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Review article



The role of impairments in self–other distinction in borderline personality disorder: A narrative review of recent evidence

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ABSTRACT

Impairments in maintaining a differentiated sense of "self" and "other" are thought to be a central feature of borderline personality disorder (BPD). However, studies directly focusing on self-other distinction (SOD) in BPD are scarce, and these findings have not yet been integrated with novel insights into the neural mechanism involved in SOD. Here, we present a narrative review of recent behavioral and neuroimaging findings focusing on impairments in SOD in BPD. Behavioral findings of SOD at the embodied level provide preliminary evidence for impairments in multisensory integration in BPD. Furthermore, both behavioral and neuroscientific data converge to suggest that SOD impairments in BPD reflect an inability to shift between self and other representations according to task demands. Research also suggests that disruptions in infant—caregiver synchrony may play a role in the development of these impairments. Based on these findings, we present a new, integrative model linking impairments in SOD to reduced neural and behavioral synchrony in BPD. The implications of these findings for future research and clinical interventions are outlined.

1. Introduction

Borderline personality disorder (BPD) is a severe psychiatric condition characterized by profound instability in affect, identity, and relationships (American Psychiatric Association, 2013). Individuals with BPD seem to be overly influenced by others' emotions, opinions, or behaviors, which may contribute to instability in their sense of self and identity (Fonagy and Luyten, 2009; Sollberger et al., 2012). Furthermore, BPD patients' self-experience seems less firmly grounded in their own body, as evidenced by high levels of dissociation in BPD (Korzekwa et al., 2009; Lyssenko et al., 2018). These individuals also often project their own emotions and mental states onto others, instead of appreciating others' perspectives as being separate from their own (Colle et al., 2018), which may relate to their profound difficulties in interpersonal relationships (Jeung and Herpertz, 2014). These clinical phenomena may be expressions of disturbances in self-other distinction (SOD) in BPD.

Indeed, many theoretical approaches assume that disturbed SOD is a central feature of BPD (Bender and Skodol, 2007; Fuchs, 2007; Jorgensen, 2010; Luyten and Blatt, 2013; Neustadter et al., 2019b), and

studies using self-report questionnaires have typically found that individuals with BPD have difficulty establishing self-other boundaries (Beeney et al., 2016, 2015). Object-relations theory, for instance, has proposed that BPD is characterized by splitting of representations of self and others as "all good" or "all bad", leading to a lack of SOD in individuals with BPD (Kernberg, 2006). Mentalizing perspectives, meanwhile, suggest that problems with SOD in BPD stem from difficulties in mentalizing, that is, reflecting upon the internal mental states of self and others (Fonagy and Luyten, 2009; Luyten et al., 2019).

However, to date, studies that have directly focused on problems with SOD in individuals with BPD are scarce. Furthermore, there is a lack of integration of findings in this area with recently emerging novel insights into the neural mechanism involved in SOD from the fields of social cognitive neuroscience and experimental psychology (Quesque and Brass, 2019; Sowden and Shah, 2014). Indeed, research efforts focused on elucidating the mechanism through which SOD is achieved at both the neural and the behavioral level has important implications for our understanding of mental disorders in which this mechanism may be impaired (Eddy, 2016; Lamm et al., 2016; Steinbeis, 2016). Yet, this framework has not yet been applied to the study of BPD.

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To bridge this gap, here we provide a narrative review of our current knowledge on SOD and existing behavioral and neuroimaging findings relating to SOD in BPD. Rather than providing a complete overview of all available studies, this selective review aims to bring together different lines of research in order to further our understanding of the mechanism of SOD and its impairment in BPD. We performed a search of Pubmed, PsycArticles and Google Scholar to identify behavioral and neural studies on SOD in BPD that (a) employ well-validated behavioral paradigms to investigate SOD or (b) investigate neural areas involved in SOD from a functional or structural perspective and (c) compare at least one clinical or non-clinical BPD group with healthy control participants. Reference lists of retrieved articles were also scrutinized.

In what follows, we first discuss recent approaches to SOD in social cognitive neuroscience. This is followed by a critical review of findings concerning SOD in BPD at both a behavioral and a neural level. Second, we review research on the developmental origins of SOD impairment in BPD. We then present a new integrative model of SOD in BPD that emphasizes an impaired ability to switch between representations of self and other, and its consequences for interpersonal attunement. We end this review with a discussion of directions for future research and clinical implications.

2. Recent approaches to self-other distinction

SOD refers to the ability to distinguish one's own body, actions, and mental states from those of others, which is essential to interacting with others while maintaining a stable sense of self (Lamm et al., 2016; Tsakiris, 2017). Humans have a remarkable capacity for sharing others' mental states through sensorimotor simulation (Decety and Sommerville, 2003; Frith and Frith, 2006; Lombardo et al., 2010) based on a so-called shared representational (SR) system (Ripoll et al., 2013). This frontoparietal mirror neuron network allows one to know how others feel "from the inside", as neural activation is similar while experiencing states of mind and observing others experiencing the same states of mind (Decety and Chaminade, 2003). This sharing of mental states facilitates empathy, connection, and cooperation. However, it also holds the risk of conflating the experience of self and others (Bird and Viding, 2014). A separate neural system, the mental state attribution (MSA) system, is hypothesized to develop with increasing (interpersonal) experience (Decety, 2010; Decety and Michalska, 2010). MSA processing allows for more cognitive and controlled reflection on mental states and is centrally involved in distinguishing between shared self and other representations (Lamm et al., 2016).

The capacity for SOD has been found to involve cortical midline structures such as the medial prefrontal cortex (mPFC) but also, importantly, the temporoparietal junction (TPJ) (Lieberman, 2007; Uddin et al., 2007; Van Overwalle, 2009). The TPJ is routinely found to be implicated in SOD tasks at different levels of processing, such as the level of perception (Heinisch et al., 2012), action (Sowden and Catmur, 2015), and mental representation (Bardi et al., 2017). Indeed, SOD seems to operate in a domain-general rather than a specific manner (Quesque and Brass, 2019), and impairments in this capacity may thus parsimoniously explain socio-cognitive deficits in different domains of functioning. The TPJ has been found to be activated either when representations of self and other are incongruent, or when a situation requires individuals to explicitly represent both self and other (Quesque and Brass, 2019). The precise mechanism through which SOD is achieved remains to be elucidated, although several options have been proposed. The TPJ and prefrontal structures may either enhance the task-relevant representation, inhibit the non-relevant one, or simply allow the individual to flexibly switch between self and other representations (Lamm et al., 2016). These suggestions are supported by the fact that the TPJ is involved in attention reorienting (Corbetta et al., 2008). Switching between representations of self and other is crucial for successful social interaction, as some interpersonal situations call for the inhibition of the self in order to take the perspective of the other, while other situations require the inhibition of the influence of the other in order to represent the self (Brass et al., 2009; Silani et al., 2013; Spengler et al., 2009). This results in the co-representation of both "self" and "other" instead of representing either "self" or "other" in a rigid manner, and this co-representation may be crucial for truly reciprocal, attuned social interaction.

Another reason why the TPJ is a privileged structure for SOD is because of its involvement in the comparison of interoceptive and exteroceptive, that is, internally and externally derived, signals and multisensory integration (Convento et al., 2018). Indeed, lower-level SOD, such as distinguishing one's own body and actions from those of others, relies on the integration and comparison of multiple sensory modalities in order to determine the degree of contingency between sensory cues (Braun et al., 2018). At the action-level, perfect action-response contingencies signal that the action is self-generated, whereas imperfect contingency corresponds to actions generated by others (Kahl and Kopp, 2018). At the perceptual level, contingency is determined between tactile stimuli on the body and visual or auditory stimuli occurring in the space close to the body, called the peripersonal space (PPS) (Serino, 2019), to uncover their cause. The higher-order distinction of mental representations of self and other is thought to develop with experience from this very basic contingency-detection mechanism supported by multisensory integration (Fotopoulou and Tsakiris, 2017).

Many of these recent advances in the understanding of the capacity for SOD have important implications for the various types of psychopathology in which SOD appears to be impaired, including BPD. In the next section, we review behavioral findings on SOD in BPD in three domains: perception, action, and mental representations.

3. Behavioral studies of self-other distinction in borderline personality disorder

3.1. SOD at the perceptual level in BPD

Perceptual SOD refers to the ability to identify one's own body and to distinguish it from others'. Although the experience that one's body is one's own may seem obvious, the sense of body ownership has been shown to be continually constructed by comparing interoceptive and exteroceptive signals (Kahl and Kopp, 2018; Tsakiris, 2017). If there is a match between these signals (e.g. perceiving and experiencing touch), it is most likely that the body part belongs to the self, whereas in the case of a mismatch (e.g. perceiving but not experiencing touch), the body part is experienced as non-self. Indeed, the classic Rubber Hand Illusion (RHI) experiment shows that, by experiencing brush strokes on one's own hand while observing temporally and spatially matched brush strokes on a fake rubber hand, illusory body ownership over the rubber hand can be induced, whereas this illusion does not occur when the rubber hand is stroked in temporal asynchrony or spatial incongruence with the own hand (i.e. mismatch between visuo-tactile stimuli) (Botvinick and Cohen, 1998).

Three studies to date have used the RHI to investigate body ownership in BPD. Bekrater-Bodmann et al. (2016) found that patients with a current BPD diagnosis (n=34) reported more proneness to experience ownership over the rubber hand after spatially congruent stroking compared to patients whose BPD was in remission (n=19) and control participants (n=25), and this was related to state and trait dissociation. Proprioceptive drift (a behavioral index of the strength of the RHI, in which participants have to blindly indicate the felt location of their real hand, which may drift towards the artificial hand) was higher in current BPD patients compared with remitted BPD patients and healthy controls, but not significantly so, as they also exhibited a larger variance in this measure. Neustadter et al. (2019a) found a greater subjective illusion strength of the RHI in a sample of 24 BPD patients compared with 21 control participants after both temporally synchronous and asynchronous stroking. Increased RHI susceptibility in the synchronous condition

was correlated with affective symptoms and psychoticism. Furthermore, controls showed less proprioceptive drift after asynchronous compared with synchronous stroking, whereas BPD patients showed no difference in drift between these conditions. The authors argue that deficits in interoceptive processing in BPD (Back and Bertsch, 2020; Löffler et al., 2018; Müller et al., 2015) may lead individuals with BPD to incorporate inconsistent exteroceptive information (i.e. an asynchronously stroked rubber hand) into the self (Neustadter et al., 2019a). Another explanation for maintained RHI in the asynchronous condition may be that BPD patients are less able to process the mismatch between seen and felt stroking as a signal that the rubber hand does not belong to the self. In a third study, a modified version of the RHI was used in a sample of 20 BPD patients and 21 controls, in which illusory body ownership and agency over a rubber hand were induced by synchronous movements of the artificial and the real hand (Möller et al., 2020). A significantly greater subjective sense of agency (e.g. "I felt as if I was controlling the rubber hand") over the artificial hand was found in the BPD group compared with the controls, as well as a greater sense of subjective ownership (e.g. "I felt as if I was looking at my own hand"), although this difference was not significant. The fact that Möller et al. (2020) did not replicate the findings from the earlier RHI studies could be explained by methodological differences or low statistical power; nevertheless, caution in the interpretation of these results is advisable.

Taken together, the findings from studies using the RHI provide some preliminary evidence for impairments in multisensory integration in BPD, which may make them more susceptible to incorporating the nonself into the self and experiencing bodily self-other overlap and thus impaired SOD at the perceptual level. The increased plasticity of the bodily self in BPD may furthermore relate to reduced certainty that own body parts belong to the self. A recent study assessed ratings of ownership for 25 body areas in current (n = 26) and remitted (n = 22) BPD patients as well as healthy controls (n = 20). Body ownership experiences were significantly reduced in current BPD patients compared to healthy controls, while there were no significant differences with the group of remitted BPD patients. Reduced body ownership was significantly related to dissociation, even when controlling for other BPD features (Löffler et al., 2020). In this context, high levels of dissociation in BPD patients seem particularly important. Dissociation refers to experiences of disconnection from the (bodily) self and the environment such as depersonalization and derealization, and occurs in up to two-thirds of BPD patients (Korzekwa et al., 2009; Lyssenko et al., 2018). Dissociation in BPD is stress-related (Stiglmayr et al., 2008) and is thought to play an important role in affect regulation to reduce emotional arousal, especially in patients with severe childhood trauma (Krause-Utz and Elzinga, 2018; Vermetten and Spiegel, 2014). From this perspective, dissociation may reflect an extreme form of detachment from one's own body (Löffler et al., 2020; Schäflein et al., 2018), while proper bodily awareness is crucial for distinguishing self and others (Palmer and Tsakiris, 2018). BPD patients' tendency to dissociate under stress may thus fundamentally hamper their capacity for perceptual SOD (Bekrater-Bodmann et al., 2016; Löffler et al., 2020), although more research is needed to determine a causal link. For instance, future studies should investigate whether the impact of stress on perceptual SOD in BPD is mediated by state-dissociation.

Perceptual SOD based on multisensory integration occurs between tactile and auditory or visual stimuli that are detected in the space close to the body (the PPS), where interactions between the self and the environment can take place (Serino, 2019). The size of the PPS is subjective and can be modulated by the interpersonal and affective context. Interestingly, in a functional magnetic resonance imaging (fMRI) study of 25 BPD patients and 25 healthy controls, all women, BPD participants reacted with increased activation in the amygdala and the somatosensory cortex when the PPS is intruded, but only in the context of facial displays of disgust (Schienle et al., 2015). In this study, BPD patients also reported a greater preferred personal distance towards an imagined other. In a live dyadic interaction task, 30 BPD patients were found to

have a twice as large preferred social distance from an unknown other compared with 23 control participants (Fineberg et al., 2018). These findings show that BPD patients' representation of the PPS seems to be enlarged, at least in the context of interacting with unknown others. PPS and perceptual SOD may be closely related as they are also found to recruit partially overlapping and interconnected neural activations in multisensory-motor and fronto-parietal regions (Grivaz et al., 2017). In the context of increased body plasticity in BPD as described above, other-generated exteroceptive signals occurring near the body may more easily be incorporated into the "self" in BPD, which may be an intrusive experience resulting in increased social distance preferences. Increased neural activation in response to PPS intrusion was recently found to be positively related to anxious attachment in a study in community young adults (Nasiriavanaki et al., 2021), suggesting that PPS representation in BPD may relate to hypervigilance to (social) threat and attachment hyperactivation strategies. Clearly, more research on the affective and interpersonal modulation of PPS in BPD is needed.

Another task that has been used to investigate perceptual SOD in BPD does not involve multisensory integration, but instead requires participants to actively discriminate visual representations of the faces of "self" and "other" in morphed self-other images (Keenan et al., 2000). In this task, participants watch a video sequence in which a picture of their own face gradually transforms into the face of an unfamiliar other (self-to-other direction) or vice versa (other-to-self direction), and indicate at which point they judge the morph to look more like the target face than the starting face. De Meulemeester et al. (2020) found that non-clinical participants high in BPD features (n = 30) needed the morph to contain more features of the other face before identifying the morph as "other" when that other was more attractive, and took longer to identify the morph as "self" in the other-to-self morphing direction when the other face was less attractive, compared with individuals without BPD features (n = 31). These observations suggest that individuals with BPD features may have difficulties both when having to shift from representing "self" to representing "other" and when shifting from "other" to "self" representations (Sowden and Shah, 2014), and that this difficulty may be modulated by characteristics of the interaction partner (e.g. the other's attractiveness).

In summary, the few behavioral studies that have been conducted suggest that there are impairments in perceptual SOD in BPD, both in terms of problems in multisensory integration – that is, in making SODs based on the match or mismatch between stimuli originating from inside and outside the body (Bekrater-Bodmann et al., 2016; Möller et al., 2020; Neustadter et al., 2019a), which may also impact their PPS representation (Fineberg et al., 2018; Schienle et al., 2015) – and in terms of discriminating visual representations of self and other in ambiguous stimuli (De Meulemeester et al., 2020). Yet, it is clear that more research in this area is needed to replicate these findings and to elucidate the impact of affective and interpersonal factors in perceptual SOD impairments in BPD.

3.2. SOD at the action level in BPD

Another important aspect of SOD is the ability to distinguish self-from other-generated motor actions. Observing another person's action generates an internal representation of that action through mirror-neuron networks (Brass et al., 2009) and this motor simulation is helpful for understanding others (Sato et al., 2013). Automatic mimicry also helps to establish affective attunement between interaction partners (Stel and Vonk, 2010). However, inhibition of these imitative tendencies is necessary when self- and other-generated actions are in conflict, to distinguish the simulation of others' actions from one's own action tendencies (Sowden and Catmur, 2015).

One study directly investigated imitation inhibition in BPD patients using the finger-tapping task, in which a simple finger-tapping response has to be performed while observing another person performing either a congruent or an incongruent finger movement (Hauschild et al., 2018).

This study reported equal response facilitation in individuals with BPD (n=26) and in control participants (n=25) in congruent trials (i.e. intact imitation), but greater interference among those with BPD during incongruent trials (i.e. impaired imitation inhibition). During incongruent trials, it is necessary for the subject to distinguish the other-generated motor action and their own motor intention in order to perform the correct finger movement; BPD patients seem to find this more difficult, as evidenced by their slower reaction times. It may be difficult for BPD patients to process the mismatch between the other-generated action and their own motor intention in the incongruent trials as a strong signal that the action is other-generated, similar to the finding of maintained body ownership for the asynchronously stroked rubber hand in the RHI (Neustadter et al., 2019a).

Imitation inhibition is also important for distinguishing one's own and others' emotions (Prochazkova and Kret, 2017). Indeed, increased mimicry of others' emotion expressions is hypothesized to play a crucial role in the increased emotional contagion that is characteristic of BPD (Herpertz and Bertsch, 2014), as the observer may mistakenly perceive the mimicked emotional state as their own (Olszanowski et al., 2019). A study in 28 adult BPD patients found that facial mimicry was enhanced for negative facial emotion expressions, and attenuated for positive expressions, compared with 28 healthy controls (Matzke et al., 2014). In 32 outpatient youths with early-stage BPD features, however, rapid facial mimicry (i.e. within 1 s after stimulus presentation) was no different from that of 47 matched controls (Pizarro-Campagna et al., 2020). This observation suggests that facial mimicry in BPD may be selectively altered (i.e. increased for negative and attenuated for positive emotion expressions) but preserved at the more unconscious level, at least early in the onset of BPD. Further research is needed to investigate facial mimicry in BPD and its relationship to emotional contagion.

Other tasks investigating SOD at the action level do not focus on imitation inhibition but rather on the experience of a sense of agency over self- versus other-generated actions. One such task relies on the phenomenon of sensory attenuation, in which the sensory consequences of self-generated actions are experienced as less intense than othergenerated stimuli (Blakemore et al., 1999). A sensory attenuation task was used in a sample of 20 individuals with BPD and 20 controls, in which participants rated the intensity of electrical stimuli that were generated by a button being pressed either by the participants themselves (self-generated) or by the experimenter (other-generated) (Colle et al., 2020). Whereas significant sensory attenuation was found in the control group, this effect was absent in participants with BPD (Colle et al., 2020), which suggests that these participants had a reduced sense of agency over their own actions. Interestingly, sensory attenuation was intact in participants with BPD who self-harmed, which the authors interpret as support for the hypothesis that individuals may self-injure to "feel real". As discussed above in the section on perceptual SOD, a greater sense of agency over actions performed by an artificial hand was reported by individuals with BPD compared with controls during an active version of the RHI, in both spatially congruent and incongruent conditions (Möller et al., 2020). These findings of altered experiences of agency in BPD (Colle et al., 2020; Möller et al., 2020) may point towards impairments in processing action-response contingencies when predicting whether an action is likely self-generated or other-generated.

3.3. Mental-state SOD in BPD

Most research has been done in the domain of mental-state SOD in BPD. Many studies in this area have focused on the role of impairments in mentalizing in BPD. Mentalizing refers to the ability to reflect on the mental states (e.g. thoughts, feelings, and intentions) of self and others (Fonagy and Luyten, 2009). Evidence suggests that mentalizing is multidimensional in nature, and that the different dimensions can be organized along the following four polarities: automatic-controlled, internal-external, cognitive-affective, and self-other (Luyten and Fonagy, 2015). In BPD, deficits in mentalizing seem to arise especially in

response to (interpersonal/attachment) stressors and in more complex tasks requiring the integration of different perspectives and mentalizing dimensions (Luyten et al., 2020; Petersen et al., 2016; Sharp and Vanwoerden, 2015).

A recent meta-analysis of studies found that the most pronounced deficits in mentalizing in BPD patients were found in tasks assessing cognitive ToM, such as the Faux Pas tests or movie- or cartoon-based mentalizing tasks, in which the participant needs to understand the intention of a character from the character's own perspective in a complex social interaction (Németh et al., 2018). For instance, one study found deficits in a sample of 18 BPD patients, compared with 20 control participants, in a joke appreciation task and in a false-belief task, but only for more complex cartoons or stories that required the simultaneous awareness and integration of the differing perspectives of multiple characters (Petersen et al., 2016). Moreover, in an interview-based study of mentalizing in 40 participants, BPD patients were found to have the greatest problems when mentalizing from the perspective of others as separate from the self (Colle et al., 2018). Individuals with BPD have also been found to report a lower tendency to take another person's perspective compared with controls, as measured with the Interpersonal Reactivity Index (Dziobek et al., 2011; Flasbeck et al., 2019b; Harari et al., 2010; New et al., 2012; Petersen et al., 2016). Reduced perspective taking suggests that BPD patients may assume that they understand others' thoughts and feelings based on their own mental states, and are less able than controls to imagine how others' mental states may be different from their own (Fonagy and Luyten, 2009). Mentalizing thus seems to be especially taxing for individuals with BPD when self and other perspectives are in conflict and need to be co-represented. This is in line with SOD impairment in BPD, since SOD, as underpinned by the TPJ, allows one to switch between self and other representations in a flexible manner (Lamm et al., 2016; Sowden and Shah, 2014).

At the same time, BPD patients report experiencing more personal distress in reaction to others' distress, compared with controls, on the Interpersonal Reactivity Index (Dziobek et al., 2011; Flasbeck et al., 2019b; Harari et al., 2010; New et al., 2012; Petersen et al., 2016). This suggests that individuals with BPD may experience others' emotions as if they are their own, a phenomenon called emotional contagion. Although emotional contagion is regarded as a key feature of BPD (Herpertz and Bertsch, 2015; Roepke et al., 2012), only one study to date has investigated emotional contagion in BPD using a behavioral paradigm, finding enhanced emotional reactions in individuals with BPD (n = 34) compared with controls (n = 32) when observing others' social communications that had a neutral verbal content but contained non-verbally expressed emotion (Niedtfeld, 2017). It may be that BPD patients automatically mirror others' non-verbally expressed emotion without being able to distinguish their own and others' emotional experience, which would reflect a deficit in SOD for emotional states of self and other. This deficit may contribute to these individuals' profound affective instability; however, more research is needed to investigate the influence of others' emotional expressions on individuals with BPD.

4. Neural underpinnings of self-other distinction in BPD

An imbalance between the two neural networks involved in self—other processing has been proposed to underlie SOD impairment in BPD (Fonagy and Luyten, 2009; Ripoll et al., 2013). First, individuals with BPD may resonate more strongly with others due to increased activation of automatic mirroring in the SR network. The SR network includes neural areas involved in emotion processing, such as the amygdala and the insula, as well as areas rich in mirror neurons (i.e. inferior parietal lobule, inferior frontal gyrus, somatosensory and sensorimotor cortices) (Ripoll et al., 2013). Second, especially under high task demands or high (attachment/interpersonal) stress (Nolte et al., 2013), BPD patients may be less able to differentiate this shared activation of others' mental states from their own experience and exert control over these self–other representations due to dysregulation in the MSA system, which comprises

the mPFC, superior temporal sulcus (STS), precuneus, and the TPJ (Luyten and Fonagy, 2015; Ripoll et al., 2013).

Consistent with these assumptions, in fMRI studies of basic mentalizing tasks involving visual socio-emotional stimuli, BPD patients have been found to recruit the somatosensory and premotor cortices and the amygdala (i.e. the SR network) to a greater degree than controls, suggesting that they resonate more strongly with others' emotions (Dziobek et al., 2011; Mier et al., 2013; Schulze et al., 2016; Sosic-Vasic et al., 2019). This hyperactivation of the SR network coincided with hypoactivation of the MSA network, notably in the STS and superior temporal gyrus (Dziobek et al., 2011; Haas and Miller, 2015; Mier et al., 2013), the right TPJ (Haas and Miller, 2015), and the inferior frontal gyrus (Mier et al., 2013; Sosic-Vasic et al., 2019), all of which have been implicated in higher-order mentalizing and SOD (van Veluw and Chance, 2014). Evidence of increased sharing of others' mental states (i. e. SR hyperactivation) combined with impaired self-other control (i.e. MSA hypoactivation) may reflect a vulnerability for self-other conflation in BPD (Luyten and Fonagy, 2015).

In imaging studies using more abstract and symbolic mentalizing tasks, however, BPD patients showed hyperactivation of the right TPJ, precuneus, and prefrontal cortices, in combination with hypoactivation of somatosensory areas (Beeney et al., 2016; Bozzatello et al., 2019). This hyperactivation of the MSA network did not relate to improved behavioral performance; instead, it was associated with reduced temporal maintenance of self-other representations (Beeney et al., 2016) and self-reported identity disturbance (Bozzatello et al., 2019). Hyperactivation of the MSA network may reflect an inefficient attempt to overcompensate for deficient SOD in BPD, leading these individuals to hypermentalize - that is, to engage in excessive and overly cognitive mentalizing that is not rooted in embodied experience (Beeney et al., 2016), as also evidenced by hypoactivation of the SR network. Studies have indeed suggested that hypermentalizing may be a key feature of BPD, particularly in response to challenging interpersonal situations or experiences (Bo et al., 2015; Sharp and Vanwoerden, 2015).

These findings suggest that BPD patients may be more vulnerable to self-other conflation due to increased resonance with others' mental states, as evidenced by hyperactivity of the SR network, and they may be less able to control these shared self-other representations due to dysregulation (i.e. both hyper- and hypoactivation) of the MSA network, particularly the prefrontal cortex and TPJ (Luyten and Fonagy, 2015; Ripoll et al., 2013). Whereas individuals with BPD may activate either the SR or the MSA network, an integrated recruitment of both networks may be more adaptive in order to integrate multiple streams of information, including information about self and others.

This SR MSA imbalance in BPD may be impacted by emotional arousal and interpersonal stressors that activate the attachment system in BPD (Fonagy and Luyten, 2009). Indeed, attachment-related stress has been found to lead to a deactivation of MSA areas crucial for SOD, namely the left TPJ and left superior temporal sulcus (STS) (Nolte et al., 2013). In BPD patients, fMRI studies show functional abnormalities in the fronto-limbic network including regions involved in emotion processing (e.g. amygdala, insula) and frontal brain regions implicated in regulatory control processes (e.g. anterior cingulate cortex (ACC), mPFC, orbitofrontal cortex, and dorsolateral prefrontal cortex) (Bertsch et al., 2018; Minzenberg et al., 2007; Posner et al., 2003; Schulze et al., 2016; van Zutphen et al., 2015). This fronto-limbic imbalance is thought to explain emotional dysregulation in BPD, although a recent review points towards several methodological issues that weaken this claim (Sicorello and Schmahl, 2021). Reduced emotion regulation may impact SOD in BPD, as reduced functional connectivity was found between the ACC and the MSA network, including areas that are part of the TPJ (O'Neill et al., 2015). Emotional dysregulation may hamper BPD patients' capacity for controlled mentalizing, including their capacity for SOD (Luyten and Fonagy, 2015). Although clinically, SOD impairment in BPD typically appears to occur in the context of emotional dysregulation, more systematic research is needed to substantiate this assumption. The context-dependency of SOD impairment may be typical for BPD, and may be less characteristic of SOD in other mental disorders, such as schizophrenia (Prikken et al., 2019) and autism spectrum disorder (ASD) (Van de Cruys et al., 2014), although it may also be typical in a subset of patients with eating disorders, particularly in those with BPD features (Barca and Pezzulo, 2020; Sacchetti et al., 2019).

As noted earlier, the TPJ is a privileged neural structure that is implicated in SOD tasks at different levels of functioning (Quesque and Brass, 2019), especially the right-hemisphere TPJ (Convento et al., 2018; Krall et al., 2015; Martin et al., 2018; Sowden and Catmur, 2015; Tsakiris et al., 2008). The right TPJ has furthermore been implicated in dissociative experiences (Blanke and Arzy, 2005). However, a meta-analysis found no important differences between the left and right TPJ during mentalizing (Quesque and Brass, 2019). In what follows, we will discuss findings on the structure and function of the bilateral TPJ in BPD.

Structurally, the parietal cortex (including the postcentral, supramarginal, and angular gyri, the TPJ, the superior parietal lobe, and the precuneus) was smaller in size and showed stronger leftward asymmetry (i.e. smaller right hemisphere parietal cortices) in 30 BPD patients compared with 25 control subjects, and leftward asymmetry was related to increased schizoid personality features and psychotic symptoms (Irle et al., 2005). Furthermore, reduced cortical thickness in the left TPJ was found in 18 individuals with BPD compared with 20 control subjects, and this was associated with self-reported difficulties in describing their own feelings as measured using the Toronto Alexithymia Scale (Bøen et al., 2014).

Functionally, hypoactivation of the right TPJ and the right STS during emotional perspective taking was found to relate to borderline features in 82 nonclinical participants (Haas and Miller, 2015). However, hyperactivation in the right TPJ was found in a study of 17 BPD participants compared with 17 healthy controls while evaluating own and others' personality traits (Beeney et al., 2016), and in 24 BPD patients compared with 24 control participants when presented with idiosyncratic unresolved life events (Bozzatello et al., 2019). It remains unclear whether TPJ hyperactivation reflects improved SOD or rather an inefficient attempt to compensate for SOD impairment. In two studies, both hypo- and hyperactivation of the TPJ were found in individuals with BPD compared with controls in the same task, depending on the emotional valence and context of the social stimuli that were presented (Flasbeck et al., 2019a; van Schie et al., 2019). For instance, when processing social feedback, BPD patients (n = 26) were more affected by, and showed right TPJ hyperactivation in response to, negative versus positive social feedback, while controls (n = 32) exhibited the opposite pattern (van Schie et al., 2019). As the TPJ is involved in reorienting attention to social cues (Igelstrom et al., 2016; Krall et al., 2016), the TPJ dysregulation found in individuals with BPD may thus also reflect aberrant attention to social stimuli compared with controls.

In conclusion, BPD patients are found to be characterized by structural and functional abnormalities in the TPJ, mostly in the right hemisphere, which plays a crucial role in SOD (Quesque and Brass, 2019). Functionally, both hypo- and hyperactivation of the right TPJ was found in BPD, often depending on the emotional and social context, as well as the specific task demands (i.e. passive viewing or active mentalizing). This dysregulation of the TPJ can be understood in the context of imbalances between the SR and MSA networks (Luyten and Fonagy, 2015; Ripoll et al., 2013), as well as fronto-limbic dysfunction in BPD (Bertsch et al., 2018). It is important to note that in the abovementioned fMRI studies, there was no explicit need for participants to distinguish between self and other representations, which hampers the ability to draw definite conclusions on TPJ activation during SOD in BPD. Furthermore, no studies to date have investigated the neural correlates of impairments in embodied SOD in BPD. Future research should investigate TPJ activation during well-validated SOD tasks in BPD.

5. Developmental origins of self-other distinction impairment in BPD

SOD is assumed to be a developmental capacity (Decety and Michalska, 2010). Indeed, the SR network, which does not differentiate between self and other agents, is present from infancy (Decety and Sommerville, 2003; Luyten and Fonagy, 2015), but it is only through repeated (interpersonal) experiences that the infant can learn to differentiate the self from the (social) environment (Fotopoulou and Tsakiris, 2017). This development is assumed to be impacted by the quality of early social interactions (Fonagy et al., 2007), specifically by the level of contingency of the caregivers' responses to the infant's actions (Gergely and Watson, 1999). "Good enough" caregivers tend to respond to the infant's actions in a way that is both contingent (i.e. attuned to the infant's actual experience) and marked (i.e. signaling parent-infant distinctiveness) (Fonagy et al., 2002). Mothers who responded in an intermittently contingent, rather than a non-contingent or perfectly contingent, manner were rated as more attuned to their infant than mothers who responded in a non-contingent or perfectly contingent manner (Bornstein and Manian, 2013). Moderate levels of parent-infant contingency, as opposed to high or low levels, have been found to predict attachment security in the infant (Beebe et al., 2010; Isabella et al., 1989; Shai and Belsky, 2017), consistent with theoretical views (Fonagy et al., 2007), but are also deemed crucial for the development of SOD (de Bézenac et al., 2018).

Infants have been found to be able to detect varying degrees of action-response contingencies (Bigelow and Rochat, 2006; Rochat, 2001) and may use them to learn to differentiate the self from the (social) environment (Bahrick and Watson, 1985; Rochat and Striano, 2002). From birth, infants are particularly focused on the perfectly contingent consequences of their own actions (e.g. kicking their legs and seeing legs kick) to develop a bodily sense of self, and have been suggested to switch to a focus on high but imperfectly contingent consequences of their actions (e.g. smiling and seeing their parent smile) to tune into their social environment at around 3-6 months of age (Hiraki, 2006; Koós and Gergely, 2001; Rochat, 2001; Zmyj et al., 2009). However, when predictable attachment figures who provide such high-but-imperfect social contingencies are not reliably available, the infant may revert to a preference for perfect imitative contingencies instead of social contingencies, which has been described as a "flickering contingency switch" or a conflict between self- and other-oriented attention (Koós and Gergely, 2001). In support of this hypothesis, a study found that infants of highly attuned mothers preferred a condition in which mothers provided "natural", intermittently contingent responses as opposed to a highly contingent (imitative) or a non-contingent condition, whereas infants who experienced less attuned interactions with their mothers did not distinguish between the conditions (Markova and Legerstee, 2006). Similarly, infants who experienced less coordination with their mother in daily life preferred to look at perfectly synchronous self-mother stimulation, in contrast to infants of more attuned mothers (Maister et al., 2020).

Problems with mutual attunement between infant and caregiver may be particularly relevant for individuals with BPD, as studies have amply demonstrated high levels of trauma (Porter et al., 2020) and/or disorganized attachment (Agrawal et al., 2004) in the developmental history of these individuals. Disorganized attachment has been associated with inconsistent parental reactions that are at times too congruent, overwhelming the infant with the parent's own distress in response to the infant's distress (i.e. lack of marking), and at other times too incongruent, by the parent being uninvolved or unable to represent the infant's subjective experience (i.e. lack of contingency) (Beebe et al., 2008; Kim et al., 2014; Lyons-Ruth et al., 1999). Along the same lines, a caregiver who is abusive or neglectful typically responds to the child in a way that is neither marked nor contingent (Luyten et al., 2019). Growing up in such a "deviant contingency environment" may have reduced BPD patients' ability to distinguish between perfect (i.e.

self-generated) and high-but-imperfect (i.e. other-generated) levels of action–response contingency, which may help explain adult BPD patients' difficulties in distinguishing between different levels of contingency in the RHI experiment (Bekrater-Bodmann et al., 2016; Neustadter et al., 2019a). Furthermore, a reduced preference for social contingencies may have hampered their ability to engage with their social environment. Lastly, it may be that individuals with BPD might not have had the same opportunities to practice making fine-grained SODs in a context that is safe and at the same time challenging, that is, high in self–other ambiguity (de Bézenac et al., 2018). However, in the absence of direct empirical studies, the assumption that disrupted contingency of caregiver responsivity and SOD impairment in BPD may be related remains speculative.

Moreover, biological predisposition may hamper SOD development, either alone or in interaction with early adversity (Gunderson and Lyons-Ruth, 2008). Indeed, several gene-environment studies have shown that genetic vulnerabilities may increase the impact of disrupted early relationships on socio-cognitive development in BPD patients (Carpenter et al., 2013; Gunderson and Lyons-Ruth, 2008; Rioux et al., 2018). For instance, a recent study found that, in both BPD and non-BPD participants, high levels of childhood trauma [as measured using the Childhood Trauma Questionnaire (CTQ)] were associated with reduced perspective taking [as measured using the Interpersonal Reactivity Index (IRI)] only in individuals who were carriers of the short (S-) allele of the 5HT serotonin transporter gene linked polymorphic region (5HTTLPR), while no relationship between trauma and perspective taking was evident in carriers of the long (L-) allele (Flasbeck et al., 2019c). A study by the same research group showed that carriers of the A-allele of the rs53576 single-nucleotide polymorphism of the oxytocin receptor gene (OXTR), especially those with BPD, rated psychologically painful and neutral interactions as more intense in a social interaction empathy task, and showed a positive association between childhood trauma (measured using the CTQ) and empathy for pain in the task, whereas no such association was present in carriers of the GG-allele (Flasbeck et al., 2018). As enhanced affective sharing and reduced perspective taking may point towards SOD impairments, these findings suggest that childhood trauma may disrupt the development of SOD in BPD only in individuals with less efficient forms of serotonergic and oxytocin system genes. Interestingly, compared with mothers carrying more efficient variants of these genes, mothers carrying the S-allele of the 5HTLLPR or the A-allele of the OXTR gene showed lower levels of sensitive responsiveness to their toddlers (Bakermans-Kranenburg and van IJzendoorn, 2008), who may have inherited their mother's genetic vulnerability and may be more affected by the impaired responsivity of their mothers. More research in this domain is needed but, based on existing findings, we propose the hypothesis that disrupted contingency of caregiver responsivity, in interaction with genetic vulnerabilities, may result in impaired SOD development in BPD.

6. A new model of impairments in switching between self and other representations and interpersonal attunement in BPD

The evidence reviewed above suggests that impaired SOD may play a key role in BPD, although more research in this area is needed. We will first discuss SOD impairments in BPD on the embodied level as supported by multisensory integration. Next, we will zoom in on BPD patients' impairments in distinguishing and switching between abstract self and other representations independent of multisensory integration and the consequences for interpersonal attunement.

Specifically, on an embodied level of SOD, that is, distinguishing one's own body and actions from those of others, behavioral evidence suggests that multisensory integration and contingency detection mechanisms may be disturbed in BPD (Bekrater-Bodmann et al., 2016; Colle et al., 2020; Hauschild et al., 2018; Löffler et al., 2020; Neustadter et al., 2019a). BPD patients were more sensitive to incorporating other-generated actions and perceptions into the self, possibly due to an

overreliance on of exteroceptive signals in the context of disturbed interoception (Back and Bertsch, 2020; Löffler et al., 2018). As a result, individuals with BPD seem to experience less ownership over their own body (Löffler et al., 2020) and less agency over their own actions (Colle et al., 2020). This shows that BPD patients' profound identity diffusion (Wilkinson-Ryan and Westen, 2000) and reduced agency over their life narratives (Lind et al., 2019) is also expressed on a very basic and embodied level.

Dissociation can be seen as an extreme loss of embodied SOD in BPD (Bekrater-Bodmann et al., 2016; Löffler et al., 2020). Dissociative experiences in BPD are often induced by stress (Stiglmayr et al., 2008), which begs the question of whether impairments in embodied SOD in BPD are trait-like or mostly transient and influenced by stress. BPD patients' lower threshold for switching from controlled to automatic mentalizing under stress (Fonagy and Luyten, 2009; Nolte et al., 2010) as a result of fronto-limbic dysfunction in BPD (Krause-Utz and Elzinga, 2018) may play an important role in this context. Non-suicidal self-injury, which is prevalent in BPD (Buelens et al., 2020), may end dissociative episodes by generating physical sensations that allow the individual to "feel real" again (Klonsky, 2007). The perfect contingency between seeing one's own action and experiencing pain during self-harm creates a salient experience of interoceptive-exteroceptive match, which may help to reestablish perceptual SOD. Indeed, the sense of agency over one's actions was found to be reduced in BPD patients, but preserved in BPD patients who self-harmed (Colle et al., 2020).

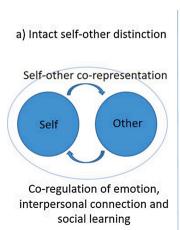
Impairments in embodied SOD in BPD may have important interpersonal consequences. As described in detail above, BPD patients were found to experience others' actions and body parts as belonging to the self (Hauschild et al., 2018; Möller et al., 2020; Neustadter et al., 2019a), showing that they are more vulnerable to experiencing embodied self-other overlap during proximal social interactions. This may relate to BPD patients' described tendency to "merge" with others and their fears of engulfment, that is, of being "subsumed" by others (Bender and Skodol, 2007). As a result of impaired embodied SOD, BPD patients may experience proximal other-generated stimuli as more intrusive (Schienle et al., 2015) and prefer unknown others to keep their distance (Fineberg et al., 2018). Embodied SOD impairment in BPD may thus result in a tendency for self-other merging on the one hand, and a defensive preference for self-other distance on the other hand. This may relate to the typical approach–avoidance dilemma's observed in BPD patients' relationships, and their use of conflicting attachment strategies (Beeney et al., 2017; Miljkovitch et al., 2018). More research is needed to elucidate the role of embodied SOD impairments in BPD patients' interpersonal functioning.

From these basic SOD capacities on the level of action and perception, more higher-order capacities for distinguishing and switching

between mental representations of self and other are assumed to develop (Krol et al., 2019; Quesque and Brass, 2019). The specific pattern of deficits found in BPD in this area are in line with an impaired capacity to switch flexibly between representations of self and other (Sowden and Shah, 2014). Whereas intact self-other switching may allow an individual to co-represent "self" and "other" simultaneously (see Fig. 1a), individuals with BPD may show impairments in this capacity and instead represent either "self" or "other" (see Fig. 1b).

On the one hand, when individuals with BPD are focused on their self-representation, they seem to have difficulty shifting from their own to another person's perspective, consistent with egocentric bias (Silani et al., 2013), as evidenced by reduced perspective-taking abilities (Colle et al., 2018; Petersen et al., 2016). This may result in them attributing their own mental states to others instead of appreciating others' perspectives as separate from their own. On the other hand, when individuals with BPD are focused on others' mental states, it may be very hard for them to inhibit the automatic resonance with others' mental states in order to represent their own, consistent with altercentric (or allocentric) bias (Hoffmann et al., 2016). This may cause them to experience personal distress in response to others' distress (Dinsdale and Crespi, 2013; Harari et al., 2010) and to mistakenly perceive others' emotions as their own (Niedtfeld, 2017). Instead of integrating self and other perspectives in a differentiated way, individuals with BPD may oscillate between representing either themselves, and assuming that others think and feel the way they do (i.e. egocentric bias), or representing others, and taking over others' mental states as if they were their own (i.e. altercentric bias) (see Fig. 1b).

According to this model, an impaired ability for flexible self-other switching in BPD may result in either egocentric or altercentric bias. Whether egocentric versus altercentric bias is expressed in BPD may depend on both state and trait self-awareness and other-awareness. Indeed, low self-awareness and high other-focus are expected to result in altercentric bias when representing one's own mental states, whereas heightened self-awareness and low other-focus should result in egocentric bias when representing others' perspective. Future studies that experimentally induce a momentary focus on the self versus a focus on the other are therefore needed, as, depending on the focus on self versus other, an altercentric or egocentric bias, respectively, should be observed in BPD patients. As outlined, other factors, such as the affective context (e.g. whether participants are in emotional hyperarousal or experiential avoidance) or the interpersonal context (e.g. the characteristics of the interaction and of the interaction partner), may also be of importance here. For instance, concerning the interpersonal context, attachment hyperactivation strategies associated with anxious attachment should be associated with an altercentric bias in BPD by increasing attention to social cues, whereas attachment deactivation strategies can be expected to lead to decreased altercentric bias by decreasing



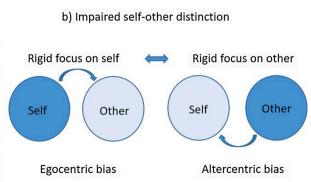


Fig. 1. Proposed model of the nature of self—other distinction (SOD) impairment in border-line personality disorder (BPD). Instead of flexibly switching between self and other representations, resulting in the co-representation of self and other (a), BPD patients seem to rigidly present either "self" or "other" (b), which may make them less able to benefit from attuned social interactions for the co-regulation of emotion and for social learning more generally, or to experience closeness to others as safe, comforting, and supportive.

attention to social cues. Hence, future studies in BPD patients might either investigate SOD impairments in patients with different attachment styles, or they might attempt to experimentally manipulate the use of different secondary attachment strategies to assess their impact on SOD.

A crucial consequence of this proposed impairment in switching between self and other representations in BPD is that it may hamper the ability of individuals with BPD to engage in truly reciprocal, attuned interaction with others. Indeed, complex social interactions are high in self-other ambiguity and require constant and flexible shifting between self and other representations in order to grasp what each interaction partner is experiencing and how these experiences impact one another. The notion of SOD being a prerequisite for interpersonal attunement is supported by recent studies showing that interpersonal attunement is underpinned by inter-brain neural synchrony (IBS), that is, synchronized brain activity between interaction partners, specifically in areas involved in SOD, that is, the TPJ and prefrontal cortex (Gvirts and Perlmutter, 2019; Shamay-Tsoory et al., 2019), and this relates to behavioral synchrony.

Gvirts and Perlmutter (2019) suggest that the TPJ may serve as a "mutual social attention" system, reorienting or shifting the individual's attention towards the social partner to tune into the interaction. Indeed, two studies have found that perspective taking (which requires SOD and is reduced in BPD) related to improved interpersonal behavior synchrony in dyads (Novembre et al., 2019; Reiss et al., 2019). SOD, in terms of shifting one's perspective from "self" to "other" and attempting to represent the other's mind as separate from the self while maintaining an intact self-representation, may be important to align oneself with an interaction partner and to coordinate one's actions with those of others. Crucially, this process was found to be disturbed in BPD. Indeed, synchronized neural responses in the TPJ during a simple joint attention task were found in dyads that included healthy controls or participants whose BPD was in remission, whereas no such IBS was found in dyads that included a participant with a current BPD diagnosis (Bilek et al., 2017). In this study, lower IBS during joint attention was associated with higher levels of childhood trauma as assessed with the CTQ. Behavioral synchrony was also found to be reduced in BPD patients during a musical improvisation (Foubert et al., 2017). Furthermore, during a naturalistic interaction with an interviewer, BPD patients' (n = 16) whole-body movements were less synchronized with those of the interviewer compared with those of control participants (n = 15) after the administration of intranasal oxytocin, and reduced synchrony was again associated with childhood trauma as measured with the CTQ (Ramseyer et al., 2020). These findings suggest that individuals with BPD show reduced interpersonal synchrony, and that this is especially prominent in individuals who experienced childhood adversity, in line with the hypothesis discussed above that disturbed contingency of caregiver responsivity may reduce BPD patients' ability to engage with their social environment (Koós and Gergely, 2001).

A reduced capacity to engage in attuned social interaction in BPD may furthermore be related to dysregulation of the attachment system, as oxytocin, a key neuromodulator of the attachment system, has been found to be related to neural IBS (Mu et al., 2016) and to behavioral synchrony (Feldman et al., 2019). Interestingly, the administration of intranasal oxytocin has been found to enhance both speed and performance in experimental SOD tasks (Colonnello et al., 2013; Tomova et al., 2019), and to reduce self-bias in the speed of labelling self-other traits (Zhao et al., 2019, 2016). Furthermore, low endogenous plasma levels of oxytocin have been related to reduced activity in the MSA network, including the TPJ, the neural substrate of SOD (Lancaster et al., 2015). Another study showed that the administration of intranasal oxytocin increased activation in the TPJ and connectivity between the TPJ and the mPFC in individuals with schizophrenia, which related behaviourally to improved SOD in a ToM task (De Coster et al., 2019).

Through its connections with the dopaminergic reward system, oxytocin is hypothesized to regulate attention to social cues by guiding

the individual as to whom to align with, through signalling which social cues and interactions are rewarding and should be selectively attended to (Shamay-Tsoory and Abu-Akel, 2016). Impairments in the attachment system in BPD, as evidenced by high reports of attachment insecurity (Agrawal et al., 2004) and dysfunction of the oxytocin system (Carrasco et al., 2020), may leave BPD patients without a "filter" to allow them to decide which interactions are safe and rewarding to tune into. Indeed, the administration of intranasal oxytocin was found to normalize approach motivation (Domes et al., 2019) and approach—avoidance behaviour (Schneider et al., 2020) in response to socio-emotional cues in individuals with BPD. However, this increased motivation may not translate into improved social alignment, as the administration of oxytocin has also been found to reduce behavioural synchrony in BPD (Ramseyer et al., 2020). Clearly, more research is needed to investigate the role of oxytocin in SOD and interpersonal synchrony in BPD.

Importantly, IBS has been found to facilitate social alignment (Shamay-Tsoory et al., 2019), emotion co-regulation (Reindl et al., 2018), and social learning (Davidesco et al., 2019; Pan et al., 2018). Reduced IBS and interpersonal synchrony in BPD may thus potentially explain why individuals with BPD seem less able to reap the benefits of social interactions in terms of emotion regulation, social learning, and experiencing closeness to others. Individuals with BPD have been found to have high levels of epistemic mistrust (Fonagy et al., 2019; Orme et al., 2019), that is, a decreased ability to learn from others and adopt their perspective, making these individuals seem "hard to reach" (Fonagy et al., 2015, 2017). Furthermore, emotion co-regulation is typically disturbed in individuals with BPD, relating to their profound affective instability (Hughes et al., 2012), and they frequently report feeling lonely and socially isolated (Liebke et al., 2017). In essence, treatment for BPD may be effective when it is aimed at restoring the patient's capacity for SOD in order to engage in attuned social interactions, so they can start to learn from others, adapt more flexibly to changing circumstances, and co-regulate their intense emotions.

7. Directions for future research

Based on our review of the existing studies on SOD in BPD and on our conceptual model of SOD impairment, we propose several recommendations for future research.

First, more efforts are needed to replicate the findings concerning SOD impairments in BPD at the perceptual and the action level using well-validated behavioral paradigms, and to investigate the purported role of interoception in these impairments. Also, more empirical work is needed to investigate the basic assumptions of the proposed model of BPD as being characterized by impairments in switching between self and other representations and an impaired ability to engage in attuned social interactions. Furthermore, there is a need to investigate neural activations in BPD patients while performing established SOD tasks in order to draw firmer conclusions about the neural underpinnings of SOD impairment in BPD.

Second, in line with calls for increased efforts towards establishing a so-called "second-person neuroscience" (Schilbach et al., 2013) there is a need to investigate SOD in BPD during real-time interactional social paradigms, instead of regarding SOD mainly as an intrapsychic mechanism. Indeed, as the present review aims to demonstrate, SOD can best be understood in the context of the dynamic interplay between self—other sharing and SOD, which may be impacted by both interaction partners and the quality of the interaction (Redcay and Schilbach, 2019). Future research should investigate neural and behavioral interpersonal synchrony in dyads including BPD patients, and its impact on social learning and emotion regulation, in order to elucidate impairments in these crucial processes in BPD.

Finally, comparative studies are needed to characterize shared and distinctive features of SOD impairment in BPD compared to other mental disorders. For instance, severe SOD impairment has also been found in schizophrenia (van der Weiden et al., 2015). Embodied SOD

impairments in BPD may reflect to some extent a transdiagnostic psychosis-proneness (Neustadter et al., 2019a). However, as we have emphasized throughout this review, a distinctive feature of SOD impairments in BPD seems to be that they may be more context-dependent and stress-induced compared to SOD impairments in psychosis (Fonagy and Luyten, 2009; Ripoll et al., 2013). Moreover, SOD impairments in psychosis also typically appear to be more extreme. Indeed, under normal circumstances, BPD patients may very well be able to distinguish their own body, actions, and mental states from those of others; however, problems may arise with increasing (attachment) stress and in challenging interpersonal contexts high in self-other ambiguity (Brüne, 2016). Furthermore, SOD impairment has also been demonstrated in anorexia nervosa (AN) using the RHI (Keizer et al., 2014), and restricted eating has been conceptualized as an active strategy to reduce interoceptive uncertainty in AN (Barca and Pezzulo, 2020). Individuals with ASD, in turn, are thought to be characterized by inflexibly precise processing of prediction errors (Van de Cruys et al., 2014), resulting in increased interoceptive awareness and less RHI proneness in ASD (Palmer et al., 2013; Schauder et al., 2015). Whether predictive processing of self-other ambiguity is highly imprecise (i.e. in BPD, schizophrenia or AN) or too precise (e.g. in ASD), these aberrancies may compromise the capacity for SOD in social interactions. The fact that SOD impairments are present in different types of mental disorders suggests that they may represent, to some extent, a transdiagnostic marker of psychopathology (Ereira et al., 2018), although differences seem to exist both in the nature of these problems and potentially also in their role.

8. Clinical implications

The proposed model of SOD impairment in BPD has important implications for the treatment of BPD. First, preliminary evidence shows that SOD may be impaired in BPD at a very basic and bodily level (Bekrater-Bodmann et al., 2016; Colle et al., 2020; Hauschild et al., 2018; Löffler et al., 2020; Neustadter et al., 2019a), calling attention to the need to consider the embodied aspects in the treatment of patients with BPD. Indeed, these patients seem to have difficulty distinguishing their own body and actions from those of others, especially during proximal embodied interactions that produce high levels of self-other ambiguity - for instance, when engaging in coordinated movements or experiencing interpersonal touch. In such circumstances, individuals with BPD may experience less ownership and agency over their own body and actions, and mistake others' actions for their own, which may be a distressing experience. Non-verbal therapies that involve the co-production of intricate joint actions, such as music therapy (Foubert et al., 2017, 2020) and dance/movement therapy (Behrends et al., 2012), may provide BPD patients with valuable opportunities to practice maintaining SOD during such challenging situations. Therapists may support this learning process by providing a safe context in order to decrease feelings of distress, and by scaffolding BPD patients' ability to focus on their own experience while engaging with others. Traditional face-to-face psychotherapy may also target BPD patients' capacity for SOD at the embodied level by providing non-verbal attunement and mirroring of the patient's experience in a way that is contingent and at the same time marked (Samuelsson and Rosberg, 2018). This approach may provide the patient with the opportunity to experience themselves as related to but at the same time distinct from the therapist, which may support the restoration of a capacity for SOD. Indeed, medium levels, as opposed to very high or low levels, of behavioral synchrony have been found to predict psychotherapy outcomes in a sample of patients with mood and anxiety disorders (Paulick et al., 2018). More research is needed to investigate the impact of patient-therapist contingency on the improvement of SOD and BPD-related symptoms.

Second, evidence suggests that BPD is characterized by a reduced capacity to distinguish and co-represent self and other mental representations (Niedtfeld, 2017; Petersen et al., 2016), emphasizing the need

for the patient and therapist to explicitly discuss and mentalize together about differing perspectives of self and other (Fonagy and Bateman, 2006). Indeed, when focused on their own narrative, individuals with BPD may assume that others think and feel the same way as they do. Validating the patient's point of view, while discussing how others' perspectives may differ, may help these individuals to integrate the two perspectives. On the other hand, when highly focused on others, BPD patients may take over others' thoughts, views, and feelings as their own. In these circumstances, exploring the patients' own thoughts and feelings, while considering how these may have been influenced by others, may repair a sense of SOD and mitigate these patients' profound sense of identity diffusion (Sollberger et al., 2012).

Different evidence-based treatments for BPD, such as transferencefocused psychotherapy (TFP), dialectical behavior therapy (DBT) or mentalization-based treatment (MBT), may currently indirectly address BPD patients' capacity for SOD. Indeed, MBT was found to significantly improve identity integration and self-control in BPD patients (Bales et al., 2012), and TFP combined with modules of DBT skills training significantly reduced BPD patients' identity diffusion and instability in sense of self and others (Sollberger et al., 2015). Although this remains to be empirically verified, interventions targeting SOD may be those directed at helping patients to distinguish between their own thoughts and feelings and those of the therapist in TFP (Levy et al., 2006), interventions aimed at fostering the patients' emotion regulation strategies in difficult interpersonal contexts in DBT (Mehlum, 2021), or interventions that help patients to reflect on their own mental states and those of others in MBT (Morken et al., 2017). A more explicit focus on strengthening SOD may enhance the effectiveness of treatment for BPD patients, although more research is needed to determine whether such interventions lead to improvements in treatment outcome.

9. Conclusions

The present study reviewed evidence of potential impairments in SOD - that is, the capacity to distinguish one's own body, actions and mental representations from those of others - in individuals with BPD. At the embodied level, existing findings suggest a reduced capacity for contingency detection and multisensory integration in BPD, resulting in reduced senses of ownership and agency and vulnerability to experiencing self-other bodily overlap. However, it is clear that more research is needed to replicate these findings. In terms of distinguishing self and other mental representations in BPD, evidence shows impaired integration of information about both self and others when self and other perspectives need to be co-represented, which is corroborated by dysregulation in the neural networks involved in self-other sharing and SOD. Based on these findings, we have presented a new model of SOD impairment in BPD as being characterized by impairments in flexibly switching between self and other representations and a reduced ability to engage in attuned, reciprocal social interaction, which may guide future research efforts.

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Declaration of Competing Interest

Patrick Luyten has been involved in the development, training, and dissemination of mentalization-based treatments.

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