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# Out of touch? How trauma shapes the experience of social touch – Neural and endocrine pathways

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ABSTRACT

Trauma can shape the way an individual experiences the world and interacts with other people. Touch is a key component of social interactions, but surprisingly little is known about how trauma exposure influences the processing of social touch. In this review, we examine possible neurobiological pathways through which trauma can influence touch processing and lead to touch aversion and avoidance in trauma-exposed individuals. Emerging evidence indicates that trauma may affect sensory touch thresholds by modulating activity in the primary sensory cortex and posterior insula. Disturbances in multisensory integration and oxytocin reactivity combined with diminished reward-related and anxiolytic responses may induce a bias towards negative appraisal of touch contexts. Furthermore, hippocampus deactivation during social touch may reflect a dissociative state. These changes depend not only on the type and severity of the trauma but also on the features of the touch. We hypothesise that disrupted touch processing may impair social interactions and confer elevated risk for future stress-related disorders.

## 1. Introduction

Interpersonal touch plays an important role in our everyday lives – a handshake as a greeting, a pat on the back after a job well done, a hug between friends or family to show one's affection or holding someone's hand to reassure them in a stressful situation. Experiencing a lack of these forms of interaction may make one feel "touch-deprived". In fact, contact restrictions and social distancing measures in the context of the COVID-19 pandemic resulted in reduced social contacts and social touch (Meijer et al., 2022), which was associated with increased feelings of loneliness, depression, and anxiety (Field et al., 2020; Meijer et al., 2022; Schneider et al., 2023; von Mohr et al., 2021).

Tactile processing is mediated by two different kinds of fibres: while discriminatory aspects of touch like location, speed, and pressure are signalled by myelinated Aβ-afferents primarily found in glabrous skin, hedonic and affective aspects of touch are facilitated by so called C-tactile (CT) afferents, a kind of unmyelinated fibre in hairy skin (see McGlone et al., 2014 and Olausson et al., 2010 for reviews). These CT-afferents are especially activated by slow, caress-like stroking (Olausson et al., 2010). Stroking speeds of 1–10 cm/s are considered to be CT-optimal touch and are perceived as pleasant (see Pawling et al., 2017 for a review). Microneurography studies show the highest firing frequency of CT-afferents in response to these stroking velocities compared to slower or faster speeds (Löken et al., 2009). When stroking a beloved person, women seem to spontaneously choose CT-optimal velocities, while they use faster, CT-suboptimal velocities for non-social stroking (Croy et al., 2016b). Besides its role in sexual behaviour (Jönsson et al., 2015), social touch can have a general affiliative function and help strengthen social bonds and attachment (see Duhn, 2010 and Jakubiak and Feeney, 2017 for reviews; Suvilehto et al., 2015, 2019). It has a communicative function and can convey emotions to another person (see Fairhurst et al., 2022 for a review; Hertenstein et al., 2006; McIntyre et al., 2022) and furthermore, it can have comforting effects (see Eckstein et al., 2020; Morrison, 2016b for reviews). In animal studies, it has also been shown to promote communicative (Tang et al., 2020) and affiliative behaviours (Huzard et al., 2022).

While social touch can have numerous positive consequences (see Suvilehto et al., 2023 for a review), these benefits might not be experienced by all people to the same extent. Previous aversive or traumatic events may influence how social touch is experienced. While not

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everyone who experiences trauma will develop psychopathology (see Ioannidis et al., 2020; Yehuda et al., 2015 for reviews), traumatic experiences pose a potent risk factor for different mental disorders such as post-traumatic stress disorder (PTSD) (see Breslau, 2009 for review), depression (see Mandelli et al., 2015; Negele et al., 2015 for reviews; O'Donnell et al., 2004), substance abuse disorders (see Brady et al., 2004 for a review; Farley et al., 2004; Min et al., 2007; Triffleman et al., 1995), and borderline personality disorder (see Ball and Links, 2009 for a review; Golier et al., 2003). Adverse life events and traumatic experiences may lead to various alterations in brain structure and functionality and these changes can occur regardless of psychopathology (Holz et al., 2023; Stark et al., 2015; Teicher et al., 2016 for review). Additionally, trauma may lead to reduced psychosocial functioning (Bolton et al., 2004) and influence different features of social interactions: it can lead to reduced interpersonal trust (Bell et al., 2019), changes in social cognition (Nietlisbach and Maercker, 2009), and alterations in the processing of and reaction to social stimuli like emotional faces (see Charuvastra and Cloitre, 2008 and Pechtel and Pizzagalli, 2011 for reviews). Both individuals with childhood maltreatment (Lüönd et al., 2022; Maier et al., 2020b) and war-veterans with PTSD (Bogovic et al., 2014) exhibit a preference for larger social distances. Importantly, more severe childhood maltreatment has been linked to a more negative attitude towards social touch (Trotter et al., 2018). Clinical interviews with caregivers provide evidence that traumatised children avoid touch from both strangers and the caregivers (Blair-Andrews et al., 2020). Furthermore, individuals with PTSD report that they avoid social touch even with their spouse and that their relationship quality suffered because of this trauma-related avoidance of touch (Nicholls and Ayers, 2007). Meta-analytic evidence indicates that perceived social support is a robust protective factor against PTSD and its symptoms (Ozer et al., 2003). Stable and reliable interpersonal connections can provide a sense of safety to an individual that can help coping with fear and anxiety after a traumatic experience (see Charuvastra and Cloitre, 2008 for a review). If social touch as a core form of emotional support is avoided, this may lead to an exacerbation of symptoms and consequences associated with trauma-exposure.

While a plethora of neuroimaging studies investigated the sequelae of trauma exposure for various domains of social processing, there have been surprisingly few attempts to assess touch processing in trauma-exposed individuals (Devine et al., 2020; Maier et al., 2020b; Strauss et al., 2019b). In the current paper, we will review the available evidence and investigate possible mechanisms that may lead to altered touch processing after trauma exposure. Given that neural changes after trauma occur regardless of subsequent development of psychopathology (Stark et al., 2015; Teicher et al., 2016 for a review), for the context of this review, we will consider findings from human studies that include a measure of trauma severity regardless of the specific psychopathology like PTSD. To investigate the relationship between trauma-exposure and the experience of touch, we will first discuss neural and hormonal mechanisms of four central pathways that might underlie the altered experience of social touch in trauma-exposed individuals: (1) the sensory processing of stimuli, (2) sensory integration and interoception, (3) the rewarding properties of social touch, and (4) its anxiolytic effects. We will also consider selected animal studies, especially regarding the neural and hormonal mechanisms involved with social touch. Then we will explore pathways of structural and functional alterations in trauma-exposed individuals and how these mechanisms may interact to result in touch aversion and avoidance.

## 2. Sensory processing

Observations from studies investigating a patient without Aβ-afferents and their brain activation patterns during CT-optimal touch indicate that Aβ- and CT-mediated touch are processed in separate systems with different connections to cortical areas (Olausson et al., 2002). Stroking with a soft brush on the forearm, a commonly used method to perform CT-optimal touch (see Maallo et al., 2022 for a review), activated the primary (S1) and secondary (S2) somatosensory cortices and the contralateral posterior insula (PI) (McGlone et al., 2012, 2014; Olausson et al., 2002). The somatosensory cortices thus seem to play a prominent role in the discriminative processing of dynamic touch stimuli on hairy skin (see Morrison et al., 2010 for a review). According to a meta-analysis, S1 is most likely active during discriminative, PI during affective, and S2 during both discriminative and affective touch processing (Morrison, 2016a).

However, there is also evidence that the role of S1 in social touch is not limited to sensory processing. While S1 did not encode the pleasantness of touch in studies that utilised a brush to touch participants (Case et al., 2016; Kryklywy et al., 2023), Gazzola et al. (2012) found that activation in S1 covaries with the pleasantness of the applied CT-optimal touch by altering the supposed sex of the caresser who touched the male participants by hand. Increased S1 activation in response to touch by a supposedly female compared to a supposedly male experimenter in heterosexual men was also observed in another study using social touch by an experimenter's hand (Scheele et al., 2014). Additionally, studies that directly compared impersonal to interpersonal touch found, for example, more pronounced neural responses in S1, S2, and the PI when women were touched by hand compared to an object (Kress et al., 2011). Furthermore, interpersonal touch can be perceived as more intense and lead to stronger signal increases in both S1 and S2 and to a stronger deactivation of the default-mode network compared with impersonal touch (Strauss et al., 2019a). Considering that S1 and the insula also seem to be differentially activated by touch performed by a stranger or a romantic partner (Suvilehto et al., 2021) and that S1 activity appears to be modulated by visual information during touch (Rosenthal et al., 2023), it seems likely that S1 is relevant for processing not only discriminative, but also affective touch. This notion is further corroborated by findings from animal studies examining pleasant touch: social touch with conspecifics lead to higher activation in S1 in rats than touch by inanimate objects or the experimenter's hand (Lenschow and Brecht, 2015). Furthermore, the firing rate of neurons in the somatosensory cortex in response to social touch has also been shown to be dependent on the sex and sexual status of the rat indicating that the variation of activity in this area could contribute to the social meaning of the interaction (Bobrov et al., 2014).

Previous multi-dimensional frameworks of mental functioning like the Research Domain Criteria did not include sensory processing as a distinct domain, but the crucial role of sensory symptoms in psychopathology is more and more recognised (Harrison et al., 2019). For instance, altered sensory processing has been identified as a key domain of autistic experience (see Robertson and Baron-Cohen, 2017 for a review). Likewise, various lines of research indicate that trauma exposure can influence sensory processing. Patients with PTSD show increased sensory sensitivity and sensation avoidance (Engel-Yeger et al., 2013), as well as difficulties with sensory filtering (Stewart and White, 2008). This phenotype may be related to defensive posturing which can result from increased reactivity to trauma-related or threatening stimuli (see Lanius et al., 2017 for review). Considering the evidence for trauma-related alterations in the brain (Holz et al., 2023; Stark et al., 2015; Teicher et al., 2016 for a review), an obvious mechanism how trauma exposure may influence the sensory processing of social touch may be based on alterations in S1 or S2 that could change the way that tactile stimuli, and more importantly CT-optimal touch, are processed. In fact, it has been suggested that abuse during childhood may act as a stressor with specific neurobiological consequences that affect sensory modalities related to the trauma if it occurs during sensitive periods in development (see Teicher, 2006 for review). Supporting evidence for this notion comes from studies showing changes in grey matter volume in visual areas after witnessing domestic violence or sexual abuse (Tomoda et al., 2009, 2012) as well as in areas associated with language and speech processing after exposure to parental verbal abuse (Tomoda et al., 2011). Moreover, Heim et al. (2013) observed cortical thinning in

S1 associated with genital representations in female victims of childhood sexual abuse.

In patients with PTSD, extensive network dysfunctions have been observed (Akiki et al., 2017 for a review; Hayes et al., 2012; Patel et al., 2012; Tursich et al., 2015; Yehuda et al., 2015 for a review). The salience network seems to be highly reactive, leading to an increased tendency to classify stimuli as threatening, whereas its modulation by both the central executive network and the default mode network is disturbed. As a result, top-down emotion-regulation, especially by the central executive network, is less effective. Hypervigilance and hyperreactivity may bias trauma-exposed individuals to experience social touch as threatening and overall aversive. Maier et al. (2020a) observed increased activation in S1 to CT-suboptimal touch (cf. Fig. 1) that significantly correlated with reduced perceived comfort in reaction to the stimulation in individuals exposed to childhood maltreatment, possibly reflecting these defensive processing patterns. Interestingly, patients with PTSD also rated tactile stimulation as more intense than healthy controls, but this effect was not evident for CT-suboptimal interpersonal touch (Strauss et al., 2019b). While (social) touch may be experienced as threatening by trauma-exposed individuals and lead to hyperreactivity and avoidance in some cases, trauma can also be associated with symptoms of emotional numbing and an overregulation of the salience network through the dorsolateral prefrontal cortex (dlPFC) and other areas of the central executive circuit (see Akiki et al., 2017; and Yehuda et al., 2015 for reviews). In patients with uni- or bipolar mood disorder self-reported lower registration of sensory input positively correlated with more severe childhood trauma (Serafini et al., 2016). Similarly, female patients with borderline personality disorder with a high rate of PTSD comorbidity perceived standardised non-social touch stimuli as less intense and pleasant (Löffler et al., 2022). Male veterans with PTSD had weaker activity in S1 in response to non-social tactile stimulation relative to veterans without PTSD (Badura-Brack et al., 2015). Taken together, trauma exposure may trigger hyperreactivity and avoidance in some cases and blunted neural activity and reduced sensory sensitivity in others. It is currently unclear if these opposing reactions in trauma-exposed individuals depend on the social nature of the interaction, the intensity and duration of the stimulus, or whether they can be explained by different psychopathologies in previous studies. Importantly, as touch is usually accompanied by additional information from other sensory modalities that provide context for the interaction - the combination of sensory input with emotional and cognitive assessments of the situation may influence the reaction pattern of trauma-exposed individuals.

## 3. Sensory integration & interoception

The insula, especially the posterior part, has been implicated in the sensory processing of social touch by integrating emotionally salient tactile inputs (McGlone et al., 2012). The PI was shown to be sensitive to stroking velocity in both observed and experienced touch if the touch was of social nature (Morrison et al., 2011a), indicating that the PI integrates visual and tactile information of the social touch interaction. Likewise, the anterior insula (AI) was active during both experienced and imagined affective touch (Lucas et al., 2015), suggesting that the AI could be involved in interpreting the affective meaning of a tactile experience. Reduced AI activity to social touch was observed in autistic children and adolescents and interpreted as evidence for a disrupted processing of the social aspect of touch (Kaiser et al., 2016).

The AI is a key part of the salience network and involved in detecting important environmental stimuli, switching between large-scale networks, and modulating physiological reactivity to stimuli (see Menon and Uddin, 2010; and Uddin, 2015 for reviews). Because of its role as a hub for input from different sensory modalities and its involvement in various subjective feelings, it has been theorised to harbour some form of a representation of self-awareness (Craig, 2002, 2009 for reviews). It is however – on top of or because of that – a key region for multisensory integration and interoception (Craig, 2009 for a review; Kurth et al., 2010; Uddin et al., 2017 for a review). While the mid-posterior insula appears to be involved in somato- and viscerosensory processing (Simmons et al., 2013), the AI has been implicated in cognitive and

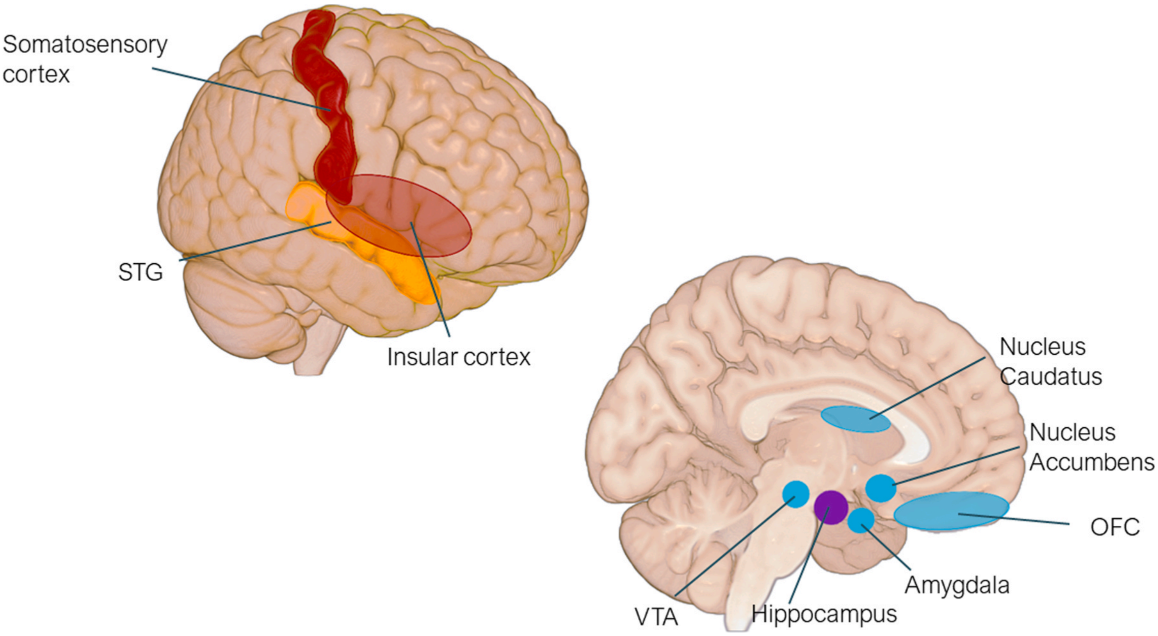

**Fig. 1.** Brain regions associated with touch processing after trauma. Red represents evidence for significant hyperactivity in response to CT-suboptimal interpersonal touch in trauma-exposed individuals, purple represents evidence for significant hypoactivity in response to CT-optimal interpersonal touch (Maier et al., 2020b). Orange indicates increased responses to interpersonal and impersonal CT-optimal and CT-suboptimal touch in the superior temporal gyrus (STG) after trauma exposure (Strauss et al., 2019b). Previous studies did not observe significant trauma-related responses to social touch in reward areas or the amygdala (marked in blue). We hypothesise that trauma-associated changes in these areas are context-dependent (e.g. changes may become evident if reward areas are more strongly activated irrespective of trauma). Abbreviations: orbitofrontal cortex (OFC), superior temporal gyrus (STG), and ventral tegmental area (VTA).

social-emotional processing and regulation (Kurth et al., 2010; Simmons et al., 2013; Uddin et al., 2017 for a review) as well as empathy (see Lamm and Singer, 2010 for a review). There seems to be a pattern of ascending complexity of interoceptive re-representations in a posterior to anterior gradient. In more posterior parts, primary interoceptive information about the current state of the body is combined with environmental conditions, as well as with motivational, social, and cognitive information to create a complete representation of an individual's feelings (see Craig, 2009 for a review). Of note, however, the insular cortex has also been divided into a ventral part that is involved mainly in homoeostatic regulation and a dorsal part that is more focused on executive mechanisms related to adaptive behaviour (see Lamm and Singer, 2010 for a review). In trauma-exposed individuals, evidence points to reduced insular volume (Akiki et al., 2017 for a review; Bromis et al., 2018), as well as altered insula functional connectivity during rest (see Akiki et al., 2017 for a review).

In recent years, more and more studies indicate that interoceptive dysfunctions (either in objective accuracy, subjective sensibility, or awareness) are a key factor influencing the development or maintenance of psychopathology (see Brewer et al., 2021 for a review). Affective touch has been brought forward as a potential tool to measure skin-mediated interoception, especially in the context of bodily awareness (see Crucianelli and Ehrsson, 2023 for a review). In individuals with childhood maltreatment, decreased cardiac interoceptive accuracy after acute social stress or pharmacologically induced noradrenergic activation has been observed (Schaan et al., 2019; Schulz et al., 2022). However, another study was unable to find similar effects of childhood maltreatment on interoceptive measures besides body dissociation (Schmitz et al., 2023). When presented with negative emotional cues, female patients with PTSD showed increased reactivity in more posterior regions of the insula compared to controls that may mirror an interaction between an exaggerated generation of interoceptive anxiety cues and heightened anxiety symptoms (Bruce et al., 2013). Similarly, individuals with high levels of childhood maltreatment showed increased reactivity to fast touch in the PI (cf. Fig. 1) that was associated with lower perceived levels of comfort of the touch (Maier et al., 2020b). PI hyperreactivity could reflect altered sensory sensitivity, but it is also consistent with the idea of disrupted multisensory integration and elevated interoceptive anxiety.

Additionally, while increased activation in the middle and anterior insula in anticipation of a negative stimulus has been observed in female PTSD patients (Simmons et al., 2008), they showed a reduced right AI and right dlPFC response during affective set shifting, indicating an impaired ability to change their interoceptive state in response to stimuli that reflect a change in affective valence (Simmons et al., 2009). Decreased functional connectivity of the vestibular system with the PI in PTSD patients has been linked to weakened interoceptive awareness that subsequently may impede multisensory integration and facilitate a disengagement from their environment (Harricharan et al., 2017). This is in line with findings of body dissociation mediating the association between traumatic childhood experiences and emotional dysregulation (Schmitz et al., 2023). Additionally, reduced connectivity between the insula and cortical areas involved in sensorimotor processing as well as increased connectivity of the PI with limbic and brainstem regions involved in evoking instinctual defensive responses have been found in PTSD patients (Harricharan et al., 2020; Nicholson et al., 2016).

Studies with monogamous prairie voles and mice indicate a key role of the hypothalamic peptide oxytocin for the formation and maintenance of pair bonds, (for a review Walum and Young, 2018, but see also Berendzen et al., 2023). Likewise, oxytocin has been implicated in parental bonding and romantic relationships in humans (see de Boer et al., 2012; Feldman, 2012; Hurlemann and Scheele, 2016; Love, 2014 for reviews). Non-social somatosensory stimulation activates parvocellular oxytocin neurons in rats (Tang et al., 2020), and embraces (Holt-Lunstad et al., 2008; Light et al., 2005; Schneider et al., 2023) and massages (Li et al., 2019; Morhenn et al., 2008) induce the release of endogenous oxytocin in humans. Emerging evidence also points to an involvement of oxytocin in multisensory integration. Both exogenous oxytocin and increased sensory experience elevated excitatory synaptic transmission in multiple sensory cortices in mice (Zheng et al., 2014). In vivo oxytocin injections even rescued the effects of sensory deprivation, indicating a function for oxytocin in promoting experience-dependent cortical development. In humans, oxytocin has been shown to increase the rubber hand illusion in which a person feels subjective ownership over an illusory body part (Crucianelli et al., 2019; Ide and Wada, 2017; Spengler et al., 2019). This effect might be due to an increased precision of top-down signals against bottom-up sensory input in visuotactile multisensory integration (Crucianelli et al., 2019). Oxytocin has also been found to influence multisensory integration in other sensory domains (Maier et al., 2019; Maier et al., 2020a). In individuals who experienced trauma, lowered oxytocin levels have been frequently observed (Carmassi et al., 2021; Donadon et al., 2018; Mizushima et al., 2015; Opacka-Juffry and Mohiyeddini, 2012). Thus, impaired oxytocin signalling may impede multisensory integration in the experience of social touch. Further support for this notion comes from studies showing that childhood maltreatment moderates the massage-induced release of oxytocin in women (Riem et al., 2020) and modulates the oxytocin effect on sensory integration in the visuo-olfactory domain (Maier et al., 2020a).

Taken together, these findings are consistent with the idea that in people with trauma experiences, altered multisensory integration because of PI hyperreactivity and decreased insular connectivity to higher-order cortical structures may result in a failure to evaluate the contextual meaning of interoceptive inferences (see Harricharan et al., 2021 for a review). On the one hand, this could mean that trauma-exposed individuals might have a reduced attunement to their own bodily states and thus show a dampened response to the interoceptive cues generated by social touch. On the other hand, they may have difficulties integrating the physical sensation with the social meaning and emotional valence of the touch. Additionally, reduced oxytocin-based modulations of top-down signals during the process of sensory integration might lead to an enhanced focus on the sensory, bottom-up component of the tactile experience.

## 4. Reward processing

It is clear from everyday experience that depending on the context, social touch can be very rewarding. For non-human primates and rodents this can mean engaging in grooming or huddling (see Dunbar, 2010 for a review). Activity dynamics of dopaminergic neurons that project from the ventral tegmental area (VTA) to the nucleus accumbens encode key features of social interactions in mice (Gunaydin et al., 2014). Surprisingly, however, evidence for touch-specific recruitment of brain reward circuits is currently scarce (see Elias and Abdus-Saboor, 2022 for a review). The human reward system is intricately connected with the VTA, dorsal striatum (DS), ventral striatum (VS), and orbitofrontal cortex (OFC). While a previous meta-analysis about whole-brain fMRI activation in response to affective and discriminative touch (Morrison, 2016a) did not detect significant involvement of reward-associated regions, several other fMRI studies found context-dependent activation of the DS (Boehme et al., 2019; Gordon et al., 2013; Mielacher et al., 2023; Sailer et al., 2016; Scheele et al., 2014; Zimmermann et al., 2019), VS (Gordon et al., 2013; May et al., 2014; Mielacher et al., 2023), and OFC (Lamm et al., 2015). Importantly, as previously discussed for S1, touch pleasantness is also processed in other brain areas. For instance, Lindgren et al. (2012) showed that a gentle caress on the arm by an experimenter led to stronger activity in the pregenual anterior cingulate cortex (ACC) and was also rated as more pleasant compared to static touch or touch by a rubber glove. Strauss et al. (2019b) found a stronger activation of the superior temporal gyrus (STG) in female PTSD patients (cf. Fig. 1) that correlated with pleasantness ratings in a quadratic manner. Furthermore, a recent study applied multivariate pattern analyses and observed distinct representations of hedonic tactile information in several frontal and temporal structures, including the insula (Kryklywy et al., 2023).

Previous studies examined a possible link between pleasant touch and the opioid system. Endogenous opioids, such as endorphins, exert their influence on the reward system by interacting with, among others, μ-opioid receptors in these brain areas. The μ-opioid receptor (MOR) system is highly involved in the regulation of social motivation, which leads to reward seeking behaviour (see Loseth et al., 2014 for a review). Interestingly, studies with human participants point to a deactivation of the endogenous μ-opioid system during pleasant social touch. Nummenmaa et al. (2016) conducted a positron emission tomography study with a MOR-specific ligand, which showed an increase in MOR availability in a broad network including the DS, VS, and OFC when men received pleasant touch from their partner. Thus, the endogenous opioid levels were lower during the social touch condition. Likewise, Case et al. (2016) found a trend for increased pleasantness of slow and fast social touch in a paradigm involving MOR blockage by an opioid antagonist. By contrast, two other studies observed no significant effect on wanting or liking ratings of social (Korb et al., 2020) or non-social touch (Loseth et al., 2019).

Research about the involvement of the dopamine system in the processing of pleasant touch is scarce. In mice, there is evidence that Mrgprb4-lineage neurons encode the rewarding quality of social touch. This class of neurons resembles c-tactile afferents in humans and induce dopamine release (Elias et al., 2023). However, the affective properties of gentle stroking in mice have also been found to be encoded by prokineticin receptor 2 (PROKR2) neurons that have also been suggested to share physiological feature with human c-tactile afferents (Liu et al., 2022). In humans, Korb et al. (2020) found no significant effect of a dopaminergic antagonist on wanting or liking ratings, but observed a decrease in positive facial expressions and physical effort to obtain reward when anticipating social touch. There is also evidence for facilitatory receptor interactions between dopamine and oxytocin in the DS and VS (Romero-Fernandez et al., 2013). In fact, activation of oxytocin receptors in the VTA is critical for social reward in female and male Syrian hamsters (Borland et al., 2019). However, oxytocin also acts as a positive allosteric modulator and enhances MOR activity (Miyano et al., 2021). Furthermore, the reinforcing properties of social interaction in male mice required coordinated activity of oxytocin and serotonin in the VS (Dölen et al., 2013). Thus, oxytocin may affect the rewarding properties of social touch via interaction with other neurotransmitters and neuropeptides. In humans, several studies found that intranasal administration of oxytocin increased pleasantness ratings of touch in a context-dependent manner (but see Ellingsen et al., 2014 for a null finding). Specifically, oxytocin enhanced the pleasure of manual (Chen et al., 2020b) and gentle massage (Chen et al., 2023), but had no significant effect on machine or pressure massages. Likewise, the framing of the touch moderated the effects of oxytocin such that oxytocin-increased pleasantness was only evident for social touch supposedly administered by an attractive opposite-sex experimenter or the romantic partner (Kreuder et al., 2017; Scheele et al., 2014). On the neural level, these behavioural effects of oxytocin were paralleled by enhanced activation in the VS (Chen et al., 2020b; Kreuder et al., 2017), DS and VTA (Chen et al., 2020b), and OFC (Chen et al., 2020a; Chen et al., 2023; Chen et al., 2020b; Scheele et al., 2014).

Anhedonia is a common symptom in PTSD (American Psychiatric Association, 2013), describing a state characterised by diminished pleasure in experiences that are generally considered pleasurable. Thus, there is a consistent pattern of reduced behavioural and neural responses to reward in trauma-exposed individuals (Sailer et al., 2008; see Lokshina et al., 2021; Nawijn et al., 2015; Seidemann et al., 2021; and Teicher et al., 2016 for reviews). More severe anhedonic symptoms have been linked to reduced functional connectivity of the fronto-striatal circuit in women with trauma experiences (Sambuco et al., 2021). Tentative evidence suggests disruptions of the opioid (Fenster et al., 2018 for a review; Liberzon et al., 2007; Torres-Berrio and Nava-Mesa, 2019 for a review) and dopamine systems in connection to the reward circuit in PTSD (see Seidemann et al., 2021 for a review). Furthermore, reduced oxytocin levels after trauma exposure have been observed (Carmassi et al., 2021; Donadon et al., 2018; Mizushima et al., 2015; Opacka-Juffry and Mohiyeddini, 2012).

Importantly, individuals with more severe childhood maltreatment differentiated less between CT-optimal and CT-suboptimal touch in pleasantness (Devine et al., 2020; Strauss et al., 2019b) and comfort ratings (Maier et al., 2020a; Mielacher et al., 2023). This effect seems to be more pronounced for social than non-social touch (Strauss et al., 2019b) and can be attributed to reduced pleasantness of CT-optimal touch (Devine et al., 2020; Strauss et al., 2019b) and decreased comfort of CT-suboptimal touch (Maier et al., 2020a; Mielacher et al., 2023). However, in a mixed sample of psychotherapy outpatients, a history of childhood maltreatment was related to enhanced affective touch awareness, defined as weighted difference of pleasantness ratings between CT-optimal and CT-suboptimal non-social touch with a brush (Croy et al., 2016a).

Surprisingly, neither Maier et al. (2020b), nor Mielacher et al. (2023) found significantly altered activity in reward-related neurocircuits in trauma-exposed individuals. Mielacher et al. detected significantly reduced VS and DS responses to social touch in patients with major depressive disorder who also reported more traumatic experiences during childhood, but the group difference compared to healthy controls was actually smaller in individuals with more severe childhood maltreatment. How can these conflicting behavioural and neural findings be reconciled? First, it is conceivable that altered pleasantness and comfort ratings can be completely explained by sensory hyperreactivity. Notwithstanding, this interpretation seems unlikely given that trauma exposure robustly dampens responses to non-touch stimuli in reward networks (Sailer et al., 2008; see Lokshina et al., 2021 Nawijn et al., 2015 ; Seidemann et al., 2021 for reviews). Second, activation in the DS, VS, and OFC is particularly influenced by signal loss due to susceptibility artifacts (Ojemann et al., 1997). Previous whole brain analysis and studies without a specific hypothesis about reward-related effects might have missed these effects. Trauma may also affect the hedonic quality of touch by modulating touch-specific responses that do not necessarily include all reward circuits to the same extent. For instance, lower ghrelin concentrations (i.e. a larger satiety response after a meal) appear to be related to higher OFC-mediated reward value of touch (Pfabigan et al., 2023), but this association was not evident in other reward areas or for non-touch social reward (Sailer et al., 2023). Third, trauma-induced impairments in oxytocin signalling may translate to context-dependent changes in reward-related activation, similar to the context-specific neural effects of intranasal oxytocin. We hypothesise that oxytocin-mediated trauma effects would become evident in a context with stronger recruitment of the dopaminergic reward circuit such as social touch by a romantic partner (cf. Fig. 1).

## 5. Anxiolysis

In addition to its rewarding properties and robust evidence for antinociceptive effects (Goldstein et al., 2018; Kreuder et al., 2019; Liljencrantz et al., 2017; López-Solà et al., 2019; Reddan et al., 2020; Von Mohr et al., 2018), social touch can have stress-dampening and anxiolytic effects. For instance, couples that touched each other more frequently during a 4-week intervention had increased salivary oxytocin levels and husbands had lower systolic blood pressure (Holt-Lunstad et al., 2008). Triscoli et al. (2017b) found that receiving touch decreased participants' heart rate. A recent meta-analysis about touch interventions yielded a medium effect size for beneficial effects on both physical and mental health (Packheiser et al., 2023).

To investigate the anxiolytic effects of touch under acute stress, previous studies implemented different paradigms which elicit social, emotional, or physical stress. These studies found decreased self-reported distress (Von Mohr et al., 2017), lower heart rate (Ditzen et al., 2007) and a decrease in cortisol levels or accelerated cortisol recovery (Berretz et al., 2022; Ditzen et al., 2007, 2019; Dreisoerner et al., 2021) if participants were touched before or during stress. Most of these studies employed some form of social touch, but CT-optimal stroking by a brush machine also increased heart rate variability (HRV) (Triscoli et al., 2017a), which is typically associated with enhanced stress-buffering.

On a neural level, there is evidence from animal models that prosocial comforting behaviour, such as allogrooming, is strongly linked to activity in the ACC, a brain area associated with bodily arousal and threat response (Burkett et al., 2016 for a review; Li et al., 2019; Wu et al., 2021). In humans, Coan et al. (2006) found attenuated ACC responses to threat of electric shock in handholding conditions compared to conditions without touch. Handholding during social rejection (Morese et al., 2019) or emotional stress (Kraus et al., 2019) also reduced activity in the AI and decreased functional connectivity between the AI and ACC (Kraus et al., 2019). Interestingly, in some studies, participants reported lower subjective distress if they experienced some form of touch (Coan et al., 2006; Kraus et al., 2019; Von Mohr et al., 2017), while other studies did not find such behavioural changes despite physiological or hormonal effects (Ditzen et al., 2007; Dreisoerner et al., 2021; Morese et al., 2019). Hence, the stress-dampening effects of social touch can extend beyond the individual's subjective awareness. Notably, psychosocial stress increased explicit wanting and anticipatory pleasure of interpersonal touch (Massaccesi et al., 2021), suggesting that individuals under stress may actively seek out touch as a form of comfort.

Not surprisingly, anxiolytic effects of social touch vary depending on context and inter-individual factors such as the relationship between the interacting individuals. Grewen et al. (2005) found that stress-buffering effects are modulated by perceived partner support, indicating that relationship quality moderates anxiolytic effects of social touch. Similarly, the touch-induced attenuation of neural threat responses was more pronounced when the person holding the hand was the husband as compared to a stranger (Coan et al., 2006). Furthermore, the touch-related decrease in insula-ACC connectivity was enhanced for more securely attached individuals (Kraus et al., 2019). These findings provide evidence that factors like intimacy, relationship satisfaction, and attachment style have a major moderating influence on stress-buffering effects of touch. It is possible that self-soothing touch has some anxiolytic properties as well, but evidence for this is currently scarce and conflicting. Dreisoerner et al. (2021) found that both self-soothing touch and receiving a hug were associated with a reduction in cortisol levels under psychosocial stress. By contrast, a significant reduction in heart rate was only evident for being stroked by a partner, but not self-touch (Triscoli et al., 2017b). Mechanistically, oxytocin enhances the stress-buffering effects of social support (Heinrichs et al., 2003) and may contribute to the context-dependent effects. In rodents, oxytocin was linked to allogrooming in stress-inducing situations (Burkett et al., 2016; Li et al., 2019). However, there is also evidence for context-dependent effects of oxytocin in animals. Oxytocin normally has the potential to dampen hypothalamic-pituitary-adrenal (HPA) axis axis reactivity, but might facilitate it during stress (see Vitale and Smith, 2022 for a review). Interestingly, oxytocin can produce anxiogenic effects in the absence of social support (Eckstein et al., 2014), but in combination with handholding with the romantic partner, it reduced the pain-associated AI response, possibly via strengthened top-down control of the prefrontal cortex (Kreuder et al., 2019).

In trauma-exposed individuals, this top-down control of limbic activation can be impaired, resulting in amygdala hyperreactivity (for a meta-analysis see Etkin and Wager, 2007) and hypervigilance for potential threats (see Lanius et al., 2017 for a review). For instance, a common finding after trauma exposure are faster behavioural reactions and enhanced activity in the amygdala in response to fearful or angry faces (Garrett et al., 2012; Maier et al., 2020a; Morris et al., 1999). Interestingly, this amygdala hyperreactivity is not limited to visual stimuli, but extends to stress-associated olfactory cues in individuals with childhood maltreatment (Maier et al., 2020a). These changes may arise to enable individuals to avoid threats (see Teicher et al., 2016 for a review), but they also cause an increased sensitivity to generally non-noxious stressors in later life.

Furthermore, it is well established that trauma exposure is associated with disturbances in reactivity of the HPA axis, but there is no consensus on the direction of effects (see Ioannidis et al., 2020 for a review). While some studies found an increase in cortisol levels (Zhong et al., 2020) in trauma exposed women, other studies obtained evidence for a blunted cortisol response in women (Metz et al., 2020). A meta-analysis by Fogelman and Canli (2018) on healthy individuals who experienced childhood maltreatment reported an association of trauma exposure with lower baseline cortisol, but increased awakening response. In addition, as discussed, lowered oxytocin levels haven been observed in individuals who experienced trauma compared to controls (Carmassi et al., 2021; Donadon et al., 2018; Mizushima et al., 2015; Opacka-Juffry and Mohiyeddini, 2012), which may hamper the oxytocin-mediated anxiolytic effects of social touch.

While touch might trigger flashbacks or trauma-related intrusions, especially if the trauma involved touch (such as sexual or physical violence), there is no evidence that individuals with trauma exposure exhibit amygdala hyperreactivity in response to touch in experimental settings (Strauss et al., 2019b). Maier et al. (2020b) even found a trend towards hypoactivation of the amygdala in response to CT-optimal touch. However, to the best of our knowledge, so far, no study has examined whether trauma exposure moderates anxiolytic and anti-stress effects of social touch. Given that negative childhood experiences influence the interaction between oxytocin and stress-protective verbal social support in women (Riem et al., 2020), we expect that trauma-exposed individuals would also benefit less from touch-based social support. Given the distinct neural response profile to self-touch including deactivation of brain areas encoding low-level sensory representations (Boehme et al., 2019), we speculate that the sequelae of traumatic experiences may differ between self-touch and touch by another person.

Furthermore, it has been suggested that a lack of nurturing touch during development could lead to attenuated sensitivity to the social value of interpersonal touch (Devine et al., 2020). Based on strong evidence for threat hypervigilance in trauma-exposed individuals, we further hypothesise that traumatic experiences may induce a bias towards negative appraisal of touch context. Thus, in addition to sensory changes, touch may be processed differently because of altered cognitive evaluation of the associated context.

## 6. Cognitive evaluation

Not only the experience of social touch but also the observation elicit activation in S1, AI, and PI (Ebisch et al., 2008; Keysers et al., 2004; Lamm et al., 2015; Morrison et al., 2011a; Riva et al., 2018; Schaefer et al., 2012; but see Ebisch et al., 2011). These activations have been related to empathising with the (pleasant) touch experience of the observed person (Morrison et al., 2011a). Interestingly, individuals with reduced density of CT afferents lack the characteristic velocity-specific pleasantness evaluation of both experienced and vicarious touch, suggesting that first-hand experience with the affective component of CT-optimal touch may be necessary to interpret the vicariously experienced touch as pleasant (Morrison et al., 2011b).

Furthermore, activations in SI during vicarious touch are modulated by the viewer's empathy (Schaefer et al., 2012, 2021), and individuals with higher levels of empathic traits assessed vicarious social touch as inciting more positive emotions (Peled-Avron et al., 2016). There is evidence that traumatic experience can reduce empathic abilities (Mazza et al., 2015; Nietlisbach and Maercker, 2009; Palgi et al., 2017). It is therefore conceivable that trauma-exposed individuals might experience difficulties predicting the positive emotions that social touch might elicit in others. Combined with negative expectations of their (social) environment, an anticipation of aversive outcomes (see Ehlers and Clark, 2000; and Yehuda et al., 2015 for reviews), general trauma-associated dissociative symptoms (Dalenberg et al., 2012; Yehuda et al., 2015 for reviews), and in light of models that conceptualise deficient context processing as a core component of PTSD (see e.g. Liberzon et al., 2007; or Maren et al., 2013 for reviews), such a dissociation of physical sensation and socio-affective meaning could additionally reduce the hedonic value or anxiolytic effects of social touch. As anxiolytic effects of touch are strongly moderated by context variables, a lack of context sensitivity might contribute to a reduction of associated stress-buffering benefits.

## 7. Consequences

Reduced pleasantness and comfort of social touch after trauma exposure may result in a negative attitude towards social touch (Maier et al., 2020b; Mielacher et al., 2023; Trotter et al., 2018) and subsequently its avoidance. Previous studies have established that trauma-exposed individuals prefer larger interpersonal distances, even with friends, and especially regarding men (Bogovic et al., 2014; Haim-Nachum et al., 2021; Lüönd et al., 2022; Maier et al., 2020b; Vranic, 2003). Patients with different stress-related disorders and more severe childhood maltreatment reported engaging in touch less frequently in daily life compared to healthy controls (Croy et al., 2016a). Traumata also have a negative impact on mother-infant interactions such as decreased and shorter duration of breastfeeding (Channell Doig et al., 2020). Additionally, past traumatisation is associated with lowered relationship quality and emotional intimacy (Davis et al., 2001; DiLillo et al., 2007; Mullen et al., 1994; Taft et al., 2011; Zamir, 2022), and reduced interpersonal trust (Bell et al., 2019). Clearly, altered social touch processing could be both the cause and consequence of these trauma sequelae (cf. Fig. 2). A reduced importance of social touch for relationships, less need for and liking of social touch, as well as feelings of loneliness have been observed in patients with borderline personality disorder who also experienced significantly more childhood maltreatment than healthy controls (Schulze et al., 2022). Interestingly, within the patient group, more severe trauma did not significantly correlate with the appraisal of interpersonal touch, which could indicate a disorder-specific disruption of touch processing or a plateau effect of traumatisation. Furthermore, touch avoidance may eventually increase the risk for stress-related disorders such as depression, given that embraces have a positive effect on daily mood and life satisfaction (Packheiser et al., 2022). Touch deprivation during COVID-19-related restrictions have been linked to worse psychological wellbeing (von Mohr et al., 2021), while affective touch during times of the pandemic and lockdown was associated with decreased self-reported anxiety, general burden, stress, and increased oxytocin levels (Schneider et al., 2023).

Finally, in the context of interpersonal traumatisation, social touch itself might pose a trigger that causes traumatic memories to resurface. Reduced hippocampal activity in response to CT-optimal touch in trauma-exposed individuals (cf. Fig. 1; Maier et al., 2020b; Strauss et al.,

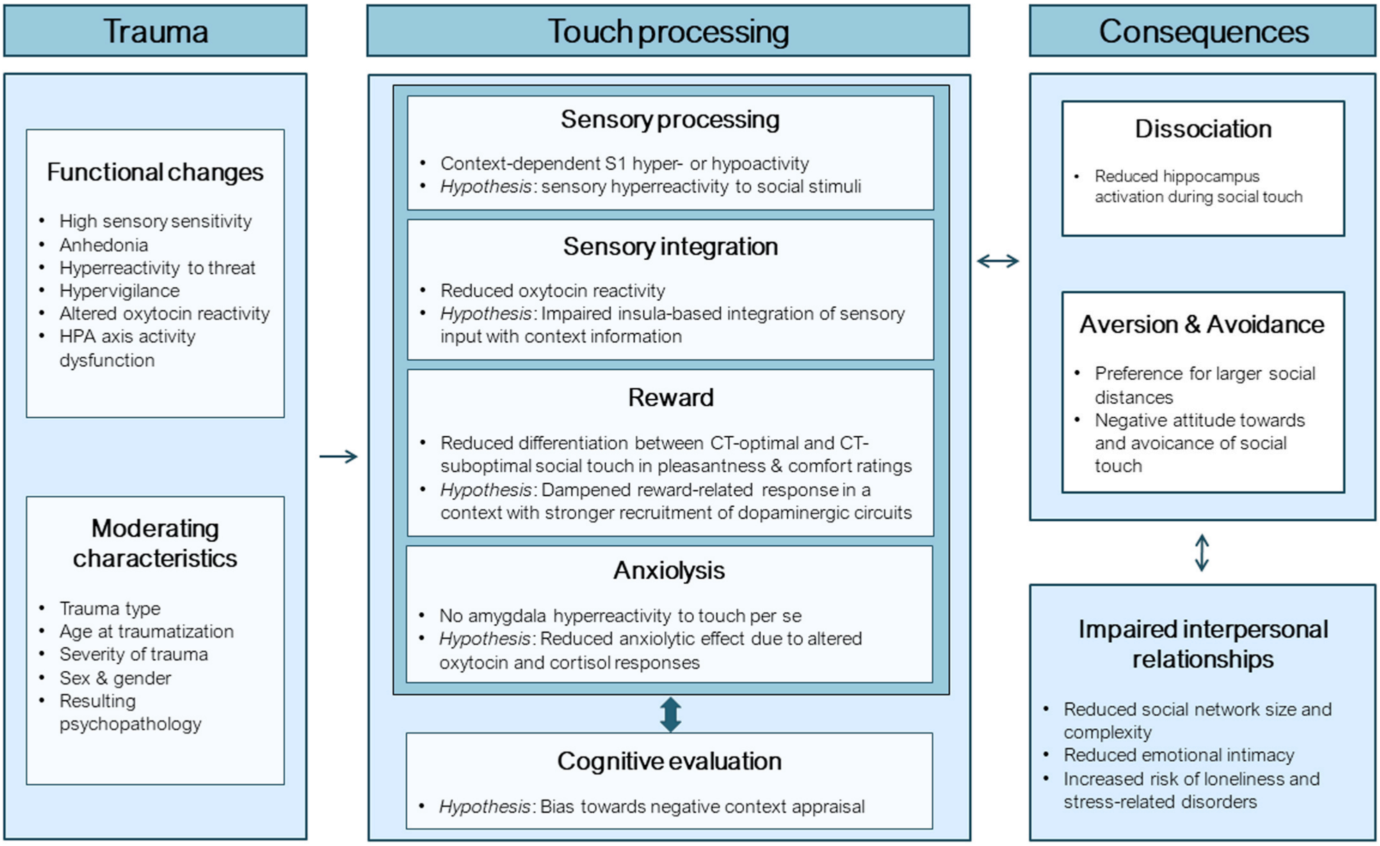

**Fig. 2.** Hypothesised influence of trauma experiences on touch processing and resulting consequences. Trauma exposure leads to functional changes that may alter sensory processing and sensory integration of touch and its rewarding and anxiolytic effects. These changes are reciprocally linked to the cognitive evaluation of touch contexts such that they may introduce a bias towards negative appraisal of touch contexts which in turn may facilitate dysfunctional touch processing. Altered touch processing may result in a dissociative state during touch and subsequently a negative attitude towards and the avoidance of touch. By impairing interpersonal relationships and exacerbating the detrimental consequences of loneliness, touch avoidance may confer vulnerability to stress-related disorders that may further amplify the hypothesised mechanisms of altered touch processing. These processes are moderated by varying characteristics of the trauma and the exposed individual.

2019b) could reflect active avoidance of traumatic memories especially since some participants experienced the emergence of unwanted memories during touch (Strauss et al., 2019b). Along these lines, direct stimulation of the amygdala has been found to trigger odour-evoked autobiographical memories (Bartolomei et al., 2017). Reduced recruitment of the amygdala during social touch in individuals with childhood maltreatment (Maier et al., 2020b) is therefore also consistent with the notion of memory avoidance. It has been proposed that the hippocampus is involved in the reenactment of traumatic body memories (see Gentsch and Kuehn, 2022 for a review), however, the observed hippocampal deactivation points to a dissociative state during acute touch in individuals with trauma experiences.

Importantly, the consequences of traumatic experiences will vary substantially depending on both features of the trauma and the context of the touch. Previous research indicates the existence of sensitive periods during which the after-effects of traumatisation may be more pronounced (see Teicher, 2006 for a review). Moreover, an individual who experienced neglect during childhood may fail to associate social touch with its rewarding or comforting properties, while an individual who experienced interpersonal violence might have developed a heightened awareness for possible threats and thus a tendency to interpret a tactile stimulus as dangerous, ultimately leading to an aversion to and avoidance of social touch.

## 8. Open questions

Despite a plethora of studies examining the neurobiological substrates of trauma exposure, there are numerous unanswered questions how trauma may affect the experience and processing of social touch. Future studies are warranted to test the hypothesised neural and hormonal pathways by which traumata may influence touch processing (cf. Fig. 1). In particular, the domain-specificity of these mechanisms needs to be tested. On the one hand, the reduced differentiation between CT-optimal and CT-suboptimal touch and the absence of amygdala hyperreactivity despite well-established amygdala-based threat hypervigilance in trauma-exposed individuals speak against domain-general effects. On the other hand, dampened responses in the reward neurocircuit and a negative cognitive evaluation bias have been reported after trauma exposure irrespective of social touch (Sailer et al., 2008; see Lokshina et al., 2021; Nawijn et al., 2015; Seidemann et al., 2021; and Teicher et al., 2016 for reviews). It is still unclear, for instance, if trauma-related changes in reward-associated neural responses are more pronounced for social touch than secondary rewards such as social appreciation or affirmation (Sailer et al., 2023).

Furthermore, previous studies do not provide conclusive evidence for trauma-specific effects. Self-reports of childhood emotional and physical neglect and emotional abuse yielded higher negative correlations with a questionnaire measuring touch experiences and attitudes compared to childhood physical and sexual abuse (Trotter et al., 2018) but participants often report multiple traumas and in the study by Maier et al. (2020b) all subtypes of maltreatment correlated negatively with comfort ratings of CT-suboptimal touch. Furthermore, deciphering trauma-specific touch effects may require area-specific analyses. For instance, remitted patients with borderline personality disorder and childhood sexual abuse showed a selective negative evaluation of sexually connoted body areas (Kleindienst et al., 2020). Clearly, a more severe traumatisation could also be associated with stronger disturbances of touch processing, but the impact of several moderating variables is still elusive. Previous studies controlled for sex as a possible confounding factor (Maier et al., 2020b), but given preliminary evidence that affective touch may be a more relevant coping mechanism for women than for men (Schirmer et al., 2022), it is conceivable that trauma exposure can have sex-specific effects on touch processing. Furthermore, trauma effects on social touch may differ between real-word settings and controlled laboratory contexts. Previous studies that explored social touch with a naturalistic approach (e.g. Murphy et al., 2018; Packheiser et al., 2021; Packheiser et al., 2022) did not consider trauma.

In addition, in line with the observation that some touch-based interventions reduce PTSD symptoms (see McGreevy and Boland, 2022 for a review), future research should investigate under which conditions the salubrious effects of social touch are preserved in trauma-exposed individuals. Specifically, little is known how trauma may influence self-soothing touch and vicarious touch, although the observation of social touch elicits similar neural responses as receiving social touch (Ebisch et al., 2011; Holle et al., 2013; Streltsova and McCleery, 2014). There is also preliminary evidence that social touch may mitigate loneliness (Heatley Tejada et al., 2020), which, in a persistent form, can hamper new social interactions (Lieberz et al., 2021; Morr, Liu, et al., 2022a) and confer vulnerability to intrusive memories after trauma exposure (Morr, Noell, et al., 2022b). Interestingly, altered oxytocin reactivity has been implicated in the neurobiology of loneliness (Lieberz et al., 2021). However, the augmentation of a group intervention for loneliness with intranasal oxytocin significantly facilitated the decrease in state loneliness and improved positive bonding between the group members, but had no significant effect on trait-like loneliness (Berger et al., 2023). Possible interactions between trauma exposure, chronic loneliness, and the oxytocinergic mechanisms of social touch have not been explored yet. In addition, we suggest comparing mechanisms involved in self-touch to other-touch with regards to trauma exposure as self-touch might bear some of the benefits of social touch while not triggering hypervigilance as much as other-touch.

## 9. Conclusion

In summary, we hypothesise that context-dependent changes in sensory sensitivity and integration combined with diminished reactivity in the reward circuit, reduced oxytocin-mediated stress buffering, dissociation-like hypoactivation of the hippocampus, and altered cognitive evaluation of the associated context can lead to a pattern of aversion and avoidance after trauma exposure (cf. Fig. 2). Put differently, in an equation weighing the pro and contra arguments of engaging in social touch, the balance might end up to the detriment of social touch and in turn of social relationships. This way, dysfunctional touch processing may confer vulnerability for loneliness and subsequently further stress-related disorders. The aspects we discussed and predictions we made in this review could be used as impulses for further research on this matter to improve our understanding of the benefits of social touch, the challenges that can arise after trauma exposure, and potential therapeutic implications to improve treatment.

## Declaration of Competing Interest

The authors declare no competing interests.

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