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Altered bodily self-consciousness and peripersonal space in autism

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Abstract

There is some evidence that disordered self-processing in autism spectrum disorders is linked to the social impairments characteristic of the condition. To investigate whether bodily self-consciousness is altered in autism spectrum disorders as a result of multisensory processing differences, we tested responses to the full body illusion and measured peripersonal space in 22 adults with autism spectrum disorders and 29 neurotypical adults. In the full body illusion set-up, participants wore a head-mounted display showing a view of their 'virtual body' being stroked synchronously or asynchronously with respect to felt stroking on their back. After stroking, we measured the drift in perceived self-location and self-identification with the virtual body. To assess the peripersonal space boundary we employed an audiotactile reaction time task. The results showed that participants with autism spectrum disorders are markedly less susceptible to the full body illusion, not demonstrating the illusory self-identification and self-location drift. Strength of self-identification was negatively correlated with severity of autistic traits and contributed positively to empathy scores. The results also demonstrated a significantly smaller peripersonal space, with a sharper (steeper) boundary, in autism spectrum disorders participants. These results suggest that bodily self-consciousness is altered in participants with autism spectrum disorders due to differences in multisensory integration, and this may be linked to deficits in social functioning.

Keywords

autism spectrum disorders, bodily self-consciousness, full body illusion, multisensory integration, peripersonal space

Introduction

Autism has long been described as a disorder of self (Asperger & Frith, 1991; Frith, 2003; Kanner, 1943). Many studies have shown altered self-processing in autism spectrum disorders (ASD), for example, weaker autobiographical memory (Crane & Goddard, 2008) and self-referenced memory (Henderson et al., 2009), deficits in emotional self-awareness (Hill, Berthoz, & Frith, 2004), lower recognition and display of 'self-conscious' emotions (Heerey, Keltner, & Capps, 2003), atypical use of personal pronouns (Lee, Hobson, & Chiat, 1994) and impairments in other aspects of self-referential cognition (Lombardo, Barnes, Wheelwright, & Baron-Cohen, 2007; Mundy, Gwaltney, & Henderson, 2010).

At the root of a cognitively 'high level' conceptual sense of self is a more basic, non-conceptual sense of self that is grounded in neural representations of the body (Bermúdez, 2018; Damasio, 2012). Basic bodily self-consciousness emerges from the integration of sensory signals, within and across different modalities, generating the feeling that we are located within a body (self-location) that we own and control, and determines the first-person perspective from which we experience the world (Blanke, 2012; Maselli & Slater, 2013; Serino et al., 2013). Surprisingly, the bodily self in ASD has received little research attention to date. Here, we addressed these issues, by measuring and manipulating the multisensory bodily self in ASD.

The bodily self has been extensively studied using different paradigms in which multisensory conflicts are used to manipulate it – that is, the rubber hand illusion (RHI) and full body illusion (FBI) (Botvinick & Cohen, 1998; Ehrsson,

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2007; Lenggenhager, Tadi, Metzinger, & Blanke, 2007), and multisensory tasks that measure peripersonal space (PPS; Canzoneri et al., 2013; Serino et al., 2013; Serino et al., 2018). Supported by studies that show that PPS and FBI arise from multisensory integration processes (Aspell, Palluel, & Blanke, 2012; Avillac, Denève, Olivier, Pouget, & Duhamel, 2005; Bernasconi et al., 2018), these experiments importantly suggest that the bodily self is malleable. For example, RHI elicits the illusion that the dummy hand is one's own hand (change in body-part ownership). Similarly, in FBI, viewing a virtual body being stroked while feeling synchronous stroking on one's own body, results in a feeling of ownership for, referral of touch to and a drift in self-location towards the virtual body (Aspell, Lenggenhager, & Blanke, 2009; Lenggenhager et al., 2007). Recently, it has also been shown that PPS – the space immediately around the body, which mediates our interaction with external objects that come within reach (Rizzolatti, Fadiga, Fogassi, & Gallese, 1997) – is extended towards the virtual body during FBI, confirming that the PPS is 'the space of the bodily self' (Noel, Pfeiffer, Blanke, & Serino, 2015; Riva, 2018; Rizzolatti et al., 1997; Salomon et al., 2017).

Differentiation between self and other underlies the development of social interaction (Decety & Chaminade, 2003; Gallagher & Meltzoff, 1996; Neisser, 1991; C. E. Palmer & Tsakiris, 2018). Indeed, in ASD, observed differences in the 'higher level' aspects of self may relate to some of the social deficits (Gillespie-Smith, Ballantyne, Branigan, Turk, & Cunningham, 2017; Henderson et al., 2009; Lombardo et al., 2007). However, the possible relationships between bodily self-consciousness and impairments in social interaction have not been investigated in ASD.

Susceptibility to body illusions may be an indirect measure of the tendency to blur the distinction between self and other. People who tend to feel other people's pain more easily are more susceptible to RHI (Derbyshire, Osborn, & Brown, 2013). Highly empathic persons show higher susceptibility to RHI and experience more vicarious pain for a rubber hand (Seiryte & Rusconi, 2015). The size of the PPS also appears to reflect the differentiation between self and other, as shown by the expansion of the PPS towards an other in social interactions (Cardellicchio, Sinigaglia, & Costantini, 2012; Teneggi, Canzoneri, di Pellegrino, & Serino, 2013), and even a remapping of another person's PPS onto one's own (Maister, Cardini, Zamariola, Serino, & Tsakiris, 2015). Together, these results suggest that altered bodily self-consciousness in ASD may underpin at least some of the social impairments seen in ASD.

The key aspects of bodily self-consciousness (Blanke, 2012) – self-identification with one's entire body and self-location – have not been researched in autism. To date, only three studies have investigated body ownership in ASD (in relation to body *parts*), using RHI (Cascio, Foss-Feig, Burnette, Heacock, & Cosby, 2012; Paton, Hohwy, & Enticott, 2012) and the 'numbness illusion' (Guerra, Spoto, Parma, Straulino, & Castiello, 2017). Cascio and colleagues (2012) found that children with ASD required a much longer stroking duration for the illusion to establish, while Paton and colleagues (2012) found that the ASD group displayed reduced proprioceptive drift towards the rubber hand. FBI, an illusion that manipulates body ownership (self-identification) and self-location, is arguably a more effective and conceptually appropriate way of investigating the bodily self than RHI – in which ownership of a single body part is altered – since one identifies one's self with one's whole body, rather than with a body part (Blanke & Metzinger, 2009). Yet FBI has not been investigated in ASD.

PPS has also not been tested in people with ASD before, although it has been suggested, based on RHI studies, that the PPS of individuals with ASD may be sharper and smaller than in the typical population (Noel, Cascio, Wallace, & Park, 2017). This might manifest as a steeper gradient from self to other: a reduced distance over which multisensory stimuli approaching PPS are integrated, reflecting less flexibility in PPS when interacting with the external world (Noel et al., 2017). This is in line with reports of individuals with ASD having difficulty respecting the personal space of others (Kennedy & Adolphs, 2014) and as more likely to approach other individuals too closely (Asada et al., 2016; Parsons, Mitchell, & Leonard, 2004). It may also be inferred from these behaviours that the size of their PPS is smaller than in typical individuals.

To summarise, we investigated, for the first time, multisensory bodily self-consciousness in individuals with ASD using FBI and PPS measurement. We expected to find evidence of altered bodily self-consciousness in individuals with ASD, manifesting as a reduced susceptibility to FBI, and a smaller PPS with steeper gradient. We also expected there would be a positive relationship between empathy and susceptibility to FBI, supporting previous suggestions that the representation of the bodily self contributes to social functioning.

Methods

Participants

A total of 22 participants with ASD and 29 participants without ASD, making a total of 51 participants (30 male), were recruited (mean age 27.1, age range 18–53). In all, 47 participants completed all parts and 4 (neurotypical) participants completed the PPS task only. The 22 ASD participants (14 male, 8 female) had a formal diagnosis of ASD given by an independent clinician. To confirm diagnosis, 19 of these participants attended an Autism Diagnostic Observation Schedule diagnostic interview (ADOS – Lord et al., 2000) with one of the authors (S.S.), and 4 met the threshold point for an autism spectrum diagnosis, while 15 met the threshold for autism. The three participants who were not able to attend the ADOS interview scored well above the ASD cut-off point of 32 on the AQ screening questionnaire (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). Participants were matched on age, ASD *M* (*SD*) = 27.0 (9.0); non-ASD *M* (*SD*) = 27.2 (6.7), *t* (49) = 0.11, *p* = 0.91), and IQ, (ASD *M* (*SD*) = 110.1 (13.0); non-ASD *M* (*SD*) = 112.7 (12.2), *t* (45) = 0.70, *p* = 0.49), as measured with the WASI II (Wechsler, 2011). All participants gave written informed consent to participate and the study was approved by the local ethics committee and conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Materials and procedure

Questionnaires. All participants completed the Autism Quotient (Baron-Cohen et al., 2001), the Toronto Alexithymia Scale (Bagby, Parker, & Taylor, 1994), the Questionnaire of Affective and Cognitive Empathy (Reniers, Corcoran, Drake, Shryane, & Völlm, 2011) and the Multidimensional Assessment of Interoceptive Awareness (MAIA – Mehling et al., 2012) measuring awareness of internal bodily sensations. MAIA has eight subscales that cannot be combined. We were primarily interested in the subscale ‘Noticing’, which measures awareness of comfortable, uncomfortable and neutral body sensations, and the subscale ‘Attention Regulation’, which measures the ability to sustain and control attention to body sensations when they are competing with exteroceptive signals, and so focus on these in the analyses.

FBI. Participants wore an Oculus Rift CV1 VR head mounted display (HMD) and were positioned 2.3 m in front of a video camera in the body condition. In the object condition, participants stood 1.0 m to the side of a tall cardboard box with a height and width similar to a person’s body. The box was positioned 2.3 m in front of the camera, such that the participant was out of view. The HMD displayed the body of the participant from the back in the body conditions, or the box in the object conditions (see Figure 1).

A custom-made program in the Unity software was used to control the timing of the visual feed to the HMD. Four conditions were presented in random order: body synchronous, body asynchronous, object synchronous and object asynchronous. In the asynchronous conditions, the visual feed was delayed by 400 ms, while there was no discernible delay (<50 ms) in the synchronous condition). In the body conditions, the experimenter stroked the back of the participant for 2 min with a stick. In the object conditions, the experimenter stroked the back of the participant and the box simultaneously in a spatially congruent manner for 2 min, using two sticks. The experimenter was out of view in all conditions. After each condition, participants were asked to close their eyes, and the HMD was removed. They were guided backwards by a distance of 1.5 m in very small steps, and then asked to return to their original position in normal steps, while keeping their eyes closed. The drift in self-location was measured as the distance in centimetres between the original and the estimated position. The FBI questionnaire (Lenggenhager et al., 2007) was administered after each condition. It contained seven statements (see Table 1) with which participants could agree/disagree on a seven point Likert-type scale from −−− to +++. The midpoint was assigned zero. The order of the items was randomised.

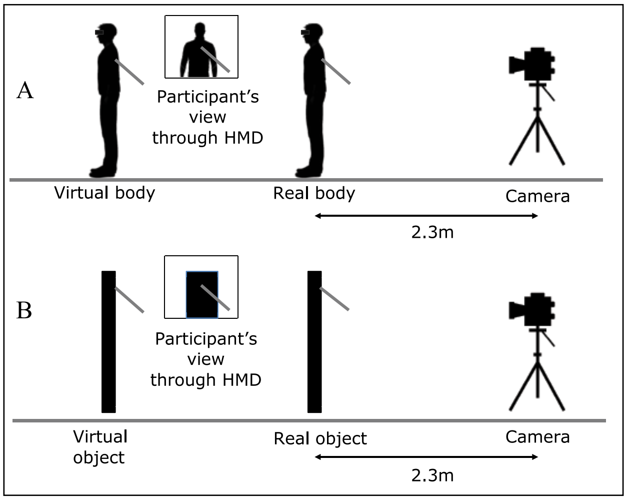

Figure 1. FBI set-up for the body condition (A) and the object condition (B).

PPS. PPS was measured prior to the FBI experiment – using an audiotactile integration task (Canzoneri, Magosso, & Serino, 2012). A custom-built small tapper attached to the right middle finger was used to administer a small tap (the drop of a 4-mm magnet). Participants were seated and blindfolded and responded as fast as possible to the tap by pressing a button with their left hand. Participants were told to ignore a sound (a pink noise) present in each trial. This sound was emitted from loudspeakers, one next to the participant’s right hand and the other 1 m further away. Modulation of the sound’s volume resulted in the impression of the sound moving towards them (Maister et al., 2015). Taps were administered at 300, 800, 1500, 2200 and 2500 ms after sound onset. Arduino board and LabView 8 (National Instruments, Austin, TX) software were used to control the sound, onset delay of the tap and record reaction times (RTs). There were 65 randomised trials in total, 10 for each onset delay and 15 no-tap catch trials.

Results

Empathy, alexithymia and interoception questionnaires

Non-ASD and ASD participants scored significantly differently on the questionnaires that measured autistic traits (AQ), empathy (QCAE), cognitive empathy (QCAEcog),

Table 1. FBI Questionnaire items. Q1–Q3 are illusion items and Q4–Q7 are control items.

	Statements
	During the experiment there were times when:
Q1	It seemed as if I were feeling the touch of the stick in the location where I saw the virtual body touched.
Q2	It seemed as though the touch I felt was caused by the stick touching the virtual body.
Q3	It felt as if the virtual body was my body.
Q4	It felt as if my (real) body was drifting towards the front (towards the virtual body).
Q5	It seemed as if the touch I was feeling came from somewhere between my own body and the virtual body.
Q6	It appeared (visually) as if the virtual body was drifting backwards (towards my body).
Q7	It seemed as if I might have more than one body.

Table 2. Means, standard deviations and comparisons between groups of questionnaire responses measuring autistic traits (AQ), alexithymia (TAS-20), empathy (QCAE), cognitive empathy (subscale of QCAE), affective empathy (subscale of QCAE), and interoceptive awareness (subscales of MAIA).

Measure	Non-ASD	ASD	Difference	*p*
	M (*SD*)	*M* (*SD*)	Mann–Whitney U	
Autistic traits	14.5 (5.8)	33.3 (7.3)	7.0	<0.001*
Alexithymia	43.9 (12.9)	61.6 (11.4)	90	<0.001*
Empathy	96.2 (10.2)	40.9 (10.7)	39.5	<0.001*
Cognitive empathy	61.5 (8.2)	40.9 (6.2)	39	<0.001*
Affective empathy	34.6 (4.4)	33.0 (6.2)	220.5	0.24
MAIA noticing	3.4 (0.9)	2.7 (1.2)	175.5	0.03
MAIA attention regulation	2.9 (0.7)	2.0 (1.1)	131	0.002*

*$p < 0.007$ (Bonferroni corrected alpha-level).

alexithymia (TAS20) and the MAIA subscale of attention regulation. No differences between groups were observed for affective empathy (QCAEaff) nor the other MAIA subscales (see Table 2).

FBI – drift

Participant's drift in self-location was measured as the distance of the participant's estimated self-location from the original position where they stood during the stroking. Subsequently, the difference in self-location drift between synchronous and asynchronous conditions was calculated by subtracting the drift in self-location of the participant in the asynchronous condition from the drift in self-location of the participant in the synchronous condition. The subtracted drift measurement was calculated because of the large variance between participants in the estimates.

Participants without ASD showed an average subtracted (synch–asynch) self-location drift in body conditions of 12.8 cm ($SD=29.6$). For ASD participants subtracted drift measurement for body conditions was 0.3 cm ($SD=16.1$). In the object conditions, non-ASD participants' subtracted drift measurement was –4.9 cm ($SD=5.4$) whereas ASD participants' subtracted drift measurement was 2.7 cm ($SD=8.2$).

For the body condition the subtracted self-location drift measurement of non-ASD participants compared with that of ASD participants was significant, $t\ (45)=1.77$, $p=0.04$, while for the object conditions, the difference in the subtracted drift measurement between groups was non-significant, $t\ (45)=0.80$, $p=0.43$. See Figure 2 for individual scores and see Figure 3 for mean scores.

FBI – questionnaire

The scale of the questionnaire was transformed from −−− to +++ into a scale from 1 to 7, with the 'neutral' midpoint acquiring a value of 4. For the analysis of the questionnaire scores, we assessed a possible response bias by calculating, per participant, an average score for the responses to the four control items for each condition, and we did the same for the three illusion items (as in, e.g. Ehrsson, 2007). For all main analysis of variance (ANOVA) analyses, the data were transformed using the ARTool aligned rank transform software (Wobbrock, Findlater, Gergle, & Higgins, 2011) to enable nonparametric factorial analysis using ANOVAs.

A four-way ANOVA (Question type × Synchrony × Display × ASD status) showed a main effect of Question type (illusion vs control), $F\ (1, 45)=92{,}27$, $p<0.001$, $\eta^2p=0.67$, a main effect of Synchrony, $F\ (1, 45)=15.80$, $p<0.001$, $\eta^2p=0.26$, a main effect of Display, $F\ (1, 45)=9.30$, $p=0.004$, $\eta^2p=0.17$, and no main effect of ASD status, $F\ (1, 45)=0.09$, $p=0.77$, $\eta^2p=0.002$.

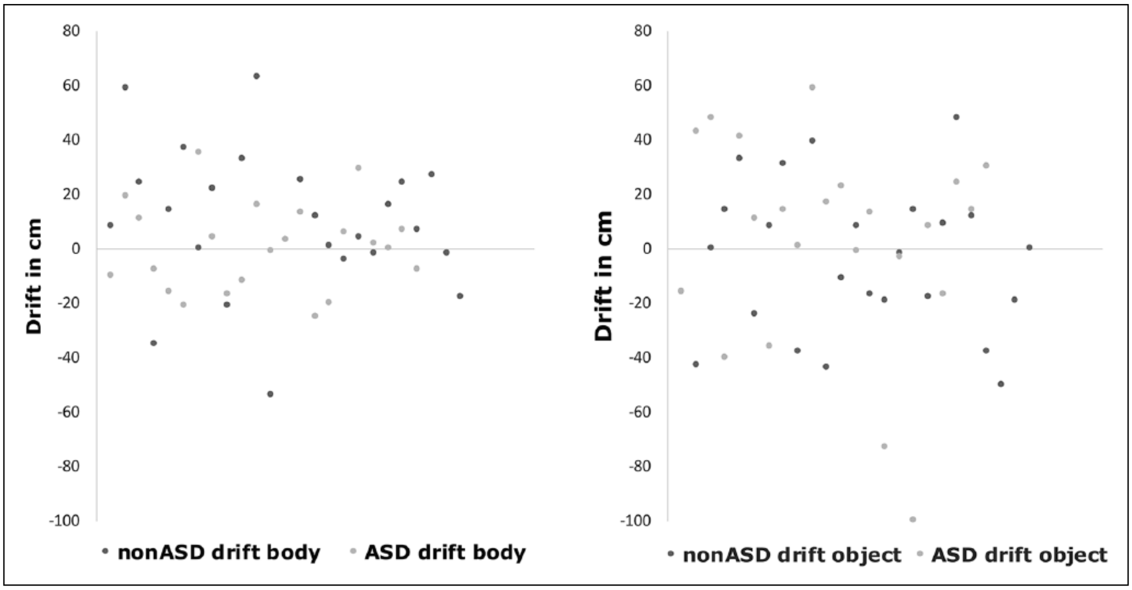

Figure 2. Individual participants' subtracted drift scores (synchronous–asynchronous) of ASD participants and non-ASD participants in the body condition and the object condition of FBI.

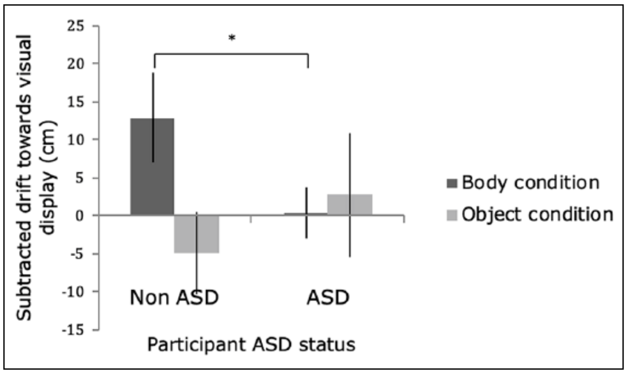

Figure 3. Subtracted drift (self-location in the asynchronous condition subtracted from self-location in the synchronous condition) for ASD participants and non-ASD participants in the body and object conditions.
$*p < 0.05$. Error bars denote *SE*.

There were several significant interaction effects: of Question type and Synchrony F (1, 45)=30.36, $p<0.001$, $\eta^2p=0.40$, of ASD status and Synchrony, F (1, 45)=4.43, $p=0.04$, $\eta^2p=0.09$, and of Question type and Display, F (1, 45)=11.51, $p=0.001$, $\eta^2p=0.20$. One three-way interaction, ASD × Question type × Synchrony, approached significance, F (1, 45)=3.38, $p=0.07$, $\eta^2p=0.07$. The remaining interactions were non-significant: Question type × ASD × Synchrony × Di splay, F (1, 45)=1.63, $p=0.21$, $\eta^2p=0.04$; Question type × Display × Synchrony, F (1, 45)=0.049, $p=0.49$, $\eta^2p=0.01$; ASD × Synchrony × Display, F (1, 45)=3.06, $p=0.09$, $\eta^2p=0.06$; ASD × Question type, F (1, 45)=0.02, $p=0.88$, $\eta^2p<0.001$; ASD × Display, F (1, 45)=1.35, $p=0.25$, $\eta^2p=0.03$; ASD × Question type × Display, F (1, 45)=0.003, $p=0.95$, $\eta^2p<0.001$; Display × Synchrony, F (1, 45)=0.27, $p=0.61$, $\eta^2p=0.006$.

In order to check for differences in response bias in the two groups, we conducted a 2 × 2 × 2 (ASD × Synchrony × Display) mixed ANOVA on the control questions only. This showed there was no significant main effect of ASD, F (3, 45)=0.11, $p=0.95$, $\eta^2p=0.001$, nor interactions of Display × ASD, F (3, 45)=0.67, $p=0.57$, $\eta^2p=0.01$, and Synchrony × ASD, F (3, 45)=0.16, $p=0.91$, $\eta^2p=0.004$, nor a three-way interaction of Synchrony × Display × ASD, F (3, 45)=0.14, $p=0.94$, $\eta^2p=0.003$, indicating that the two groups responded in a similar way to the control questions and a correction for a response bias was unnecessary.

Planned comparisons with Wilcoxon signed rank tests showed that for the non-ASD participants, the average ratings for the illusion questions in the synchronous body condition were significantly higher, M (SD)=5.53 (1.12), than in the asynchronous body condition, M (SD)=3.97 (1.70), $Z=3.33$, $p=0.001$. However, ASD participants' ratings in the synchronous body condition, M (SD)=4.63 (1.64) were not significantly different from their ratings in the asynchronous body condition, M (SD)=4.26 (1.64), $Z=0.64$, $p=0.52$. Concerning the average ratings for illusion items in the object conditions, non-ASD participants' ratings were significantly higher in the synchronous condition, M (SD)=4.4 (1.4) than in the asynchronous condition, M (SD)=3.1 (1.4), $Z=3.60$, $p=0.001$. ASD participants also had significantly higher scores in the synchronous condition M (SD)=4.3 (2.0) than in the asynchronous condition, M (SD)=3.5 (2.0), $Z=2.78$, $p=0.005$, when viewing the object.

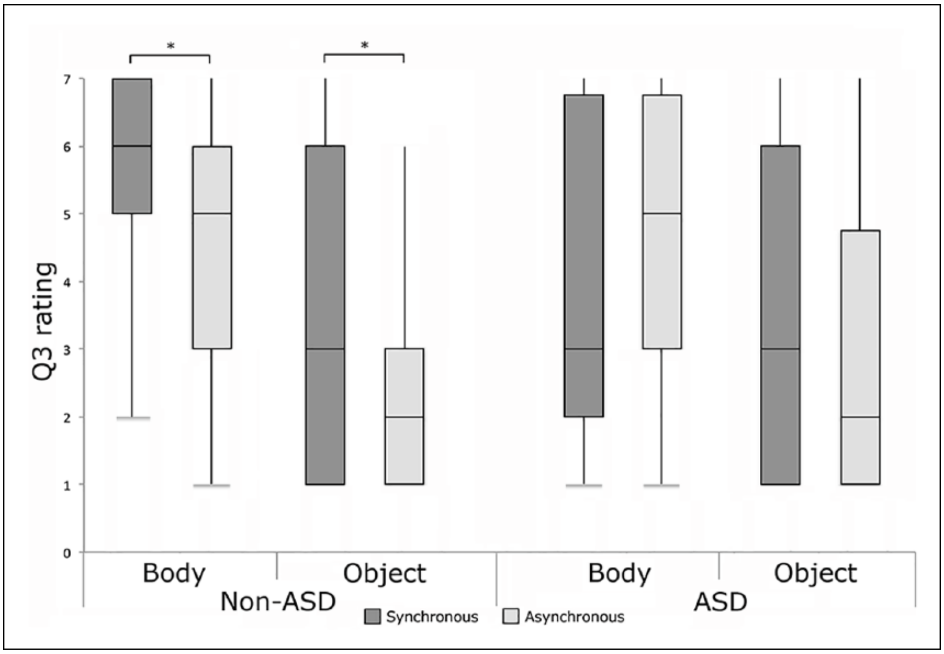

Figure 4. Group medians (horizontal lines) and interquartile ranges of questionnaire responses to Q3 'It felt as if the virtual body/object was my body'.
Whiskers denote 1st and 4th quartile ranges.
*$p < 0.012$ (Bonferroni corrected alpha level).

To further explore the data we examined differences in ratings for the 'self-identification' question, Q3 ('It felt as if the body/object was my body'). Wilcoxon signed rank tests were planned per group for Q3, comparing the synchronous vs asynchronous for the body and object. The alpha-level was Bonferroni corrected to 0.012.

In response to Q3 Wilcoxon signed rank tests showed that the response of non-ASD participants in the synchronous body condition, *M* (*SD*) = 5.76 (1.39), was significantly higher than in the asynchronous body condition, *M* (*SD*) = 4.32 (2.10), *Z* = 3.07, *p* = 0.001. However, for ASD participants, the difference between the synchronous body condition, *M* (*SD*) = 3.86 (2.42) and the asynchronous body condition, *M* (*SD*) = 4.68 (2.01) was not significant, *Z* = 0.64, *p* = 0.52. In the object conditions, non-ASD participants showed a significant difference, showing higher ratings in the synchronous condition *M* (*SD*) = 3.40 (2.24) than in the asynchronous condition, *M* (*SD*) = 2.40 (1.76), *Z* = 2.64, *p* = 0.008. In contrast, ASD participants showed similar levels of self-identification with the object in the synchronous condition *M* (*SD*) = 3.50 (2.58) as in the asynchronous condition *M* (*SD*) = 2.91 (2.16), *Z* = 1.08, *p* = 0.28 (see Figure 4).

PPS

Participants' RTs were recorded per tapping delay after sound onset. Trials that were faster or slower than 2.5 *SD* of their average RT for that onset delay were removed (fewer than 5% of all trials). The data of two non-ASD participants were rejected due to equipment malfunction.

A 2 × 5 mixed ANOVA, with ASD status (ASD vs non-ASD participants) as the between subjects factor, and tap delay after sound onset as the within-subjects factor (300, 800, 1500 ms, 2200 and 2500 ms) was run. Results revealed a significant main effect of tap delay, *F* (4, 47) = 25.51, $p < 0.001$, $\eta^2p = 0.35$ and a significant main effect of ASD status: ASD participants tended to have slower RTs than non-ASD participants, *F* (4, 47) = 7.11, *p* = 0.01, $\eta^2p = 0.13$ and RTs tended to become faster with each consecutive delay (see Table 3). Importantly, a significant interaction ASD status × tap delay was found, *F* (4, 47) = 3.47, *p* = 0.04, $\eta^2p = 0.07$, which means that the effect of delay on RTs was different for each group. To test the robustness of the interaction effect specifically, we calculated log-transformed RT values and repeated the ANOVA with these new values. The interaction effect was borderline significant with the transformed data, *F* (4, 47) = 2.95, *p* = 0.05, $\eta^2p = 0.06$.

To analyse this further, in each group, we ran four paired sample *t*-tests to compare RTs between each consecutive delay, that is, we compared RT at 300 ms with RT at 800 ms, RT at 800 ms with RT at 1500 ms and so on. The alpha-level was Bonferroni corrected to *p* = 0.006 for multiple comparisons. For ASD participants, RTs at 1500 ms were significantly faster than the RTs at 800 ms, *t* (21) = 3.62, *p* = 0.002, but there was no significant difference between RTs at 300 and 800 ms, *t* (21) = 1.86, *p* = 0.08, between RTs at 1500 and 2200 ms, *t* (21) = 2.49, *p* = 0.02, and between RTs at 2200 and 2500 ms, *t* (21) = 1.14, *p* = 0.27. For non-ASD participants, RTs at 800 ms were

Table 3. Reaction time (in ms) at tap delay after sound onset, for ASD and non-ASD participants.

Tap delay	300 ms	800 ms	1500 ms	2200 ms	2500 ms
	M (*SD*)	*M* (*SD*)	*M* (*SD*)	*M* (*SD*)	*M* (*SD*)
Non-ASD	1109 (107)	1070 (104)	1043 (80)	1037 (74)	1017 (73)
ASD	1272 (286)	1220 (216)	1147 (218)	1112 (198)	1093 (183)

significantly faster than RTs at 300 ms, $t\ (26)=3.16$, $p=0.004$, but there was no significant difference between RTs at 800 and 1500 ms, $t\ (26)=1.61$, $p=0.12$, between RTs at 1500 and 2200 ms, $t\ (26)=0.82$, $p=0.42$, and between RTs at 2200 and 2500 ms, $t\ (26)=2.66$, $p=0.01$. This means that in the two groups, tactile processing is differently boosted by co-occurring sounds, with a facilitation effect of sound on RTs occurring between 800 and 1500 ms for ASD participants, whereas for non-ASD participants the facilitation occurred between 300 and 800 ms. In this way, if we take the critical distance where the sound speeds up tactile RTs as a proxy of the PPS boundary (Canzoneri et al., 2012; Teneggi et al., 2013), we can conclude that the PPS size of ASD participants is smaller.

Using a MATLAB curve fitting tool, we fitted the data of the two groups to a linear function to assess if the slope of the PPS gradient as the sound approached was steeper for ASD participants than for non-ASD participants. The linear function was described by the following equation: $y(x)=y_0+kx$, where x represents the tap delay, y the RT, y_0 the intercept at $x=0$ and k the slope of the function. After removing the data of individuals with a poor fit (adjusted $R^2<0.2$, 6 participants in each group) the ASD linear equation could be described as $y=1340-0.11x$, and the non-ASD linear equation could be described at $y=1142-0.05x$. Importantly, the slope of the function was significantly different for the two groups, $t\ (33)=2.67$, $p=0.01$, with the slope of ASD participants being steeper ($k=-0.11$) than the slope of non-ASD participants ($k=-0.05$). See Figure 5.

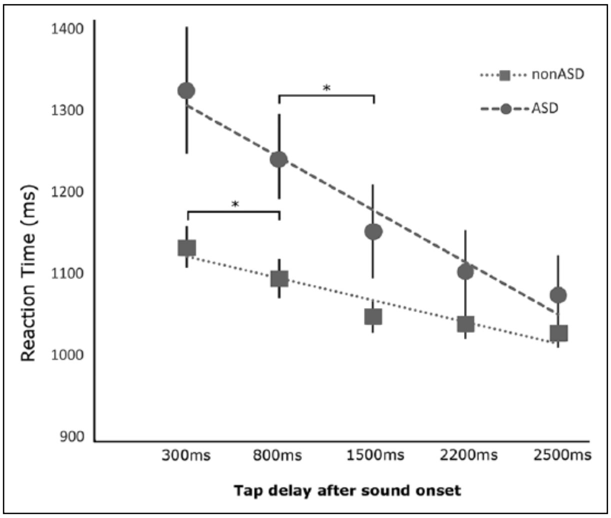

Figure 5. Reaction time of participants in response to taps after sound onset. Dotted lines depict the linear function.
Error bars denote 1 *SE*.
$^*p<0.006$ (Bonferroni corrected alpha level).

Correlations

Relationships between illusion strength in the body conditions, drift in self-location, PPS slope and questionnaire measures of interoceptive awareness, autistic traits, empathy and alexithymia were investigated with Spearman's correlations for the full sample of participants. Illusion strength – calculated as the subtracted score (synch–asynch) for Q3 (self-identification) in the body condition – showed a significant negative correlation with severity of autistic traits and a significant positive correlation with empathy ratings. No other correlations were significant (see Table 4).

To address the hypothesis that bodily self-consciousness may contribute to empathy, we conducted a stepwise multiple regression, with the predictor variables of autistic traits (AQ), alexithymia (TAS-20), IQ scores and the scores of FBI self-identification (Q3), and with empathy scores (QCAE) as the dependent variable. This showed that autistic traits and FBI self-identification are significant predictors of empathy, $F\ (2, 44)=42.27$, $p<0.001$, explaining 66% of the variance of empathy. The relationship between autistic traits and empathy is negative, while the relationship between self-identication and empathy is positive. Alexithymia and IQ do not significantly explain any additional variance of empathy after AQ and Q3 scores were modelled. See Table 5 for the regression coefficients.

Discussion

In this study we investigated bodily self-consciousness in ASD by measuring responses to the FBI and the extent of PPS in participants with the condition. Overall, our results show that individuals with ASD are much less susceptible to FBI than are typical control participants. Consistent with this, our data also show that the PPS of ASD participants is smaller and shows a steeper gradient at its boundary, indicating a more pronounced self-other distinction in ASD. The representation of the bodily self therefore seems to be less malleable in ASD participants and these 'low-level' differences in self may relate to (and partly underlie) the ability to empathise with others.

Table 4. Spearman's correlations and *p* values of the subtracted FBI scores (synchronous–asynchronous) for self-location drift and combined illusion questions ratings in the body condition, Question 3 (self-identification) and PPS slope, with scores measuring autistic traits (AQ), alexithymia (TAS20) and empathy (QCAE) and interoceptive awareness (MAIA subscales).

	Drift		Illusion questions		Q3		PPS slope	
	rho	*p*	*rho*	*p*	*rho*	*p*	*rho*	*p*
Autistic traits	0.23	0.11	−0.27	0.07	−0.46	0.001*	−0.10	0.51
Alexithymia	−0.08	0.59	−0.27	0.08	−0.26	0.06	−0.11	0.48
Empathy	0.26	0.08	0.37	0.01	0.49	<0.001*	0.05	0.75
Cognitive empathy	0.25	0.09	0.36	0.01	0.47	<0.001*	0.12	0.45
Affective empathy	0.07	0.64	0.13	0.37	0.18	0.22	−0.19	0.20
MAIA Noticing	−0.07	0.67	0.21	0.16	0.22	0.14	−0.06	0.69
MAIA attention regulation	0.11	0.46	0.18	0.23	0.27	0.07	0.12	0.44

$^*p < 0.002$ (Bonferroni corrected alpha level).

Table 5. Regression model showing the contributions of autistic traits (AQ) and FBI self-identification (Q3) to empathy (QCAE).

	β	*SE β*	*β*
Step 1			
Constant	110.55	3.24	
AQ	−1.06	0.13	−0.78***
Step 2			
Constant	100.32	5.44	
AQ	−0.95	0.13	−0.71***
Q3	1.58	0.69	0.22*

$R^2 = 0.62$, $p < 0.001$ for Step 1. $\Delta R^2 = 0.04$, $p = 0.03$ for Step 2.
$^*p < 0.05$.
$^{***}p < 0.001$.

The FBI data show that agreement with illusion statements was signfiicantly higher in synchronous than in asynchronous body conditions in the non-ASD group – as found previously (Aspell et al., 2012; 2013; Cowie, McKenna, Bremner, & Aspell, 2017; Ionta et al., 2011; Lenggenhager et al., 2007) – but did not differ in the ASD group. Moreover, neurotypical participants showed significantly greater self-identification with the virtual body in the synchronous condition and a greater self-location drift towards the virtual body during the synchronous condition, but this was not found for ASD participants. In keeping with this, we found a strong and highly significant negative correlation of autistic traits with self-identification ratings.

Surprisingly, non-ASD participants also responded with higher ratings after synchronous stroking on the summated illusion questionnaire items and on the self-identification item Q3, in the object condition. However, the actual score of these participants in the object condition on Q3 indicated a negative agreement with the statement (lower than 4 which equates to the neutral point), and only in the body condition did they positively agree with the Q3 self-identification statement. Similarly, ASD participants showed higher scores in the synchronous condition than the asynchronous condition for the summated illusion scores. But their score on Q3 in the synchronous object condition was also below 4, and therefore a negative agreement. In sum, only non-ASD participants identified more with the virtual body after synchronous stroking, while neither group identified with the object. This suggests that, whereas non-ASD participants have a tendency to self-identify with the virtual body and localise their self closer to it following synchronous stimulation, ASD participants do not appear to have a bodily self-representation that adapts to changes in multisensory input so readily. This is in line with the finding that ASD participants show a lower susceptibility to RHI (Cascio et al., 2012; Paton et al., 2012), and suggests that ASD participants have an altered bodily self-representation that encompasses their whole body.

Confirming our other hypotheses, and in line with recent predictions about the slope of PPS in ASD (Noel et al., 2017), the results of the PPS task demonstrated that ASD participants exhibited a steeper slope in their RTs as a function of the temporal delay of the tap, as the sound approached their body. Also, their PPS boundary was closer to the body than for non-ASD participants. A smaller PPS may partly underlie certain behaviours sometimes seen in individuals with ASD, such as approaching others closer than social norms prescribe, or having difficulty considering communications outside personal space as directed towards themselves (Asada et al., 2016; Kennedy & Adolphs, 2014; Parsons et al., 2004).

The reduced susceptibility to FBI we found for ASD participants fits with the steeper PPS slope of these participants and may indicate a generally less flexible representation of the bodily self. The slope of the PPS indicates the distance over which the facilitatory effect on RT via the integration of touch and sound manifests: it occurs over a greater distance in a shallow slope than it does in a steep slope (found for ASD participants). Therefore conceptually, the slope of the PPS may indicate the flexibility of the boundary between one's self and an other (Noel et al., 2017). It has been shown that PPS extends towards others in social interactions

(Teneggi et al., 2013) and that others' PPS can even sometimes be remapped onto one's own (Maister et al., 2015). Having a steeper, less flexible boundary between the self and other would mean that the PPS boundary of individuals with ASD would not change to the same extent in social interactions or during shared sensory experiences.

A limitation of the study, however, is that our results refer to the 'peri-hand' PPS, and not to the 'full body' PPS that can be measured by stimulating the trunk (Serino et al., 2015). Therefore, our conclusions about the PPS modulation in ASD participants only relate to the peri-hand portion of the space around the body. A recent paper by Serino et al. (2015) showed that the PPS size changes according to the body part around which the PPS is measured (i.e. face or hand or trunk), with the hand-PPS being the smallest, the face-PPS being larger and the trunk-PPS the largest. This is thought to reflect the different portions of space in which a body part mostly interacts with external objects: whereas the hand interacts with objects in a very limited area, that is, only when the hand is touching an object, the trunk is usually involved in interactions that occur over a larger area. Despite the different sizes of the body-part centred PPSs, we expect the full-body PPS in ASD participants to be modulated as the peri-hand one, that is, being smaller in ASD than in non-ASD participants. This is because the sizes of different body-part PPSs are not fully independent of each other (Serino et al., 2015), and are in line with our interpretation and previous studies, that the smaller PPS in ASD participants may reflect their often-observed anomalous social interactions – such as 'invading' others' personal space – where the whole body as well as the hands are similarly involved (Asada et al., 2016; Kennedy & Adolphs, 2014; Parsons et al., 2004).

An explanation for the reduced susceptibility to FBI in ASD is offered by findings that individuals with ASD have a wider temporal binding window (TBW) in which temporally close sensory signals are 'bound' into a single perceived event (Greenfield, Ropar, Smith, Carey, & Newport, 2015; Kwakye, Foss-Feig, Cascio, Stone, & Wallace, 2011; Noel, Stevenson, & Wallace, 2018; Stevenson et al., 2014). A wider TBW would impair the ability to integrate multisensory information and may lead to a lower ability to discriminate between the synchronous and asynchronous conditions of body illusions. This explanation is supported by our findings that on all measures, the difference between the synchronous and asynchronous conditions was smaller for ASD participants.

In addition, it has been suggested – following the finding of an inverse relationship between interoceptive sensitivity and susceptibility to the RHI (Tsakiris, Tajadura-Jimenez, & Costantini, 2011) – that an individual's bodily self is more robust and stable if interoceptive cues are more accurately /precisely represented relative to exteroceptive stimuli, making them less susceptible to body illusions (C. E. Palmer & Tsakiris, 2018; Tajadura-Jiménez & Tsakiris, 2014 ; Tsakiris et al., 2011). In a predictive coding approach, C. E. Palmer and Tsakiris (2018) propose that probabilistic representations of the bodily self-emerge from the integration of top-down predictions and bottom-up prediction errors across all modalities, including interoceptive. They suggest that the balance in saliency of interoceptive relative to exteroceptive prediction errors will determine the malleability of the representation of self, with the interoceptive prediction errors providing stability and continuity of the representation of self in the face of exteroceptive uncertainty. In this account, the brains of individuals with lower interoceptive accuracy would rely less on the prediction errors generated by interoceptive senses, awarding more saliency to exteroceptive signals. Therefore, representations of self would be updated based on conflicting exteroceptive signals, thus generating stronger body illusions. The opposite would be true for individuals with high interoceptive accuracy.

However, in this study we did not find relationships between susceptibility to FBI and interoceptive awareness. Furthermore, autistic individuals tend to have *lower* interoceptive sensitivity and awareness than the typical population (DuBois, Ameis, Lai, Casanova, & Desarkar, 2016; Mul, Stagg, Herbelin, & Aspell, 2018; Shah, Hall, Catmur, & Bird, 2016), yet our findings are in line with previous research that shows that they are *less* susceptible to body illusions, not more (Cascio et al., 2012; Guerra et al., 2017; Paton et al., 2012). It is worth noting that an exceptionally wide temporal binding window for interoceptive and exteroceptive (cardio-visual) signals has been shown in ASD. This may affect the balance of interoceptive and exteroceptive processing in terms of saliency and integration (Noel, Lytle, Cascio, & Wallace, 2018). Our ASD participants scored significantly lower on the MAIA dimension of Attention Regulation, which captures how well individuals can control or maintain focus on interoceptive sensations. Thus, individuals with ASD may be less able to sustain attention to interoceptive signals.

Taken together, these findings support suggestions that the saliency of interoceptive versus exteroceptive prediction errors may differ in ASD (Noel, Lytle, et al., 2018), and/or that the strength of top-down predictions (priors) versus the saliency of bottom-up sensory prediction errors is different, as proposed by the so-called hypo-prior model of autism (Lawson, Rees, & Friston, 2014; Pellicano & Burr, 2012). Usually, the experience of the FBI results from an optimal top-down resolution (update) to the prediction errors the multisensory conflict of the illusion generates. However, it has been proposed that in ASD, bottom-up sensory signals outweigh top-down priors: an inflexibility in adapting higher order cognitions to novel sensory signals results (Lawson, Mathys, & Rees, 2017; Lawson et al., 2014). This might explain both a less flexible sense of bodily self as evidenced by a reduced susceptibility to FBI, and a reduced flexibility in self–other boundaries as suggested by our finding of a steeper slope of the PPS boundary.

It is worth noting that these findings are in line with suggestions that a low-level mechanism that differentiates between representations of self and other may be anomalous in ASD (Lamm, Bukowski, & Silani, 2016; Lombardo et al., 2010; Sowden & Shah, 2014). In particular, it is widely agreed that successful social interactions are reliant on the ability to flexibly switch between neural representations of self and others. This mechanism, referred to as 'self-other control' (Decety & Sommerville, 2003), has been hypothesised to be altered in ASD participants (Bird & Cook, 2012). Importantly, several studies have tried to identify the neural basis of this 'self-other control' mechanism, reaching a widely agreed conclusion that the two main areas involved are the medial prefrontal cortex and the temporoparietal junction (Brass, Ruby, & Spengler, 2009; Spengler, von Cramon, & Brass, 2009). These regions are critical in mentalising, theory of mind and perspective taking, that is, in those processes for which a flexible yet well-controlled distinction between self and others is needed. We therefore speculate – given the purely behavioural nature of our investigation – that a dysfunction in these key regions for controlling self-other distinction underpins the observed reduced malleability of bodily self-representations in ASD participants (Lombardo et al., 2010; Uddin, 2011).

Our final hypothesis, that altered bodily self-consciousness would be related to social functioning in ASD, is supported by our findings. The strength of the experienced illusion as indicated by the self-identification question (Q3) was negatively related to autistic traits and positively related to empathy. Our multiple regression showed that both autistic traits and the tendency to self-identify with the vitual body contributed significantly to empathy scores. This link with empathy suggests that altered bodily self-consciousness has social implications. Empathy involves the understanding and sharing of the emotion of an other, a process in which one's own emotional experience and that observed in an other are both neurally represented (Bird & Viding, 2014; Decety & Jackson, 2006; Sowden & Shah, 2014). We can speculate that the reduced flexibility of bodily self-representation in ASD may hamper the ability to represent another flexibly as well. Indeed, the social environment provides more unpredictable and novel situations than any other, and it has been suggested that the consequences of altered predictive coding in the brain are not restricted to perception, but also affect aspects of behaviour and social interaction (Balsters et al., 2016; Kilner, Friston, & Frith, 2007; Lawson et al., 2014; C. J. Palmer, Lawson, & Hohwy, 2017).

However, it was somewhat surprising to find that, in our sample, while autistic traits and the tendency to self-identify with the virtual body did contribute to empathy, alexithymia did not contribute significantly to empathy in our multiple regression model, which is in contrast to previous results (e.g. Bird et al., 2010; Mul et al., 2018; Shah et al., 2016). This may be due to differences in the way empathy was measured, that is, state empathy for pain specifically in response to visual stimuli versus trait empathy by questionnaire. Alternatively, or additionally, our sample may not have been large enough to find a relationship. Mul and colleagues (2018) and Aaron, Benson, and Park (2015) did find a relationship between empathy and alexithymia, which was partly independent from the relationship with autistic traits, all of which were measured by questionnaire, the latter in a sample of 139 non-ASD adults.

We note a number of limitations of this study. The use of self-report measures of emotion understanding, although widely used, may produce unreliable (underestimated or overestimated) responses from some ASD participants. In this vein, it would be useful if future studies use an additional implicit measure of susceptibility to FBI, such as changes in skin temperature (Salomon, Lim, Pfeiffer, Gassert, & Blanke, 2013), skin conductance response to threat to the virtual body (Ehrsson et al., 2008) or crossmodal congruency effects (Aspell et al., 2009). The relatively small size of our sample, and the fact that our non-ASD group did not have similar levels of alexithymia as the ASD group, means that our study is limited in regard to conclusions that can be drawn on the contributions of alexithymia and autistic traits to empathy.

In conclusion, our findings suggest that individuals with ASD have altered bodily self-consciousness, likely due to differences in multisensory integration, which may have a cascading effect on social functioning. Participants with ASD showed reduced susceptibility to FBI and had a smaller PPS with a steeper slope than the control participants. These results might be explained by wider temporal binding windows in ASD and/or a hypo-prior predictive coding account of autism, and may be compounded by impairments in mechanisms underlying 'self-other control' (Decety & Sommerville, 2003) in autism.

We suggest that the observed differences may be indicative of a less flexible representation of the bodily self in ASD. The integration of interoceptive and exteroceptive signals and the contribution of these integrated signals to bodily self-consciousness may also differ in ASD, and this warrants further investigation. Finally, further research into if and how an altered bodily self affects higher order self-processing would also be informative, as this would not only increase our understanding of autism and other disorders of self, but also deepen our insight into the nature of self.

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