

Neuroscience of Consciousness, 2019, 5(1): niz017

doi: 10.1093/nc/niz017 Research article

Induced illusory body ownership in borderline personality disorder

Eli S. Neustadter () ^{1,2,*,†}, Sarah K. Fineberg () ^{1,†}, Jacob Leavitt³, Meagan M. Carr^{1,4} and Philip R. Corlett¹

¹Yale Department of Psychiatry, Yale University, 300 George St., Suite 901, New Haven, CT 06511, USA; ²Yale School of Medicine, Yale University, 333 Cedar St., New Haven, CT 06510, USA; ³Department of Psychology, University of Houston, Heyne Building, #126, Houston, TX 77204, USA; ⁴Department of Psychology, Eastern Michigan State University, 341 Science Complex, Ypsilanti, MI 48197, USA

*Correspondence address. Yale Department of Psychiatry, Yale University, 300 George St., Suite 901, New Haven, CT 06511, USA. Tel: 203-974-7265; E-mail: eli.neustadter@yale.edu

[†]These authors contributed equally to this work.

Abstract

One aspect of selfhood that may have relevance for borderline personality disorder (BPD) is variation in sense of body ownership. We employed the rubber hand illusion to manipulate sense of body ownership in BPD. We extended previous research on illusory body ownership in BPD by testing: (i) two illusion conditions: asynchronous and synchronous stimulation, (ii) relationship between illusion experience and BPD symptoms, and (iii) relationship between illusion experience and maladaptive personality traits. We measured illusion strength (questionnaire responses), proprioceptive drift (perceived shift in physical hand position), BPD symptoms (Revised Diagnostic Interview for Borderlines score), and maladaptive personality traits (Personality Inventory for DSM-5) in 24 BPD and 21 control participants. For subjective illusion strength, we found main effects of group (BPD > healthy control, F(1, 43) = 11.94, P = 0.001) and condition (synchronous > asynchronous, F(1, 43) = 22.80, P < 0.001). There was a group × condition interaction for proprioceptive drift (F(1, 43) = 6.48, P = 0.015) such that people with BPD maintained illusion susceptibility in the asynchronous condition. Borderline symptom severity correlated with illusion strength within the BPD group, and this effect was specific to affective (r = 0.45, P < 0.01). Across all participants, trait psychoticism correlated with illusion strength (r = 0.44, P < 0.01). People with BPD are more susceptible to illusory body ownership than controls. This is consistent with the clinical literature describing aberrant physical and emotional experiences of self in BPD. A predictive coding framework holds promise to develop testable mechanistic hypotheses for disrupted bodily self in BPD.

Keywords: rubber hand illusion; borderline personality disorder; body ownership; psychoticism; predictive coding; self

Introduction

Aberrations of self-experience and identity are considered core symptoms of borderline personality disorder (BPD) (Gunderson et al. 2018). Self-disturbance is characterized by a markedly persistent unstable sense of self that can be realized by dramatic shifts in self-image, shifting goals and values, and feelings of emptiness, dissociation, and even non-existence (Fuchs 2007; Kerr et al. 2015). One aspect of selfhood that may have relevance for pathologies of self in BPD is the experience of body ownership. Indeed, abnormal bodily experiences in BPD are common, including bodily dissociation (Korzekwa et al. 2009), altered pain

© The Author(s) 2019. Published by Oxford University Press.

This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (http://creativecommons.org/ licenses/by-nc/4.0/), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact journals.permissions@oup.com

Received: 7 May 2019; Revised: 26 October 2019. Accepted: 28 October 2019

Highlights

- · The rubber hand illusion allows measurement of self-disturbance.
- People with borderline personality disorder (BPD) had greater illusion susceptibility and this correlated with affective symptoms.
- Interoception stabilizes representations of body ownership and is impaired in BPD.
- Illusion strength correlates with psychotic traits across levels of psychopathology.
- Predictive coding frameworks can probe mechanisms of altered body ownership in psychopathology.

perception (Schmahl et al. 2010), and deficits in interoception (the awareness and processing of internal bodily signals) (Loffler et al. 2018).

Mechanistically, sense of body ownership is constituted by the integration of sensorimotor (external) and interoceptive (internal) signals (Tsakiris 2017). Neural computations on these signals generate a probabilistic, and therefore dynamic, model of self-representation (Seth 2013). While sense of body ownership is stable and taken for granted in everyday circumstances, experimental paradigms, such as body illusion tasks that directly manipulate sensorimotor integration, can affect the experience of body ownership. As such, these paradigms have the potential to elucidate aberrations in embodied self-experience in BPD.

Body illusion tasks can test the plasticity of body ownership by manipulating the integration of self and non-self stimuli. One paradigmatic body illusion is the rubber hand illusion (RHI) (Botvinick and Cohen 1998). During the task, a participant's hidden hand is stroked in synchrony with an appropriately positioned and visible rubber hand. The RHI can induce the feelings that the rubber hand belongs to the participant (subjective illusion) and that the participant's own hand has moved toward the rubber hand (proprioceptive drift). Typically, the RHI is measured by a self-report questionnaire of illusory experience (adapted from Botvinick and Cohen 1998) and the spatial magnitude of proprioceptive drift (Thakkar et al. 2011).

It is theorized that the RHI results from the multimodal (e.g. visuo-tactile) integration of sensory events in peri-personal space: an area including and immediately surrounding the body that is implicated in maintaining a dynamic cortical representation of the body (Holmes and Spence 2004). RHI induction is sensitive to visuospatial plausibility and the timing of sensory stimulation, such that unrealistic placement of the rubber hand and temporally asynchronous stroking have been found to attenuate illusory body ownership in healthy participants (Costantini and Haggard 2007; Morgan et al. 2011). Eshkevari et al. (2012) highlight two factors that promote induction of the rubber hand illusion. One factor, "visual capture," occurs prior to visuo-tactile stimulation, whereby a sense of body ownership results from overweighting of the visual stimulus of the rubber hand over proprioceptive information of the real hand. The other factor, which entails simultaneous seen and felt touch of the fake and real hand during simultaneous stroking, results in the illusion of rubber hand ownership via the multisensory integration of temporally co-occurring visual and tactile stimulation. Empirical data from healthy participants, and computational modeling of rubber hand ownership, demonstrate that the illusion can occur without tactile stimulation (first factor) (Ferri et al. 2013) and is enhanced by temporally synchronous (vs. asynchronous) stroking of fake and real hands (Samad et al. 2015). Importantly, increased susceptibility to the first factor, which occurs in both synchronous and asynchronous conditions (as it occurs prior to tactile stimulation) may indicate imprecise bodily

representations that result in the overweighting of exteroceptive information (Eshkevari et al. 2012; Samad et al. 2015). Investigating RHI responses in both conditions in BPD may illuminate potential mechanisms of altered sense of body ownership in the condition.

The RHI has been conducted across a range of mental disorders in which anomalous self-experience has been implicated and which share clinical overlap with BPD, including schizophrenia (Thakkar et al. 2011), body dysmorphic disorder (BDD) (Kaplan et al. 2014), and eating disorders (Eshkevari et al. 2012; Keizer et al. 2014). These conditions are associated with increased susceptibility to the RHI as measured by self-report questionnaire (Keizer et al. 2014), proprioceptive drift (Kaplan et al. 2014), or both (Thakkar et al. 2011; Eshkevari et al. 2012). Increases in subjective measures of the illusion and proprioceptive drift have also been demonstrated in pharmacological models of psychosis (i.e. ketamine) in healthy participants, implicating N-methyl-D-aspartate (NMDA) hypofunction and augmented neural oscillations in the gamma-range that promote cross-modal binding (Morgan et al. 2011). This interpretation was bolstered by the finding of maintained illusory experience in an asynchronous version of the RHI with pharmacologic challenge, highlighting the methodological importance of administering the task in both synchronous and asynchronous versions.

The vividness of the illusion has also been linked to schizotypy in healthy participants (Asai et al. 2011), suggesting that altered body ownership may be a marker of psychosis-proneness. However, the interpretation of these results is limited as task demand characteristics of the illusion questionnaire may not have been controlled for. In particular, the original Botvinick and Cohen (1998) questionnaire was designed to include target and nontarget items to control for suggestibility and to our knowledge no clinical study has adequately assessed group differences in the relative endorsement of target and non-target items on the RHI questionnaire. Another consideration is that responses to non-target items may be linked to altered sense of body ownership and that clinical populations may have atypical responses to RHI procedures (Thakkar et al. 2011). Furthermore, target items (which probe the illusions of touch, causality, and ownership, respectively) sequentially probe qualitatively more encompassing aspects of the illusion. For example, people who minimally experience the illusion may only endorse the illusion of touch (feeling the touch on the location where the rubber hand is touched), while those who experience a stronger illusory experience may also endorse ownership of the rubber hand (that the rubber hand is their hand). However, specific hypotheses regarding the differential endorsement of target items in clinical groups have not been previously tested. Close examination of target item responses and attention to dimensional symptomology can reveal trait markers across diagnostic thresholds that may influence illusion susceptibility.

To date, there has been one study examining illusory body ownership using the RHI in people with current and remitted BPD (Bekrater-Bodmann et al. 2016). That study analyzed findings in a synchronous version of the task only, and found increased subjective experience of the illusion, but similar proprioceptive drift, in people with BPD compared to healthy controls (HCs). However, group differences in the relative endorsement of target and nontarget items were not assessed. Additionally, the authors found a small but significant correlation between illusory body ownership and state and trait dissociation after controlling for BPD symptom severity. We extend these findings by (i) testing group differences in the relative endorsement of target vs. non-target items, (ii) probing responses to individual target items to explore more granular group differences in illusory experience, (iii) directly testing hypotheses about asynchronous stimulation, and (iv) exploring relationships between illusory body ownership and BPD symptom phenotypes and dimensional measures of maladaptive personality. In the current study, we conducted the RHI task with people with BPD and HCs in temporally synchronous and asynchronous conditions. We made the following hypotheses:

H1. Illusion strength would be greater in BPD vs. HC in both synchronous and asynchronous conditions as measured by questionnaire response (H1.1) and proprioceptive drift (H1.2).

Given that there are interoceptive deficits in BPD, we hypothesized that relative overweighting of exteroceptive input would result in increased susceptibility in both conditions, rather than specifically in the synchronous condition.

H2. The illusion of ownership (Q1), but not the illusions of perception (Q2) or causality (Q3), will be more strongly endorsed in BPD than in HC.

Given self-disturbance in BPD, we hypothesized specific increased endorsement of Q3 in BPD vs. HC.

H3. Illusion strength would positively correlate to psychotic-like symptoms and traits.

We hypothesized that RHI illusion strength would correlate with psychotic-like experiences across all participants, as well as the cognitivedisturbance symptom cluster in BPD group.

Methods

Participants

This study was approved by the Yale Institutional Review Board. Results for this study were collected as part of a larger battery of experimental tasks. Results from those tasks as well as the recruitment strategy for these participants are described in detail elsewhere (Fineberg et al. 2018a,b). Briefly, women aged 18–65 were recruited from the community. HCs had no current psychiatric conditions, and BPD participants had no current substance dependence and no primary psychotic disorder according to intake interview assessment (see Supplementary material S1). We report results here from the 24 BPD and 21 HC participants who completed RHI procedures.

Symptom and self-report scales

HC and BPD participants completed a series of well-validated self-report symptom scales and structured clinical interviews including: the Beck Anxiety Inventory (BAI) (Beck *et al.* 1988), the Beck Depression Inventory (BDI-II) (Beck *et al.* 1996), the Personality Inventory for DSM-5 (PID-5) (Krueger *et al.* 2012), the Structured Clinical Interview for DSM-IV Personality Questionnaire (Ekselius *et al.* 1994), and the Revised Diagnostic Interview for Borderlines (DIB-R) (Zanarini *et al.* 1989). Please refer to Supplementary material S2 for information on scale validation and subscales.

Rubber hand illusion paradigm

Participants wore a non-latex glove on their right hand, sat in front of a table, and placed their right hand into an open cardboard box (Fig. 1). All participants underwent RHI procedures on their right hand only as it was previously demonstrated that laterality and handedness had no effect on the subjective experience of the illusion or magnitude of proprioceptive drift, the two main outcomes measures for the task in the current study (Smit et al. 2017).

In the box, the participant's right hand was occluded from their view, but not from the view of the experimenter who sat across the table facing the participant. A gloved life-sized rubber hand was positioned so that the hand was visible to the participant on the medial end of the box. A cloth was then draped over the participant's shoulder covering both the real right arm and the arm of the rubber hand. In this setup, participants saw a rubber hand and a box under which their real hand is hidden. A cloth occluded the real arm and wrist up to the box edge, and also hid the wrist of the rubber hand, giving the impression that the rubber hand may extend from the participant's arm under the cloth. During measurements, the positions of the real and rubber hands remained the same. Participants saw a ruler which we placed on top of the box, and which they used to verbally indicate the spatial location of their real index finger. Before induction of the illusion, participants made an initial estimate of the spatial location on their hidden right index finger. Each participant then underwent synchronous and asynchronous versions of the task, each lasting 3 min. The order of condition administration varied across participants in each group. In the synchronous condition, an experimenter used the brush of a paintbrush to provide soft simultaneous touch at 1Hz frequency in the proximal to distal direction along the middle

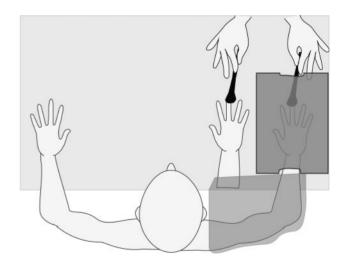


Figure 1. Rubber hand illusion setup. Participant's gloved right hand is placed in cardboard box obstructing it from view. A life-like gloved rubber hand is placed medial to the box. A cloth is draped across right shoulder, covering the wrist of the rubber hand and the cardboard box proximally, where the participant's real hand enters. During illusion induction, the participant is instructed to visually focus on the rubber hand while an experimenter provides brushstrokes to the middle phalanges of the real hand (through an opening in the cardboard box) and an equivalent location on the rubber hand for 3 min. Hand localization ("drift") estimates are taken at 30-s intervals. The questionnaire is administered once after each stimulation condition (synchronous, asynchronous). phalanges of the real index finger and an equivalent location on the rubber hand. Procedures for the asynchronous condition were identical except that brush strokes were offset in time by 0.5 s (resulting in alternating touch on the real and rubber hands).

Measure of subjective experience of the illusion

After synchronous and asynchronous conditions, participants completed a questionnaire adapted from Botvinick and Cohen (1998) to assess their subjective experience of the illusion (Table 1). Variations of this questionnaire have been used widely in RHI research (Kaplan et al. 2014). Similar to previous studies, the first three items ("target") were used to create an index score as they are more strongly and consistently endorsed than the other items, and they reflect expected illusory experience (Kaplan et al. 2014). The remaining items ("non-target") have historically been included to control for suggestibility and task demand characteristics as they are endorsed only minimally by healthy samples (Kaplan et al. 2014). However, they are often endorsed in clinical psychiatric populations and during pharmacologic challenges (e.g. ketamine) (Morgan et al. 2011). For each condition, a cumulative "target item" score was created as the average rating across items 1-3 and a cumulative "non-target item" score was created as the average rating across items 4-9. Significantly higher target scores compared to non-target scores were used as an indicator of successful induction of the illusion.

Measure of proprioceptive drift

Proprioceptive drift refers to the extent to which participants estimated their hand as being closer to the rubber hand after induction of the illusion. Participants estimated the position of their hidden right index finger before stimulation, and then at 30-s intervals during stimulations (six times over 3 min of stimulation) by referring to a numbered ruler placed on top of the box. At each interval, participants were reminded not to move their hand. At each interval, the position of the ruler was jittered to prevent participants from anchoring on previous estimates (Schütz-Bosbach et al. 2009). Proprioceptive drift was calculated as the difference in estimated hand location between the baseline estimate and average of the six post-trial estimates for each condition. This value was used in subsequent analyses of proprioceptive drift. Positive values refer to post-trial estimates that are closer to rubber hand than the baseline estimate and are consistent with successful induction of the illusion.

| Table 1: RHI questionnaire items | (target items in bold) |
|----------------------------------|------------------------|
|----------------------------------|------------------------|

| Item | Wording | | | | |
|------|--|--|--|--|--|
| 1 | It seemed as if I were feeling the touch of the paint brush in the location where I saw the rubber hand touched. | | | | |
| 2 | It seemed as though the touch I felt was caused by the paint brush touch the rubber hand. | | | | |
| 3 | I feel as if the rubber hand were my hand. | | | | |
| 4 | I felt as if my real hand was drifting toward the rubber hand. | | | | |
| 5 | It seemed as if I might have more than one right hand or arm. | | | | |
| 6 | It seemed as if the touch I was feeling came from some- where between my own hand and the rubber hand. | | | | |
| 7 | It felt as if my real hand were turning "rubbery." | | | | |
| 8 | It appeared visually as if the rubber hand was drifting to- wards my hand. | | | | |
| 9 | The rubber hand began to resemble my own real hand, in terms of shape, texture, or some other visual feature. | | | | |

Planned statistical analyses

Parametric tests were conducted for analyses on main outcome variables (subjective experience questionnaire and proprioceptive drift) as values for skewness and kurtosis were all within -2 to 2, indicating normal univariate distribution (George and Mallery, 1999).

A 2 \times 2 repeated measures analysis of variance (ANOVA) was used to assess impact of group (HC vs. BPD) and condition (synchronous vs. asynchronous) on target item endorsement (Hypothesis H1.1). To assess the relative endorsement of target vs. non-target items, we performed a one-way analysis of co-variance (ANCOVA) to assess for group differences (HC vs. BPD) in target item endorsement in the synchronous condition (the more illusion-inducing condition) using non-target item endorsement as a covariate. A separate 2 \times 2 repeated measures ANOVA was used to assess impact of group and condition on proprioceptive drift (Hypothesis H1.2).

Two separate 2 group \times 3 target items ANOVAs were employed to test for differential endorsement of individual target items in the synchronous and asynchronous conditions, respectively (Hypothesis H2).

Lastly, we performed Pearson correlations to explore the relationships between RHI measures and symptom scales that were normally distributed. Two DIB-R subscales (affect and cognition) demonstrated significant kurtosis, and as such, Kendall's tau correlation were used to explore the relationship between target items and these symptom subscales. Correlations were one-tailed to test for positive correlations unless stated otherwise.

Alpha values were set to 0.05 for primary analyses and, more conservatively, to 0.01 for *post hoc* analyses and correlations. We report effect sizes using Cohen's D for t-tests, and partial η^2 for ANOVAS.

Results

Participant characteristics

Twenty-four women were enrolled in the BPD group, and 21 women were enrolled in the HC group. HC and BPD groups were matched on age, years of education, and race (Table 2). The BPD group was significantly more symptomatic on measures of BPD

 Table 2: Participant characteristics: mean results are reported followed by standard deviations in parentheses

| | BPD | HC | Statistics |
|---------------------|----------------|---------------|----------------------|
| n | 24 | 21 | |
| Age (years) | 33.17 (12.47) | 31.10 (13.13) | t = 0.54; P = 0.59 |
| Education (years) | 13.96 (2.46) | 15.02 (2.45) | t = -1.45; P = 0.15 |
| Race | | | Chi square = 3.19; |
| Asian | 8.30% | 9.50% | df = 2; P = 0.74 |
| Black | 16.70% | 28.60% | |
| Hispanic | 4.20% | 19% | |
| White | 66.70% | 42.90% | |
| Not reported | 4.20% | 0% | |
| BAI | 24. 83 (12.80) | 7.35 (10.05) | t = 4.92; P < 0.001 |
| BDI | 23.04 (12.71) | 2.52 (4.52) | t = 7.39; P < 0.001 |
| DIB-R (unscaled) | 28.00 (6.55) | 3.19 (4.17) | t = 14.90; P < 0.001 |
| SCID-II self-report | 9.75 (3.51) | 0.95 (1.40) | t = 11.31; P < 0.001 |
| BSL-23 | 36.25 (21.42) | 3.95 (4.32) | t = 7.219; P < 0.001 |

Note: Groups were matched on age, education, and race. All participants were female. BPD group participants reported significantly more anxiety, depression, and BPD symptoms than did HC participants.

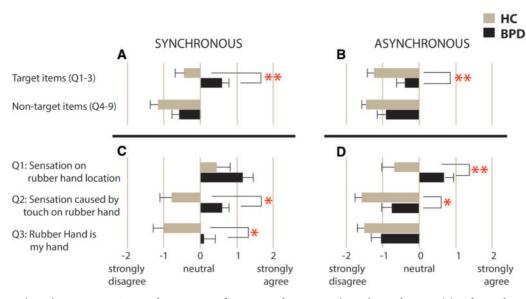


Figure 2. RHI questionnaire responses. Averaged mean scores for target and non-target items in synchronous (A) and asynchronous conditions (B). Error bars denote standard error of the mean. Means for individual target items are displayed for both synchronous (C) and asynchronous (D) conditions. *P < 0.05; **P < 0.01.

symptom severity (SCID-II, BSL, DIB-R), depression (BDI), and anxiety (BAI) (Table 2).

Self-Report RHI questionnaire

H1.1 Subjective illusion strength would be greater in BPD vs. HC groups in both synchronous and asynchronous conditions.

We tested for group differences in mean target item endorsement (H1.1) using a 2 group × 2 condition repeated measures ANOVA (Fig. 2A and B). We found a significant main effect of group (BPD > HC, F(1, 43) = 11.94, P = 0.001, $\eta^2 = 0.22$) and of task condition (synchronous > asynchronous, F(1, 43) = 22.80, P < 0.001, $\eta^2 = 0.35$). No significant interaction was found (F(1, 43) = 1.72, P = 0.681, $\eta^2 < 0.01$).

In the RHI literature, a standard set of items has been used to test for group differences in target item endorsement that may be accounted for by task demand characteristics or suggestibility. Focusing on the more illusion-inducing (synchronous) condition, We conducted a one-way ANCOVA to test for a difference between BPD and HC groups in target item endorsement while controlling for responses to non-target items. We found that the effect of group remained significant when we controlled for the non-target items (F(1, 42) = 4.40, P = 0.042, $\eta^2 < 0.1$) suggesting that group differences in target item responses do reflect differences in the magnitude of illusory experience rather than a non-specific positive response bias.

Confirming that the RHI was successfully induced in our sample, t-tests demonstrated that both BPD and HC groups endorsed target items more strongly than non-target items in the synchronous condition (Fig. 2A, BPD: t(23) = 5.64, P < 0.001, d = 1.15; HC: t(20) = 3.19, P = 0.005, d = 0.70). This result, together with the finding above that target item endorsement is greater in the synchronous condition compared to the asynchronous, suggests that we were able to successfully induce the RHI in our participants.

H2. Greater subjective illusion in BPD would be accounted for by the ownership illusion (Q3).

To examine hypothesis H2, we conducted two separate 2 group \times 3 target items ANOVAs for the synchronous and asynchronous conditions, respectively. We expected that group differences in target item endorsement would be unique to Q3. In the synchronous condition, we found a main effect of group $(F(1, 43) = 8.92, P = 0.005, \eta^2 = 0.17)$ and item (F(1, 43) = 17.37,P < 0.001, η^2 = 0.29). The group × item interaction was not significant (F(1, 43) = 0.33, P = 0.57). As described above, the main effect of group was that overall target item endorsement was greater in BPD than control. Post hoc tests to examine the main effect of items revealed that Q1 was significantly more endorsed that Q2 (P = 0.002) and Q3 (P < 0.001), but that Q2 and Q3 were not statistically significantly different in participant endorsement (P = 0.124). In the asynchronous condition, we found a main effect of group (F(1, 43) = 7.56, P = 0.009, η^2 = 0.15) and item $(F(1, 43) = 19.77, P < 0.001, \eta^2 = 0.32)$. The group × item interaction was not significant (F(1, 43) = 2.05, P = 0.15). As reported above (and as in the synchronous condition), the main effect of group is that target item endorsement in the asynchronous condition was greater in BPD than control. Also here, as in the synchronous condition, endorsement of Q1 was significantly different from Q2 (P < 0.001) and Q3 (P < 0.001), but Q2 and Q3 were not statistically significantly differently endorsed (P = 0.44)

In summary, contrary to our hypothesis, group differences in target item endorsement do not appear to be driven by a specific target item (no significant group \times item interaction). However, both groups endorse Q1 (tactile illusion) more than they do Q2 (illusion of causality) or Q3 (illusion of ownership).

Proprioceptive drift

H1.2. Proprioceptive illusion strength would be greater in BPD vs. HC groups in both synchronous and asynchronous conditions.

To test hypothesis H1.2., we explored group differences in proprioceptive drift using a 2 × 2 repeated measures ANOVA (group × condition) (Fig. 3). Main effects of group (BPD vs. HC, F(1, 43) <0.001, P = 0.99, η^2 < 0.01) and of task condition (synchronous vs. asynchronous, F(1, 43) = 2.19 P = 0.15, η^2 = 0.05) were not significant. However, a significant group × condition interaction

was found (F(1, 43) = 6.48, P = 0.015, η^2 = 0.13). Post hoc paired sample t-tests demonstrated that, contrary to our hypothesis, while the HC group had significantly reduced proprioceptive drift in the asynchronous condition (t(20) = 2.90, P = 0.009, d = 0.63), the BPD group had no significant difference in drift across conditions (t(23) = 0.75, P = 0.462, d = 0.094) (Fig. 3). To assess differences in drift estimates over time, we also conducted a 2 group (HC vs. BPD) × 2 condition (sync vs. async) × 6 trial (6 poststimulation estimates) repeated measures ANOVA, which found that the effect of trial reached only trend-level significance (P = 0.051; see Supplementary material S3). We also found weak to moderate relationships between target item endorsement and

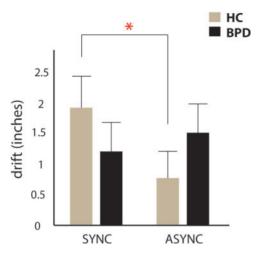


Figure 3. Proprioceptive drift. Mean drift toward rubber hand following six 30-s trials of synchronous (sync) or asynchronous (async) stimulation. Error bars represent standard error of the mean. *P < 0.05.

S

proprioceptive drift that did not meet our significance cut-off of P < 0.01 (see Supplementary material S4).

Symptom/trait correlations

H3. Illusion strength would positively correlate to psychotic-like symptoms and traits.

BPD symptoms

We investigated whether BPD symptom severity and BPD symptom clusters relate to illusion strength in the clinical group. To do so, we conducted one-tailed Pearson correlations between DIB-R total (unscaled score) and subscale (affect, cognition, impulsivity, and interpersonal relationship sections) scores (unscaled) and the following RHI measures: target-item score, item-3 ("I felt as if the rubber hand was my hand") and proprioceptive drift in the synchronous condition (statistics in Fig. 4). We limited correlations to the synchronous condition to limit multiple comparisons and to focus on the more illusioninducing condition. At the $\alpha = 0.01$ level, we found that targetitem score and item-3 endorsement were related to the affect and cognition subscales with correlations in the medium to large effects range. Proprioceptive drift was not related to BPD symptom severity or symptom clusters within the clinical group.

Dimensional personality assessment

Next, we examined the relationship between RHI and dimensional measures of maladaptive personality traits across all participants. To do so, we conducted one-tailed Pearson correlations between PID-5 personality trait domains (negative affect, detachment, antagonism, disinhibition, and psychoticism) and the following RHI measures: target-item score, item-3 ("I felt as if the rubber hand was my hand") and proprioceptive

| | Scale | (s) Drift | (s) target | (s) Q3 |
|----------------|--------------------|-----------|------------|---------|
| BPD | DIB: Total score | 0.019 | .384* | 0.400* |
| | DIB: Affect | 0.133 | 0.454** | 0.619** |
| | DIB: Cognition | 0.091 | 0.457** | 0.429** |
| | DIB: Impulsivity | 0.283 | 0.256 | 0.075 |
| | DIB: Interpersonal | 0.095 | 0.041 | 0.107 |
| | Scale | (s) Drift | (s) target | (s) Q3 |
| | NegativeAffect | 0.172 | 0.309* | 0.183 |
| Total ample | Detachment | 0.026 | 0.368* | 0.325* |
| | Antagonism | 0.335* | 0.256 | 0.121 |
| | Disinhibition | 0.067 | 0.228 | 0.173 |
| | Psychoticism | 0.101 | 0.440** | 0.393** |

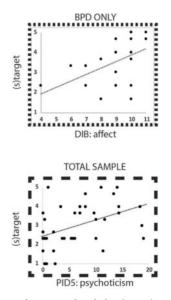


Figure 4. Relationship between synchronous condition illusion susceptibility, BPD symptom clusters, and maladaptive traits. On the left, correlation coefficients between proprioceptive drift, target-item endorsement, item three endorsement in the synchronous condition, and clinical/personality variables are presented. On the right side are the scatterplots for the relationship between average target item endorsement in the synchronous condition and DIB-R affect in the BPD group (upper panel) and trait psychoticism as measured by PID-5 in the whole sample (lower panel). *P < 0.05, one-tailed; ** P < 0.01, one-tailed. Note: DIB-R = Diagnostic Interview for Borderlines-revised. DIB-R includes affect, cognition, impulsivity, and interpersonal subscales. PID-5 = Personality Inventory for DSM-5 which has scales for the following maladaptive traits: negative affect, detachment, an-tagonism, disinhibition, and psychoticism. (s) Drift = proprioceptive drift in synchronous condition. (s) targ = average target-item response in synchronous condition. (s) Q3 = response to item 3 on RHI questionnaire in the synchronous condition: "I feel as if the rubber hand were my own."

drift in the synchronous condition (Fig. 4). At the $\alpha = 0.01$ level, only trait psychoticism was significantly related to the targetitem score and item-3 endorsement, with correlations observed in the medium-effect range. Proprioceptive drift was not significantly related to clinical traits at the P < 0.01 level.

Of note, six participants (four BPD and two HC) did not complete the PID-5. The two HC participants were comparable to other HCs in age, education, BDI, BAI, and RHI outcomes. The four BPD participants were both highly symptomatic and appeared to have higher target item endorsement in the synchronous condition. Note that the very small sample size was prohibitive of inferential statistics.

Discussion

In this study, we have extended the previous investigation of illusory body ownership in BPD by directly assessing findings in the asynchronous condition, analyzing differential endorsement of self-report items, and identifying further associations with clinical and personality trait variables. In the paragraphs to follow, we will interpret RHI behavior in BPD within a predictive coding account of bodily self (Apps and Tsakiris, 2014; Palmer and Tsakiris, 2018), which posits that representations of self are probabilistically generated through integration of top-down predictions about the body and bottom-up "prediction errors" of sensory inputs across interoceptive and exteroceptive domains.

We hypothesized that compared to HC, people with BPD would have greater target item endorsement (H1.1) and larger proprioceptive drift (H1.2) in both synchronous and asynchronous conditions. H1.1 was supported: BPD had greater target item endorsement in both conditions. Contrary to H1.2, we found a significant group \times condition interaction on drift measurements: BPD and HC had comparable drift during synchronous stimulation. However, during asynchronous stimulation, BPD had maintained drift while HC had significantly reduced drift.

As hypothesized, we found increased body plasticity in BPD as measured by subjective endorsement of illusory experience. Bekrater-Bodmann et al. (2016) reported increased subjective experience of the illusion; we clarified this finding by demonstrating that this group difference remained significant after controlling for the endorsement of non-target items, suggesting that increased target item response reflects alterations in the magnitude of illusory experience. We also extend their findings by demonstrating increased susceptibility in both synchronous and asynchronous conditions, indicating that illusion susceptibility occurs generally, rather than specifically during synchronous stimulation. While Bekrater-Bodmann et al. (2016) employed asynchronous stimulation merely as a manipulation check, others have compared RHI results across conditions (e.g. Morgan et al. 2011; Eshkevari et al. 2012; Kaplan et al. 2014) to elucidate possible mechanisms underlying abnormalities in illusory body ownership. For example, Morgan et al. (2011) found maintained illusory experience from synchronous to asynchronous stimulation during ketamine (an NMDA antagonist) challenge in healthy participants. NMDA antagonism (a model for early psychotic illness) is thought to weaken top-down signaling, leading to over-weighting of bottom-up input, even when the bottom-up signals are inconsistent (such as in the asynchronous RHI condition). In BPD, illusion susceptibility across synchronous and asynchronous conditions may similarly indicate weak top-down signaling regarding body ownership.

RHI induction is hypothesized to arise from two processes (Eshkevari et al. 2012): (i) visual capture, which occurs prior to

tactile stimulation, whereby rubber hand ownership is experienced via integration of visual and proprioceptive inputs of the fake and real hands, respectively; and (ii) temporal integration of visual and tactile input during synchronous stroking. Studying RHI in eating disorders, Eshkevari et al. (2012) interpreted maintained illusion susceptibility in the asynchronous condition as a heightened sensitivity to visual capture over distorted bodily signals. This interpretation was bolstered by the finding that interoceptive deficits were a significant predictor of illusory body ownership in eating disorders. Importantly, interoception (i.e. the processing and awareness of internal bodily signals) is theorized as a central modality in stabilizing mental representations of bodily self in predictive coding frameworks (e.g. Tsakiris 2017; Fotopoulou and Tsakiris 2017; Palmer and Tsakiris 2018). Accordingly, the precision associated with prediction error of sensory input-the confidence or uncertainty ascribed to it-modulates the integration of bottom-up and topdown information flow, such that low precision-weighted prediction errors are less likely to update (top-down) prior beliefs. In the RHI, the stability of body ownership is maintained by the relative precision of interoceptive vs. exteroceptive input. Reduced certainty, or "trustworthiness," ascribed to interoceptive signals leads to the overweighting of exteroceptive input (e.g. seeing the rubber hand) during the task, resulting in increased susceptibility to the illusion (see Tajadura-Jiménez and Tsakiris 2014 for empirical support). BPD is associated with deficits in interoceptive processing (Müller et al. 2015). However, the relationship between interoception and body plasticity was not directly assessed in this study. Future research can assess the extent to which interoceptive processing [e.g. as measured by heartbeat evoked potentials (Müller et al. 2015; Khalsa et al. 2018), or heartbeat detection (Tsakiris et al. 2011), though see Ring et al. 2015 for methodological limitations], mediates illusory body ownership in BPD and serves as a common mechanism of illusion susceptibility across personality, eating, and body-image disorders, for which there are symptomatic and clinical overlap (Rosenvinge et al. 2000; Sansone et al. 2010).

Contrary to H1.2, we found that BPD had comparable drift in both task conditions, while HC had significantly reduced drift in the asynchronous condition. While in previous studies, drift has been used as a "behavioral proxy" of rubber hand ownership (e.g. Tsakiris and Haggard 2005; Kammers et al. 2009), Rohde et al. (2011) found subjective endorsement of the illusion and drift to be separate and dissociable phenomena. In our sample, drift magnitude did not significantly correlate with endorsement of RHI questionnaire items. Interestingly, Kaplan et al. (2014) found that individuals with BDD demonstrate similar findings to our BPD sample such that they evidenced comparable drift in both conditions. They interpret this result in light of findings in healthy participants (Rohde et al. 2011), that proprioceptive drift occurs to an equal extent during synchronous stroking and in a "just vision" condition (wherein participants estimate hand location after looking at rubber hand without tactile stimulation), while asynchronous stroking reduces drift by disrupting visio-proprioceptive integration. Kaplan et al. (2014) posit that with regards to bodily awareness, people with BDD are less susceptible to the illusion-extinguishing effects of the asynchronous condition. If BPD shares a similar mechanism underlying maintained drift across conditions with BDD, this would be consistent with our proposed BPD self-model that is biased towards incorporating (even inconsistent) exteroceptive information in the setting of interoceptive deficits.

We hypothesized that greater subjective illusion strength in BPD would be accounted for by the illusion of ownership (H2). Contrary to our hypothesis, we found no group by item interaction: though there was a main effect of group (BPD > HC) and of condition (Q1 > (Q2 = Q3)), the relative endorsement of the three target items was similar as a function of group. These findings are consistent with a predictive coding account of selfrecognition (Apps and Tsakiris 2014), wherein more abstract multimodal self-representations are encoded at higher levels within a hierarchical model of self-processing. Intermediatelevel beliefs are constrained by top-down expectations as well as sensory bottom-up information lower in the hierarchy. We propose that during synchronous stroking, the prediction error caused by RHI procedures could be accounted for at the level of a perceptual experience for healthy participants (i.e. endorsement of Q1); whereas in BPD, RHI procedures lead to updating of more abstract self-representations, and therefore endorsement of causation and ownership illusions (Q2 and Q3 endorsement was greater than "neutral", in the "agree" range Fig. 2c). Similarly, while asynchronous stroking was sufficient to eradicate the illusion in HCs, the BPD group maintained an attenuated experience of the illusion (Q1 endorsement in the "agree" range, Fig. 2D) related to perceptual experience. One limitation of this interpretation is that differences in individual item endorsement may be due in part to how the questions are worded. While descriptively, absolute endorsement of Q1 > Q2 > Q3, future research may benefit from an expanded RHI questionnaire to probe differentially encompassing aspects of the illusion, e.g., the illusion of perception, causality, and ownership, respectively.

Lastly, we performed exploratory correlations to assess the relationship between clinical traits and illusory experience. We hypothesized that psychotic-like experiences would be uniquely related to RHI illusion strength (H.3). In addition to linking illusion strength with psychotic-like experiences, we also found strong associations with affective symptoms in both the BPD group (as measured by the DIB-R affect subscale) and across the whole sample (as measured by PID-5 trait negative affect). While the link between psychotic-spectrum experience and RHI has been demonstrated in other settings (e.g. Asai et al. 2011; Morgan et al. 2011), we are the first to demonstrate this association within BPD, providing further evidence that body plasticity may track psychosis-proneness trans-diagnostically. Finding a link between dissociation and RHI susceptibility in BPD, Bekrater-Bodman et al. (2016) posit that altered NMDA neurotransmission may underlie altered body plasticity in the condition. This suggestion is bolstered by neurochemical evidence (Hoerst et al. 2010) implicating glutamatergic signaling in the anterior cingulate cortex (ACC) in BPD. Importantly, the ACC and the insular cortex have been identified as central structures for interoception (Müller et al. 2015). Computational perspectives on mood and emotion suggest that emotional states reflect the certainty (or precision) regarding the interoceptive consequences of action, such that negative emotions "contextualize events that induce expectations of unpredictability" (Clark et al. 2018, p. 2278). Thus, state negative affect may contribute to overweighting of exteroceptive input during RHI procedures in the setting of low precision-weighted interoceptive input. Clarifying the contribution of state (e.g. affect) and trait (e.g. emotion regulation Müller et al. 2015) characteristics to the plasticity of body ownership also may elucidate the relationship between emotion arousal and clinical states such as the dissociation and depersonalization associated with BPD (Korzekwa et al. 2009). Alterations in body plasticity may also inform our understanding of interpersonal difficulties in the condition. BPD is associated with a 2-fold increase in preferred interpersonal distance in live dyadic contexts compared to HCs, suggesting alteration in embodied peri-personal space (Fineberg *et al.* 2018). Given the theoretical links between interoception, emotion, and theory of mind (Ondobaka *et al.* 2017), targeting body awareness (e.g. through mindfulness practice; Farb *et al.* 2012; Bornemann *et al.* 2015) may be an important focus, especially for people with BPD whose symptom profiles are high in self-disturbance and psychoticism.

The correlation we observe between illusion susceptibility and psychotic-like traits here points at another mechanistic path through predictive coding to the observed results. We have written elsewhere about the critical role of priors in explanation-making in the face of a chaotic environment. For example, people with early psychosis suffer a barrage of difficult to explain perceptual experiences, likely related to aberrant signaling of prediction errors. We and others have demonstrated that top-down suppression of aberrant prediction error is a mechanism of odd belief formation, especially delusions in psychosis and psychotic-like states (Corlett et al. 2006; Honey et al. 2008; Corlett et al. 2010; Corlett and Fletcher 2012). Strong priors for predictable causality may, by this logic, drive acceptance of the rubber hand as one's own hand (as a way of explaining the conflicting visual and tactile cues). This may serve as an alternative common mechanism of illusory body ownership across a wide variety of people with psychotic-like traits.

The findings from this work are best understood within the context of several limitations. Sample size was small, and participants were all women. The small sample size prohibits examination of the impacts of potentially interesting demographics (race, sexual orientation, age) and co-morbidities on outcome, as well as more stable estimates of the correlation between illusory body ownership and measures of maladaptive personality and BPD symptom clusters (Schönbrodt and Perugini 2013). Inclusion of only biologically female, female-identified participants for the study was important to decrease potential sources of variability in results given the small sample, but does limit generalizability of results.

Another potential limitation of our study arises from our use of non-target items to control for suggestibility while assessing RHI subjective experience. While this questionnaire has been used many times in RHI research, there is no consensus on how it is best analyzed. A common method, which we follow, is to create a target-item score which averages responses to the first three items. The use of the remaining items to control for suggestibility is thought to be justified by the finding that they are less commonly endorsed by HC subjects (Kaplan et al. 2014). However, the phenomenology of the RHI is nuanced, and may include endorsement of statements of non-target items. Furthermore, Thakkar et al. (2011) report a case study of an individual with schizophrenia, who has an out-of-body experience during RHI procedures, suggesting that the task may induce atypical experiences in clinical populations. Thus, increased endorsement of non-target items in BPD may reflect increased suggestibility or a more expansive subjective experience arising from RHI procedures. Future phenomenological and qualitative research on induced illusory body ownership can clarify experiential correlates of questionnaire item endorsement (Lewis and Lloyd 2010).

Also, Lush et al. (2019) recently provided empirical evidence that susceptibility to the RHI is predicted by self-report measures of hypnotizability. They posit that responses to the RHI, and to tasks probing embodied phenomenology more generally, are influenced by participants' trait dispositions to generate experiences to meet expectancies—a top-down process they call "phenomenological control." Hypnotizability is a particular instance of this process. Comparing relative responses to synchronous and asynchronous conditions may not sufficiently account for these trait level differences, as participants may have different illusion expectancies for each condition. We suggest that future RHI research include measurement of phenomenological control (e.g. self-reported suggestibility) to assess the contribution of this generalized process to observed differences in embodied experience.

From a task setup perspective, we did not include a baseline acclimation period to test for illusion induction from visual stimulus alone prior to tactile stimulation. This has been done in a non-clinical sample (Samad *et al.* 2015) and would enable the direct assessment of the relative contribution of visual capture vs. integration of visuo-tactile stimulation in producing enhanced illusory experience in clinical populations. Furthermore, in a computational model, Samad *et al.* (2015), demonstrated that the perception of body ownership as measured by the RHI can be described as a Bayesian causal inference. Future research applying modeling techniques to clinical data can further probe the extent to which increased body plasticity in BPD is driven by weakening of top-down representations of body-schemas, strong priors for rubber hand ownership, and/or bottom-up integration of interoceptive and exteroceptive input.

Data availability

Data will be made readily available upon request to the corresponding author.

Supplementary data

Supplementary data is available at NCONSC Journal online.

Conflict of interest statement. None declared.

Acknowledgments

We would like to thank Ada Umuego for her help creating figures. We also thank our research participants. This work was supported by the Yale School of Medicine Medical Student Research Fellowship to E.S.N.; the National Institutes of Mental Health (5T32MH019961 to S.K.F.); a National Alliance for Research on Schizophrenia and Depression Young Investigator Award (NARSAD) from the Brain and Behavior Research Foundation to S.K.F.; the National Institute on Drug Abuse (5T32DA01042615 to M.M.C.); an International Mental Health Research Organization/Janssen Rising Star Translational Research Award to P.R.C.; a Clinical and Translational Science Award (L1TR000142) from the National Center for Research Resources and the National Center for Advancing Translational Science, components of the National Institutes of Health and the National Institutes of Health Roadmap for Medical Research to P.R.C.; and the National Institutes of Mental Health (R01MH112887 to P.R.C.). This work was funded in part by the State of Connecticut, Department of Mental Health and Addiction Services. This publication does not express the views of the NIH, the Department of Mental Health and Addiction Services or the State of Connecticut, or other funding agencies. The views and opinions expressed are those of the authors.

References

- Apps MAJ, Tsakiris M. The free-energy self: a predictive coding account of self-recognition. Neurosci Biobehav Rev 2014;41: 85–97.
- Asai T, Mao Z, Sugimori E, Tanno Y. Rubber hand illusion, empathy, and schizotypal experiences in terms of self-other representations. *Conscious Cogn* 2011;**20**:1744–50.
- Beck AT, Epstein N, Brown G, Steer RA. An inventory for measuring clinical anxiety: psychometric properties. J Consult Clin Psychol 1988;56:893–7.
- Beck AT, Steer RA, Brown GK. Beck Depression Inventory-II, Vol. **78**(2). San Antonio: The Psychological Corporation, 1996, 490–8.
- Bekrater-Bodmann R, Chung BY, Foell J. et al. Body plasticity in borderline personality disorder: a link to dissociation. *Compr Psychiatry* 2016;**69**:36–44.
- Bornemann B, Herbert BM, Mehling WE, Singer T. Differential changes in self-reported aspects of interoceptive awareness through 3 months of contemplative training. Front Psychol 2015;5:1504.
- Botvinick M, Cohen J. Rubber hands 'feel' touch that eyes see. Nature 1998;**391**:756.
- Clark JE, Watson S, Friston KJ. What is mood? A computational perspective. Psychol Med 2018;48:2277–84.
- Corlett PR, Honey GD, Aitken MR. *et al*. Frontal responses during learning predict vulnerability to the psychotogenic effects of ketamine: linking cognition, brain activity, and psychosis. *Arch Gen* Psychiatry 2006;**63**:611–21.
- Corlett PR, Taylor JR, Wang XJ. et al. Toward a neurobiology of delusions. Prog Neurobiol 2010;**92**:345–69.
- Corlett PR, Fletcher PC. The neurobiology of schizotypy: frontostriatal prediction error signal correlates with delusion-like beliefs in healthy people. *Neuropsychologia* 2012;**50**:3612–20.
- Costantini M, Haggard P. The rubber hand illusion:sensitivity and reference frame for body ownership. *Conscious Cogn* 2007; **16**:229–40.
- Ekselius L, Lindström E, Knorring LV. et al. A principal component analysis of the DSM-III-R axis II personality disorders. J Pers Disord 1994;8:140–8.
- Eshkevari E, Rieger E, Longo MR. et al. Increased plasticity of the bodily self in eating disorders. Psychol Med 2012;**42**:819–28.
- Farb NAS, Segal ZV, Anderson AK. Mindfulness meditation training alters cortical representations of interoceptive attention. Soc Cogn Affect Neurosci 2012;8:15–26.
- Ferri F, Chiarelli AM, Merla A. *et al*. The body beyond the body: expectation of a sensory event is enough to induce ownership over a fake hand. Proc Biol Sci 2013;**280**:20131140.
- Fineberg SK, Leavitt J, Stahl DS. *et al*. Differential valuation and learning from social and nonsocial cues in borderline personality disorder. *Biol Psychiatry* 2018a;**84**:838–45.
- Fineberg SK, Leavitt J, Landry CD. et al. Individuals with borderline personality disorder show larger preferred social distance in live dyadic interactions. *Psychiatry Res* 2018b;**260**:384–90.
- Fotopoulou A, Tsakiris M. Mentalizing homeostasis: the social origins of interoceptive inference. *Neuropsychoanalysis* 2017;**19**: 3–28.
- Fuchs T. Fragmented selves: temporality and identity in borderline personality disorder. *Psychopathology* 2007;**40**:379–87.
- George D, Mallery P. SPSS[®] for Windows[®] Step by Step: A Simple Guide and Reference. Needham Heights, MA: Allyn & Bacon, 1999.
- Gunderson JG, Herpertz SC, Skodol AE. et al. Borderline personality disorder. Nat Rev Dis Primers 2018;4:18029.

- Hoerst M, Weber-Fahr W, Tunc-Skarka N. et al. Correlation of glutamate levels in the anterior cingulate cortex with selfreported impulsivity in patients with borderline personality disorder and healthy controls. Archiv Gen Psychiatry 2010;67: 946–54.
- Holmes NP, Spence C. The body schema and multisensory representation(s) of peripersonal space. *Cogn Process* 2004;5:94–105.
- Honey GD, Corlett PR, Absalom AR. et al. Individual differences in psychotic effects of ketamine are predicted by brain function measured under placebo. J Neurosci 2008;**28**:6295–303.
- Kammers MPM, de Vignemont F, Verhagen L, Dijkerman HC. et al. The rubber hand illusion in action. *Neuropsychologia* 2009; **47**:204–11.
- Kaplan RA, Enticott PG, Hohwy J. et al. Is body dysmorphic disorder associated with abnormal bodily self-awareness? A study using the rubber hand illusion. *PLoS One* 2014;**9**:e99981.
- Keizer A, Smeets MAM, Postma A. et al. Does the experience of ownership over a rubber hand change body size perception in anorexia nervosa patients? Neuropsychologia 2014;62:26–37.
- Kerr IB, Finlayson-Short L, McCutcheon LK. et al. The 'self' and borderline personality disorder: conceptual and clinical considerations. Psychopathology 2015;48:339–48.
- Khalsa SS, Adolphs R, Cameron OG. et al. Interoception and mental health: a roadmap. *Biol Psychiatry* 2018;**3**:501–13.
- Korzekwa MI, Dell PF, Pain C. Dissociation and borderline personality disorder: an update for clinicians. Curr Psychiatry Rep 2009;11:82–8.
- Krueger RF, Derringer J, Markon KE. et al. Initial construction of a maladaptive personality trait model and inventory for DSM-5. Psychol Med 2012;42:1879–90.
- Lewis E, Lloyd DM. Embodied experience: a first-person investigation of the rubber hand illusion. *Phenomenol Cogn Sci* 2010;**9**: 317–39.
- Loffler A, Foell J, Bekrater-Bodmann R. Interoception and its interaction with self, other, and emotion processing: implications for the understanding of psychosocial deficits in borderline personality disorder. *Curr Psychiatry Rep* 2018;**20**: 1–9.
- Lush P, Botan V, Scott RB, et al. Phenomenological control: response to imaginative suggestion predicts measures of mirror touch synaesthesia, vicarious pain and the rubber hand illusion. PsyArXiv 2019, doi: 10.31234/osf.io/82jav.
- Morgan HL, Turner DC, Corlett PR, *et al*. Exploring the impact of ketamine on the experience of illusory body ownership. *Biol Psychiatry* 2011;**69**:35–41.
- Müller LE, Schulz A, Andermann M. *et al.* Cortical representation of afferent bodily signals in borderline personality disorder: neural correlates and relationship to emotional dysregulation. JAMA Psychiatry 2015;**72**:1077–86.
- Ondobaka S, Kilner J, Friston K. The role of interoceptive inference in theory of mind. Brain Cogn 2017;**112**:64–8.

- Palmer CE, Tsakiris M. Going at the heart of social cognition: is there a role for interoception in self-other distinction? *Curr Opin* Psychol 2018;**24**:21–6.
- Ring C, Brener J, Knapp K, Mailloux J. Effects of heartbeat feedback on beliefs about heart rate and heartbeat counting: a cautionary tale about interoceptive awareness. *Biol Psychol* 2015; 104:193–8.
- Rohde M, Luca MD, Ernst MO. The rubber hand illusion: feeling of ownership and proprioceptive drift do not go hand in hand. PLoS One 2011;6:e21659.
- Rosenvinge JH, Martinussen M, Østensen E. The comorbidity of eating disorders and personality disorders: a metaanalytic review of studies published between 1983 and 1998. Eat Weight Disord 2000;5:52–61.
- Samad M, Chung AJ, Shams L. Perception of body ownership is driven by Bayesian sensory inference. PLoS One 2015;10: e0117178.
- Sansone RA, Chu JW, Wiederman MW. Body image and borderline personality disorder among psychiatric inpatients. Compr Psychiatry 2010;51:579–84.
- Schmahl C, Meinzer M, Zeuch A. et al. Pain sensitivity is reduced in borderline personality disorder, but not in posttraumatic stress disorder and bulimia nervosa. World J Biol Psychiatry 2010;**11**:364–71.
- Schönbrodt FD, Perugini M. At what sample size do correlations stabilize? J Res Pers 2013;47:609–12.
- Schütz-Bosbach S, Tausche P, Weiss C. Roughness perception during the rubber hand illusion. Brain Cogn 2009;**70**:136–44.
- Seth AK. Interoceptive inference, emotion, and the embodied self. Trends Cogn Sci 2013;17:565–73.
- Smit M, Kooistra DI, van der Ham IJM, Dijkerman HC. Laterality and body ownership: effect of handedness on experience of the rubber hand illusion. *Laterality* 2017;**22**:703–24.
- Tajadura-Jiménez A, Tsakiris M. Balancing the "inner" and the "outer" self: interoceptive sensitivity modulates self-other boundaries. *J Exp Psychol* 2014;**143**:736–44.
- Thakkar KN, Nichols HS, McIntosh LG, Park S. Disturbances in body ownership in schizophrenia: evidence from the rubber hand illusion and case study of a spontaneous out-of-body experience. PLoS One 2011;6:e27089.
- Tsakiris M, Haggard P. The rubber hand illusion revisited: visuotactile integration and self-attribution. J Exp Psychol 2005;**31**:80–91.
- Tsakiris M, Tajadura-Jimenez A, Costantini M. Just a heartbeat away from one's body: interoceptive sensitivity predicts malleability of body-representations. Proc R Soc B 2011;**278**:2470–6.
- Tsakiris M. The multisensory basis of the self: from body to identity to others. QJ Exp Psychol 2017;**70**:597–609.
- Zanarini MC, Gunderson JG, Frankenburg FR, Chauncey, DL. The revised diagnostic interview for borderlines: discriminating BPD from other axis II disorders. J Pers Disord 1989;3: 10–8.