same stimuli were also delivered to the participants themselves. The results showed that both felt and seen pleasant touch significantly activated the mOFC/vmPFC region, which is associated with hedonic and pleasant feelings, as well as reward valuation (Haber and Knutson, 201; Bhanji and Delgado, 2014; Fareri and Delgado, 2014; Berridge and Kringelbach, 2015). On the other hand, empathy for unpleasant touch shared with felt unpleasant touch activation within the fronto-insular cortex (similar to IFO in Jabbi et al., 2007), the MCC, and in motor areas, probably because of the involvement of this latter set of regions in withdrawal responses to fist-hand experience of unpleasant stimuli (Lamm et al., 2015).

4.5. Conclusions and future directions

In this review, we set the stage for a much-needed scientific exploration of empathy for positive emotions and rewards. Most of the literature has focused on the sharing and understanding of others' pain, or other negative emotions. However, there is no particular reason to leave out of the "empathy picture" the important aspect of sharing others' positive feelings. Here, we discussed that positive empathy is a separable construct – from negative empathy, but also from other related positive concepts (Morelli et al., 2015). Furthermore, the main features of the widely accepted shared representations hypothesis for empathy seem to hold in the case of positive empathy as well. Future studies will have to start from this crucial evidence to shed light on the psychological, neuroscientific, and evolutionary aspects of sharing positive emotions and perhaps apply the knowledge thus gathered to understand failures of empathizing with others' positive experiences (e.g., Greene et al., 2020).

5. Motor facilitation following pleasant social touch observation

5.1. Introduction

According to the "skin as a social organ" hypothesis (Morrison et al., 2010), the sense of touch should be considered as an extremely important facet constituting the world of social interactions. The affective component of touch ranges from extreme unpleasantness (e.g., pain, disgust) to the extreme pleasantness (e.g., consolatory stimuli) and may largely shape our interpersonal behaviour (Gallace and Spence, 2010). Social touch is a fundamental drive of human development that starts with the mother-infant dyadic relationship and continues to modulate interactive behaviours throughout the lifespan (Cascio et al., 2019) and it is thought to encourage cooperative, affiliative, and sexual behaviour (Suvilehto et al., 2015). Importantly, social touch constitutes a channel through which we communicate and share our emotions with conspecifics (Hertenstein et al., 2009; Kirsch et al., 2018).

Humans and other animals are endowed with the ability to understand others' feelings and sensations, which helps them to efficiently navigate the social world (Decety and Jackson, 2004; Gallese et al., 2004; de Vignemont and Singer, 2006; Keysers and Gazzola, 2009). There is now general consensus that, when witnessing others' emotions and sensations, people may share the target feeling on two levels: on one hand, affective sharing allows the observer to evaluate the valence of the observed affect, whereas on the other, sensorimotor resonance permits to share its sensory and motor consequences (Keysers and Gazzola, 2009; Keysers et al., 2010; Betti and Aglioti, 2016). Working together, these processes ultimately allow individuals to grasp what another person is experiencing in its totality.

The theory of embodied simulation provides an interesting theoretical framework for these phenomena. This account postulates that the understanding of others' emotions and sensations relies on the automatic and unconscious activation of individual embodied representations associated with the very same event (Keysers and Gazzola, 2009; Gallese and Sinigaglia, 2011; Gallese and Ebisch, 2013). For instance, the first-hand experience of pain is characterized by an ensemble of bodily sensations, sensorimotor reactions, and conscious affect (Iannetti and Mouraux, 2010) that is automatically re-enacted when witnessing someone else in pain, thus aiding the understanding of others' feelings in painful situations. Moreover, a specific prediction of this theory is that the same neural structures involved in our own experiences also underlie the automatic understanding of the emotions and sensations of other individuals (see Betti and Aglioti, 2016, for an extensive review of pain empathy studies). This was demonstrated utilizing various neuroscientific techniques, including fMRI and TMS. A pivotal study investigating the neural correlates of empathy for pain was run by Singer and colleagues (2004). The authors reported that harmful stimulations (electric shocks) delivered on participants' hands elicited brain activations (as measured via fMRI) that were very similar to those yielded by the same stimuli delivered to participants' romantic partners. Here, it was systematically shown, for the first time, that first-hand pain and empathy for pain shared neural activation in insular and cingulate cortices, brain areas known to underlie various aspects of affective processing (Singer et al., 2004). In another seminal work by Avenanti and colleagues (2005), the observation of others' tactile pain elicited an enhancement of somatotopic corticospinal inhibition induced via the application TMS over sensorimotor areas. This modulation was thought to represent the mapping of others' somatic experiences in one's own sensorimotor system (sensorimotor resonance; Avenanti et al., 2005). Many more studies followed, which provided support to the shared representations account (Morrison et al., 2004; Botvinick et al., 2005; Jackson et al., 2005; Morrison and Downing, 2007; Lamm et al., 2011; Betti and Aglioti, 2016).

Recent evidence has extended the shared embodied representations hypothesis to pleasant touch observation and scholars have postulated that people come to understand others' tactile experiences through the implementation of cognitive and somatic representations that are also involved in the first-hand perception of similar somatic events (Keysers et al., 2010; Peled-Avron and Woolley, 2022). This hypothesis has been initially supported by fMRI studies showing overlapping brain activation for personal and observed neutral and pleasant touch, which included higher-order and limbic areas but, importantly, also sensorimotor brain regions (such as premotor areas, SI, SII, posterior insula, inferior frontal gyrus) (Blakemore et al., 2005; Ebisch et al., 2011; Morrison et al., 2011; Schaefer et al., 2012; Lamm et al., 2015). Crucial evidence in this sense stems also from electrophysiology and neural stimulation studies, which have highlighted the sensorimotor resonance mechanisms at play and, consequently, the recruitment of the sensorimotor system when observing others' neutral and pleasant touch experiences (Wood et al., 2010; Bolognini et al., 2013; Peled-Avron et al., 2016, 2019; Schirmer et al., 2019).

This set of studies proves that others' tactile experiences are automatically mapped onto our own sensorimotor system. However, little is known on how the functional significance of this sensorimotor resonance mechanism extends to the behavioural domain. In two studies on empathy for tactile pain, Morrison and colleagues (Morrison et al., 2007a, 2007b) showed that pain observation was associated with motor facilitation in simple motor tasks. Using Go/No-go paradigms, Galang and colleagues (2017, 2021) replicated these findings and showed that this motor facilitation effect was not dependent on the effector (hand vs. foot) nor on the timing of Go stimulus presentation (0 ms vs 500 ms after pain video). The aim of the present work was to extend the findings discussed above and demonstrate a motor facilitation effect following the observation of pleasant touch on others. To do so, we implemented a similar paradigm to that used by Galang and colleagues (2017) for pain observation. However, our task was different in that only one effector, the right hand, was tested and the Go/No-go stimuli always appeared 500 ms after the target videos (as Galang and colleagues report a main effect of timing whereby participants were overall faster in responding to Go stimuli when these were presented 500 ms after the videos). Moreover, to test the effect of longer exposure to pleasant touch, we tested half of the participants with 1800 ms videos (as in Galang et al., 2017) and the remaining half with 3000 ms videos. We hypothesized that reaction times to Go stimuli would be faster following the observation of pleasant touch on others' hands (compared to no-touch), especially for the hand congruent with the effector used to carry out the task – in our case, the participants' right hand – and for longer exposure to touch – 3000 ms videos. Moreover, if pleasant touch observation elicits a general motor facilitation in the self, we would expect higher accuracy along with increased speed for touch conditions. Finally, as we consider the embodied sensorimotor resonance to observed pleasant touch a form of positive empathy (Morelli et al., 2015), we expected the motor facilitation effect to be associated with individual levels of empathy, interoceptive sensibility, and propensity to social touch.

5.2. Materials and methods

5.2.1. Participants

Participants included 120 right-handed adults (18+; 52 females, mean age = 25 years, SD = 6.90, range = 18-61 years). They were recruited through the online participant recruitment platform Prolific and were paid £4.20 (£6 per hour) for their participation. The sample size was estimated using MorePower 6.0 software, which indicated that a sample of ~120 participants was sufficient to detect a medium effect (e.g., $\eta 2$ = 0.06) with at least 80% power.

The experimental protocol was approved by the ethics committee of the Psychology Department of City, University of London and followed the ethical standards of the 2013 Declaration of Helsinki. All participants gave their informed consent to take part in the study and were naïve to the purposes of the research.

5.2.2. General procedures

The study was run online. The primary task consisted of a Go/No-Go RTs task wherein participants had to respond as quick and accurate as possible to the appearance of a Go stimulus with their right hand and refrain from responding when seeing the No-Go stimulus. The Go and No-Go stimuli consisted of an orange and a blue square alternating in different mini-blocks (randomized across participants). The ratio of Go/No-go stimuli was 3:1. To investigate the effect of pleasant touch observation on RTs, the Go/No-go trials were preceded by videos depicting: i) either a right or left hand being caressed on their back (*touch videos*); ii) the caressing hand making the same movements but not actually touching the still hands (right or left; *no-touch videos*). The caresses had a velocity of approximately 3cm/s, regarded as one of the main features of pleasant affective touch (Löken et al., 2009). The videos were created specifically for this study (see Appendix C for snapshots of the videos). Figure 5.1 shows a schematic representation of the experimental procedure. A similar paradigm was implemented by Galang and colleagues (2017) to investigate motor facilitation following pain observation. In their work, the authors report a main effect of post-video delay (0 vs 500 ms) on RTs – motor facilitation for 500 ms post-video delay. Thus, based on this result, we decided to reduce the complexity of our design by implementing only 500 ms-delayed conditions. Moreover, differently from Galang and colleagues (2017), we utilized videos having a length of 1800 ms (as in Galang et al., 2017) and 3000 ms to examine the effect of prolonged exposure to pleasant touch on motor facilitation (this was a between-subjects factor).

To summarize the experimental design, participants completed four Go/No-go blocks of 64 trials each. In two of these blocks, the caressed (or not caressed) hand the participants had to observe before the motor task was a right hand (*congruent condition*, as the participants always responded with the right hand); in the remainder, it was a left hand (*incongruent condition*). Each block included two types of videos: *touch* and *no-touch*. Depending on the participant, these videos could have a length of 1800 ms or 3000 ms (between-subjects factor). Thus, our design included three main factors: Video type (*touch/no-touch*), Hand laterality (*congruent/incongruent*) and Length (*1800 ms/3000 ms)*. At the end of the main task, participants had to rate how pleasant they found the touch videos utilizing a visual analogue scale (VAS). The experiment was programmed and run using PsychoPy and Pavlovia (https://pavlovia.org/).

The second part of the study consisted of the completion of various questionnaires, i.e.: the Interpersonal reactivity index (IRI, Davis et al., 1983), the Multidimensional assessment of interoceptive awareness-Version 2 (MAIA-2, Mehling et al., 2018), the Positive empathy scale (PES, Morelli et al., 2015), and the Touch experiences and attitudes questionnaire (TEAQ, Trotter et al., 2018).

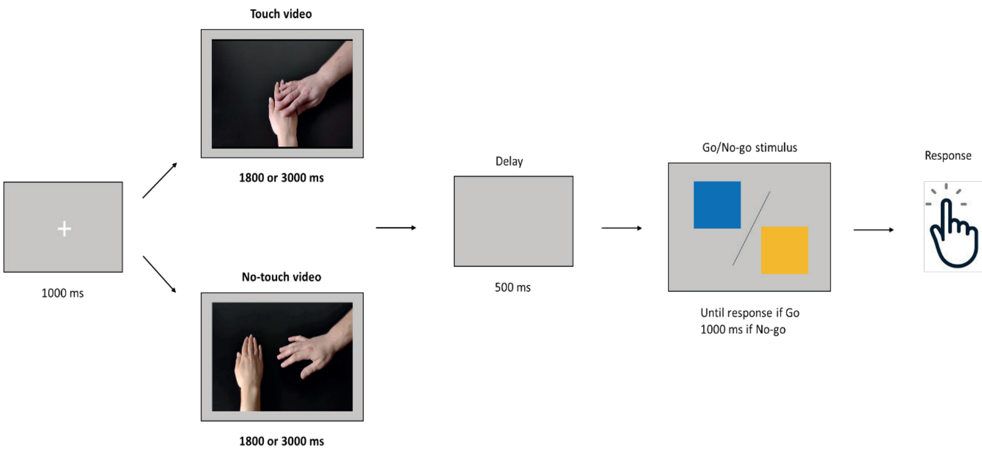


Fig. 5.1. Schematic representation of the experimental paradigm.

5.2.3. Questionnaires

5.2.3.1. IRI. The IRI (Davis, 1983) is a measure of dispositional empathy. It consists of four subscales, each tapping into a separate aspect of empathy: the perspective taking (PT) scale measures the tendency to adopt the psychological point of view of others; the empathic concern (EC) scale measures feelings of sympathy and compassion for unfortunate others; the personal distress (PD) scale assesses the tendency to experience personal distress in response to distress in others; finally, the fantasy (FS) scale measures the tendency to imagine oneself in fictional situations.

5.2.3.2. MAIA-2. The MAIA-2 (Mehling et al., 2018) is a 32-item questionnaire measuring eight different dimensions of interoception (subscales: Noticing, Not distracting, Not worrying, Attention regulation, Emotional awareness, Self-regulation, Body listening, Trusting), and specifically interoceptive sensibility.

5.2.3.3. PES. The PES (Morelli et al., 2015) is a 7-item questionnaire measuring trait positive empathy.

5.2.3.4. TEAQ. The TEAQ (Trotter et al., 2018) is a 57-item self-report assessing six dimensions of experiences and attitudes concerning social touch. For our purposes, we focused on three subscales, i.e., Friends and family touch, Childhood touch, Attitude to unfamiliar touch.

5.2.4. Data analysis

The data were pre-processed in Python and analysed in RStudio (R Core Team, 2021). The pre-processing steps included the extraction of individual data files from an online database (Pavlovia) and the creation of subject-wise data matrices.

RTs often have a skewed distribution and linear modelling of such data seldomly meet basic statistical assumptions (e.g., normally distributed model residuals). Lo and Andrews (2015) report that non-linear transformations of RTs are utilized throughout the psychology literature to overcome these issues, but this practice has important theoretical implications that can lead to misinterpretations of statistical results. The authors suggest that a better practice is to implement generalized linear modelling, as within this context transformations of the outcome variable are not needed, and a specific probability distribution can be assumed to underlie the data (Lo and Andrews, 2015). In this work, we applied Lo and Andrew (2015)'s approach in conjunction with minimal a-priori screening and model criticism, a practice suggested by Baayen and Milin (2010) for RTs analysis. First, RTs below 200 ms were discarded (trimming; 0.05% of the total) and the remaining data were modelled using the function lmer() from the lme4 package (Bates et al., 2014). The resulting statistical models did not meet model assumptions and had goodness-of-fit of $R^2 = 0.30$. Following Baayen and Milin (2010), the next step involved removing data points with absolute standardized residuals exceeding 2.5 standard deviations (model criticism step). The resulting dataset (Fig. 5.2) was modelled utilizing the glmer() function for generalized linear models and assuming a gamma distribution underlying our RTs data. The resulting models had a goodness-of-fit of $R^2 = 0.44$. Model complexity was gradually increased by inserting the fixed effects and their interactions to check for the model that best fitted the data. The different statistical models were compared using the anova() function from the stats package (R Core Team, 2021).

AIC, BIC, and Chi-square statistics informed us on which model best fitted the data compared to the previous ones in the hierarchy. All fitted models included by-subject intercepts.

Accuracy and commission error data were modelled using the glmer() function and assuming a binomial distribution underlying the data, as binomial generalized linear models are ideal for proportion outcomes expressed as counts (i.e., with a known total number of observations or trials).

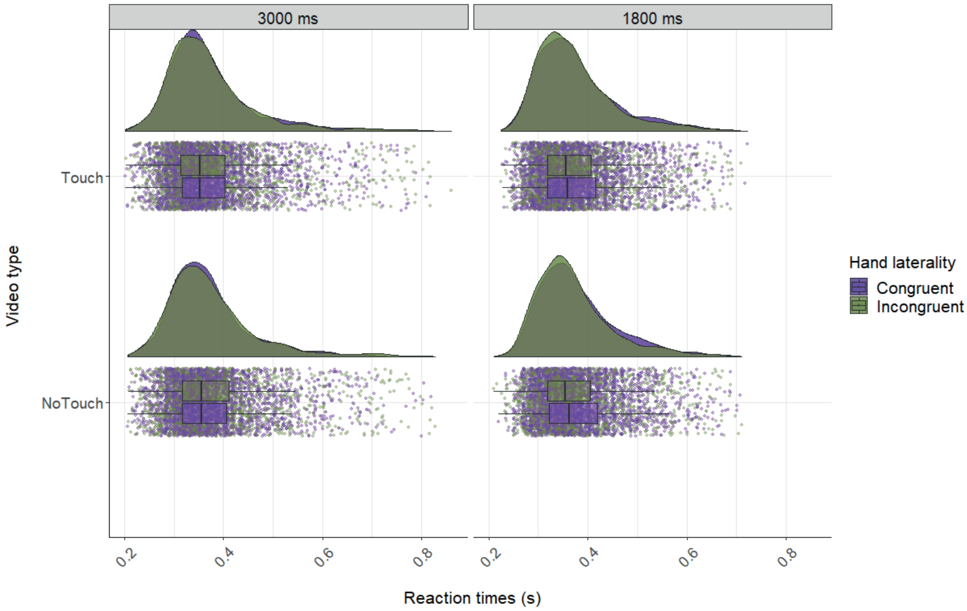


Fig. 5.2. Distribution of RT data following removal of data points with absolute standardized residuals exceeding 2.5 standard deviations (model criticism).

5.3. Results

5.3.1. RTs

Participants were faster at responding to Go targets following observation of pleasant touch [main effect of Video type: $\chi^2(1) = 6.42$, p-value = 0.01; mean = 359.4 ± 5.6 ms, CI (348.6, 370.9)] compared to following a video of no touch [mean = 361.3 ± 5.7 ms, CI (350.4, 372.9)]. We also found a main effect of Hand laterality ($\chi^2(1) = 11.23$, p-value < 0.001) whereby participants were slower at responding to Go targets when they had to pay attention to a right hand [either caressed or not caressed; Congruent condition: mean = 361.7 ± 5.7 ms, CI (350.8, 373.4)] compared to a left hand [Incongruent condition: mean = 359.1 ± 5.6 ms, CI (348.2, 370.5)]. Moreover, Hand laterality interacted with Length ($\chi^2(1) = 19.29$, p-value < 0.001) as participants' RTs were slower for congruent conditions compared to incongruent conditions only for 1800-ms videos. Finally, a three-way interaction between Video type, Hand laterality and Length ($\chi^2(1) = 3.97$, p-value = 0.04) was found. As figure 5.3 shows, while RTs were overall shorter for 3000 ms-videos, the reduction of RTs for touch conditions (compared to no-touch) during 1800-videos was greater for congruent compared to incongruent conditions. It is worth noting that we controlled for fatigue and learning effects by including trial number and block number as covariates in all statistical models. We found that both trial number (t-value = -3.84, p-value < 0.001) and block number (t-value = 3.67, p-value < 0.001) had a significant effect on RTs. In each block, RTs increased with increasing trial number, likely representing a fatigue effect. On other hand, RTs decreased with block number, likely representing a learning effect.

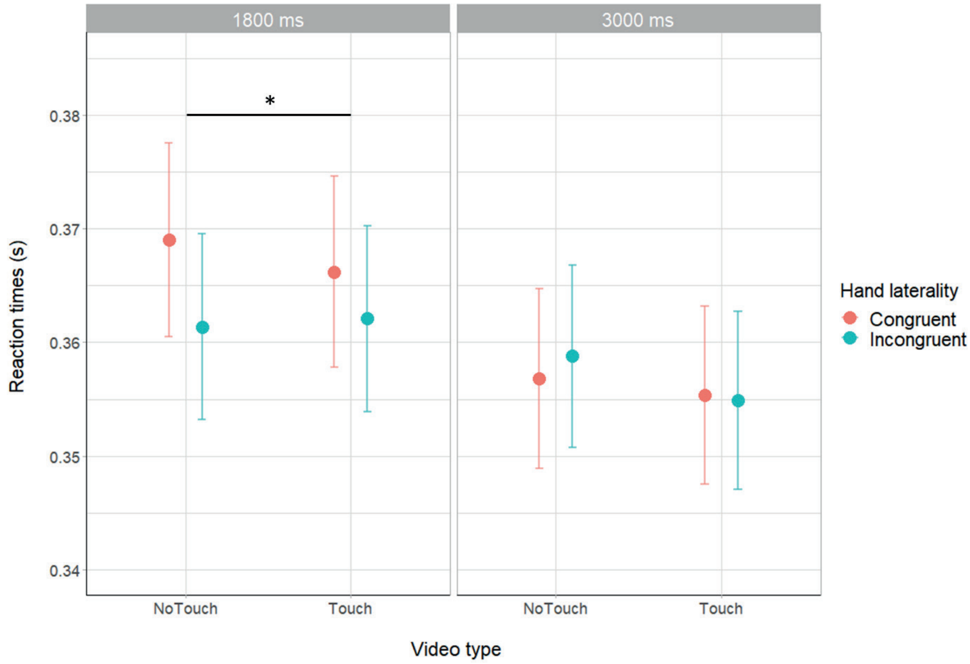


Fig. 5.3. Graph showing the three-way interaction between Video type, Hand laterality, and Video length on RTs.

To test the effect of multiple exposures to pleasant touch on RTs, we ran a separate model with a predictor we defined *Seriality*. This represented the coupling of each trial with the preceding one, so that this factor consisted of four levels: touch/touch, touch/no-touch, no-touch/touch, no-touch/no-touch. We found an effect of Seriality ($\chi^2(3)$ = 11.27, p-value = 0.01), which was explained by faster RTs when a touch video was preceded by another touch video [touch/touch; z-ratio = -3.28, p-value = 0.006; mean = 358.7 ± 5.6 ms, CI (347.9, 370.3)] compared to when a no-touch video was preceded by a touch video [touch/no-touch; mean = 362.2 ± 5.8 ms, CI (351.2, 373.9)] (Fig. 5.4).

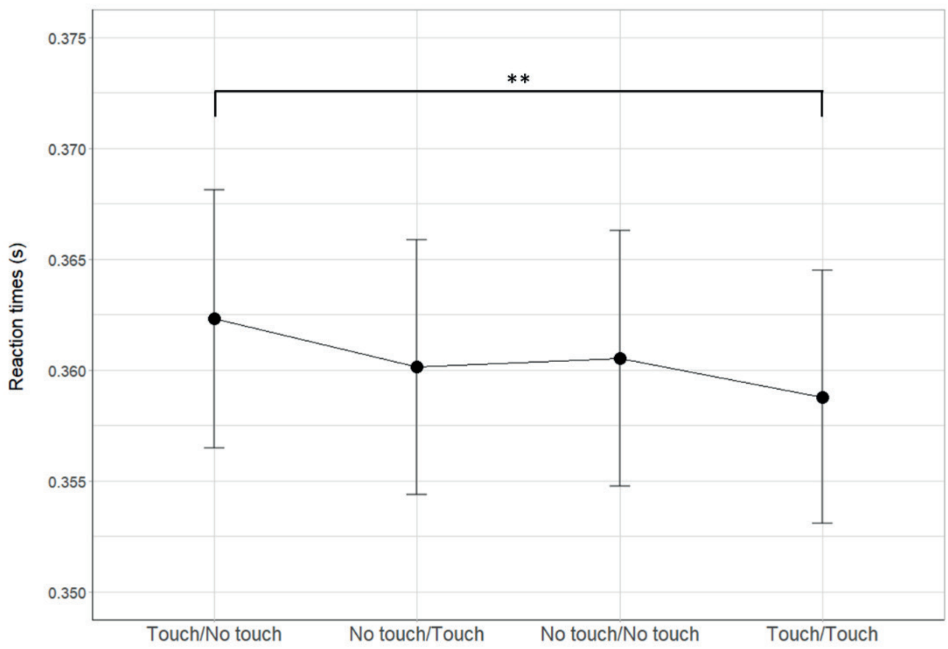


Fig. 5.4. Effects of Seriality on RTs. Participants were faster in responding to Go stimuli when a touch video was preceded by another touch video (compared with the touch/no-touch condition).

5.3.2. Accuracy and commission errors

The accuracy rate for Go stimuli within our sample was 98%. The commission errors rate for No-go stimuli was 3%.

As concerns accuracy for Go stimuli, we found a main effect of Video type ($\chi^2(1) = 5.28$, p-value = 0.02), whereby accuracy was higher after watching pleasant touch videos [mean = 99.45 ± 0.11%, CI (99.18, 99.63)] compared to no-touch videos [mean = 99.30 ± 0.13%, CI (98.97, 98.52)], and a main effect of Hand laterality ($\chi^2(1) = 9.15$, p-value = 0.002), explained by higher accuracy following videos in which participants had to pay attention to a right hand [mean = 99.48 ± 0.1 %, CI (99.23, 99.65)] compared to a left hand [mean = 99.28 ± 0.13%, CI (98.95, 99.51)].

We found no significant differences between conditions for commission errors.

5.3.3. Correlation analyses

We calculated an empathy-for-pleasant touch index for each participant by subtracting their RTs in the touch condition from the RTs in the no-touch condition and we correlated it with the questionnaires using Spearman's rank method. FDR correction was applied to deal with multiple comparisons. We found no significant correlations (all p-values > 0.1). We also correlated the pleasantness ratings for the touch videos with the same questionnaires. We found that pleasantness ratings positively correlated with MAIA-2 ($\varrho = 0.19$, p-value = 0.02) and TEAQ ($\varrho = 0.28$, p-value = 0.002) scores and negatively correlated with the PD subscale of the IRI ($\varrho = -0.21$, p-value = 0.02). See Appendix C for results on pairwise correlations between questionnaires.

5.4. Discussion

5.4.1 What we know from pain observation studies

The only evidence on a motor facilitation effect following observation of others' tactile events comes from studies on tactile pain (Morrison et al., 2007a, 2007b; Galang et al., 2017). In Morrison et al. (2007a), participants were asked to press a button when a video depicted an item either hitting (in one block) or missing (in another block) a finger. The authors found that button presses were faster when participants saw the item hit the finger compared to when the item missed it. In another study using a Go/No-go task, Morrison and colleagues (2007b) found that key releases were faster and key presses were slower when the participants saw a hand getting pricked by a needle compared to getting touched by a Q-tip. They postulated that these results could reflect a slowing of approach and a facilitation of withdrawal behaviours elicited by viewing painful stimulations on other people (Morrison et al., 2007b). These results on a facilitation effect of tactile pain observation on motor performance seem to contradict the neural stimulation studies whereby a general muscle-specific corticospinal inhibition was found contingent to the observation of pain in others (e.g., Avenanti et al., 2005, 2010). However, these studies involve the passive observation of pain videos, where participants are in a relaxed state and the motor system is characterized by low levels of pre-activation (Galang et al., 2017). Drawing on this, Galang and colleagues (2017) set out to explore whether existing levels of motor activity would modulate the effect that pain observation has on the motor system and overt behaviour. Using a Go/No-go paradigm, they found that people responded faster to Go stimuli following the observation of a hand being pricked by a needle compared to getting touched by a Q-tip, thus confirming the original results on this motor facilitation effect by Morrison and colleagues (Morrison et al., 2007a, 2007b). This effect was not dependent on the effector (hand vs. foot) nor on the timing of Go stimulus presentation (0 ms vs 500 ms after pain video) (Galang et al., 2017). Finally, the same research group replicated the findings on a general motor facilitation effect after observing pain in others while they did not find differential effects of pain observation on withdrawal-like and approach-like movements (Galang et al., 2021).

The interpretation of the motor facilitation effect following tactile pain observation is hitherto undetermined. One hypothesis suggests that sharing the affective and the sensorimotor consequences of others' pain eventually leads to the implementation of coherent adaptive reactions, which can be conveniently reduced to increased withdrawal-like movements and decreased approach-like movements. Galang and colleagues (2021) call this the Natural-Mappings hypothesis. The evidence for this account is however contradictory: for instance, while Morrison and colleagues (2007b) found that withdrawal-like movements were faster and approach-like movements were slower when participants saw a hand getting pricked by a needle, Galang and colleagues (2021), using a similar paradigm, failed to replicate these results. On the other hand, the evidence for a general motor facilitation effect that is independent by the type of associated action is, as we saw, consistent across the literature (Morrison et al., 2007a, 2007b; Galang et al., 2017, 2020, 2021). Galang and colleagues (2021) propose two diverging hypothesis to account for the functional significance of this effect. The first, less likely, possibility is that higher arousal levels, as induced by the observation of pain in others, lead to motor activation and consequently to faster reaction times (Martinie et al., 2010). While this is a potentially correct interpretation, the evidence supporting it is inconsistent, as it has been shown that high arousal can also lead to slower reaction times (e.g., in Houwer and Tibboel, 2010). On the other hand, a general motor facilitation effect following pain observation could be functionally associated with reducing one's own personal distress while empathizing with others. This would in turn maximize the self-other distinction necessary for empathic responses, which may be hindered by personal distress reactions (see Han et al., 2017 for details on this account).

5.4.2 Vicarious feelings

In the present study, we found that the observation of pleasant social touch on someone else's hand triggered faster reaction times and higher accuracy for Go stimuli compared to a no-touch condition. This result mimics the one discussed above for pain observation and demonstrates that both negative and positive tactile experiences observed in others are associated with motor facilitation in the self.

Accumulating evidence has shown that the embodied shared representations hypothesis holds true also for the understanding of others' pleasant tactile experiences (Keysers and Gazzola, 2009; Keysers et al., 2010). A pivotal study that supports this hypothesis was run by Morrison and colleagues (Morrison et al., 2011). While under the fMRI scanner, participants underwent both the experience of being caressed by a brush and the observation of someone else's hand being caressed by another hand (Experiment 1). The velocity of the caresses, either felt or seen, could be 3 cm/s, a known feature of pleasant touch, or 30 cm/s, mostly considered not pleasant (Löken et al., 2009). The authors found that for both felt and seen pleasant touch involved the activation of a very similar region in the posterior insula, a brain area that underlies the affective processing of first-hand pleasant touch (Morrison et al., 2011; Gordon et al., 2013). Importantly, the modulation of this area by observed pleasant touch only occurred when the caress had a social nature (a hand caressing another hand) (Morrison et al., 2011). Importantly, Ebisch and colleagues (2008, 2011) extended these findings by reporting a selective involvement of sensorimotor areas (such as SI, SII, and the ventral postcentral gyrus) for the observation of social touch.

Crucial for our discussion are studies demonstrating a relation between touch observation and the sensorimotor system. In an early study on neutral touch observation, Wood and colleagues (2010) showed that the inhibition of the motor cortex (M1) excitability – as induced via TMS – was enhanced during observation of touch on another's hand. This effect was congruent with the laterality of the stimulated M1 and thought to depend on the modulation exerted by touch observation on somatosensory cortices and, consequently, on M1 (Wood et al. 2010). It is worth noting that this inhibitory modulation of M1 brought about by neutral touch observation mirrors the muscle-specific corticospinal inhibition found contingent to pain observation (e.g., Avenanti et al., 2005, 2010) and might be related to low levels of motor system pre-activation due to passive observation of touch videos (Galang et al., 2017). Tellingly, Bolognini and colleagues (2013) demonstrated a causal role of the right SI in encoding the affective valence of others' touch by showing that repeated TMS over this area slowed down participants' reaction times in response to both pleasant (social) and unpleasant touch. Finally, the observation of social touch elicits desynchronizations of pericentral Rolandic rhythms (mu and beta rhythms, 10-20 Hz; Peled-Avron et al., 2016; Schirmer et al., 2019), which underlie increased activity of sensorimotor areas and are associated with mirror properties of the human brain (Fox et al., 2016).

Our results provide further evidence that the observation of pleasant social touch is associated with the activation of the sensorimotor system and extends this finding to the behavioural level. As in the case of motor facilitation following pain observation (Galang et al., 2021), the functional significance of this effect might be related, on a more complex level, to higher order cognitive processes. We believe that the enhanced motor system activity is a direct effect of the recruitment of first-hand sensorimotor representations that are at play when empathizing with others' tactile experiences (Keysers and Gazzola, 2009; Keysers et al., 2010). In this scenario, the motor facilitation effect is a non-causal after-product of shared embodied representations mechanisms. However, one interesting consequence we want to discuss, which draws from studies on empathy for pain, is the approach/withdrawal hypothesis – what Galang and colleagues (2021) have defined as Natural-Mappings hypothesis. We apply this framework to the pleasant social touch domain, and postulate that the resonance with others' positive tactile experiences via shared representations mechanisms leads to the activation of a set of adaptive motor reactions that include approach-like and withdrawal-like behaviours. As pleasant touch is intrinsically a positive experience, we speculate that the general motor facilitation effect found in the present study might be functionally related to the activation of higher-order approach-like tendencies. In support of this, several studies have shown that the perception of positive stimuli (such as facial expressions, words, food, and so on) leads to enhanced approach-like movements and behaviours (Warriner et al., 2017; Fini et al., 2020). More specifically, the observation of pleasant social touch might activate personal tendencies to engage in the same tactile behaviour or "reciprocate". While this hypothesis represents an interesting possibility to explain the enhanced motor activity after pleasant social touch observation, there is currently no study investigating this issue. To shed light on this, future studies will have to expand on our findings by combining pleasant social touch observation and motor tasks in which approach-like and withdrawal-like movements are tested (as in Galang et al., 2021, for pain observation).

In our study, we also theorized that a motor facilitation effect could be restricted to observing a caress on the hand congruent to the effector used to carry out the motor task – the right hand – and that it would be enhanced by longer exposure to social touch (3000ms vs 1800 ms videos). Studies on pain and touch empathy provide mixed evidence for a somatotopic nature of empathic response to others' tactile experiences. Avenanti and colleagues (2005, 2010) and Wood and colleagues (2010) report a muscle-specific corticospinal inhibition for pain observation and an effector-specific corticospinal inhibition for touch observation, respectively. On the other hand, Galang and colleagues (2017) found that the motor facilitation effect after pain observation was not dependent on the effector used to carry out the motor task (hand or foot). We found no direct link between touch conditions and hand laterality (two-way interaction). However, we report a three-way interaction whereby the reduction in response latencies for the touch condition was specific for congruent conditions (caress on right hand) and for 1800 ms videos. As concerns the effect of longer exposure, Triscoli and colleagues (2017) showed that long-lasting first-hand pleasant touch was associated with increased autonomic activity as indicated by increased heart rate variability. We did not find a direct link between pleasant touch observation and length of touch videos (two-way interaction). However, as figure 3 shows, reaction times were overall faster for 3000 ms videos, including touch conditions. Moreover, we show that multiple exposure to pleasant social touch also leads to faster reaction times (as indicated by our results concerning the Seriality factor). Taken together, these findings partly confirm our hypotheses and pave the way for future investigations aimed at systematically exploring whether motor facilitation following pleasant touch observation is effector-specific and how longer exposure to pleasant touch might modulate the motor system activity.

We consider the embodied simulation of affective touch a form of positive empathy (Morelli et al., 2015). Empathy and interoception, the sense of the internal state of the body (Craig, 2002, 2009), are tightly linked (Fukushima et al., 2011; Ernst et al., 2013; Grynberg and Pollatos, 2015). Tellingly, both first-hand and observed affective touch activate a widespread neural system involved in interoception (Ebisch et al., 2011; Morrison et al., 2011). Accordingly, our correlation analysis shows that higher pleasantness for others' touch is linked to higher trait interoceptive sensibility, to higher first-hand positive social touch attitudes and experiences, and to lower personal distress in response to distress in others. On the other hand, we did not find any association between the motor facilitation effect and individual traits of empathy, social touch, and interoceptive sensibility, which is in line with previous studies on pain observation and reaction times (Galang et al., 2017, 2021).

5.4.3 Limitations

The results on a motor facilitation effect reported in the present study are based on comparisons between touch and no-touch conditions. We decided to implement the no-touch condition to try and reduce any possible confounding effect due to the mirroring of motor features in the videos (Calvo-Merino et al., 2005, 2006) – i.e., belonging to the hand caressing, as opposed to hand being caressed. As we controlled for this, we believe our results represent a pure effect of sensorimotor resonance of pleasant social touch. The comparison between touch and no-touch conditions, in both pain and pleasant touch observation studies, has been widely utilized (e.g., Peled-Avron et al., 2016, Schirmer et al., 2019). As Peled-Avron and colleagues (2016) before us, we are aware that the inclusion of a touch-on-object condition might have benefitted our experimental design and possibly led to more complete results. However, our study was run online, and we decided to balance length of the online experiment and design completeness to maintain the length of the experiment to below 1 hour and increase participants' compliance. Furthermore, our decision is supported by previous findings by Morrison and colleagues (2011), who showed that shared representations mechanisms for affective touch observation were at play only during social touch (a hand caressing another hand) and not during a touch on an object.

We would also like to note that, for similar time management reasons, we decided to implement a between-subject factor for Video length. This might have slightly affected the validity of our results, as it is known that within-subjects designs are statistically more powerful and less affected by individual differences (Charness et al., 2012).

5.5. Conclusions and future directions

In the present study, we built on previous evidence showing motor facilitation contingent to empathy for pain (Morrison et al., 2007a, 2007b; Galang et al., 2017, 2021) and examined the possibility that the observation of pleasant social touch would also be associated with enhanced motor activation. We indeed found, utilizing a Go/No-go paradigm, that observing a hand being caressed in a pleasant way led to faster reaction times and higher accuracy for Go stimuli compared with no-touch conditions. Moreover, participants were faster in responding when a touch video was followed by another touch video, highlighting the effect of multiple exposures to pleasant touch on motor behaviour.

Our findings bring about new evidence in support of the embodied simulation account (Keysers et al., 2010; Gallese and Sinigaglia, 2011; Gallese and Ebisch, 2013) on a behavioural level. In fact, we postulate that the activation of embodied sensorimotor representations underlies the motor facilitation effect found in the present study. Furthermore, we propose that this enhanced motor activity might be functionally related to more complex behavioural inclinations arising from empathizing with others, such as approach-like tendencies. Future studies should address this issue by implementing paradigms aimed at examining response-specific effects of pleasant touch observation.

Appendix C – Supplementary material for Chapter 3

Snapshots of experimental videos

Fig. C1. snapshots of the experimental videos

A: touch on right hand condition (Touch congruent)

B: touch on left hand condition (Touch incongruent)

C: no-touch – right hand condition (No-touch congruent)

D: no-touch – left hand condition (No-touch incongruent)

		1800 ms videos		3000 ms videos	
		Congruent (mean ± SE)	**Incongruent** (mean ± SE)	**Congruent** (mean ± SE)	**Incongruent** (mean ± SE)
Reaction times (ms)	**Touch**	366.2 ± 8.38	362.1 ± 8.20	355.3 ± 7.84	354.8 ± 7.82
	No-touch	369.0 ± 8.51	361.3 ± 8.17	356.7 ± 7.90	358.7 ± 7.99
Accuracy (%)	**Touch**	99.52 ± 0.14	99.32 ± 1.93	99.55 ± 0.13	99.41 ± 0.17
	No-touch	99.44 ± 0.16	99.13 ± 2.41	99.35 ± 0.18	99.27 ± 0.20
Commission errors (%)	**Touch**	1.71 ± 0.45	1.49 ± 0.41	1.77 ± 0.45	1.99 ± 0.49
	No-touch	1.64 ± 0.43	1.34 ± 0.38	1.85 ± 0.46	2.07 ± 0.50

Tab. C1: Estimated means and SEs for reaction times, accuracy, and commission errors measures.

Correlation analysis between questionnaires. We ran correlations between pairs of questionnaires using Spearman's rank correlation and FDR correction to account for multiple comparisons. The PES positively correlated with the IRI subscales PT (ϱ = 0.44, p-value < 0.001), FS (ϱ = 0.29, p-value = 0.001), and EC (ϱ = 0.59, p-value < 0.001), with the MAIA (ϱ = 0.50, p-value < 0.001), and with the TEAQ (ϱ = 0.46, p-value <

0.001); the IRI subscale PT positively correlated with the IRI subscale EC (ϱ = 0.43, p-value < 0.001), with the MAIA (ϱ = 0.30, p-value = 0.001), and with the TEAQ (ϱ = 0.27, p-value = 0.003); the IRI subscale FS positively correlated with the IRI subscales EC (ϱ = 0.36, p-value < 0.001), and PD (ϱ = 0.25, p-value = 0.006), and with the MAIA (ϱ = 0.21, p-value = 0.02); the IRI subscale EC positively correlated with the IRI subscale PD (ϱ = 0.29, p-value = 0.001), with the MAIA (ϱ = 0.25, p-value = 0.006), and with the TEAQ (ϱ = 0.24, p-value = 0.01); the IRI subscale PD negatively correlated with the MAIA (ϱ = -0.20, p-value = 0.02); the MAIA positively correlated with the TEAQ (ϱ = 0.34, p-value < 0.001) (see Fig. C2 for a graphical representation of the correlation matrix).

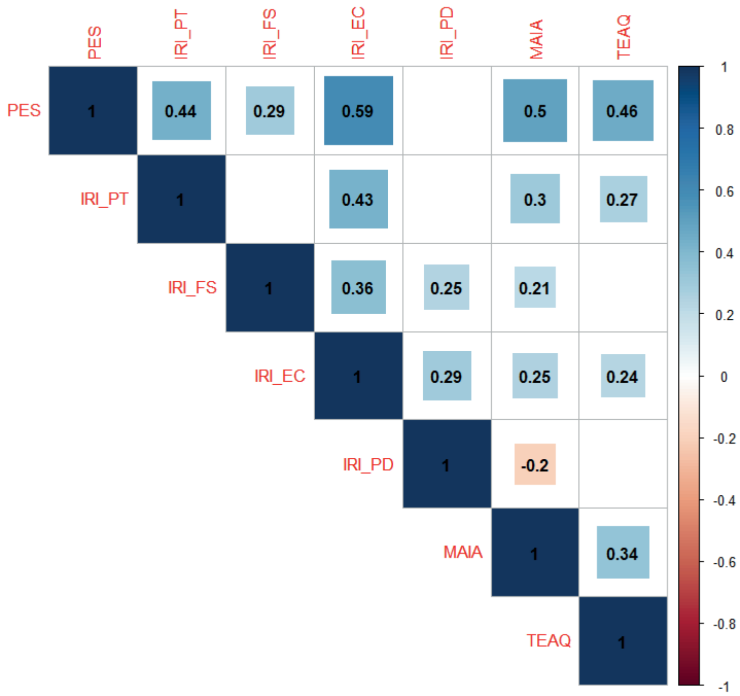


Fig. C2. Graphical representation of the pairwise correlation matrix.

6. Research proposal: Does positive empathy enhance prosocial behaviour? A combined virtual reality-EEG study

6.1. Background

6.1.1. Sharing others' emotions

Humans are endowed with the fundamental ability of sharing and understanding others' affective states, that is empathy (Preston and de Waal, 2002; de Vignemont and Singer, 2006; Decety, 2009; Zaki and Ochsner, 2012; Betti and Aglioti, 2016). The past few decades have witnessed a growth in scientific inquiries on this specific theme, especially in social sciences. This originated not only from a pure interest in comprehending what makes us a well-functioning social species, but also in examining the behavioural consequences of sharing others' emotions, and how this might be applied for societal reasons (Decety, 2009).

According to an influential and widely accepted view, put forward by de Vignemont and Singer (2006), an interpersonal reaction to someone displaying an emotion can be properly defined as empathy when i) the reaction itself consists of being in an emotional state, ii) which is isomorphic to the one just observed (or imagined), and iii) is accompanied by the awareness that the other person is the source of this reaction (de Vignemont and Singer, 2006). Despite being rather strict, this definition of empathy enables differentiations from related, although different, concepts, such as emotional contagion, compassion, and perspective-taking (de Vignemont and Singer, 2006; Batson, 2009).

Since its early stages, the study of cognitive and neural mechanisms of empathy has benefitted from the ideas put forward within a new theory of social cognition, which postulates that humans come to understand others' minds through mental representation sharing (Gallese et al., 2004). In a nutshell, observing others' actions and feelings would elicit activation in certain brain areas that are also involved in the processing of the first-hand experience of that same action or emotion (shared circuits). This similarity between first-person and third-person brain representations (also defined as vicarious activation) would help people interpret others' behaviour and feelings. Mirror neurons systems (MNS), discovered in monkeys in the 1990s

(Di Pellegrino et al., 1992), fuelled the development of this view, providing a possible neural correlate for emotional sharing phenomena (Gallese et al., 2004; Keysers and Gazzola, 2006; Keysers et al., 2010).

6.1.2. Positive empathy

In spite of the increased attention that has been paid to the investigation of empathy, progresses in the field are still held back by at least two factors: i) the focus on empathy for negatively-valenced events; ii) the detachment of emotional processing from its outcomes, i.e., behavioural reactions to the observation of others' emotions, such as prosocial behaviours. Indeed, although the study of empathy has mainly focused on the subjective perception of others' negative feelings, and specifically pain (Betti and Aglioti, 2016), the spectrum of emotions an individual can empathize with ranges from extreme negativity/unpleasantness (e.g., pain, sadness) to extreme positivity/pleasantness (happiness, erogeneity) (Fan et al., 2011; Bernhardt and Singer, 2012; Morelli et al., 2015).

Positive empathy refers to the process of vicariously sharing and understanding an observed or imagined positive emotion (Morelli et al., 2015). Thus defined, positive empathy clearly differs from the negative counterpart, in that the target emotion the observer empathizes with has positive valence and not negative valence (Andreychik and Migliaccio, 2015; Morelli et al., 2015; Andreychik and Lewis, 2017). Coherently, it has been argued that people might be more motivated to empathize with positive emotions, compared to negative ones, in that doing so involves low costs but high benefits – the experience of positive affect – which might be highly rewarding (Duan, 2000; Telle and Pfister, 2016).

First evidence originating from studies investigating the neural correlates of positive empathy suggests that the shared representations model can be also applied to the interpersonal sharing of others' positive emotions (Jabbi et al., 2007; Mobbs et al., 2009; Morelli et al., 2014; Lamm et al., 2015; Morelli, Sacchet, and Zaki, 2015; Chiesa et al., 2017). A recent meta-analysis, conducted by Morelli and colleagues (Morelli, Sacchet, and Zaki, 2015), confirms that personal and vicarious reward – in other words, first-hand positive affect and positive empathy – share common brain activations. Specifically, both experiencing first-hand rewarding outcomes and observing these on another person activates, among the others, the vmPFC, the bilateral amygdala, the AI, and the dACC. On the other hand, whereas personal reward selectively activates the NAcc, activity in dmPFC and pSTS, involved in representing others' beliefs and intentions, is only reported contingent to witnessing others' positive outcomes (Morelli, Sacchet, and Zaki, 2015). Furthermore, along with the affective component, positive empathy has been found to activate sensorimotor brain areas, especially when the rewarding outcome is related to an apparent body part. This has been taken as a confirmation of sensorimotor mirroring during the observation of others' reward (Keysers et al., 2010; Morrison et al., 2011; Chiesa et al., 2017; Schirmer et al., 2019).

6.1.3. Pleasant social touch

Social touch, when pleasant, is considered a highly rewarding outcome. Indeed, along with the sensory-discriminative function, human development and social interaction are strongly influenced by the motivational-affective component of touch (Dunbar, 2010; Gallace and Spence, 2010; Morrison et al., 2010; Pawling et al., 2017). Skin-to-skin contact during mother-infant interactions is now considered essential for healthy human development, and touch deprivation during childhood has been linked to people's social functioning and well-being (Gallace and Spence, 2010, Cascio et al., 2019). Moreover, touch is a preferred channel through which we communicate our emotions, feelings, and thoughts (Hertenstein et al., 2006, 2009; Kirsch et al., 2018), the understanding of which is a quintessential feature of empathy.

Importantly, it has been demonstrated that social affective touch may have positive, appetitive, and soothing effects influencing people's social behaviour. For example, Pawling and colleagues (2017) showed that pictures of neutral faces paired with pleasant affective touch (3 cm/s velocity; Löken et al., 2009) were evaluated as more approachable than faces paired with non-affective touch (30 cm/s velocity). In another study (von Mohr et al., 2017), pleasant affective touch (3 cm/s velocity) had the effect of reducing social exclusion as induced through a Cyberball task. Thus, the rewarding effect of pleasant social touch embraces not only an individual's personal experience, but also his relationship with others.

6.1.4. Electrophysiological components of empathy for pleasant touch

Differently from empathy for pain, the investigation of neural mechanisms underlying positive empathy is still at its early stages. Specifically, few studies have tried to shed light on the electrophysiological features associated with the observation of pleasant touch (Peled-Avron et al., 2016, 2018; Pisoni et al., 2018; Schirmer et al., 2019). Early evidence, interpreted within the shared representations and simulation hypotheses of sensorimotor events (Gallese et al., 2004; Keysers and Gazzola, 2006, 2009; Keysers et al., 2010), shows the crucial role of somatosensory areas: indeed, early physiological activation (around 50-100 ms) and alpha/mu suppression over central brain areas in correspondence of S1 has been reported contingent to the observation of neutral touch (e.g. Pisoni et al., 2018) and pleasant social touch (Peled-Avron et al., 2016; Schirmer et al., 2019). Moreover, a late affective response to observed pleasant touch has been observed, both in the time domain (late positive potential, LPP) and in the time-frequency domain (theta-band synchronization) (Schirmer et al., 2019). Crucially, EEG offers not only the possibility to efficiently investigate the timing of a neural response to observed pleasant touch, but also to examine brain oscillations patterns underlying the communication between different brain regions within widespread neural networks (Varela et al., 2001). This can become particularly useful when investigating the mirror and simulation properties of sensorimotor areas, such as S1. Indeed, even though activation of similar brain regions has been observed, mainly using fMRI, during felt and seen pleasant touch (e.g., Morrison et al., 2011), differences might or might not arise when looking at the different brain connectivity patterns that characterize the two events (Zaki et al., 2007; Pisoni et al., 2018).

6.1.5. Positive empathy and prosocial behaviour

Prosocial behaviour is defined as a collection of acts aimed at benefitting others (individuals or whole groups) (Batson and Powell, 2003; Eisenberg, 2006). Although the link between empathy and prosocial behaviour has long been known to be a tight one, most of the evidence of this interplay comes from studies examining the consequences of negative empathy (Telle and Pfister, 2016). Importantly, the type of empathic responding to someone else's emotion seems to be crucial for the subsequent prosocial engagement: while empathic concern for a person experiencing a negative emotion often results in prosocial and helping behaviours, personal distress is more frequently associated with withdrawal from the stressing circumstances, especially if it is difficult for the empathizer to gain rewards for helping (Batson, 2014; Grynberg and López-Pérez, 2018). If this is the case, then empathizing with negative versus positive emotions might result in very different prosocial tendencies. In fact, this seems to be the case: recent evidence highlights that positive empathy is, differently from negative empathy, associated with little personal distress reactions and, consequently, with a higher probability of engaging in daily prosocial behaviour (Morelli et al., 2014; Morelli et al., 2015; Morelli et al., 2018). However, while much work has been done on relating negative empathy to prosocial behaviour (Decety et al., 2016; Weisz and Zaki, 2018), still little is known on how positive empathy might be associated to prosociality (Morelli et al., 2015; Telle and Pfister, 2016).

A recent model put forward by Telle and Pfister (2016) postulates that prosocial behaviour is, in some cases, driven by the positive affect that stems from witnessing another's positive emotion or reward. Specifically, following the mood maintenance hypothesis, this model claims that i) witnessing a person displaying a positive emotion triggers vicarious positive affect in the observer – that is, positive empathy; ii) this feeling facilitates positive thoughts and behaviour, which are likely to be felt as rewarding; iii) in order to maintain this positive state, the empathizer engages in prosocial acts, either directly formulated or when an occasion spontaneously arises. This empathy-driven prosocial behaviour can be either directed to the person experiencing the positive affect in the first place, or to another recipient (Telle and Pfister, 2016). It is worth noting that this model directly draws on the assumption that people seek to maintain a rewarding state, that is they aim at increasing pleasant affect while decreasing unpleasant affect. Thus, although prosocial behaviour is essentially an other-related phenomenon, the link between positive empathy and prosocial acts might in fact reflect egoistic tendencies. Alternatively, it has been suggested that prosocial behaviour following positive empathy might derive from a conscious or unconscious desire of further amplifying others' positive feelings (just like when, for example, one throws a surprise birthday party for a friend). These motives might be further incentivized by the anticipation of the positive emotional reaction in the other person, thus generating a loop of positive feelings feeding in positive empathy (Telle and Pfister, 2016).

6.2. Research questions and objectives

The purpose of the present research project is to shed light on the relationship between positive empathy and prosocial behaviour. We will look at a specific type of stimuli, that is pleasant touch, which can be considered a rewarding stimulation (see Background). To this aim, we will take advantage of an IVR paradigm. Different from common social neuroscience experimental protocols, which have primarily relied on the presentation of static, unimodal, and decontextualized social and affective stimuli (Zaki and Ochsner, 2009), IVR allows the implementation of virtual environments that can efficiently simulate real-life social interactions, enabling both high experimental control and appropriate ecological validity (Parsons, 2015). In our case, IVR will permit us to implement a more realistic empathic scenario, which should be characterized by participants' feeling of "being there" in the virtual environment (Sanchez-Vives and Slater, 2005). This is expected to amplify the desired emotional reactions and make them more similar to real-life sensations. Moreover, by adopting EEG, we will set out to explore the dynamical temporal features of processing others' rewards and how the neural response to this type of stimulation predicts subsequent prosocial behaviour.

A secondary aim of the present work relates to the differentiation between vicarious and personal reward, at both behavioural and neural levels. By having our participants embody a virtual body in first-person perspective (1PP), we will be able to examine the different behavioural and neural reactivity associated with experiencing pleasant touch on the virtual self and the virtual other. Despite virtual touch cannot be fully considered a tactile experience, previous evidence has demonstrated that IVR is able to elicit a strong feeling of ownership over a virtual body in 1PP, which is further associated with increased pleasantness for touches delivered upon it (Fusaro et al., 2016; Fusaro et al., 2019; Fusaro et al., 2021; Mello et al., 2022).

Based on the literature summarized above, and given the aims we set out to pursue, the present research project will try and address the following research questions:

1. Is positive empathy a main drive of prosocial behaviour? Specifically, does witnessing others' rewards, in the form of pleasant touch, increases prosocial choices? By adopting a charitable donation task, we will try and demonstrate a link between empathy for others' rewards and prosocial behaviour.

2. Is prosocial behaviour predicted by specific neural activity, as measured via EEG, to others' rewards? We will use EEG to elucidate the neural mechanisms underlying positive empathy. Moreover, we will investigate how the neural response to others' rewards predicts subsequent prosocial choices.

3. Can first-hand pleasant experience and positive empathy be dissociated at the behavioural and neural level? And how the two types of pleasant outcomes differentially relate to prosocial behaviour? To address this research question, we will have our participants embody an avatar in 1PP and experience virtual touches on their virtual self. This will allow us to disentangle the behavioural and neural components associated with self and other reward.

6.3. Materials and methods

6.3.1. General set-up

Through a head-mounted display (HMD), participants will enter a virtual environment and embody a demographically matched avatar in 1PP. According to the experimental block, they will observe pleasant and neutral touches delivered on either their virtual right hand or the right hand of a virtual character sitting on the other side of a desk (to control for intervening factors, the face of the other character will not be visible). After each trial, participants will be asked to provide ratings about the pleasantness of the virtual touch, as well as about their general affect. Moreover, participants will complete a donation task (similar to Tusche et al., 2016) during some of the trials (after the virtual touch and the questions are delivered). The trials including the donation task will vary randomly across participants. After the main experimental task, questionnaires concerning trait empathy, prosocial behaviour, and other related constructs will be delivered to the participants (see below for further details on the various experimental tasks). The EEG of the participants will be registered across the whole experiment.

6.3.2. Virtual touch stimuli

Pleasant touch is defined by specific physical parameters (Löken et al., 2009). A crucial one is velocity. Indeed, it has been demonstrated that subjective ratings of pleasantness for both felt and observed touch are specifically high when the tactile stimulation has a velocity of 1-10 cm/s, with a maximum peak at around 3 cm/s (Löken et al., 2009; Morrison et al., 2011; Walker et al., 2017). Thus, our experimental stimuli will be represented by virtual touches delivered at 3 cm/s. This type of stimuli will be compared to two different control conditions: i) a virtual touch having 18 cm/s velocity, which is out of the pleasantness range; ii) a touching virtual ball, which does not have social characteristics that can be considered pleasant. The choice of implementing two different control conditions is justified by the aim of fully controlling for the pleasantness of a social stimulus. While, on one hand, the comparison with a virtual touch with 18 cm/s velocity can control for the pleasantness of a tactile stimulation, the comparison with a virtual ball can ensure that any effect of the experimental task is not the result of merely observing a social stimulus, as it can be a virtual hand.

6.3.3. Main experimental task

The main task will consist of two experimental blocks, one in which participants will observe virtual pleasant and neutral touches on another character's virtual hand, and one in which the same stimulation will be delivered on participants' virtual hand. Block order will be counterbalanced across participants. The number of trials in each block will be set at an amount that represents a compromise between the length of the experience in IVR and the right number of trials needed for reliable EEG analyses. In each of the two blocks, every virtual touch will be followed by a question evaluating the subjective feeling of pleasantness for that stimulation – "How pleasant was the touch/stimulation?". Moreover, general affect will be evaluated through the following questions: “To what extent did you experience positive emotions during the touch/stimulation?”.

Some of the trials will further include a donation task, in which participants will be asked to share a sum of virtual money (10 euros) with different charitable organizations (Tusche et al., 2016). It has been demonstrated that economic prosocial tasks, including sharing a sum of money with another person, or a bigger entity, such as a charitable organization, do in fact well capture prosocial tendencies (Christov-Moore and Iacoboni, 2016; Klimecki et al., 2016; Tusche et al., 2016; Gallo et al., 2018; Ioumpa et al., 2019). In each of the trials including a donations task, the target charitable organization’s name and a description of its purposes will be displayed (for a similar paradigm see Tusche et al., 2016). Before starting the main experimental task, participants will be informed that one donation trial per block will be selected randomly at the end of the experiment, which will define the amount of real money donated and kept. This will ensure that participants will treat each trial equally and will make coherent choices.

Finally, after the main experimental task, participants will fill in questionnaires regarding positive empathy (Positive Empathy Scale, PES; Morelli et al., 2015), prosocial tendencies (Prosocialness Scale; Caprara et al., 2005), social touch (Social Touch Questionnaire, STQ; Wilhelm et al., 2001), and related concepts, such as well-being and life satisfaction (Morelli et al., 2015).

Participants’ EEG will be continuously registered via a 64-channels Brain Vision system. Electrodes will be positioned according to the international 10-20 placement system. Electrical impedance will be checked at the beginning of each block and kept below the 5 kΩ threshold.

6.4. Expected results

As concerns behavioural manipulations, we predict that the pleasantness ratings to virtual touch will be significantly higher during the 3 cm/s touch conditions, compared to both the control conditions. Moreover, we also expect that pleasant touch will specifically increase general affect. As empathy has been shown to modulate pleasantness ratings for social touch (e.g., Peled-Avron et al., 2016), we further predict that higher scores on our empathy measure (PES) will be associated with higher pleasantness ratings for observed pleasant touch.

The primary aim of the present work is to demonstrate a relationship between interpersonal sharing of positive outcomes, i.e., positive empathy, and prosocial behaviour. If a positive relationship does exist, then to a higher interpersonal reactivity to observed pleasant touch should correspond a more pronounced tendency to share a sum of money during the donation task. This is in fact what we predict. Again, we expect this relationship to be modulated by general levels of trait empathy.

As concerns electrophysiological results, our predictions parallel existing works on the observation of pleasant touch on others. Specifically, following the simulation hypothesis of sensorimotor events, we expect that witnessing slow pleasant touch on others will result in enhanced early neural activation (around 50-100 ms; P50/P100) and alpha/mu-band suppression over somatosensory areas, such as S1, as compared to neutral non-pleasant touch. As alpha/mu-band suppression has also been reported for first-hand tactile experiences, a similar pattern of results found for vicarious tactile experiences would provide further evidence for the shared representations and simulation hypothesis. Moreover, it would confirm that, when witnessing others' reward, not only people share the affective component of that emotional event, but also its somatosensory outcomes, especially when an apparent body part is involved. Related to the latter point, we in fact also expect a late affective response to others' pleasure: specifically, a modulation of the LPP and an increase in power of oscillations in the theta-band, both previously associated with affective reactivity to pleasant social touch (Schirmer et al., 2019). Finally, we predict that different quantitative and qualitative aspects of the electrophysiological reactivity to pleasant touch on others will be predictive of behavioural outcomes during the prosocial task.

As concerns the third research question, we predict both qualitative and quantitative differences between first-hand virtual pleasant touch and the same stimulation on others. Pleasantness ratings are expected to be higher during the first-hand experience of pleasant touch, while general affect should not be affected, or marginally so, by the different conditions. On the other hand, positive empathy for others' pleasant touch is expected to elicit higher prosocial behaviour (Telle and Pfister, 2016), although it has been suggested that first-hand affective touch might be tightly linked to pro-social behaviour as well (Su and Su, 2018). At the brain level, similar local patterns of neural activity are expected for both first-hand and observation of pleasant touch, coherently with the shared representations hypothesis. Despite this, in depth network-based investigations might reveal different brain connectivity patterns between conditions, which might differ both in space and in time (Pihko et al., 2010; Pisoni et al., 2018).

6.5. Pioneering features

First, the present work is innovative in that it takes advantage of IVR, a new tool in neuroscientific research that allows to create experimental scenarios that can replace classic social neuro-science paradigms, without losing in the process ecological validity and experimental control (Parsons, 2015). IVR can induce a strong sense of embodiment over virtual full bodies and body parts, overall increasing the sense of "being there" in the virtual environment. We will exploit this to examine behavioural and neural reactions to others' reward and personal reward (pleasant touch).

Importantly, our work seeks to provide new evidence and insights about the behavioural and neural mechanisms of understanding others' positive emotions and rewards, as well as about the desirable outcomes associated with it. In an essentially social species like ours, prosocial behaviour highly contributes to social bonding and trust among individuals. Shedding light on the association between positive empathy and prosocial behaviour can be relevant not only to increase our knowledge regarding human nature (and its disfunctions), but also to better understand what underlies and motivates the implementation of other-directed actions, with an eye to applicative purposes.

7. General discussion and conclusions

7.1. General discussion

The aim of the present thesis was to characterize pleasant social touch as an embodied phenomenon, critically depending on the many ways we perceive and interact with our own body and grounded in somato-motor representations of the self (Wilson, 2002; Gallagher, 2006; Goldman and de Vignemont, 2009; Shapiro, 2014).

The embodied cognition (EC) account arose in opposition to what Goldman and de Vignemont (2009) call classical cognitivism (CC), which assumes that cognition is separable from the physical body, and its interactions with the environment, and sees the body as a mere hardware enacting the commands dictated by the mind (the software). But any given mental act unfolds within an experiencing and acting body, and the idea that all cognitive functions – including socially oriented ones – are deeply rooted in perception and action through the body gained much attention thanks to the EC perspective (Wilson, 2002; Gallagher, 2006; Goldman and de Vignemont, 2009; Shapiro, 2014).

Perhaps, the sense of touch represents the best instance of embodied phenomenon: there is no touch without a body, and there is no body (and self) without touch (Serino and Haggard, 2010; de Haan and Dijkerman, 2020). Since the pre-natal period, and throughout human and other species life, tactile experiences with other individuals represent a critical element contributing to neural, individual, and social development (Bales et al., 2018; Gliga et al., 2019; Cascio et al., 2019). These interactions give life to an ensemble of somatic sensations, conscious and unconscious feelings, and sensorimotor correlates forming embodied mental representations that shape intrapersonal and interpersonal processes (Serino and Haggard, 2010; Gallese and Ebisch, 2013; de Haan and Dijkerman, 2020).

When touch has a social nature (Gallace and Spence, 2010; Morrison et al., 2010), its personal experience is inextricably determined by the body location wherein the touch is delivered, demonstrating a first crucial link between touch and the body. In the first work constituting this thesis – Chapter 2 –, we presented evidence showing that social touch preferences pertaining different social contexts and, importantly, specific body locations differ in typically developing and autistic adults. Touch is the first sense to develop (Gallace and Spence, 2010; Cascio et al., 2019), and while the importance of in-utero tactile stimulations is inseparable from other sensory sources (e.g., vestibular and proprioceptive signals), the impact of interpersonal touch on post-natal development is conspicuous (Bales et al., 2019; Gliga et al., 2019; Cascio et al., 2019). Mother-infant tactile interactions represent a main force of healthy neural and social development, driving secure attachment, helping the formation of emotional bonds, and possibly setting the stage for the associative learning of social reward. Importantly, these initial interpersonal touch experiences provide the scaffolding for later social exchanges, such as those occurring during adolescence and adulthood (Cascio et al., 2019). In chapter 2, we presented recent evidence suggesting that socio-affective touch processing might be compromised in ASD, with the roots of this impairment deep into basic sensory processing difficulties and its consequences leading to long-term complex social disabilities (Foss-Feig et al., 2012; Lundqvist, 2015; Kadlaskar et al., 2019). Few studies have investigated affective touch processing in ASD and have reported abnormal behavioural reactions to and neural processing of socio-affective touch compared with typically developed individuals (Cascio et al., 2016; Kaiser et al., 2016; Masson et al., 2019). Here, we proposed that social touch experiences – in terms of appropriateness, pleasantness, and erogeneity of touch – of ASD individuals would differ from those of NT individuals depending on body location and social context. First, we showed that the level of each touch-related feeling we examined was diminished in the ASD compared with the NT group – i.e., autistic people experienced overall less appropriateness, pleasantness, and erogeneity for interpersonal touch. Furthermore, we confirmed that: i) social contexts characterized by a higher socio-affective meaning, namely friendly and intimate situations, were those that most differentiated between the two groups; ii) within these contexts, specific body areas (e.g., intimate areas within the intimate scenario) were associated with the diminished feelings of appropriateness, pleasantness, and erogeneity for touch. Finally, we showed that touch preferences were dependent on people's autistic traits, although social touch aversion (and social anxiety in the case of appropriateness) strongly mediated this relationship. The study presented in Chapter 2 thus highlights and clarifies the peculiarities of social touch processing in ASD and our results might be further useful for interventions aimed at easing autistic people's daily tactile interactions (Cullen et al., 2005).

The relation between touch and one's own body is more or less straightforward when it comes to experienced feelings for touch in specific body locations. On a more intricate level, how does the *perception* of and the *sense of ownership* for our bodies affect touch experiences? Chapter 3 dealt with this fascinating topic. It was framed within the overarching perspective that, while we usually think of the ownership of our own body as a rather stable construct, the ensemble of feelings and perceptions constituting it are in fact drastically modified by brain damage and body ownership illusions (Maister et al., 2015). Importantly, studies have shown that illusory ownership over a virtual body can affect people's perceptions and behaviour, as well as their implicit attitudes, depending on conspicuous features of the virtual body they are embodying (Maister et al., 2015), such as ethnicity (Peck et al., 2013), age (Banakou et al., 2013), shape (Van Der Hoort et al., 2011), size (Preston and Ehrsson, 2014; Provenzano et al., 2020), and sex (Slater et al., 2010; Peck et al., 2020). In the study constituting Chapter 3, we utilized immersive virtual reality and the full-body illusion (Maselli and Slater, 2013) to exploit the possibility of replacing heterosexual participants' real bodies with a virtual version that could either match or not their sex – body swapping. Within this context, we investigated social touch experiences for touches delivered by virtual avatars – either male or female. As hypothesized, we found that wearing a virtual body belonging to the opposite sex changed participants' touch preferences for same-sex touch in a coherent way – i.e., men rated touches by male avatars as more erogenous, pleasant, and appropriate when they embodied a woman, and so did women for female avatars when they embodied a man. Furthermore, these effects were related to participants' feeling of ownership over the virtual bodies and were predicted by specific physiological activity. These results bring about new important evidence on the embodied nature of social touch and demonstrate that body ownership, and the various individual characteristics associated with it such as sexual orientation and gender, plays a crucial role in touch experiences.

Chapter 4 represented a bridging element between first-hand embodied experiences – including tactile ones – and the re-enactment of the resulting cognitive representations for the understanding of others' feelings and sensations. Scholars call this embodied simulation (Gallese et al., 2004; Gallese, 2005; Keysers and Gazzola, 2009; Gallese and Sinigaglia, 2011). Chapter 4, in fact, examined the new emerging topic of positive empathy – of which empathy for pleasant touch is a special case – by comparing it to the much more beaten and fruitful (at least for now!) field of empathy for pain (Betti and Aglioti, 2016). Here, we argued that embodied simulation mechanisms, at the basis of emotional sharing and widely accredited as concerns negative empathy, are likewise at play during the perception and understanding of others' positive emotions (Morelli, Sacchet, and Zaki, 2015) and sensations like pleasant touch (Keysers et al., 2010). This provides important support to the claim that socio-affective touch experiences are embodied, and that cognitive simulations based on embodied representations help us navigate the social world (Gallese et al., 2004). Thus, the review presented in Chapter 4 served the purpose of facilitating the passage from first-hand tactile experiences (Chapter 2 and 3) to tactile events that occur to others (Chapter 5).

As said, first-hand tactile experiences are associated with an ensemble of bodily sensations, feelings, and sensorimotor consequences forming cognitive representations that are automatically re-enacted when witnessing touch on others. This results in individual states of affective sharing and sensorimotor resonance, which lead eventually to the understanding of others' tactile experience (Keysers and Gazzola, 2009). The embodied simulation account has received much attention within the field of empathy for pain (Betti and Aglioti, 2016). Thanks to the renewed interest in the role of somatosensation in social perception, studies have confirmed that this approach holds also for the sharing and understanding of others' socio-affective touch (Keysers and Gazzola, 2009). Neuroimaging and electrophysiology studies have demonstrated that brain areas that are involved in the first-hand perception of pleasant social touch – such as the insular and cingulate cortices, primary and secondary somatosensory areas, motor and premotor regions – are also activated by the observation of pleasant social touch on others (Morrison et al., 2011; Ebisch et al., 2011; Walker et al., 2017). In chapter 5, we were interested in examining the role of sensorimotor mechanisms in the observation of pleasant social touch. In the study constituting this chapter, we postulated that the activation of sensorimotor representations when observing other's touch would result in a generalized motor activation in the self that would eventually lead to a motor facilitation effect when carrying out a motor task. This hypothesis was mainly based on previous studies on empathy for pain showing indeed motor facilitation following the observation of others' pain (Morrison et al., 2007a, 2007b; Galang et al., 2017, 2021). Here, we demonstrated that also the observation of pleasant social touch is associated with motor facilitation in the self as we reported faster reaction times and higher accuracy following touch observation (compared to no-touch conditions) in a Go/No-go task. Furthermore, repeated exposure to touch led to faster reaction times as well. These results suggest that, when observing social touch experiences, embodied sensorimotor resonance is a likely mechanism contributing to the sharing and understanding of others' tactile experiences (Keysers and Gazzola, 2009). The functional significance of this enhanced motor activity in response to others' socio-affective touch might extend to the activation of approach-like tendencies, but more studies are definitely needed to argue that this is indeed the case.

Finally, we proposed a research project aimed at examining the relation between positive empathy and prosocial behaviour in Chapter 6. Positive empathy is a rather emerging topic in social neuroscience (Morelli et al., 2015) and, while a huge amount of work has been dedicated to exploring the prosocial consequences of empathizing with others' negative emotions (and for a good reason!), still very little is known on how sharing others' positive emotions and sensations might foster prosociality. A first attempt in this sense comes from Telle and Pfister (2016), who postulated that prosocial behaviour might be driven by the positive affect that stems from witnessing another's positive emotion or reward. Following the mood maintenance hypothesis, their model claims that positive empathy facilitates positive thoughts and behaviour, which are likely to be felt as rewarding, and to maintain this positive state, the empathizer engages in prosocial acts. This empathy-driven prosocial behaviour can be either directed to the person experiencing the positive affect in the first place, or to another recipient (Telle and Pfister, 2016). The study proposed in Chapter 6 is specifically aimed at demonstrating a link between empathy for pleasant touch and prosocial behaviour. Su and Su (2018) recently proposed a model of human prosociality that sees its roots in the early tactile interactions – e.g., infant-mother interactions – that characterize human lives. According to the authors, prosociality is "touch-scaffolded" (Su and Su, 2018). Thus, based on this premises, we argue that empathizing with others' pleasant touch activates a series of positively valenced embodied representations that would eventually culminate in heightened tendencies to act prosocially. We believe this represents a fascinating topic that is worth exploring in future.

6.2. Conclusions

The series of studies presented in this thesis provides important evidence in support of the embodied nature of social touch by focusing on both first-hand and others' tactile experiences. We showed that mental body representations associated with the perception and ownership of our own body affect how social touch, concerning ourselves and others, is perceived. Chapter 2 – *Social touch experiences of neurotypical people and people on the autism spectrum are differentially affected by social context and body location* – is a journey into core differences in social touch perception between typically developing and autistic adults. The daily life abounds with tactile interactions, but interpersonal touch has the tricky feature of resulting pleasant or unpleasant, appropriate or inappropriate depending on a series of dispositional and contextual factors (Gallace and Spence, 2010). And autistic people seem to struggle even more with grasping the socio-affective meaning of touch (Kaiser et al., 2016; Cascio et al., 2019). Our findings bring about clarification on how social touch in different social contexts and pertaining the whole body is perceived in ASD. Based on this, future studies may want to examine the link between social touch preferences and long-term social impairments in ASD in more depth and perhaps apply the knowledge thus gathered to develop targeted interventions to facilitate daily tactile interactions in ASD.

Chapter 3 – *Wearing same- and opposite-sex virtual bodies and seeing them caressed in intimate areas* – reported a clear instance of the effect of body ownership modifications on cognition and attitudes. If mental body representations play a crucial role in cognition, then it follows that conspicuous changes in how people perceive and interact with their bodies will have important effects on how we think and behave (Wilson, 2002; Gallagher, 2006; Goldman and de Vignemont, 2009; Shapiro, 2014). We showed that this was indeed the case as concerns social touch preferences. We want to focus on one important point in this conclusions section: immersive virtual reality provides an extremely useful tool for investigating the effect of embodiment on cognition and behaviour (Maister et al., 2015). In fact, it enables people to undergo body ownership illusions constituted by changes in one's body that are otherwise impossible to reach with common methodologies (Maselli and Slater, 2013). We thus suggest that studies of embodied social cognition take more advantage of this technique to shed light on the bodily influences on the human mind.

Chapter 5 – *Motor facilitation following pleasant social touch observation* – transferred the attention from personally-experienced to others' touch, and presented results suggesting that individual sensorimotor representations are involved in the observation of pleasant social touch on others. We postulate, in fact, that the activation of these representations underlies the motor facilitation effect we found when participants carried out a simple motor task. While future studies will definitely need to replicate these results, the functional significance (or, if you prefer, the functional consequence) of the enhanced motor activation when witnessing others' pleasant social touch might be explored in relation to approach-like and prosocial tendencies.

The fundamental relation between touch and the body has been widely addressed in the cognitive and social neuroscience literature, where it has been shown that mental body representations are formed by converging exteroceptive and interoceptive signals, including tactile ones, and that in turn these representations can greatly shape how a tactile event is perceived and interpreted (Serino and Haggard, 2010; de Haan and Dijkerman, 2020). I would like to conclude this thesis with a suggestion for future research. Tactile experiences are inextricably linked to feelings and sensations – either negatively or positively valenced – elicited by them, and I hope this thesis clarified and shed new light on this important aspect of social touch. However, the interrelation between socio-affective touch and the body from an embodied cognition perspective has not been widely addressed and it is important that future studies focus on this to elucidate and enhance our knowledge on how the body shapes, and it shaped, by social touch.

References

Aleong R., and Paus T. (2010). Neural correlates of human body perception. Journal of Cognitive Neuroscience, 22(3), 482–495.

Andreychik, M. R., and Lewis, E. (2017). Will you help me to suffer less? How about to feel more joy? Positive and negative empathy are associated with different other-oriented motivations. *Personality and Individual Differences, 105*, 139-149.

Andreychik, M. R., and Migliaccio, N. (2015). Empathizing with others' pain versus empathizing with others' joy: Examining the separability of positive and negative empathy and their relation to different types of social behaviours and social emotions. *Basic and Applied Social Psychology, 37*(5), 274-291.

Avenanti, A., Bueti, D., Galati, G., and Aglioti, S. M. (2005). Transcranial magnetic stimulation highlights the sensorimotor side of empathy for pain. *Nature Neuroscience, 8*(7), 955-960.

Avenanti, A., Paluello, I. M., Bufalari, I., and Aglioti, S. M. (2006). Stimulus-driven modulation of motor-evoked potentials during observation of others' pain. *Neuroimage, 32*(1), 316-324.

Avenanti, A., Sirigu, A., and Aglioti, S. M. (2010). Racial bias reduces empathic sensorimotor resonance with other-race pain. *Current Biology, 20*(11), 1018-1022.

Azevedo, R. T., Macaluso, E., Avenanti, A., Santangelo, V., Cazzato, V., and Aglioti, S. M. (2013). Their pain is not our pain: brain and autonomic correlates of empathic resonance with the pain of same and different race individuals. *Human Brain Mapping, 34*(12), 3168-3181.

Baayen, R. H., and Milin, P. (2010). Analyzing reaction times. *International Journal of Psychological Research, 3*(2), 12-28.

Bagby, R. M., Parker, J. D., and Taylor, G. J. (1994). The twenty-item Toronto Alexithymia Scale—I. Item selection and cross-validation of the factor structure. *Journal of Psychosomatic Research, 38*(1), 23-32.

Bales, K. L., Witczak, L. R., Simmons, T. C., Savidge, L. E., Rothwell, E. S., Rogers, F. D., ... and Del Razo, R. A. (2018). Social touch during development: Long-term effects on brain and behavior. *Neuroscience & Biobehavioral Reviews, 95*, 202-219.

Banakou D., Groten R., and Slater M. (2013). Illusory ownership of a virtual child body causes overestimation of object sizes and implicit attitude changes. Proceedings of the National Academy of Sciences (PNAS) USA, 110(31), 12846–12851.

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., and Clubley, E. (2001). The autism-spectrum quotient (AQ): Evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders, 31*(1), 5-17.

Barrett, L. F., and Satpute, A. B. (2013). Large-scale brain networks in affective and social neuroscience: towards an integrative functional architecture of the brain. *Current Opinion in Neurobiology, 23*(3), 361-372.

Barton K. (2020). MuMIn: multi-model inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn.

Bates D., Sarkar D., Bates M. D., and Matrix L. (2014). The lme4 package. R package version, 2(1), 74.

Batson, C. D. (2009). These things called empathy: Eight related but distinct phenomena. In: *The Social Neuroscience of Empathy*, ed. J. Decety, W. Ickes, pp. 16–31. Cambridge, MA: MIT Press

Batson, C. D. (2014). *The altruism question: Toward a social-psychological answer*. Psychology Press..

Batson, C. D., and Powell, A. A. (2003). Altruism and prosocial behaviour. *Handbook of Psychology*, 463-484.

Batson, C. D., Batson, J. G., Slingsby, J. K., Harrell, K. L., Peekna, H. M., and Todd, R. M. (1991). Empathic joy and the empathy-altruism hypothesis. *Journal of Personality and Social Psychology, 61*(3), 413.

Bejerot, S., Eriksson, J. M., & Mörtberg, E. (2014). Social anxiety in adult autism spectrum disorder. *Psychiatry Research, 220*(1-2), 705-707.

Berlucchi G., and Aglioti S. M. (2010). The body in the brain revisited. Experimental Brain Research, 200(1), 25.

Bernhardt, B. C., and Singer, T. (2012). The neural basis of empathy. *Annual review of neuroscience, 35*, 1-23.

Berridge, K. C., and Kringelbach, M. L. (2015). Pleasure systems in the brain. *Neuron, 86*(3), 646-664.

Betti, V., and Aglioti, S. M. (2016). Dynamic construction of the neural networks underpinning empathy for pain. *Neuroscience and Biobehavioural Reviews, 63*, 191-206.

Betti, V., Zappasodi, F., Rossini, P. M., Aglioti, S. M., and Tecchio, F. (2009). Synchronous with your feelings: sensorimotor γ band and empathy for pain. *Journal of Neuroscience, 29*(40), 12384-12392.

Bhanji, J. P., and Delgado, M. R. (2014). The social brain and reward: social information processing in the human striatum. *Wiley Interdisciplinary Reviews: Cognitive Science, 5*(1), 61-73.

Bird, G., Silani, G., Brindley, R., White, S., Frith, U., and Singer, T. (2010). Empathic brain responses in insula are modulated by levels of alexithymia but not autism. *Brain, 133*(5), 1515-1525.

Blakemore, S. J., Bristow, D., Bird, G., Frith, C., and Ward, J. (2005). Somatosensory activations during the observation of touch and a case of vision–touch synesthesia. *Brain, 128*(7), 1571-1583.

Blanke O., Landis T., Spinelli L., and Seeck M. (2004). Out-of-body experience and autoscopy of neurological origin. *Brain, 127*(2), 243–258.

Bolognini, N., Rossetti, A., Convento, S., and Vallar, G. (2013). Understanding others' feelings: the role of the right primary somatosensory cortex in encoding the affective valence of others' touch. *Journal of Neuroscience, 33*(9), 4201-4205.

Botvinick M., and Cohen J. (1998). Rubber hands "feel" touch that eyes see. *Nature, 391*(6669), 756–756.

Botvinick, M., Jha, A. P., Bylsma, L. M., Fabian, S. A., Solomon, P. E., and Prkachin, K. M. (2005). Viewing facial expressions of pain engages cortical areas involved in the direct experience of pain. *Neuroimage, 25*(1), 312-319.

Bradley M. M., Codispoti M., Cuthbert B. N., and Lang P. J. (2001). Emotion and motivation I: defensive and appetitive reactions in picture processing. *Emotion, 1*(3), 276.

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., ... and Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal, 9*(2), 378-400.

Brown, C., and Dunn, W. (2002). Adolescent/adult sensory profile. San Antonio, TX: Pearson.

Bufalari, I., Aprile, T., Avenanti, A., Di Russo, F., and Aglioti, S. M. (2007). Empathy for pain and touch in the human somatosensory cortex. *Cerebral Cortex, 17*(11), 2553-2561.

Burke, S. M., Majid, D. A., Manzouri, A. H., Moody, T., Feusner, J. D., and Savic, I. (2019). Sex differences in own and other body perception. *Human Brain Mapping, 40*(2), 474-488.

Bush, G., Luu, P., and Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences, 4*(6), 215-222.

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., and Haggard, P. (2005). Action observation and acquired motor skills: an FMRI study with expert dancers. *Cerebral Cortex, 15*(8), 1243-1249.

Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., and Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology, 16*(19), 1905-1910.

Carey, M., Crucianelli, L., Preston, C., and Fotopoulou, A. (2019). The effect of visual capture towards subjective embodiment within the full body illusion. *Scientific Reports, 9*(1), 1-12.

Carey, M., Crucianelli, L., Preston, C., and Fotopoulou, A. (2021). The role of affective touch in whole-body embodiment remains equivocal. *Consciousness and Cognition, 87*, 103059.

Cascio, C. J., Lorenzi, J., and Baranek, G. T. (2016). Self-reported pleasantness ratings and examiner-coded defensiveness in response to touch in children with ASD: effects of stimulus material and bodily location. *Journal of Autism and Developmental Disorders, 46*(5), 1528-1537.

Cascio, C. J., Moore, D., and McGlone, F. (2019). Social touch and human development. *Developmental ognitive Neuroscience, 35*, 5-11.

Cascio, C., McGlone, F., Folger, S., Tannan, V., Baranek, G., Pelphrey, K. A., and Essick, G. (2008). Tactile perception in adults with autism: a multidimensional psychophysical study. *Journal of Autism and Developmental Disorders, 38*(1), 127-137.

Charness, G., Gneezy, U., and Kuhn, M. A. (2012). Experimental methods: Between-subject and within-subject design. *Journal of Economic Behavior & Organization, 81*(1), 1-8.

Cheng, Y., Yang, C. Y., Lin, C. P., Lee, P. L., and Decety, J. (2008). The perception of pain in others suppresses somatosensory oscillations: a magnetoencephalography study. *Neuroimage, 40*(4), 1833-1840.

Chiesa, P. A., Liuzza, M. T., Macaluso, E., and Aglioti, S. M. (2017). Brain activity induced by implicit processing of others' pain and pleasure. *Human Brain Mapping, 38*(11), 5562-5576.

Christov-Moore, L., and Iacoboni, M. (2016). Self-other resonance, its control and prosocial inclinations: Brain–behavior relationships. *Human Brain Mapping, 37*(4), 1544-1558.

Christov-Moore, L., Simpson, E. A., Coudé, G., Grigaityte, K., Iacoboni, M., and Ferrari, P. F. (2014). Empathy: gender effects in brain and behaviour. *Neuroscience and Biobehavioural Reviews, 46*, 604-627.

Coll, M. P. (2018). Meta-analysis of ERP investigations of pain empathy underlines methodological issues in ERP research. *Social Cognitive and Affective Neuroscience, 13*(10), 1003-1017.

Constantino, J. N., and Gruber, C. P. (2012). Social responsiveness scale: SRS-2. Torrance, CA: Western Psychological Services.

Corradi-Dell'Acqua, C., Hofstetter, C., and Vuilleumier, P. (2011). Felt and seen pain evoke the same local patterns of cortical activity in insular and cingulate cortex. *Journal of Neuroscience, 31*(49), 17996-18006.

Costantini, M., and Haggard, P. (2007). The rubber hand illusion: sensitivity and reference frame for body ownership. *Consciousness and Cognition, 16*(2), 229-240.

Craig, A. D. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. *Nature Reviews Neuroscience, 3*(8), 655-666.

Craig, A. D. (2009). How do you feel--now? The anterior insula and human awareness. *Nature Reviews Neuroscience, 10*(1).

Crucianelli, L., Metcalf, N. K., Fotopoulou, A. K., and Jenkinson, P. M. (2013). Bodily pleasure matters: velocity of touch modulates body ownership during the rubber hand illusion. *Frontiers in Psychology, 4*, 703.

Crusco, A. H., and Wetzel, C. G. (1984). The Midas touch: The effects of interpersonal touch on restaurant tipping. *Personality and Social Psychology Bulletin, 10*(4), 512-517.

Cullen, L. A., Barlow, J. H., & Cushway, D. (2005). Positive touch, the implications for parents and their children with autism: an exploratory study. *Complementary Therapies in Clinical Practice, 11*(3), 182-189.

Davis, M. H. (1983). Measuring individual differences in empathy: Evidence for a multidimensional approach. *Journal of Personality and Social Psychology, 44*(1), 113.

de Borst A. W., Sanchez-Vives M. V., Slater M., and de Gelder B. (2020). First-Person Virtual Embodiment Modulates the Cortical Network that Encodes the Bodily Self and Its Surrounding Space during the Experience of Domestic Violence. *eNeuro, 7*(3).

de Haan, E. H., and Dijkerman, H. C. (2020). Somatosensation in the brain: A theoretical reevaluation and a new model. *Trends in Cognitive Sciences, 24*(7), 529-541.

De Houwer, J., and Tibboel, H. (2010). Stop what you are not doing! Emotional pictures interfere with the task not to respond. *Psychonomic Bulletin & Review, 17*(5), 699-703.

De Vignemont, F., and Singer, T. (2006). The empathic brain: how, when and why? *Trends in Cognitive Sciences, 10*(10), 435-441.

de Waal, F. B., and Preston, S. D. (2017). Mammalian empathy: behavioural manifestations and neural basis. *Nature Reviews Neuroscience, 18*(8), 498-509.

Decety J., and Lamm C. (2007). The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. *Neuroscientist, 13*(6), 580–593.

Decety, J. E., and Ickes, W. E. (2009). *The social neuroscience of empathy*. Cambridge, MA: MIT Press.

Decety, J., and Jackson, P. L. (2004). The functional architecture of human empathy. *Behavioral and Cognitive Neuroscience Reviews, 3*(2), 71-100.

Decety, J., Bartal, I. B. A., Uzefovsky, F., and Knafo-Noam, A. (2016). Empathy as a driver of prosocial behaviour: highly conserved neurobehavioural mechanisms across species. *Philosophical Transactions of the Royal Society B: Biological Sciences, 371*(1686), 20150077.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., and Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental Brain Research, 91*(1), 176-180.

Dijkerman, H. C., and De Haan, E. H. (2007). Somatosensory processing subserving perception and action: Dissociations, interactions, and integration. *Behavioral and Brain Sciences, 30*(2), 224-230.

Dorros, S., Hanzal, A., and Segrin, C. (2008). The Big Five personality traits and perceptions of touch to intimate and nonintimate body regions. *Journal of Research in Personality, 42*(4), 1067-1073.

Duan, C. (2000). Being empathic: The role of motivation to empathize and the nature of target emotions. *Motivation and Emotion, 24*(1), 29-49.

Dunbar, R. I. (2010). The social role of touch in humans and primates: behavioural function and neurobiological mechanisms. *Neuroscience & Biobehavioral Reviews, 34*(2), 260-268.

Ebisch, S. J., Ferri, F., Salone, A., Perrucci, M. G., D'Amico, L., Ferro, F. M., ... and Gallese, V. (2011). Differential involvement of somatosensory and interoceptive cortices during the observation of affective touch. *Journal of Cognitive Neuroscience, 23*(7), 1808-1822.

Ebisch, S. J., Perrucci, M. G., Ferretti, A., Del Gratta, C., Romani, G. L., and Gallese, V. (2008). The sense of touch: embodied simulation in a visuotactile mirroring mechanism for observed animate or inanimate touch. *Journal of Cognitive Neuroscience, 20*(9), 1611-1623

Edition, Fifth. (2013). Diagnostic and statistical manual of mental disorders. *American Psychiatric Assocociation*, *21*.

Eisenberg, N. (2006). Prosocial behavior.

Eisenberg, N. (2006, December). Empathy-related responding and prosocial behaviour. In *Novartis Foundation Symposium* (Vol. 278, p. 71). Chichester; New York; John Wiley; 1999.

Eisenberg, N., and Morris, A. S. (2001). The origins and social significance of empathy-related responding. A review of empathy and moral development: implications for caring and justice by ML Hoffman. *Social Justice Research, 14*(1), 95-120.

Erceau, D., and Guéguen, N. (2007). Tactile contact and evaluation of the toucher. *The Journal of Social Psychology, 147*(4), 441-444.

Ernst, J., Northoff, G., Böker, H., Seifritz, E., and Grimm, S. (2013). Interoceptive awareness enhances neural activity during empathy. *Human Brain Mapping, 34*(7), 1615-1624.

Fabi, S., and Leuthold, H. (2017). Empathy for pain influences perceptual and motor processing: Evidence from response force, ERPs, and EEG oscillations. *Social Neuroscience, 12*(6), 701-716.

Fan, Y., and Han, S. (2008). Temporal dynamic of neural mechanisms involved in empathy for pain: an event-related brain potential study. *Neuropsychologia, 46*(1), 160-173.

Fan, Y., Duncan, N. W., de Greck, M., and Northoff, G. (2011). Is there a core neural network in empathy? An fMRI based quantitative meta-analysis. *Neuroscience and Biobehavioural Reviews, 35*(3), 903-911.

Fareri, D. S., and Delgado, M. R. (2014). Social rewards and social networks in the human brain. The *Neuroscientist, 20*(4), 387-402.

Feldman, R., Singer, M., and Zagoory, O. (2010). Touch attenuates infants' physiological reactivity to stress. *Developmental Science, 13*(2), 271-278.

Fini, C., Fischer, M., Bardi, L., Brass, M., and Moors, A. (2020). Support from a TMS/MEP study for a direct link between positive/negative stimuli and approach/avoidance tendencies. *Neuropsychologia, 143*, 107496.

Fisher, J. D., Rytting, M., and Heslin, R. (1976). Hands touching hands: Affective and evaluative effects of an interpersonal touch. *Sociometry*, 416-421.

Foss-Feig, J. H., Heacock, J. L., and Cascio, C. J. (2012). Tactile responsiveness patterns and their association with core features in autism spectrum disorders. *Research in Autism Spectrum Disorders, 6*(1), 337-344.

Fox, N. A., Bakermans-Kranenburg, M. J., Yoo, K. H., Bowman, L. C., Cannon, E. N., Vanderwert, R. E., ... and Van IJzendoorn, M. H. (2016). Assessing human mirror activity with EEG mu rhythm: A meta-analysis. *Psychological Bulletin, 142*(3), 291.

Fukushima, H., Terasawa, Y., and Umeda, S. (2011). Association between interoception and empathy: evidence from heartbeat-evoked brain potential. *International Journal of Psychophysiology, 79*(2), 259-265.

Fusaro M., Tieri G., and Aglioti S. M. (2016). Seeing pain and pleasure on self and others: behavioural and psychophysiological reactivity in immersive virtual reality. *Journal of Neurophysiology, 116*(6), 2656–2662.

Fusaro M., Tieri G., and Aglioti S. M. (2019). Influence of cognitive stance and physical perspective on subjective and autonomic reactivity to observed pain and pleasure: an immersive virtual reality study. *Consciousness and Cognition, 67*, 86–97.

Fusaro, M., Lisi, M. P., Tieri, G., and Aglioti, S. M. (2021). Heterosexual, gay, and lesbian people's reactivity to virtual caresses on their embodied avatars' taboo zones. *Scientific Reports, 11*(1), 1-12.

Fusco G., Tieri G., and Aglioti S. M. (2020). Visual feedback from a virtual body modulates motor illusion induced by tendon vibration. *Psychological Research*, 1–13.

Gaigg, S. B., Cornell, A. S., & Bird, G. (2018). The psychophysiological mechanisms of alexithymia in autism spectrum disorder. *Autism, 22*(2), 227-231.

Galang, C. M., Naish, K. R., Arbabi, K., and Obhi, S. S. (2017). Observing painful events in others leads to a temporally extended general response facilitation in the self. *Experimental Brain Research, 235*(11), 3469-3477.

Galang, C. M., Pichtikova, M., Sanders, T., and Obhi, S. S. (2021). Investigating the effects of pain observation on approach and withdrawal actions. *Experimental Brain Research, 239*(3), 847-856.

Gallace A., and Spence C. (2010). The science of interpersonal touch: an overview. *Neuroscience and Biobehavioural Reviews, 34*(2), 246–259.

Gallagher, S. (2006). *How the body shapes the mind*. Clarendon Press.

Gallese, V. (2005). Embodied simulation: From neurons to phenomenal experience. *Phenomenology and the Cognitive Sciences, 4*(1), 23-48.

Gallese, V., and Ebisch, S. (2013). Embodied simulation and touch: The sense of touch in social cognition. *Phenomenology and Mind*, (4), 196-210.

Gallese, V., and Sinigaglia, C. (2011). What is so special about embodied simulation? *Trends in Cognitive Sciences, 15*(11), 512-519.

Gallese, V., Keysers, C., and Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences, 8*(9), 396-403.

Gallo, S., Paracampo, R., Müller-Pinzler, L., Severo, M. C., Blömer, L., Fernandes-Henriques, C., ... and Gazzola, V. (2018). The causal role of the somatosensory cortex in prosocial behaviour. *Elife, 7*, e32740.

Gladney, K., and Barker, L. (1979). The effects of tactile history on attitudes toward and frequency of touching behavior. *Sign Language Studies, 24*(1), 231-252.

Glick P., and Fiske S. T. (1996). The ambivalent sexism inventory: differentiating hostile and benevolent sexism. *Journal of Personality and Social Psychology, 70*(3), 491.

Gliga, T., Farroni, T., and Cascio, C. J. (2019). Social touch: A new vista for developmental cognitive neuroscience? *Developmental Cognitive Neuroscience, 35*, 1.

Goldman, A., and de Vignemont, F. (2009). Is social cognition embodied? *Trends in Cognitive Sciences, 13*(4), 154-159.

Gordon, I., Voos, A. C., Bennett, R. H., Bolling, D. Z., Pelphrey, K. A., and Kaiser, M. D. (2013). Brain mechanisms for processing affective touch. *Human Brain Mapping, 34*(4), 914-922.

Greene, R. K., Damiano-Goodwin, C. R., Walsh, E., Bizzell, J., & Dichter, G. S. (2020). Neural Mechanisms of Vicarious Reward Processing in Adults with Autism Spectrum Disorder. *Autism Research and Treatment*, 2020.

Greenwald A. G., McGhee D. E., and Schwartz J. L. (1998). Measuring individual differences in implicit cognition: the implicit association test. *Journal of Personality and Social Psychology, 74*(6), 1464.

Gross, J., Schnitzler, A., Timmermann, L., and Ploner, M. (2007). Gamma oscillations in human primary somatosensory cortex reflect pain perception. *PloS Biology, 5*(5).

Grynberg, D., & Pollatos, O. (2015). Perceiving one's body shapes empathy. *Physiology & behavior, 140*, 54-60.

Grynberg, D., and López-Pérez, B. (2018). Facing others' misfortune: Personal distress mediates the association between maladaptive emotion regulation and social avoidance. *PLoS One, 13*(3), e0194248.

Guéguen, N. (2004). Nonverbal encouragement of participation in a course: The effect of touching. *Social Psychology of Education, 7*(1), 89-98.

Guéguen, N., and Fischer-Lokou, J. (2003). Another evaluation of touch and helping behavior. *Psychological Reports, 92*(1), 62-64.

Haber, S. N., and Knutson, B. (2010). The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology, 35*(1), 4-26.

Haggarty, C. J., Malinowski, P., McGlone, F. P., and Walker, S. C. (2020). Autistic traits modulate cortical responses to affective but not discriminative touch. *European Journal of Neuroscience, 51*(8), 1844-1855.

Han, X., He, K., Wu, B., Shi, Z., Liu, Y., Luo, S., ... and Han, S. (2017). Empathy for pain motivates actions without altruistic effects: evidence of motor dynamics and brain activity. *Social Cognitive and Affective Neuroscience, 12*(6), 893-901.

Hertenstein, M. J., Holmes, R., McCullough, M., and Keltner, D. (2009). The communication of emotion via touch. *Emotion, 9*(4), 566.

Hertenstein, M. J., Keltner, D., App, B., Bulleit, B. A., and Jaskolka, A. R. (2006). Touch communicates distinct emotions. *Emotion, 6*(3), 528.

Hillis, A. E. (2014). Inability to empathize: brain lesions that disrupt sharing and understanding another's emotions. *Brain, 137*(4), 981-997.

Hilton, C. L., Harper, J. D., Kueker, R. H., Lang, A. R., Abbacchi, A. M., Todorov, A., and LaVesser, P. D. (2010). Sensory responsiveness as a predictor of social severity in children with high functioning autism spectrum disorders. *Journal of Autism and Developmental Disorders, 40*(8), 937-945.

Iannetti, G. D., and Mouraux, A. (2010). From the neuromatrix to the pain matrix (and back). *Experimental Brain Research, 205*(1), 1-12.

Ioumpa, K., Graham, S. A., Clausner, T., Fisher, S. E., Van Lier, R., and Van Leeuwen, T. M. (2019). Enhanced self-reported affect and prosocial behaviour without differential physiological responses in mirror-sensory synaesthesia. *Philosophical Transactions of the Royal Society B, 374*(1787), 20190395.

Jabbi, M., Bastiaansen, J., and Keysers, C. (2008). A common anterior insula representation of disgust observation, experience and imagination shows divergent functional connectivity pathways. *PloS One, 3*(8).

Jabbi, M., Swart, M., and Keysers, C. (2007). Empathy for positive and negative emotions in the gustatory cortex. *Neuroimage, 34*(4), 1744-1753.

Jablonski, N. G. (2021). Social and affective touch in primates and its role in the evolution of social cohesion. *Neuroscience, 464*, 117-125.

Jackson, P. L., Meltzoff, A. N., and Decety, J. (2005). How do we perceive the pain of others? A window into the neural processes involved in empathy. *Neuroimage, 24*(3), 771-779.

Joule, R. V., and Guéguen, N. (2007). Touch, compliance, and awareness of tactile contact. *Perceptual and Motor Skills, 104*(2), 581-588.

Kadlaskar, G., Seidl, A., Tager-Flusberg, H., Nelson, C. A., and Keehn, B. (2019). Atypical response to caregiver touch in infants at high risk for autism spectrum disorder. *Journal of Autism and Developmental Disorders, 49*(7), 2946-2955.

Kaiser, M. D., Yang, D. Y. J., Voos, A. C., Bennett, R. H., Gordon, I., Pretzsch, C., ... and Pelphrey, K. A. (2016). Brain mechanisms for processing affective (and nonaffective) touch are atypical in autism. *Cerebral Cortex, 26*(6), 2705-2714.

Kandel, E. R., Koester, J. D., Mack, S. H., and Siegelbaum, S. A. (Eds.). (2021). *Principles of neural science*. New York: McGraw-Hill.

Keenaghan, S., Bowles, L., Crawfurd, G., Thurlbeck, S., Kentridge, R. W., and Cowie, D. (2020). My body until proven otherwise: Exploring the time course of the full body illusion. *Consciousness and Cognition, 78*, 102882.

Kennett, S., Taylor-Clarke, M., and Haggard, P. (2001). Noninformative vision improves the spatial resolution of touch in humans. *Current Biology, 11*(15), 1188-1191.

Keysers, C., an Gazzola, V. (2009). Expanding the mirror: vicarious activity for actions, emotions, and sensations. *Current Opinion in Neurobiology, 19*(6), 666-671.

Keysers, C., and Gazzola, V. (2006). Towards a unifying neural theory of social cognition. *Progress in Brain Research, 156*, 379-401.

Keysers, C., Kaas, J. H., and Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience, 11*(6), 417-428.

Kilteni K., Maselli A., Kording K. P., and Slater M. (2015). Over my fake body: body ownership illusions for studying the multisensory basis of own-body perception. Frontiers in Human Neuroscience, 9, 141.

Kilteni, K., Normand, J. M., Sanchez-Vives, M. V., and Slater, M. (2012). Extending body space in immersive virtual reality: a very long arm illusion. *PloS One, 7*(7), e40867.

Kinnaird, E., Stewart, C., & Tchanturia, K. (2019). Investigating alexithymia in autism: a systematic review and meta-analysis. *European Psychiatry, 55*, 80-89.

Kinsey A. C., Pomeroy W. R., and Martin C. E. (2003). Sexual behaviour in the human male. *American Journal of Public Health, 93* (6), 894–898.

Kirsch, L. P., Krahé, C., Blom, N., Crucianelli, L., Moro, V., Jenkinson, P. M., and Fotopoulou, A. (2018). Reading the mind in the touch: Neurophysiological specificity in the communication of emotions by touch. *Neuropsychologia, 116*, 136-149.

Klimecki, O. M., Mayer, S. V., Jusyte, A., Scheeff, J., and Schönenberg, M. (2016). Empathy promotes altruistic behavior in economic interactions. *Scientific Reports, 6*(1), 1-5.

Körner, A., Topolinski, S., and Strack, F. (2015). Routes to embodiment. *Frontiers in Psychology, 6*, 940.

Kurosaki M., Shirao N., Yamashita H., Okamoto Y., and Yamawaki S. (2006). Distorted images of one's own body activates the prefrontal cortex and limbic/paralimbic system in young women: a functional magnetic resonance imaging study. *Biological Psychiatry, 59*(4), 380–386.

Lamm, C., Decety, J., and Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *Neuroimage, 54*(3), 2492-2502.

Lamm, C., Silani, G., and Singer, T. (2015). Distinct neural networks underlying empathy for pleasant and unpleasant touch. *Cortex, 70*, 79-89.

Legrain, V., Iannetti, G. D., Plaghki, L., and Mouraux, A. (2011). The pain matrix reloaded: a salience detection system for the body. *Progress in Neurobiology, 93*(1), 111-124.

Lenth R. V. (2017). Using lsmeans. *Journal of Statistical Software, 69*, 1–33.

Lenth R. V. (2020). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.2-1. https://CRAN.R-project.org/package=emmeans.

Liebowitz, M. R. (1987). Social phobia. *Modern Problems of Pharmacopsychiatry.*

Light, S. N., Moran, Z. D., Swander, L., Le, V., Cage, B., Burghy, C., ... and Davidson, R. J. (2015). Electromyographically assessed empathic concern and empathic happiness predict increased prosocial behaviour in adults. *Biological Psychology, 104*, 116-129.

Lipps, T. (1903). Einfühlung, innere nachahmung und organenempfindungen.

Lo, S., and Andrews, S. (2015). To transform or not to transform: Using generalized linear mixed models to analyse reaction time data. *Frontiers in Psychology, 6*, 1171.

Löken L. S., Wessberg J., McGlone F., and Olausson H. (2009). Coding of pleasant touch by unmyelinated afferents in humans. *Nature Neuroscience, 12*(5), 547.

Maister, L., Slater, M., Sanchez-Vives, M. V., and Tsakiris, M. (2015). Changing bodies changes minds: owning another body affects social cognition. *Trends in Cognitive Sciences, 19*(1), 6-12.

Major, B., Schmidlin, A. M., and Williams, L. (1990). Gender patterns in social touch: The impact of setting and age. *Journal of Personality and Social Psychology, 58*(4), 634.

Manganelli Rattazzi A. M., Volpato C., and Canova L. (2008). L'atteggiamento ambivalente verso donne e uomini. Un contributo alla validazione delle scale ASI e AMI. *Giornale Italiano di Psicologia, 35*(1), 217–246.

Martinie, M. A., Olive, T., and Milland, L. (2010). Cognitive dissonance induced by writing a counterattitudinal essay facilitates performance on simple tasks but not on complex tasks that involve working memory. *Journal of Experimental Social Psychology, 46*(4), 587-594.

Maselli, A., and Slater, M. (2013). The building blocks of the full body ownership illusion. *Frontiers in Human Neuroscience, 7*, 83.

Masson, H. L., Pillet, I., Amelynck, S., Van De Plas, S., Hendriks, M., Op de Beeck, H., and Boets, B. (2019). Intact neural representations of affective meaning of touch but lack of embodied resonance in autism: a multi-voxel pattern analysis study. *Molecular Autism, 10*(1), 1-14.

Masten, C. L., Morelli, S. A., and Eisenberger, N. I. (2011). An fMRI investigation of empathy for 'social pain'and subsequent prosocial behaviour. *Neuroimage, 55*(1), 381-388.

McGlone, F., Vallbo, A. B., Olausson, H., Loken, L., and Wessberg, J. (2007). Discriminative touch and emotional touch. *Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale, 61*(3), 173.

McGlone, F., Wessberg, J., and Olausson, H. (2014). Discriminative and affective touch: sensing and feeling. *Neuron, 82*(4), 737-755.

Mehling, W. E., Acree, M., Stewart, A., Silas, J., and Jones, A. (2018). The multidimensional assessment of interoceptive awareness, version 2 (MAIA-2). *PloS One, 13*(12), e0208034.

Mello, M., Fusaro, M., Tieri, G., and Aglioti S. M. (2022). Wearing same- and opposite-sex virtual bodies and seeing them caressed in intimate areas. *Quarterly Journal of Experimental Psychology, 75*(3).

Menon, V., and Uddin, L. Q. (2010). Saliency, switching, attention and control: a network model of insula function. *Brain Structure and Function, 214*(5-6), 655-667.

Meyer, M. L., Masten, C. L., Ma, Y., Wang, C., Shi, Z., Eisenberger, N. I., and Han, S. (2013). Empathy for the social suffering of friends and strangers recruits distinct patterns of brain activation. *Social cognitive and Affective Neuroscience, 8*(4), 446-454.

Mikkelsen, M., Wodka, E. L., Mostofsky, S. H., and Puts, N. A. (2018). Autism spectrum disorder in the scope of tactile processing. *Developmental Cognitive Neuroscience, 29*, 140-150.

Mobbs, D., Yu, R., Meyer, M., Passamonti, L., Seymour, B., Calder, A. J., ... and Dalgleish, T. (2009). A key role for similarity in vicarious reward. *Science, 324*(5929), 900-900.

Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., and Grafman, J. (2006). Human fronto–mesolimbic networks guide decisions about charitable donation. *Proceedings of the National Academy of Sciences (PNAS), 103*(42), 15623-15628.

Moll, J., Zahn, R., de Oliveira-Souza, R., Bramati, I. E., Krueger, F., Tura, B., ... and Grafman, J. (2011). Impairment of prosocial sentiments is associated with frontopolar and septal damage in frontotemporal dementia. *Neuroimage, 54*(2), 1735-1742.

Monti A., and Aglioti S. M. (2018). Flesh and bone digital sociality: On how humans may go virtual. *British Journal of Psychology, 109*(3), 418-420.

Monti A., Porciello G., Tieri G., and Aglioti S. M. (2020). The “embreathment” illusion highlights the role of breathing in corporeal awareness. *Journal of Neurophysiology, 123*(1), 420–427.

Morelli, S. A., Knutson, B., and Zaki, J. (2018). Neural sensitivity to personal and vicarious reward differentially relate to prosociality and well-being. *Social Cognitive and Affective Neuroscience, 13*(8), 831-839.

Morelli, S. A., Lieberman, M. D., and Zaki, J. (2015). The emerging study of positive empathy. *Social and Personality Psychology Compass, 9*(2), 57-68.

Morelli, S. A., Rameson, L. T., and Lieberman, M. D. (2014). The neural components of empathy: predicting daily prosocial behaviour. *Social Cognitive and Affective Neuroscience, 9*(1), 39-47.

Morelli, S. A., Sacchet, M. D., and Zaki, J. (2015). Common and distinct neural correlates of personal and vicarious reward: A quantitative meta-analysis. *NeuroImage, 112*, 244-253.

Moro, V., Pernigo, S., Tsakiris, M., Avesani, R., Edelstyn, N. M., Jenkinson, P. M., and Fotopoulou, A. (2016). Motor versus body awareness: voxel-based lesion analysis in anosognosia for hemiplegia and somatoparaphrenia following right hemisphere stroke. *Cortex, 83*, 62-77.

Morrison I., Björnsdotter M., and Olausson, H. (2011). Vicarious responses to social touch in posterior insular cortex are tuned to pleasant caressing speeds. *Journal of Neuroscience, 31*(26), 9554–9562.

Morrison I., Löken L. S., and Olausson H. (2010). The skin as a social organ. *Experimental Brain Research, 204*(3), 305–314.

Morrison, I., and Downing, P. E. (2007). Organization of felt and seen pain responses in anterior cingulate cortex. *Neuroimage, 37*(2), 642-651.

Morrison, I., Lloyd, D., Di Pellegrino, G., and Roberts, N. (2004). Vicarious responses to pain in anterior cingulate cortex: is empathy a multisensory issue?. *Cognitive, Affective, and Behavioural Neuroscience, 4*(2), 270-278.

Morrison, I., Peelen, M. V., and Downing, P. E. (2007a). The sight of others' pain modulates motor processing in human cingulate cortex. *Cerebral Cortex, 17*(9), 2214-2222.

Morrison, I., Poliakoff, E., Gordon, L., and Downing, P. (2007b). Response-specific effects of pain observation on motor behavior. *Cognition, 104*(2), 407-416.

Mountcastle, V. B. (2005). *The sensory hand: neural mechanisms of somatic sensation.* Harvard University Press.

Neyret, S., Navarro, X., Beacco, A., Oliva, R., Bourdin, P., Valenzuela, J., ... and Slater, M. (2020). An embodied perspective as a victim of sexual harassment in virtual reality reduces action conformity in a later Milgram obedience scenario. *Scientific Reports, 10*(1), 1-18.

Nilsen, W. J., and Vrana, S. R. (1998). Some touching situations: The relationship between gender and contextual variables in cardiovascular responses to human touch. *Annals of Behavioral Medicine, 20*(4), 270-276.

Nummenmaa, L., Suvilehto, J. T., Glerean, E., Santtila, P., and Hietanen, J. K. (2016). Topography of human erogenous zones. *Archives of Sexual Behavior, 45*(5), 1207-1216.

Olausson, H., Wessberg, J., McGlone, F., & Vallbo, Å. (2010). The neurophysiology of unmyelinated tactile afferents. *Neuroscience & Biobehavioral Reviews, 34*(2), 185-191.

Otti, A., Guendel, H., Läer, L., Wohlschlaeger, A. M., Lane, R. D., Decety, J., ... and Noll-Hussong, M. (2010). I know the pain you feel—how the human brain's default mode predicts our resonance to another's suffering. *Neuroscience, 169*(1), 143-148.

Parsons, T. D. (2015). Virtual reality for enhanced ecological validity and experimental control in the clinical, affective and social neurosciences. *Frontiers in Human Neuroscience, 9*, 660.

Pavone, E. F., Tieri, G., Rizza, G., Tidoni, E., Grisoni, L., and Aglioti, S. M. (2016). Embodying others in immersive virtual reality: electro-cortical signatures of monitoring the errors in the actions of an avatar seen from a first-person perspective. *Journal of Neuroscience, 36*(2), 268-279.

Payne, B. K., Cheng, C. M., Govorun, O., and Stewart, B. D. (2005). An inkblot for attitudes: affect misattribution as implicit measurement. *Journal of Personality and Social Psychology, 89*(3), 277.

Peck T. C., Doan M., Bourne K. A., and Good J. J. (2018). The effect of gender body-swap illusions on working memory and stereotype threat. *IEEE Transactions on Visualization and Computer Graphics, 24*(4), 1604–1612.

Peck T. C., Good J. J., and Bourne K. A. (2020). Inducing and mitigating stereotype threat through gendered virtual body-swap illusions. *Proceedings of the 2020 CHI Conference on Human Factors in Computing Systems*, Honolulu, HI, USA.

Peck T. C., Seinfeld S., Aglioti S. M., and Slater M. (2013). Putting yourself in the skin of a black avatar reduces implicit racial bias. *Consciousness and Cognition, 22*(3), 779–787.

Peled-Avron, L., & Woolley, J. D. (2022). Understanding others through observed touch: neural correlates, developmental aspects, and psychopathology. *Current Opinion in Behavioral Sciences, 43*, 152-158.

Peled-Avron, L., and Shamay-Tsoory, S. G. (2017). Don't touch me! autistic traits modulate early and late ERP components during visual perception of social touch. *Autism Research, 10*(6), 1141-1154.

Peled-Avron, L., Glasner, L., Gvirts, H. Z., and Shamay-Tsoory, S. G. (2019). The role of the inferior frontal gyrus in vicarious social touch: A transcranial direct current stimulation (tDCS) study. *Developmental Cognitive Neuroscience, 35*, 115-121.

Peled-Avron, L., Goldstein, P., Yellinek, S., Weissman-Fogel, I., and Shamay-Tsoory, S. G. (2018). Empathy during consoling touch is modulated by mu-rhythm: An EEG study. *Neuropsychologia, 116*, 68-74.

Peled-Avron, L., Levy-Gigi, E., Richter-Levin, G., Korem, N., and Shamay-Tsoory, S. G. (2016). The role of empathy in the neural responses to observed human social touch. *Cognitive, Affective, & Behavioral Neuroscience, 16*(5), 802-813.

Penfield, W., and Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain, 60*(4), 389-443.

Petkova V. I., and Ehrsson H. H. (2008). If I were you: perceptual illusion of body swapping. *PloS One, 3*(12), e3832.

Pihko, E., Nangini, C., Jousmäki, V., and Hari, R. (2010). Observing touch activates human primary somatosensory cortex. *European Journal of Neuroscience, 31*(10), 1836-1843.

Pisoni, A., Lauro, L. J. R., Vergallito, A., Maddaluno, O., and Bolognini, N. (2018). Cortical dynamics underpinning the self-other distinction of touch: A TMS-EEG study. *NeuroImage, 178*, 475-484.

Poquérusse, J., Pastore, L., Dellantonio, S., & Esposito, G. (2018). Alexithymia and autism spectrum disorder: a complex relationship. *Frontiers in Psychology, 9*, 1196.

Prehn-Kristensen, A., Wiesner, C., Bergmann, T. O., Wolff, S., Jansen, O., Mehdorn, H. M., ... and Pause, B. M. (2009). Induction of empathy by the smell of anxiety. *PloS One, 4*(6).

Preston, C., and Ehrsson, H. H. (2014). Illusory changes in body size modulate body satisfaction in a way that is related to non-clinical eating disorder psychopathology. *PloS One, 9*(1), e85773.

Preston, S. D., and De Waal, F. B. (2002). Empathy: Its ultimate and proximate bases. *Behavioural and Brain Sciences, 25*(1), 1-20.

Prochazkova, E., and Kret, M. E. (2017). Connecting minds and sharing emotions through mimicry: A neurocognitive model of emotional contagion. *Neuroscience and Biobehavioural Reviews, 80*, 99-114.

Provenzano, L., Porciello, G., Ciccarone, S., Lenggenhager, B., Tieri, G., Marucci, M., ... and Bufalari, I. (2020). Characterizing body image distortion and bodily self-plasticity in anorexia nervosa via visuo-tactile stimulation in virtual reality. *Journal of Clinical Medicine, 9*(1), 98.

Pyasik, M., Tieri, G., and Pia, L. (2020). Visual appearance of the virtual hand affects embodiment in the virtual hand illusion. *Scientific Reports, 10*(1), 1-11.

R Core Team (2021). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Riečanský, I., and Lamm, C. (2019). The role of sensorimotor processes in pain empathy. *Brain Topography*, 1-12.

Riečanský, I., Paul, N., Kölble, S., Stieger, S., and Lamm, C. (2015). Beta oscillations reveal ethnicity ingroup bias in sensorimotor resonance to pain of others. *Social Cognitive and Affective Neuroscience, 10*(7), 893-901.

Rudman L. A., Greenwald A. G., and McGhee D. E. (2001). Implicit self-concept and evaluative implicit gender stereotypes: self and ingroup share desirable traits. Personality and Social Psychology Bulletin, 27(9), 1164–1178.

Russo V., Ottaviani C., and Spitoni G. F. (2019). Affective touch: a meta-analysis on sex differences. *Neuroscience and Biobehavioural Reviews, 108*, 445–452.

Saarinen, A., Harjunen, V., Jasinskaja-Lahti, I., Jääskeläinen, I. P., and Ravaja, N. (2021). Social touch experience in different contexts: A review. *Neuroscience & Biobehavioral Reviews, 131*, 360-372.

Sanchez-Vives M. V., Spanlang B., Frisoli A., Bergamasco M., and Slater M. (2010). Virtual hand illusion induced by visuomotor correlations. *PLoS One, 5*(4), e10381.

Sanchez-Vives, M. V., and Slater, M. (2005). From presence to consciousness through virtual reality. *Nature Reviews Neuroscience, 6*(4), 332-339.

Schaefer, M., Heinze, H. J., and Rotte, M. (2012). Embodied empathy for tactile events: interindividual differences and vicarious somatosensory responses during touch observation. *Neuroimage, 60*(2), 952-957.

Scheele, D., Kendrick, K. M., Khouri, C., Kretzer, E., Schläpfer, T. E., Stoffel-Wagner, B., ... and Hurlemann, R. (2014). An oxytocin-induced facilitation of neural and emotional responses to social touch correlates inversely with autism traits. *Neuropsychopharmacology, 39*(9), 2078-2085.

Schirmer, A., and McGlone, F. (2019). A touching sight: EEG/ERP correlates for the vicarious processing of affectionate touch. *Cortex, 111*, 1-15.

Schirmer, A., Reece, C., Zhao, C., Ng, E., Wu, E., and Yen, S. C. (2015). Reach out to one and you reach out to many: Social touch affects third-party observers. *British Journal of Psychology, 106*(1), 107-132.

Seinfeld, S., Arroyo-Palacios, J., Iruretagoyena, G., Hortensius, R., Zapata, L. E., Borland, D., ... and Sanchez-Vives, M. V. (2018). Offenders become the victim in virtual reality: impact of changing perspective in domestic violence. *Scientific Reports, 8*(1), 1-11.S.

Serino, A., & Haggard, P. (2010). Touch and the body. *Neuroscience & Biobehavioral Reviews, 34*(2), 224-236.

Serino, A., Farnè, A., Rinaldesi, M. L., Haggard, P., and Làdavas, E. (2007). Can vision of the body ameliorate impaired somatosensory function? *Neuropsychologia, 45*(5), 1101-1107.

Shamay-Tsoory, S. G., Aharon-Peretz, J., and Perry, D. (2009). Two systems for empathy: a double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. *Brain, 132*(3), 617-627.

Shapiro, L. A. (Ed.). (2014). *The Routledge handbook of embodied cognition*.

Shu, J., Hassell, S., Weber, J., Ochsner, K. N., and Mobbs, D. (2017). The role of empathy in experiencing vicarious anxiety. *Journal of Experimental Psychology: General, 146*(8), 1164.

Singer, T., and Klimecki, O. M. (2014). Empathy and compassion. Current Biology, 24(18), R875-R878.

Singer, T., and Lamm, C. (2009). The social neuroscience of empathy. *Annals of the New York Academy of Sciences, 1156*(1), 81-96.

Singer, T., Critchley, H. D., and Preuschoff, K. (2009). A common role of insula in feelings, empathy and uncertainty. *Trends in Cognitive Sciences, 13*(8), 334-340.

Singer, T., Seymour, B., O'Doherty, J. P., Stephan, K. E., Dolan, R. J., and Frith, C. D. (2006). Empathic neural responses are modulated by the perceived fairness of others. *Nature, 439*(7075), 466-469.

Singer, T., Seymour, B., O'doherty, J., Kaube, H., Dolan, R. J., and Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science, 303*(5661), 1157-1162.

Slater M., and Sanchez-Vives M. V. (2014). Transcending the self in immersive virtual reality. *Computer, 47*(7), 24–30.

Slater M., Spanlang B., Sanchez-Vives M. V., and Blanke O. (2010). First person experience of body transfer in virtual reality. *PloS One, 5*(5).

Smith, K. D., Keating, J. P., and Stotland, E. (1989). Altruism reconsidered: The effect of denying feedback on a victim's status to empathic witnesses. *Journal of Personality and Social Psychology, 57*(4), 641.

Spain, D., Sin, J., Linder, K. B., McMahon, J., & Happé, F. (2018). Social anxiety in autism spectrum disorder: A systematic review. *Research in Autism Spectrum Disorders, 52*, 51-68.

Stier D. S., and Hall J. A. (1984). Gender differences in touch: an empirical and theoretical review. *Journal of Personality and Social Psychology, 47*(2), 440.

Suvilehto, J. T., Glerean, E., Dunbar, R. I., Hari, R., and Nummenmaa, L. (2015). Topography of social touching depends on emotional bonds between humans. *Proceedings of the National Academy of Sciences, 112*(45), 13811-13816.

Tacikowski P., Fust J., and Ehrsson H. H. (2020). Fluidity of gender identity induced by illusory body-sex change. *Scientific Reports, 10*, 14385.

Telle, N. T., and Pfister, H. R. (2016). Positive empathy and prosocial behaviour: A neglected link. *Emotion Review, 8*(2), 154-163.

Tesio, V., Goerlich, K. S., Hosoi, M., and Castelli, L. (2019). Alexithymia: State of the Art and Controversies. Clinical and Neuroscientific Evidence. *Frontiers in Psychology, 10*, 1209.

Titchener, E. B. (1909). *Lectures on the experimental psychology of the thought-processes*. Macmillan.

Triscoli, C., Croy, I., Steudte-Schmiedgen, S., Olausson, H., and Sailer, U. (2017). Heart rate variability is enhanced by long-lasting pleasant touch at CT-optimized velocity. *Biological Psychology, 128*, 71-81.

Tsakiris, M., and Haggard, P. (2005). The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance, 31*(1), 80.

Tsuchiya, N., and Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience, 8*(8), 1096-1101.

Tusche, A., Böckler, A., Kanske, P., Trautwein, F. M., and Singer, T. (2016). Decoding the charitable brain: empathy, perspective taking, and attention shifts differentially predict altruistic giving. *Journal of Neuroscience, 36(*17), 4719-4732.

Ujiie, Y., and Takahashi, K. (2022). Associations between self-reported social touch avoidance, hypersensitivity, and autistic traits: Results from questionnaire research among typically developing adults. *Personality and Individual Differences, 184*, 111186.

Valentini, E., Betti, V., Hu, L., and Aglioti, S. M. (2013). Hypnotic modulation of pain perception and of brain activity triggered by nociceptive laser stimuli. *Cortex, 49*(2), 446-462.

Valeriani, M., Betti, V., Le Pera, D., De Armas, L., Miliucci, R., Restuccia, D., ... and Aglioti, S. M. (2008). Seeing the pain of others while being in pain: a laser-evoked potentials study. *Neuroimage, 40*(3), 1419-1428.

Vallar G., and Ronchi R. (2009). Somatoparaphrenia: a body delusion. A review of the neuropsychological literature. *Experimental Brain Research, 192*(3), 533–551.

Vallbo, Å. B., Olausson, H., and Wessberg, J. (1999). Unmyelinated afferents constitute a second system coding tactile stimuli of the human hairy skin. *Journal of Neurophysiology, 81*(6), 2753-2763.

Van Der Hoort, B., Guterstam, A., and Ehrsson, H. H. (2011). Being Barbie: the size of one's own body determines the perceived size of the world. *PloS One, 6*(5), e20195.

van Stralen, H. E., van Zandvoort, M. J., Hoppenbrouwers, S. S., Vissers, L. M., Kappelle, L. J., & Dijkerman, H. C. (2014). Affective touch modulates the rubber hand illusion. *Cognition, 131*(1), 147-158.

Varela, F., Lachaux, J. P., Rodriguez, E., and Martinerie, J. (2001). The brainweb: phase synchronization and large-scale integration. *Nature Reviews Neuroscience, 2*(4), 229-239.

Verkuilen, J., & Smithson, M. (2012). Mixed and mixture regression models for continuous bounded responses using the beta distribution. *Journal of Educational and Behavioral Statistics, 37*(1), 82-113.

von Mohr, M., Kirsch, L. P., and Fotopoulou, A. (2017). The soothing function of touch: affective touch reduces feelings of social exclusion. *Scientific Reports, 7*(1), 1-9.

Voos, A. C., Pelphrey, K. A., and Kaiser, M. D. (2013). Autistic traits are associated with diminished neural response to affective touch. *Social Cognitive and Affective Neuroscience, 8*(4), 378-386.

Vrana, S. R., and Rollock, D. (1998). Physiological response to a minimal social encounter: Effects of gender, ethnicity, and social context. *Psychophysiology, 35*(4), 462-469.

Walker S. C., Trotter P. D., Woods A., and McGlone F. (2017). Vicarious ratings of social touch reflect the anatomical distribution and velocity tuning of C-tactile afferents: a hedonic homunculus? *Behavioural Brain Research, 320*, 91–96.

Wang H., Callaghan E., Gooding-Williams G., McAllister C., and Kessler K. (2016). Rhythm makes the world go round: an MEG-TMS study on the role of right TPJ theta oscillations in embodied perspective taking. *Cortex, 75*, 68–81 (2016).

Warriner, A. B., Shore, D. I., Schmidt, L. A., Imbault, C. L., and Kuperman, V. (2017). Sliding into happiness: A new tool for measuring affective responses to words. *Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale, 71*(1), 71.

Weisz, E., and Zaki, J. (2018). Motivated empathy: a social neuroscience perspective. *Current Opinion in Psychology, 24*, 67-71.

Wheelwright, S., Auyeung, B., Allison, C., and Baron-Cohen, S. (2010). Defining the broader, medium and narrow autism phenotype among parents using the Autism Spectrum Quotient (AQ). Molecular Autism, 1(1), 1-9.

Wicker, B., Keysers, C., Plailly, J., Royet, J. P., Gallese, V., and Rizzolatti, G. (2003). Both of us disgusted in My insula: the common neural basis of seeing and feeling disgust. *Neuron, 40*(3), 655-664.

Wilhelm, F. H., Kochar, A. S., Roth, W. T., and Gross, J. J. (2001). Social anxiety and response to touch: incongruence between self-evaluative and physiological reactions. *Biological Psychology, 58*(3), 181-202.

Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin & Review, 9*(4), 625-636.

Wood, R., Gallese, V., and Cattaneo, L. (2010). Visuotactile empathy within the primary somatosensory cortex revealed by short-latency afferent inhibition. *Neuroscience Letters, 473*(1), 28-31.

Zaki, J., and Ochsner, K. (2009). The need for a cognitive neuroscience of naturalistic social cognition. *Annals of the New York Academy of Sciences, 1167*, 16.

Zaki, J., and Ochsner, K. N. (2012). The neuroscience of empathy: progress, pitfalls and promise. *Nature Neuroscience, 15*(5), 675-680.

Zaki, J., Ochsner, K. N., Hanelin, J., Wager, T. D., and Mackey, S. C. (2007). Different circuits for different pain: patterns of functional connectivity reveal distinct networks for processing pain in self and others. *Social Neuroscience, 2*(3-4), 276-291.

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List of papers constituting this thesis

I. **Mello, M.**, Fusaro, M., Aglioti, S. M., and Minio-Paluello, I. Social touch experiences of neurotypical people and people on the autism spectrum are differentially affected by social context and body location. *In preparation.* (Chapter 2).

II. **Mello, M.**, Fusaro, M., Tieri, G., and Aglioti, S. M. (2022). Wearing same- and opposite-sex virtual bodies and seeing them caressed in intimate areas. Quarterly Journal of Experimental Psychology, 75(3). (Chapter 3).

III. **Mello, M.**, and Aglioti, S. M. The interpersonal sharing of positive emotions: a scoping review. In preparation. (Chapter 4).

IV. **Mello, M.**, Gaigg, S., and Calvo-Merino, B. Motor facilitation following pleasant social touch observation. In preparation. (Chapter 5).

Other papers

i. **Mello, M.***, Dupont, L.*, Engelen, T., Acciarino, A., de Borst, A., and de Gelder, B. (2021, November 3). Human freezing responses to virtual characters in immersive virtual reality are impacted by body expression, group affiliation and threat proximity. *Under review.* Pre-print: https://doi.org/10.31234/osf.io/cr7x9.

ii. Nicolardi, V., Tieri, G., **Mello, M.**, Lisi, M., Fusaro, M., and Aglioti, S. M. Vicarious neural reactivity to pleasant and unpleasant touch: a combined IVR-EEG study. *In preparation.*

iii. Era, V*., Fini, C*., Cuomo, G., **Mello, M.**, Boukarras, S., Mazzuca, C., Borghi, A. M., and Candidi, M. On-line conversations about abstract concepts

modulate the inclusion of the interlocutor in the representation of the narrative and bodily self. *In preparation.*

Opera sottoposta a peer review. Il Consiglio scientifico-editoriale, anche attraverso i comitati scientifici di serie, assicura una valutazione trasparente e indipendente delle opere sottoponendole in forma anonima a due valutatori ignoti agli autori e ai curatori. Per ulteriori dettagli si rinvia al sito: www.editricesapienza.it

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Nico Michele Schiavone

164. One protein many functions: the non-canonical interactions of SHMT1
The structural and functional characterization of SHMT1 interactions with RNA and in the *de novo* thymidylate synthesis complex
Sharon Spizzichino

Studi e Ricerche

From infancy to adulthood, touch shapes our understanding of self and others, influencing social interactions and emotional bonds. This work delves into the embodied nature of pleasant social touch. Through a series of innovative studies, the author investigates how social context and body location affect touch preferences in typically developing and autistic adults, as well as the influence of virtual body ownership on social touch perception. The thesis also explores the role of embodied simulation in empathy for pleasant touch and examines motor facilitation effects during the observation of others' tactile experiences. Furthermore, it proposes a potential link between empathy for pleasant touch and prosocial behaviour. By combining cutting-edge techniques with established experimental paradigms, this thesis offers insights into the intricate relationship between touch, body representations, and social cognition. From exploring the roots of touch processing difficulties in autism spectrum disorders to uncovering the neural mechanisms underlying positive empathy, this work bridges crucial gaps in our understanding of social touch. Whether you're a researcher in neuroscience and psychology, or simply curious about the power of human touch, this thesis provides a comprehensive and thoughtprovoking exploration of how our tactile experiences shape our social world. Discover the embodied phenomenon of pleasant social touch and its implications for human interaction.

Manuel Mello, born in Naples, Italy in 1993, is a cognitive neuroscientist, currently working as a postdoctoral researcher at the Laboratory of Cognitive Neuropsychology and Development, Institut des Sciences Cognitives "Marc Jeannerod", Centre National de la Recherche Scientifique (CNRS) in Lyon, France. Prior to his current position, M. Mello held postdoctoral and research fellowships at the Italian Institute of Technology in Rome. M. Mello holds a joint Ph.D. in Psychology and Social Neuroscience from the University of Rome "La Sapienza" and City, University of London. His research interests focus on social perception, behavior, and cognition in adults, infants, and atypically developing individuals. He has published in peer-reviewed journals and presented his work at international conferences, and he has lectured various academic courses, contributing to both research and teaching in his field.

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