Interoceptive influences on peripersonal space boundary.

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ABSTRACT

Integration of body-related signals within the peripersonal space (PPS) contributes to bodily self-awareness. Whereas several studies have shown how individual PPS extension is shaped by external factors, e.g. during interactions with people and objects, no studies have looked at interoceptive influences on PPS extension. We exposed participants to an audio-tactile interaction task, to measure their PPS boundary (Session 1), and to a heartbeat counting task and a time estimation task, to specifically assess their interoceptive accuracy (Session 2). Participants' traits of private self-consciousness and social anxiety were also evaluated, to account for their possible effect on the relation between interoception and PPS representation. We found that higher interoceptive accuracy specifically predicts narrower PPS boundary. Moreover, this relation is moderated by individual traits of private self-consciousness, but not social anxiety. Extending the concept of interoceptive influences on exteroceptive body representations to PPS, our results, first, support the idea that a dynamic balance between intero-exteroceptive processing might represent a general principle underlying bodily self-awareness; second, they shed light on how interoception may affect also the way we interface with the external world. Finally, showing that, in order for interoceptive accuracy to be effective on the intero-exteroceptive balance, it is important that individuals tend to focus on inner sensations and feelings, our results suggest that a comprehensive intero-exteroceptive model of bodily self-awareness should be (at least) a three-dimensional model that includes individual self-consciousness traits.

1.INTRODUCTION

Bodily self-awareness is a central aspect of our sense of self as subject of experience distinct from others. It refers to the feeling of being situated within a body that we own, and that occupies a specific location in space (Noel, Pfeiffer, Blanke, & Serino, 2015). The experience of being a bodily self in space depends on the integration of multisensory signals occurring within the peripersonal space (PPS). PPS is a limited portion of the space immediately surrounding the body that has been functionally described in different ways, specifically as the space for goal-directed action (reaching space), protection (defensive space) and joint action (social space) (de Vignemont & Iannetti, 2015; di Pellegrino & Ladavas, 2015; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). Also, PPS can be anchored to different body parts (hand, arm, face etc. (Fogassi et al., 1996; Graziano, Hu, & Gross, 1997)). Interestingly, recent studies have shown that PPS is centered at the subjectively perceived location of the bodily self, rather than at the location of the physical body (Noel et al., 2015). Moreover, the extension of PPS boundary is not fixed. Rather, it is dynamically shaped during interactions with objects - both real (Ladavas & Serino, 2008; Martel, Cardinali, Roy, & Farne, 2016) and virtual (Bassolino, Serino, Ubaldi, & Ladavas, 2010; Sengul et al., 2012) - and after interactions with other persons (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013). Thus, PPS, as the space of the bodily self (Noel et al., 2015), also mediates the interactions with other people and the environment. However, and most importantly, before any dynamic modulation induced by social and non-social interactions, the extension of PPS boundary largely varies across persons (Ferri, Costantini, et al., 2015) depending on several individual characteristics. For instance, studies suggest that it is affected by individual personality traits: people with larger PPS boundary report higher levels of anxiety (Sambo & Iannetti, 2013) and claustrophobia (Lourenco, Longo, & Pathman, 2011). Moreover, PPS boundary adapts to the physical dimensions of the individual's body (Longo & Lourenco, 2007). However, if also interoceptive abilities (i.e., to sense physiological signals originating inside the body) affect the extension of PPS boundary is currently unknown. This knowledge would also shed light on how interoception may affect the way we interface with the external world. In the present study we aim at investigating the relationship between interoceptive accuracy (IAcc;

(Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015)) and extension of PPS boundary, in healthy individuals.

Why do we expect interoceptive accuracy to affect the extension of PPS boundary?

IAcc is commonly taken as a proxy for trait-like sensitivity to one's visceral signals, and usually determined using heartbeat tracking (i.e., silent counting of heartbeats in specified time windows (Schandry, 1981)). As such, IAcc is thought to play a ubiquitous role not only in emotional (Dunn, Galton, et al., 2010; Herbert & Pollatos, 2012; Wiens, 2005) and cognitive (Garfinkel et al., 2013; Umeda, Tochizawa, Shibata, & Terasawa, 2016) processing, but also in bodily self-awareness. According to a recent proposal (Tsakiris, 2017), IAcc may constrain the effects of ever-changing exteroceptive signals (e.g., visual, tactile) on body awareness. By counteracting exteroceptive influences, interoception would serve the necessary balance between adaptability and stability of the bodily self.

The first study that tested the interaction between interoceptive and exteroceptive representations of the bodily self compared individual IAcc with the change in body ownership induced by the rubber hand illusion (RHI; (Tsakiris, Tajadura-Jimenez, & Costantini, 2011)). The study revealed that individuals with lower IAcc experience a stronger RHI. This evidence certainly supports the idea of a dynamic intero-exteroceptive balance: the absence of accurate interoceptive representations would make one's sense of body ownership more malleable and unstable against exteroceptive bodily signals. Specifically, lack of co-weighting of interoceptive and exteroceptive signals or more attentional resources allocated to exteroceptive multi-sensory input during body-perception may explain the observed negative correlation between IAcc and RHI (Suzuki, Garfinkel, Critchley, & Seth, 2013; Tsakiris et al., 2011).

Body ownership is only one of the manifold exteroceptive representations of the bodily self though. If the dynamic balance between intero-exteroceptive processing is a general principle underlying bodily self-awareness, then it should apply also to other aspects of the bodily self. In this study, we test its validity for the subjectively perceived space of the bodily self, the PPS.

Empirical evidence suggesting that there might be a relation between IAcc and PPS extension concerns the contribution of IAcc in the demarcation of self-other boundary. Similar to the RHI, individual traits of IAcc were shown to negatively predict the flexibility of self-other boundary during the enfacement illusion (Tajadura-Jimenez, Longo, Coleman, & Tsakiris, 2012; Tajadura-Jimenez & Tsakiris, 2014), an illusion that investigates the plasticity of self-face identity. Hence, interoception was proposed as an element of stability of the bodily self also against self-other blurring (Tsakiris, 2017). Interestingly, the plasticity of PPS extension seems to play a crucial role in setting self-other boundaries during social interactions (Teneggi et al., 2013). However, whether individual traits of IAcc may influence the demarcation of self-other - or self-world - boundary also in terms of plasticity of PPS extension is still unknown.

Our study is the first to investigate the interaction between individual boundary of PPS and different degrees of IAcc. First, we hypothesize that individuals with higher IAcc may show narrower PPS boundary than individuals with lower IAcc. A stronger ability to sense internal signals in the former might support the co-weighting of interoceptive and exteroceptive signals. In contrast, individuals with lower IAcc might rely mainly on, and better integrate, external input occurring far from the body. However, strong interoceptive skills may not be enough to counterbalance exteroceptive influences on bodily self-awareness. For instance, this could be the case of individuals who, regardless of their interoceptive skills, tend to allocate attentional resources and attribute more salience to external stimuli, rather than focus on inner sensations and feelings. In other words, and this is our second hypothesis, specific individual traits may bias top-down attentional effects on the intero-exteroceptive balance. Interestingly, it is known that individual traits of social anxiety and private self-consciousness affect PPS extension (Iachini, Ruggiero, Ruotolo, Schiano di Cola, & Senese, 2015; Sambo & Iannetti, 2013) and IAcc (Ainley, Maister, Brokfeld, Farmer, & Tsakiris, 2013; Ainley, Tajadura-Jimenez, Fotopoulou, & Tsakiris, 2012; Dunn, Stefanovitch, et al., 2010; Ehlers & Breuer, 1992; Pollatos, Traut-Mattausch, & Schandry, 2009; Stevens et al., 2011; Weisz, Balazs, & Adam, 1988; Zoellner & Craske, 1999) separately. Therefore, they might influence also the possible correlation between IAcc and PPS boundary, for instance, explaining (or facilitating) it. To exclude this possibility, we will adopt a partial correlation approach using social anxiety and private self-consciousness scores as variables of no interest. Most interestingly, however, individual traits might also moderate (or change) the possible relation between IAcc and PPS boundary, at certain levels. This would be the case if, as hypothesized above, in order for interoceptive signals to counterbalance exteroceptive input, it is essential that individuals show an adequate inclination to private self-focus. If this is the case, a moderation analysis using private self-consciousness scores as moderating variable should reveal the level of private self-consciousness that makes the relationship between IAcc and PPS possible.

2.METHODS

2.1 Participants

Forty-one healthy right-handed volunteers (16 females, mean age 21.8, age range 20-31 years) participated in the study after providing written informed consent. Each participant took part in two sessions. During Session 1, participants performed a Peripersonal Space task (Figure 1, top). During Session 2, the same participants performed a Heartbeat Counting task and a Time Estimation task (Figure 1, bottom). Participants were also assessed by the Self-Consciousness Scale (Fenigstein, Scheier, & Buss, 1975). The experimental protocol was approved by the local institutional ethics committee.

2.2 Session 1: Peripersonal space task

Auditory stimuli were samples of pink-noise (or 1/f noise) of 3000 ms duration, with flat or increasing (looming) intensity levels. The sounds were sampled at 44.1 kHz. Sound intensity was manipulated by using the Soundforge 4.5 software (Sonic Foundry, Madison, WI), so that “looming sounds” had exponentially rising acoustic intensity from 55 to 70 dB, while “flat sounds” had constant 62.5 dB acoustic intensity.

Tactile stimuli were delivered by means of constant-current electrical stimulators (DS7A, Digitimer, Hertfordshire, United Kingdom), via pairs of electrodes placed on the hairy surface of the index fingers. The electrical stimulus was a single, constant voltage, rectangular monophasic pulse. At the beginning of Session 1, the tactile stimulus was set individually for each participant at the intensity of the weakest, non-painful, stimulus that was clearly above threshold (Canzoneri, Magosso, & Serino, 2012). Intensity for the tested participants ranged between 60 and 90 mA. Stimulus duration was equal to 100 μs. The presentation of auditory and tactile stimuli, as well as the recording of participants’ responses, was controlled by custom software implemented in Matlab.

Apparatus and Procedure. During the task, participants were blindfolded and comfortably seated beside a table, with their right arm resting palm down. The audiotactile apparatus, which was mounted on the table, consisted of two loudspeakers - one placed near to the participants' right hand, while the other at a distance of 100 cm from the near loudspeaker, thus far from the participant - and a constant-current electrical stimulator controlling a pair of neurological electrodes attached on the participant's right index finger. During each trial, either a looming or a flat sound was presented. Along with the auditory stimulation, in the 60% of trials participants were also presented with a tactile stimulus. According to prior studies using the same task (e.g., (Canzoneri et al., 2012; Ferri, Costantini, et al., 2015)), the remaining trials (40% of total) were catch trials with auditory stimulation only. The tactile stimulus was delivered at different temporal delays from the onset of the auditory stimulus. Five different temporal delays (T1, 300 ms; T2, 800 ms; T3, 1500 ms; T4, 2200 ms; and T5, 2700 ms) were used. Each trial was followed by an intertrial interval of 1000 ms. Each participant was presented with 18 target stimuli for each combination of temporal delays (T1-T5) and sounds (looming, flat) randomly intermingled with the catch trials. Trials were equally divided into three blocks. Participants were asked to respond as fast as possible to the tactile target, when present, by pressing a button on a response box (Cedrus RB-834) with their left index finger, trying to ignore the auditory stimulus. Session 1 lasted approximately 30 minutes.

Estimation of individual PPS boundary. Mean RTs to tactile targets were calculated for every temporal delay (T1 – T5), separately for looming and flat sounds. Then, they were fitted to a sigmoidal function (Canzoneri et al., 2012): $y(x) = (y_{min} + y_{max} * e^{(x-x_c)/b}) / (1 + e^{(x-x_c)/b})$, where x represents the independent variable (timing of touch delivery in ms), y the dependent variable (reaction time), y_{min} and y_{max} the lower and upper saturation levels of the sigmoid, x_c the value of the abscissa at the central point of the sigmoid (value of x at which $y = (y_{min}+ y_{max})/2$) and b establishes the slope of the sigmoid at the central point. For each participant we took x_c, hereafter the Central Point of the curve (CP; Figure 1, top-right), as an estimation of the individual boundary of PPS representation (Canzoneri et al., 2012; Ferri, Costantini, et al., 2015; Ferri, Tajadura-Jiménez, Väljamäe, Vastano, & Costantini, 2015). To check that the sigmoid function, compared to a linear function ($y(x) = y_0 + kx$), provided a better description of the relationship between tactile RTs and timing at which the tactile stimuli were delivered along with looming sounds, we compared the root mean square error (RMSE), an index of goodness of fit, between the two models by means of a paired t test analysis (Canzoneri et al., 2012; Ferri, Costantini, et al., 2015).

2.3 Session 2

2.3.1 Heartbeat Counting Task

To assess interoceptive accuracy, we used the Mental Tracking Method (Schandry, 1981).

Apparatus and Procedure. Heart rate was monitored with three 10 mm Ag/AgCl pre-gelled electrodes attached to the participants' shoulders and left ankle according to the Einthoven's triangle configuration (PowerLab, AD Instruments, UK). In twelve trials, participants silently counted how many heartbeats they felt over varying time intervals (three 25-s trials, three 35-s trials, three 45-s trials, three 100-s trials). The presentation order of the different time intervals was randomized. They were instructed to count their heartbeats without taking their pulse. Responses were then compared with how many heartbeats were measured by ECG.

Estimation of individual IAcc. Heartbeat traces were analysed using LabChart5. For each participant, the number of R-wave peaks was counted on the heart trace recorded in each trial. The individual IAcc was calculated as the mean score of the heartbeat perception intervals (Schandry, 1981): (1/12 Σ(1 − (|recorded heartbeats − counted heartbeats| / recorded heartbeats)). Thus, IAcc values varied between 0 and 1, with higher scores indicating better interoceptive accuracy.

2.3.2 Time Estimation task

To make allowance for participants' potential use of time-estimation strategies during the Heartbeat Counting task (Dunn, Stefanovitch, et al., 2010), participants were asked to perform a Time Estimation Task.

Apparatus and Procedure. Participants were asked to estimate the length of the same time intervals (three 25-s trials, three 35-s trials, three 45-s trials, three 100-s trials) presented in the Heartbeat Counting task. Responses were then compared with the actual duration of the trials.

Estimation of individual TEAcc. The individual Time Estimation Accuracy was calculated as the mean score of the time estimation intervals: (1/12 Σ(1 − (|estimated

elapsed time−actual elapsed time | / actual elapsed time)). Thus, TEAcc values varied between 0 and 1, with higher scores indicating better time estimation accuracy.
Overall, Session 2 lasted approximately 30 minutes.

2.4 Self-consciousness scale (SCS)

The Self-Consciousness Scale (SCS; (Fenigstein et al., 1975)) consists of three subscales, designed to measure self-focused attention. The Social Anxiety subscale (6 items) measures distress caused by interacting with other people. The Private Self-Consciousness subscale (10 items) assesses the extent to which individuals focus on internal thought, sensations and feelings. The Public Self-Consciousness subscale (7 items) concerns the propensity to focus on oneself as an object of an observer's scrutiny. Participants respond on a 5-point Likert scale (from 0 = extremely uncharacteristic of me to 4 = extremely characteristic). Higher scores indicate greater self-consciousness/social anxiety. The SCS has fairly good reliability, with Cronbach's alpha ranging from .73 to .84 (Mor & Winquist, 2002). Based on prior evidence suggesting that both peripersonal space extension and interoception are affected by anxiety and private self-consciousness (Iachini et al., 2015; Sambo & Iannetti, 2013); (Ainley et al., 2013; Ainley et al., 2012; Dunn, Stefanovitch, et al., 2010; Ehlers & Breuer, 1992; Pollatos et al., 2009; Stevens et al., 2011; Weisz et al., 1988; Zoellner & Craske, 1999), we focused on the Social Anxiety and the Private subscales of the SCS to investigate whether these specific traits affect the relationship between multisensory PPS boundary and interoceptive accuracy.

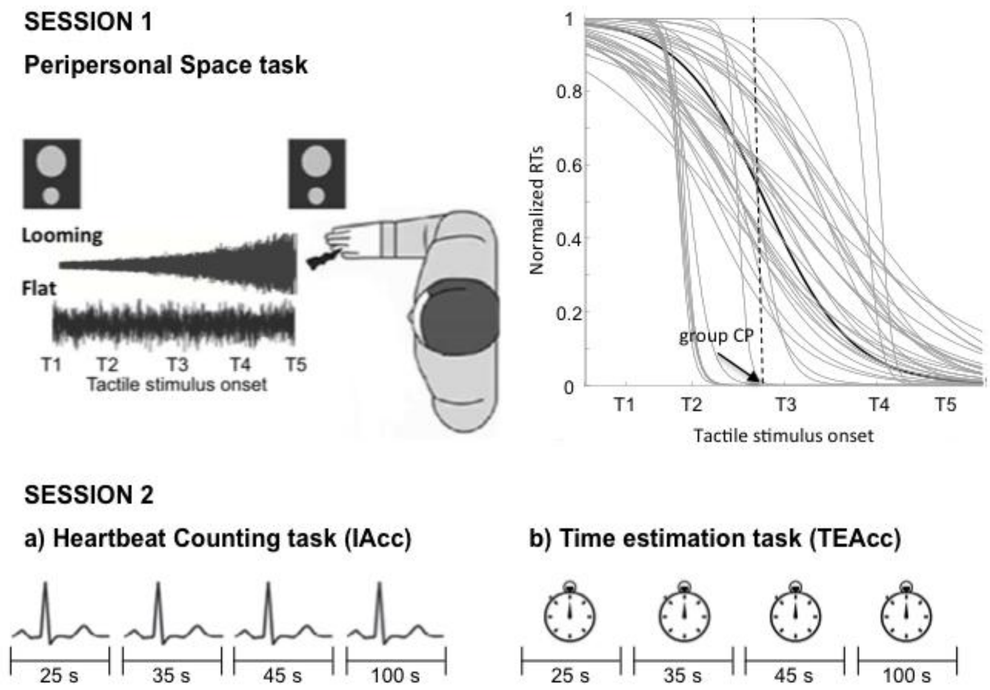

Figure 1: Illustration of the tasks performed by each participant.
Session 1. PPS task. Left: at each trial, participants were presented with either a looming or a flat sound delivered by loudspeakers. At different delays from the onset of the sound (T1-T5), a tactile stimulus was also delivered. Participants were asked to respond as fast as possible to the tactile target. Right: Individual sigmoid fits obtained from normalized RTs. CP = Central Point. *Session 2. a) Heartbeat counting task.* Participants were instructed to silently count their heartbeats over varying time intervals, while their actual heartbeat was recorded. IAcc = Interoceptive Accuracy. *b) Time estimation task.* Participants were instructed to estimate the length of varying time intervals, while the actual length of the time intervals was measured. TEAcc = Time Estimation Accuracy.

2.5 Data Analysis

2.5.1 Relationship between individual PPS boundary and IAcc. We first performed correlations between individual measures of CP and IAcc. Then, since standard correlation analyses are particularly sensitive to deviant observations (Rousselet & Pernet, 2012), especially bivariate outliers, to confirm and refine the robustness of our results, we computed also skipped correlations (Wilcox, 2004) using the Robust Correlation toolbox (Pernet, Wilcox, & Rousselet, 2012). Moreover, we conducted null hypothesis statistical significance testing using the nonparametric percentile bootstrap test (2000 resamples; 95% confidence interval, corresponding to an alpha level of .05), which is more robust against heteroscedasticity compared with the traditional t-test (Pernet et al., 2012).

Then, to account for potential confounds of the heartbeat counting task, due to time estimation strategies (Dunn, Stefanovitch, et al., 2010), we performed a partial correlation with TEAcc as a covariate of non-interest between CP and IAcc.

Finally, the correlation coefficients resulting from standard bivariate and partial correlations were statistically compared through Williams' test (Williams, 1959) for non-independent coefficients. The 95% confidence interval for their difference was estimated by means of Zuo's method (Zou, 2007).

2.5.2 Effect of Social Anxiety and Private Self-Consciousness traits on the relationship between PPS boundary and IAcc.

Partial correlation analyses. Partial correlation analyses were performed also to investigate whether individual's Social Anxiety or Private Self-Consciousness traits facilitated the relation between CP and IAcc. To this aim, we measured the association between CP and IAcc, while adjusting the effect of either Social Anxiety scores or Private Self-Consciousness scores. Then, the correlation coefficients showed by partial and bivariate correlations were statistically compared through Williams' test (Williams, 1959) for non-independent coefficients. The 95% confidence interval for their difference was estimated by means of Zuo's method (Zou, 2007).

Moderation analyses. Moderation analyses (Model 1 in the SPSS PROCESS macro; (Hayes, 2013)) were performed to separately probe moderation by individual's Social Anxiety and Private Self-Consciousness traits of the relation between IAcc and CP. Significant interactions between individual traits and IAcc were further probed using the Johnson-Neyman (J-N) method (Johnson & Fay, 1950) as implemented in the SPSS MODPROBE macro (Hayes & Matthes, 2009). The J-N method calculates the critical moderator variable values at which the relationship between the focal predictor (IAcc) and the dependent variable (CP) changes significance. J-N regions of significance are reported using standardized Z scores.

3. RESULTS

3.1 Measures of CP, IAcc, TEAcc.

3.1.1 Individual PPS boundary (CP). To estimate the location of PPS boundary, for each participant, the mean RTs to the tactile targets delivered along with looming sounds were fitted to a sigmoidal function. Five participants were excluded from further analysis, as the goodness-of-fit of the sigmoid model for them was questionable, being r^2 < .70. This threshold was chosen based on previous studies that used the same PPS task (see Table 1 in (Ferri, Costantini, et al., 2015)). The average goodness-of-fit of the sigmoid models in the remaining participants (N = 36) was excellent (r^2 = .92). Consistent with previous literature (Canzoneri et al., 2012; Ferri, Costantini, et al., 2015; Teneggi et al., 2013), the sigmoid model provided a better description of the relationship between tactile RTs and timing at which the tactile stimuli were delivered, compared to a linear model (RMSE: 21.92 ms vs 27.67 ms; $t_{34} = -4.51$, $p < .001$ two-tailed, 95% CI [-8.37, -3.38]). Next, to estimate the individual boundaries of PPS representation, we computed the CP of the sigmoid curve for each participant (Canzoneri et al., 2012; Ferri, Costantini, et al., 2015; Teneggi et al., 2013). The average CP was 1356 ± 437 ms (± SD) ranging from 708 to 2227 ms. As a control, for each participant, also the mean RTs to the tactile targets delivered along with flat sounds were fitted to a sigmoidal function. As expected, in this case the goodness-of-fit of the model was unacceptable in all the participants (all r^2 values < .50).

3.1.2 <u>*Interoceptive Accuracy (IAcc).*</u> For each participant, the mean heartbeat tracking accuracy across the twelve perception intervals was computed. The average IAcc was .67 ± .20 (± SD) ranging from .29 to .96.

3.1.3 <u>*Time Estimation Accuracy (TEAcc).*</u> For each participant, the mean accuracy in appraising the duration of temporal intervals across the twelve time estimation trials was computed. The average TEAcc was .68 ± .17 (± SD) ranging from .24 to .87.

3.2 Relationship between individual PPS boundary and IAcc.

None of the continuous variable distributions violated assumptions of normality (Gravetter & Wallnau, 2014; Trochim & Donnelly, 2006): CP (skewness = .21, SE = .39; kurtosis = -.93, SE = .77), IAcc (skewness = -.27, SE = .39; kurtosis = -.82, SE = .77) and TE (skewness = -1.15, SE = .39; kurtosis = .67, SE = .77). Hence, we performed parametric analyses.

Standard Pearson's correlation between individual measures of CP and IAcc showed a positive association between PPS boundary and interoceptive accuracy ($r_{CP,IAcc} = .37$, $p = .02$ two-tailed): individuals with narrower PPS boundary (higher CP values) were more accurate in tracking their heartbeats (higher IAcc values) (Figure 2). The robustness of this result was also confirmed by skipped Pearson's correlation ($r_{CP,IAcc}$ = .37, 95% CI [.05, .62]). Partial correlation analysis with TEAcc as a covariate of non-interest did not substantively alter the relationship between CP and IAcc ($r_{CP,IAcc|TEAcc}$ = .38, p = .02 two-tailed, 95% CI [.03, .68]). Indeed, Williams' test showed no significant difference between partial and bivariate correlation coefficients (t_{33} = .13; p = .89; $r_{CP,IAcc}$ -$r_{CP,IAcc|TEAcc}$ 95% CI [-.29, .33]), thus, proving that participants' performance during the heartbeat counting task was not confounded by time estimation strategies (Dunn, Stefanovitch, et al., 2010).

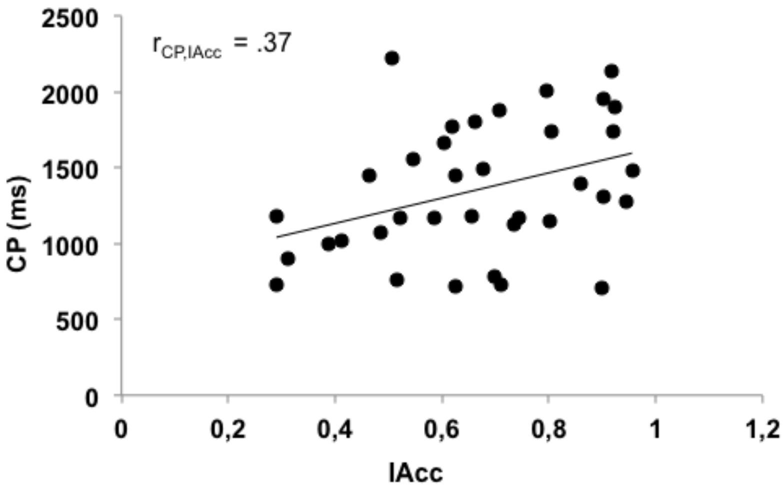

Figure 2: Correlation between participants' PPS boundary and their interoceptive accuracy. Correlation coefficients from skipped parametric ($r_{CP,IAcc}$) and nonparametric ($\rho_{CP,IAcc}$) correlations are reported. CP = Central Point; IAcc = Interoceptive Accuracy.

3.3 Social Anxiety and Private Self-Consciousness traits do not explain the relationship between PPS boundary and IAcc.

Both Private Self-Consciousness scores (PSC) and Social Anxiety sores (SA) were normally distributed (Gravetter & Wallnau, 2014; Trochim & Donnelly, 2006): PSC (skewness = -.003, SE = .393; kurtosis = 1.06, SE = .77), SA (skewness = .14, SE = .39; kurtosis = -.59, SE = .77).

Partial correlation analysis with Private Self-Consciousness scores as a control variable did not essentially alter the association between CP and IAcc ($r_{CP,IAcc|PSC}$ = .37, p = .03 two-tailed, 95% CI [.05, .63]). Indeed, Williams' test showed no significant difference between partial and bivariate correlation coefficients (t_{33} = .00; p = 1; $r_{CP,IAcc}$ -$r_{CP,IAcc|PSC}$ 95% CI [-.40, .40]). Similar results were obtained using Social Anxiety sores as a control variable for the association between CP and IAcc ($r_{CP,IAcc|SA}$ = .33, p = .05 two-tailed, 95% CI [.01, .59]). Also in this case, Williams' test showed no significant difference between partial and bivariate correlation coefficients (t_{33} = .16; p = .87; $r_{CP,IAcc}$ -$r_{CP,IAcc|SA}$ 95% CI [-.43, .51]). All in all, these results rule out the possibility that either Private Self-Consciousness or Social Anxiety traits might explain the relationship between PPS and IAcc.

3.4 Private self-consciousness traits moderate the relationship between PPS boundary and IAcc.

To test the hypothesis that a certain inclination to private self-focus is required, in order for interoceptive signals to counterbalance exteroceptive input, we applied a moderation analysis. A significant interaction emerged between individual Private Self-Consciousness scores and IAcc predicting CP (ΔR^2=.10, b=.36, p=.05, R^2=.25), wherein higher IAcc was associated with higher CP values (narrower PPS boundary) only for participants with relatively high Private Self-Consciousness scores (e.g., 1 s.d. above the mean; see Figure 3 for 95% confidence intervals). Specifically, J-N region of significance analyses indicated that higher IAcc was associated with narrower PPS boundary in participants with Private Self-Consciousness scores above 0.08 (mean-centred around 0). Importantly, the interaction term explained significant CP variance above and beyond the main effects of individual Private Self-Consciousness scores (b=.03, p=.87) and IAcc (b=.29, p=.08). In contrast to the individual Private Self-Consciousness scores, no significant interaction was found between individual Social Anxiety scores and IAcc (ΔR^2=.006, b=-.07, p=.63, R^2=.18).

These results show that relatively high levels of Private Self-Consciousness traits are essential to make the relationship between PPS and IAcc possible. More specifically, they show that through its interaction with interoceptive accuracy, Private Self-Consciousness allow interoceptive signals to counterbalance exteroceptive input, rather than the opposite. Indeed, when we ran a moderation analysis with CP as independent variable, IAcc as dependent variable and Private Self-Consciousness traits as moderator, no significant interaction emerged between individual Private Self-Consciousness scores and CP predicting IAcc (p=.07).

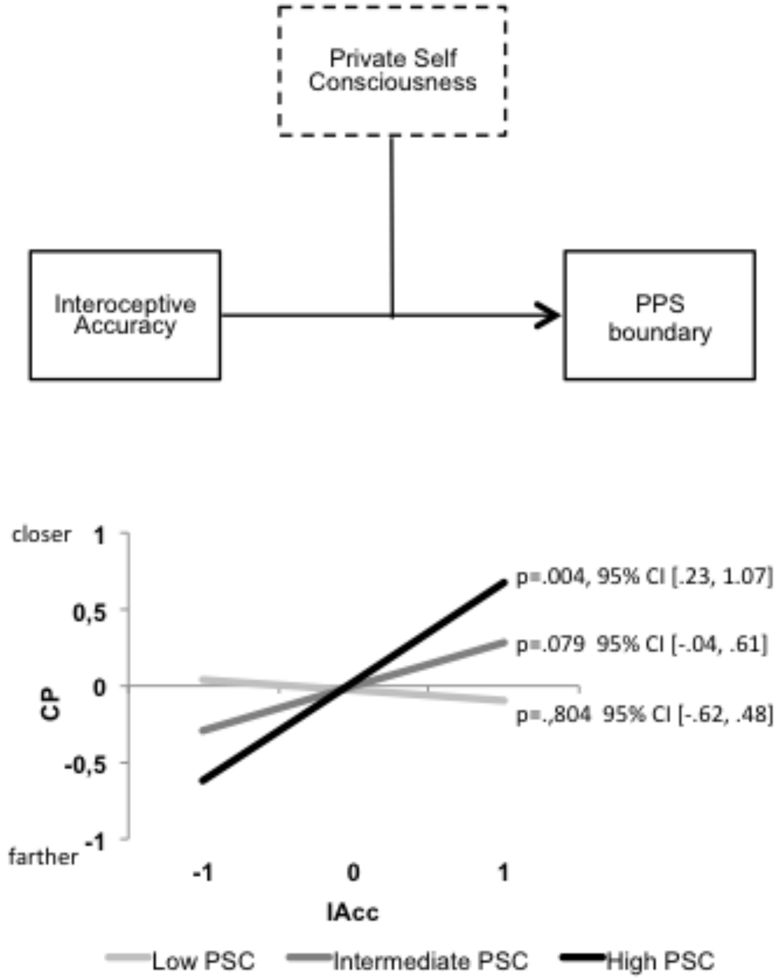

Figure 3. Moderation of the effect of IAcc on PPS boundary by individual Private Self-Consciousness (PSC) levels. *Top:* Conceptual depiction of the model tested. *Bottom:* illustration of the IAcc*PSC interaction effect on individual PPS boundary. IAcc was positively correlated with PPS boundary in individuals with relatively High PSC score (1 SD above mean; black line), but not in those with Intermediate (mean levels; dark grey line) and Low (1 SD below mean; light grey line) PSC. Notably, IAcc became a significant positive predictor of PPS boundary at PSC score values > .08 SD above the mean (not visualized). Statistical analyses were carried out with standardized values for all the variables. 95% CIs based on 5000 bootstrap iterations (bias-corrected) are reported. Notably, for visualization purposes, slope estimates are presented at discrete values of the moderator (mean levels ± 1SD away from the mean). However, these estimates are based on the linear trends present in the entire sample (i.e., no arbitrary splitting of the sample was performed). CP = Central Point; IAcc = Interoceptive Accuracy; PPS = Peri-Personal Space.

4. DISCUSSION

Peripersonal space is one of the manifold exteroceptive representations of the bodily self. It is the space around the body where sensory signals are more efficiently processed and integrated: the wider the PPS boundary, the farther the stimuli integrated. Prior studies showed that the extension of individual PPS boundary is affected by several factors, such as social interactions (Teneggi et al., 2013), tool-use (Ladavas & Serino, 2008), personality traits (Lourenco et al., 2011; Sambo & Iannetti, 2013), physical dimensions of the body (Longo & Lourenco, 2007). For the first time, we revealed specific interoceptive influences on the extension of individual PPS boundary. Precisely, our results show that higher interoceptive accuracy, likely reflecting more attentional resources allocated to internal than external input, predicts narrower PPS boundary. This evidence suggests that the role of interoception in counteracting exteroceptive influence on body representation (Tsakiris, 2017) might represent a general principle underlying bodily self-awareness. Far from being confined to body ownership (Tsakiris et al., 2011), it rather extends to at least another aspect of the bodily self, that is, the extension of individual PPS boundary. This evidence is consistent with prior studies showing that body ownership and PPS representation, despite underlying distinct functions, seem to interact (Ferri, Chiarelli, Merla, Gallese, & Costantini, 2013) and share some brain substrates (Grivaz, Blanke, & Serino, 2017).

What would interoceptive influences on the extension of PPS boundary be for? A proposal has been made that, in general, interoception supports the balance between stability and adaptability of the bodily self (Tsakiris, 2017). In the specific case of PPS representation, higher IAcc associated to narrower PPS boundary would indeed enable adaptability, in the sense of potentiality for extension of PPS boundary, where non-social (Ladavas & Serino, 2008; Martel et al., 2016) and social (Teneggi et al., 2013) circumstances demand it. Conversely, lower IAcc is associated to wider and thus less adaptable PPS boundary. The idea that good interoception supports adaptability of PPS boundary is also in agreement with recent evidence on the neural mechanism underlying individual differences in PPS extension (Ferri, Costantini, et al., 2015). Individuals with narrower PPS boundaries, and higher interoceptive accuracy, also show increased neural response variability to far stimuli in sensorimotor regions supporting PPS representation (Ferri, Costantini, et al., 2015).

Importantly, neural response variability is known to enable dynamic adaptation of sensorimotor representations (Knill & Pouget, 2004; Mandelblat-Cerf, Paz, & Vaadia, 2009), which include the representation of PPS (de Vignemont & Iannetti, 2015; di Pellegrino & Ladavas, 2015; Rizzolatti et al., 1997). In sum, there is enough evidence to support the idea that higher IAcc in individuals with narrower PPS boundary might help the balance between stability and adaptability of the space of the bodily self. Specifically, IAcc would help increase the stability of the representation of near body space (associated to lower neural variability; (Ferri, Costantini, et al., 2015)), while leaving the representation of far body space (associated to higher neural variability; (Ferri, Costantini, et al., 2015)) potentially adaptable to all contexts. Less attentional resources allocated to far exteroceptive stimuli, compared to bodily interoceptive input, may play a crucial role in this balance between stability and adaptability of PPS boundary in high interoceptive individuals. From what has been said it follows that interoception may represent an element of stability/adaptability of "spatial", in addition to "identity" (Tsakiris, 2017), self-other boundaries in social contexts. Teneggi et al (Teneggi et al., 2013) showed that presence of and interaction with others shape PPS extension, causing it to narrow or expand, respectively. Higher IAcc may stabilize narrower PPS boundaries, when subjects face another individual, while allowing PPS boundaries between self and other to merge, if the other behaves cooperatively. Again, adaptation to the presence of a cooperative other, in individuals with higher IAcc and narrower PPS boundary, would be enabled by enhanced neural response variability. However, before drawing any conclusions about the neural mechanisms associated to interoceptive influences on individual PPS boundary, in social and non-social contexts, one should specifically test the relationship between IAcc, neural response variability and PPS boundaries measured in both contexts. All this will be the focus of future investigations.

A second aim of our study was to explore whether specific individual traits, such as high social anxiety and private self-focus levels, may bias attentional effects on the intero-exteroceptive balance - i.e. individuals' inclination to allocate attentional resources to either external or internal input. Partial correlation and moderation analyses excluded any significant effects of social anxiety. This might seem at odds with prior evidence of more extended PPS boundary in individuals with higher levels of anxiety (Iachini et al., 2015; Sambo & Iannetti, 2013). A crucial difference between our study and those by Iachini et al (Iachini et al., 2015) and Sambo et al (Sambo & Iannetti, 2013), which may account for the apparent discrepancy in results, is that we focused on a different peripersonal space (de Vignemont & Iannetti, 2015). While we measured the boundary of a multisensory peripersonal space centered on the participant's hand and in the context of no interaction, both Iachini et al (Iachini et al., 2015) and Sambo et al (Sambo & Iannetti, 2013) focused more on a peripersonal space centered on the participant's face, and functionally identifiable as an interaction space or a defensive space, respectively. In their studies, the interaction with either people or objects (Iachini et al., 2015), as well as the threatening stimuli approaching participants' face (Sambo & Iannetti, 2013), might have emphasized the effect of individual anxiety traits on PPS boundary. Still, in our study social anxiety traits could affect the relation between individual PPS boundary and IAcc also through their impact on the latter. Indeed, there appears to be a tendency for better interoceptive awareness among patients with anxiety disorders (Dunn et al., 2010b; Ehlers and Breuer, 1992; Pollatos et al., 2009; Stevens et al., 2011; Weisz et al., 1988; Zoellner and Craske, 1999). However, this evidence comes from studies on clinical populations. It is entirely possible that subclinical levels of social anxiety do not affect IAcc and, consequently, its impact on individual PPS boundary.

Regarding the effects of individual traits of Private Self-Consciousness, our results reveal that, through its interaction with IAcc, Private Self-Consciousness changes the relation between IAcc and PPS boundary. Specifically, only in participants with relatively high Private Self-Consciousness scores, who tend to allocate attentional resources to inner sensations and feelings, rather than to external stimuli, higher IAcc is associated with narrower PPS boundary. Prior studies consistently demonstrated that private self-focus enhances interoceptive sensitivity, as reflected by higher interoceptive accuracy when attending to pictures of self, self-referential words (Ainley et al., 2013) or own face in a mirror (Ainley et al., 2012; Weisz et al., 1988). Differently, contrasting evidence exists in the literature on whether and how private self-focus affects perception of exteroceptive input (Mirams, Poliakoff, Brown, & Lloyd, 2012, 2013). Recently, Durlik et al (Durlik, Cardini, & Tsakiris, 2014) proposed that a distinct mode of self-focus, meaning the social rather than private mode, predicts exteroception. Hence, while interoception would be enhanced by private self-focus - which implies individuals' attention directed to inner aspects of the self -, exteroception would be enhanced by social self-focus - which implies individuals' attention directed to observable to others aspects of the self. We suggest a third possibility that goes beyond this dichotomy and takes the well-recognized interaction between interoception and exteroception into account (Adler, Herbelin, Similowski, & Blanke, 2014; Crucianelli, Krahe, Jenkinson, & Fotopoulou, 2017; Simmons et al., 2013; Zamariola, Cardini, Mian, Serino, & Tsakiris, 2017). Indeed, according to our results from the moderation analysis, through its interaction with individual interoceptive accuracy, private self-consciousness indirectly affects also the exteroceptive representation of the body (i.e., PPS extension).

Overall, our results demonstrate that the individual extension of peripersonal space boundary is affected by interoceptive accuracy. Thus, they extend the concept of interoceptive influences on exteroceptive bodily self-representation, so far only shown for body ownership (Tsakiris et al., 2011), to another aspect of the bodily self. Moreover, they reveal that such influences are conditioned by individual traits, especially the tendency to introspect and examine one's inner self and feelings. Hence, an intero-exteroceptive model of bodily self-awareness should be (at least) a three-dimensional model that includes also individual self-consciousness traits. A practical implication is that possible intervention strategies that aim at improving interoceptive accuracy to consequently affect exteroceptive representations of the bodily self should take individual traits into account, and train them in parallel. For instance, one may want to improve individuals' private self-focus using mirrors to direct their attention to inner aspects of the self (Ainley et al., 2012; Davies, 2005).

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