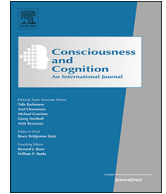




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Audio-visual sensory deprivation degrades visuo-tactile peri-personal space

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ABSTRACT

Self-perception is scaffolded upon the integration of multisensory cues on the body, the space surrounding the body (i.e., the peri-personal space; PPS), and from within the body. We asked whether reducing information available from external space would change: PPS, interoceptive accuracy, and self-experience. Twenty participants were exposed to 15 min of audio-visual deprivation and performed: (i) a visuo-tactile interaction task measuring their PPS; (ii) a heartbeat perception task measuring interoceptive accuracy; and (iii) a series of questionnaires related to self-perception and mental illness. These tasks were carried out in two conditions: while exposed to a standard sensory environment and under a condition of audio-visual deprivation. Results suggest that while PPS becomes ill defined after audio-visual deprivation, interoceptive accuracy is unaltered at a group-level, with some participants improving and some worsening in interoceptive accuracy. Interestingly, correlational individual differences analyses revealed that changes in PPS after audio-visual deprivation were related to interoceptive accuracy and self-reports of “unusual experiences” on an individual subject basis. Taken together, the findings argue for a relationship between the malleability of PPS, interoceptive accuracy, and an inclination toward aberrant ideation often associated with mental illness.

1. Introduction

Prominent models of self-consciousness stress the role of integration between multisensory exteroceptive (i.e., processing of external sensory stimuli; Blanke, 2012; Blanke, Slater, & Serino, 2015; Bermudez et al., 1995) and interoceptive (i.e., processing of sensory stimuli from within the body; Damasio, 2010; Seth, 2011; Craig, 2002, 2009; Critchley & Seth, 2012) signals as essential in the formation of a pre-reflexive form of bodily self-consciousness (BSC). BSC includes the feeling of owning a body, of being at a specific location in space, and of experiencing the world from a particular first-person perspective (Blanke & Metzinger, 2009). Intriguingly, signals relevant for BSC are not limited to the body itself – with crucial contributions from the tactile, proprioceptive and

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thermo-nocioceptive systems (see Haggard, Iannetti, & Longo, 2013 and Legrain, 2017, for theoretical postulates casting nociception as inherently multisensory, fundamental in body representation, and most importantly for the current purpose, with a double function both in exteroception and interoception) - but they equally extend within one's peri-personal space (PPS; Blanke et al., 2015; Noel, Grivaz, et al., 2015, Noel, Pfeiffer, et al., 2015; Salomon et al., 2017; Bernasconi et al., 2018); that is, the space immediately adjacent to and surrounding the body (Di Pellegrino, Ladavas, & Farne, 1997; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997; Serino et al., 2015). Indeed, all physical interactions between the individual's body and the external environment take place within the PPS. Accordingly, by modulating multisensory cues not only from the body, but also within the PPS, it is possible to alter the different components of BSC (Noel, Grivaz, et al., 2015, Noel, Pfeiffer, et al., 2015; Salomon et al., 2017). For example, by manipulating visuo-tactile spatio-temporal congruencies (tactile on the body and visual in the PPS) it is possible to induce ownership for an artificial hand (as in the rubber hand illusion; RHI, Botvinick & Cohen, 1998), face (as in the enfacement illusion; Tsakiris, 2008) or even the whole body (as in the body-swap illusion, Petkova & Ehrsson, 2008). Further, the administration of controlled multisensory cues at the body and within the PPS may even shift the perceived location of the self in space (as in the full body illusion; FBI, Lenggenhager et al., 2007; Noel, Grivaz, et al., 2015, Noel, Pfeiffer, et al., 2015; Salomon et al., 2017) and the direction of the first-person perspective (Petkova & Ehrsson, 2008; Ionta et al., 2011).

On the other hand, focusing on internal as opposed to external bodily cues, experimentally induced altered states of BSC due to the administration of conflicting exteroceptive sensory signals (Botvinick & Cohen, 1998; Lenggenhager et al., 2007; Ehrsson, 2007) have been shown to affect aspects of interoception such as autonomic responses (Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007) and neural representations of cardiac afferents (Park et al., 2016). In the case of the RHI (Botvinick & Cohen, 1998), for instance, illusory ownership for a rubber hand is associated with a reduction of the skin temperature of the participant's real hand (Moseley et al., 2008, but see de Haan et al., 2017) and an increase in its histamine reactivity (Barnsley et al., 2012). Similar temperature effects have been reported for the FBI (Salomon, Lim, Pfeiffer, Gassert, & Blanke, 2013). In addition, there exists a negative relation between an individual's capacity for interoceptive accuracy (in this case operationalized as the ability to detect their own heartbeats without measuring their pulse) and their proneness to the RHI (Tsakiris, Tajadura-Jimenez, & Costantini, 2011) and the enfacement illusion (Tajadura-Jimenez et al., 2012, 2013). These results suggest that individuals with low interoceptive accuracy might rely more heavily on external sensory cues in forming a representation of their bodily self, and hence be more prone to illusions mediated by multisensory external cues. More directly, recent data demonstrated a strong relationship between exteroceptive and interoceptive sensory signals in giving rise to BSC (Suzuki, 2013; Aspell, 2013; Adler, Herbelin, Similowski, & Blanke, 2014). Indeed, artificially introduced matches (illusion condition; vs. mismatches or control condition) between cardiac and visual signals provoke the RHI (Suzuki et al., 2013) and the FBI (Aspell et al., 2013; see also Adler et al. (2014) for a FBI using respiratory signals), much in the same way that spatially concordant visual-tactile stimuli promote the illusion. Thus, it appears that there are strong relationships between the manner in which individuals process exteroceptive and interoceptive sensory signals, and in addition, this relationship appears to modulate BSC.

Although prior studies have attempted to manipulate interoceptive accuracy in order to measure concomitant body representation changes (Ainley, Tajadura-Jiménez, Fotopoulou, & Tsakiris, 2012, 2013; Stevens et al., 2011; Khasha et al., 2008; Fairclough & Goodwin, 2007; Maister & Tsakiris, 2013) few have studied the relationship between the processing of interoceptive and exteroceptive signals within and beyond the PPS. Indeed, within this framework, Legrain and colleagues have highlighted the nociceptive system as one straddling interoceptive and exteroceptive domains (Haggard et al., 2013) to demonstrate that visual stimuli within but not beyond the PPS modulates nociceptive processing, in particular in the temporal dimension (De Paepe, Crombez, Spence, & Legrain, 2014, 2017; Filbrich et al., 2017; further see Bultitude, Walker, & Spence, 2017 for recent corroborative evidence from a different group). Nonetheless, a direct causal manipulation offsetting the weighting between exteroceptive and interoceptive signaling, and subsequently measuring the impact of this remapping on PPS and BSC is lacking. Indeed, while the relationship between interoceptive accuracy and BSC has been described in prior work (Tsakiris et al., 2011; Tajadura-Jimenez et al., 2012, 2013; Aspell et al., 2012), only a single study (Ferri, Ardizzi, Ambrosecchia, & Gallese, 2013) has attempted to investigate whether interoceptive accuracy was associated with an autonomic response (more precisely, respiratory sinus arrhythmia) indexing PPS. Further, while the above mentioned study (Ferri et al., 2013) showed a positive association between interoceptive accuracy and an autonomic response to interpersonal stimulation (i.e., another person's hand approaching the participant's body) at the boundary of the PPS anchored on the hand (i.e., the peri-hand space; see Serino et al., 2015), no study has investigated the relation between interoception and fundamental characteristics of an individual's PPS, such as its size (i.e., the spatial extent over which exteroceptive signals modulate somatosensory processing on the body) or its gradient (i.e., the sharpness in the division between peri- and extra-personal space), as well as their respective link (interoception and PPS) to the experience of the self in space.

Indeed, if the neural encoding of the PPS (and thus the boundary between the peri- and extra-personal space) is conceived as encoding the interface between the individual's body (or body-related space) and the environment, it is possible that PPS and interoceptive accuracy interact in building one's BSC (see Noel, De Nier, Lazzara, & Wallace, 2017, for a similar argument). If true, one would expect a relationship between the spatial extent (i.e., size) and/or shape (i.e., gradient or the way in which 'far' and 'near' space are distinguished) of one's PPS and interoceptive accuracy. Further, it may be that certain PPS representations, such as the peritrunk space (i.e., the PPS anchored on the trunk) – due to its association with self-location (Blanke, 2012; Blanke et al., 2015) – and not others, such as the peri-face space (i.e., the PPS anchored on the face), are related to interoception accuracy and BSC.

As a result of these questions, the first aim of this study is to highlight potential relationships between PPS, interoceptive accuracy, and BSC by attempting to manipulate the relative strength of exteroceptive and interoceptive signals. To this aim, we submitted healthy subjects to a short session of audio-visual deprivation in an anechoic chamber, in an attempt to reduce exteroceptive processing and hence potentially enhance interoception processing. That is, we conceived that the most direct approach in testing the

relation between interoception and exteroception in shaping PPS and BSC was to eliminate or reduce the degree of exteroceptive signals available, potentially enhancing interoceptive processing (either due to the fact that the degree of exteroceptive information is reduced or as a consequence of a homeostatic process). After audio-visual deprivation in the anechoic chamber or after the same amount of time in a normal environment (as a control condition) – but importantly while still in either the anechoic or standard room – we assessed (1) participant’s interoceptive accuracy by means of a heartbeat-counting task (Schandry Task; Schandry, 1981), (2) the size and gradient of their peri-face and peri-trunk representation by means of a visuo-tactile space-dependent interaction task (for analogous task in the auditory domain see Noel, Grivaz, et al., 2015, Noel, Pfeiffer, et al., 2015, Galli, Noel, Canzoneri, Blanke, & Serino, 2015, Serino et al., 2017), and (3) their phenomenological experience of the self-in-space during audio-visual deprivation. We hypothesized that as a consequence of the degraded exteroceptive signals; (1) audio-visual deprivation would result in (1) degraded division between the near and far space (i.e., shallower PPS gradients) for both the peri-face and peri-trunk, and (2) enhanced interoceptive accuracy – as other sensory evidence is diminished. Further, we predict that (3) audio-visual deprivation will result in anomalies of the phenomenology of the “self-in-space”, which would be most readily related to the PPS representation around the trunk (Noel, Grivaz, et al., 2015, Noel, Pfeiffer, et al., 2015; Serino et al., 2015; Salomon et al., 2017) than the face.

Furthermore, the manner in which the nervous system represents the body and integrates information from distinct sensory modalities has also been postulated to impact individual differences in personality traits (Damasio, 2010; Seth et al., 2011; James, 1890; Damasio, 2000; Seth, 2013; Berlucchi & Aglioti, 2010) and higher-order levels of cognition (Canzoneri, di Pellegrino, Herbelin, Blanke, & Serino, 2016; Stevenson et al., 2014, 2017; Postmes et al., 2014; Noel et al., 2016; Noel, Cascio, et al., 2017, Noel, Blanke, et al., 2017, Noel, Lytle, et al., 2017). In fact, prior studies have demonstrated a specific interplay between personality traits, the valence of stimuli utilized (e.g., spider vs. butterfly; de Haan et al., 2016), and PPS representation (Sambo et al., 2013; Fossataro, Sambo, Garbarini, & Iannetti, 2016; Iachini, Ruggiero, Ruotolo, Schiano di Cola, & Senese, 2015). Similarly, studies have linked interoceptive accuracy with emotional processing (Pollatos, Traut-Mattausch, Schroeder, & Schandry, 2007; Critchley et al., 2011; Werner, Kerschreiter, Kindermann, & Duschek, 2013; Durlak & Tsakiris, 2015) and have attempted to establish a functional relationship between interoceptive measures and psychopathology (Pollatos et al., 2007; Dunn, Dalgleish, Ogilvie, & Lawrence, 2007; Mussgay, Klinkenberg, & Rüdell, 1999; Domschke, Stevens, Pfeleiderer, & Gerlach, 2010; Ehlers & Breuer, 1992; Noel et al., 2017). Therefore, in the present study we also tested how changes in exteroceptive and interoceptive processes induced by audio-visual deprivation affects personality traits by administering personality questionnaires (Mason, Claridge, & Jackson, 1995; Claridge et al., 1996; Morrison, Wells, & Nothard, 2002; Launay & Slade, 1981) after audio-visual deprivation or the control condition. The questionnaires administered indexed psychosis-proneness, principally Schizotypy (Claridge et al., 1996, Mason et al., 1995) and hallucinations (Morrison et al., 2002). Similarly to above, we hypothesized that audio-visual deprivation would accentuate Schizotypic and hallucinatory reports, and that these would be closely tied to PPS representation and the experience of the “self-in-space”.

2. Methods

2.1. Participants

Twenty healthy participants (6 females, mean age 24 ± 2.1 years old) partook in this study. All participants were right-handed, had normal or corrected-to-normal visual acuity, and reported normal touch, as well as no history of psychiatric or neurological impairment. History of cardiac disease was not formally queried, and hence was not an exclusion criterion for the present study. This sample size was determined given prior effect sizes of our work delineating PPS representation (Serino et al., 2015; Noel, Grivaz, et al., 2015, Noel, Pfeiffer, et al., 2015; Galli et al., 2015; Pfeiffer, Noel, Serino, & Blanke, 2018; average partial eta-squared = 0.59) and calculated via G*power 3.1 to achieve a power of 0.90. Stopping rule regarding data collection was a priori set to $N = 20$. All participants gave informed consent to take part in this study, which was approved by the local ethics committee – The Brain Mind Institute Ethics Committee for Human Behavioral Research at EPFL – and conducted in line with the Declaration of Helsinki. All participants were remunerated with 20 Swiss Francs per session for their time.

2.2. Audio-visual deprivation protocol

Each subject partook in two experimental sessions separated by 7–10 days. Both sessions were identical with the exception of the environmental surrounding in which it took place. One session was carried out inside an anechoic room (see Fig. 1, ambient noise = 16 dB (A) due to experimental testing devices) while the other took place in a standard room (ambient noise = 45 dB (A); see Noel & Wallace, 2016 for a similar approach). Session order was counterbalanced across participants. Upon arriving at the experimental location, if being tested in the anechoic room session, participants were first asked to simply relax and stand quietly, blindfolded, in the center of the room for 15 min. Lights were turned off. In this manner participants received limited external visual and auditory input – on the other hand, tactile sensation was present (e.g., at the sole of their feet, clothing on their body, and thermo-sensation), as were proprioceptive and vestibular signals. In fact, it may be argued that these latter inputs were exacerbated due to the demand of remaining standing in an exteroceptive (auditory and visual) impoverish environment. Contrarily, when partaking in the standard room condition, participants were simply instructed to stand in the middle of the room and relax. No effort was made to avoid auditory and visual sensory input in this condition. After the exposure phase to the audio-visual deprivation environment or the control environment, participants were invited to sit comfortably as interoceptive accuracy and PPS representations (around the face and the trunk) were measured, as well as changes in their subjective experience of the self-in-space and personality traits (see below). Importantly, while we explicitly consider the duration of audio-visual deprivation (or exposure to

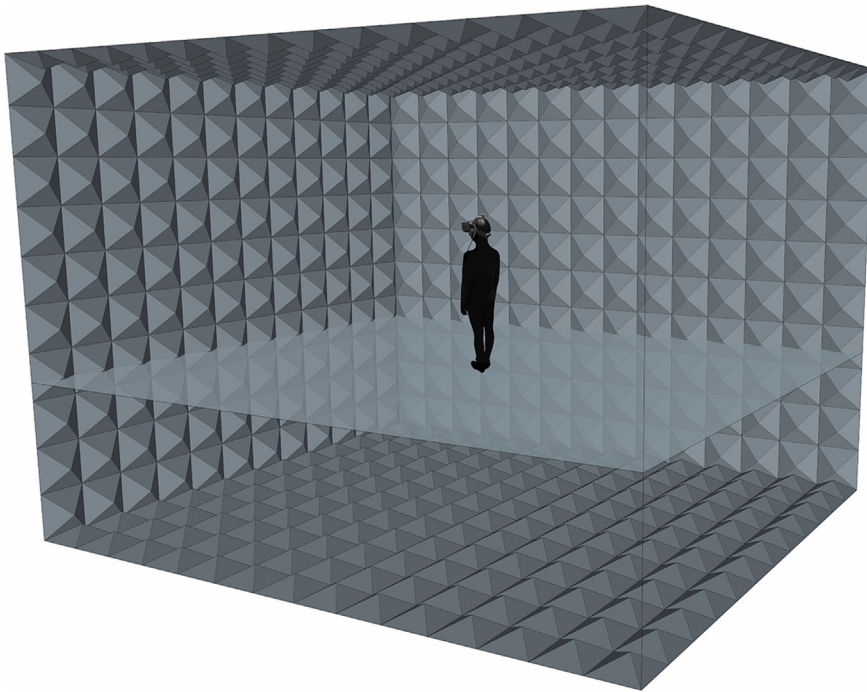


Fig. 1. *Depiction of the anechoic chamber.* Participants submitted to a short session (15 min) of exteroceptive audio-visual deprivation, by placing them standing inside and anechoic room and requesting them to close their eyes. In this manner visual stimulation was absent, while auditory and tactile stimulation were minimized. After exteroceptive audio-visual deprivation, during the experiment, participants wore a head-mounted display (HMD; depicted), and looming stimuli were presented in virtual reality in order to measure peri-personal space representation.

the standard environment) to last 15 min (the duration without any other task but to “experience the environment”), testing of interoceptive accuracy, PPS, and questionnaires measures were all undertaken while remaining in the environment participants were exposed to for the particular condition. That is, PPS measurement, for instance, was in fact measured while participants were in the anechoic chamber.

2.3. Materials and procedure

2.3.1. Interoceptive accuracy

Immediately following audio-visual deprivation (or after the control condition), interoceptive accuracy (IAcc) was measured using the Mental Tracking Method (Schandry, 1981, Knoll & Hodapp, 1992). Participants sat on a chair, placed three recording electrodes on their chest (two at the level of the left and right clavicles, the third one on the left side at the last rib), and were instructed to silently count the number of heartbeat events between an auditory start and finish cue. They were asked to close their eyes and not to monitor their pulse. The task consisted of four unique repetitions of different durations (25 s, 35 s, 45 s, and 100 s) presented in a random order across participants. After each trial participants reported vocally the number of heartbeats counted and the experimenter recorded the number mentioned. This particular task has been widely used to assess interoceptive accuracy and has good test–retest reliability ($r = .80$ in Werner et al., 2013; $r = 0.71$ in Knoll & Hodapp, 1992). On the other hand, the strength of its relation to other heartbeat discrimination tasks (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004) is mixed (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015) and authors have questioned its independence to belief biases or cognitive systems (e.g., knowledge that heart rhythm is higher after physical activity; Ring & Brener, 1996; see discussion). Raw electrocardiogram (ECG) data were acquired by means of an Arduino™ microcontroller (<http://arduino.cc>) mounted with an e-Health Sensor Shield V2.0 from Libelium™ (www.libelium.com) and driven by in-house software (ExpyVR, <http://Inco.epfl.ch/expyvr>) at 100 Hz. The detection of heartbeats was performed by identification of the R-wave in the QRS complex, defined as an amplitude change of over 80% of the difference between the exponential moving averages of the maxima and minima of the raw signal (see Ronchi et al., 2017 for a similar approach). This approach in identifying heart rhythm was offline confirmed by peak detection (R-wave) via MATLAB's (MathWorks) *findpeaks.m* function between the time periods of count initiation and termination. Both approaches yield identical heartbeat counts. This task took approximately 4 min.

2.3.2. Peripersonal space (PPS)

Following the IS task, two blocks of peripersonal space measurement were conducted to measure the effects of audio-visual deprivation on the representation of the PPS around the face and around the trunk. As mentioned in the introduction, the latter is

considered a more global representation of the space around the individual, to which smaller, body-parts centered PPSs are referenced, and hence we hypothesize more interesting changes due to audio-visual deprivation for the trunk than for the face PPS (Serino et al., 2015). The two blocks (i.e., measuring PPS around the face and trunk) were identical with exception of the location of vibrotactile stimulation (face or trunk) and were run in counterbalanced order across participants. Subjects were instructed to respond as fast as possible to tactile stimulation (tactile reaction times were measured) and wore a HMD (VR1280, Virtual Research Systems Inc., California, USA; 1280 x 1024 display resolution per eye, 60° field of view) via which looming visual stimuli were presented. Participants were informed that the approaching visual stimulus was task irrelevant. The onset of a fixation cross indicated initiation of a trial. Participants fixated on the cross as a looming ball approached their face (100 cm/s). At a particular interval of time after trial onset (T1 = 0.25 s, T2 = 0.50 s, T3 = 0.75 s, T4 = 1.0 s, T5 = 1.25 s, T6 = 1.50 s, T7 = 1.75 s); a brief vibrotactile stimulation was given (100 ms). As the ball loomed toward the participant linearly, the temporal interval between trial onset and touch delivery matched linearly and negatively with the spatial distance between the location of somatosensory and visual stimuli. That is, T1 through T7 map onto D7 through D1. In addition to these visuo-tactile experimental PPS trials, unimodal tactile and visual trials were conducted, respectively as baseline and catch trials. The baseline conditions were probed at T1 and T7 in order to assure that a putative modulation of visuo-tactile spatiotemporal separation on tactile detection reaction time was in fact a multisensory distance-dependent effect and not merely an expectancy effect (see Kandula, van der Stoep, Hofman, & Dijkerman, 2017). Catch trials in which no tactile stimulation was given, and therefore participants were to withhold response, were included in order to avoid an automatic association between visual presentation and motor response (see Serino et al., 2017). Inter-trial interval was set randomly to either 0.8 or 1.2 s. Each condition (experimental D1 through D7, baseline T1 and T7, and catch trial) was repeated 16 times resulting in 160 trials per PPS block. Measurement of both the peri-face and peri-trunk took approximately 15 min total.

2.3.3. Questionnaires

Lastly, in order to measure subjective changes in personality states and experience of the self-in-space due to audio-visual deprivation subjects also completed three questionnaires. First, participants completed an adapted version of the BSC questionnaire (Lenggenhager et al., 2007, Ehrsson, 2007), previously used to measure changes in bodily experience due to multisensory bodily illusions. Participants responded to this questionnaire on a scale from 1 (not at all) to 10 (completely agree), and it was designed to probe at subjects' experience of their body in space – a component of BSC. Different items on this questionnaire were designed to probe the experience of the “self-in-space” generally (e.g., “How strong was the feeling that you had more than one body?”), specifically during the audio-visual deprivation experience (e.g., “How strong was the feeling that you were lost in space?”), or as control questions (e.g., “How strong was the feeling that you could hear your blood flow through your veins?”). All items administered in this questionnaire may be viewed in Fig. 4A.

Next, subjects completed the Oxford-Liverpool Inventory of Feelings and Experiences (O-LIFE) questionnaire (Claridge et al., 1996, Mason et al., 1995) – a questionnaire designed for measuring psychosis-proneness, principally schizotypy. This questionnaire contains four subscales; (1) Unusual Experiences, (2) Cognitive Disorganization, (3) Introverted Anhedonia, and (4) Impulsive Nonconformity. The scale is binary and subjects reported either with an affirmative or with a negative answer. The items of the O-LIFE (e.g., “Are your thoughts sometimes so strong that you can almost hear them?” or “Do you often have difficulties in controlling your thoughts?”) have been deliberately chosen to make the measure suitable for tapping into psychotic characteristics in healthy individuals (Mason & Claridge, 2006).

Finally, participants completed the Revised Hallucinations Scales (RHS; Morrison et al., 2002). This questionnaire is based on the Launay-Slade Hallucination Scale (Launay et al., 1981) and captures individual's proneness to experience hallucinations. Participants responded to this scale on a 4-point scale (1 = never, to 4 = almost always). Example items for questionnaire are; “I have had the experience of hearing a person's voice and then found that there was no one there” or “My thoughts seem as real as actual events in my life”.

All questionnaires were administered in English and all instructions (in order: IAcc task, PPS task, and questionnaires) were given before the start of the experiment in order to avoid unnecessary verbal communication (and therefore auditory input) during the course of the experiment. This precaution was taken in both sessions (inside and outside the anechoic room).

2.4. Analyses

2.4.1. Interoceptive accuracy

Interoceptive accuracy (IAcc) was calculated as the mean absolute difference between recorded and counted heartbeats across the four repetitions of the interoceptive accuracy task according to Eq. (1). This transformation yields a scores between 0 and 1, with higher scored indicating a smaller discrepancy between recorded and counted heartbeats, and hence a higher interoceptive accuracy (Tsakiris et al., 2011; Werner et al., 2013). The change in interoceptive accuracy due to audio-visual deprivation is of interest here, and therefore the difference between interoceptive accuracy after audio-visual deprivation (inside anechoic room) and after regular sensory conditions (outside anechoic room) was calculated for each participant.

$$\frac{1}{4} \sum \left(1 - \frac{|\text{recorded heartbeats} - \text{counted heartbeats}|}{\text{recorded heartbeats}} \right) \quad (1)$$

2.4.2. Peripersonal space

Individual subject condition-wise averages were fitted to a sigmoidal function (Eq. (2)),

$$y(x) = \frac{y_{\min} + y_{\max} \times e^{(x-x_c)/b}}{1 + e^{(x-x_c)/b}} \quad (2)$$

where x represents the distance between visual and tactile stimuli and $y(x)$ is the RT to touch at a given visual distance x . y_{\min} and y_{\max} are saturation points of the sigmoidal fixed to the slowest and fastest average RT in the experimental trials, while x_c and b respectively represent the central point and the slope of the sigmoidal at x_c and are free to vary. The central point of this function is taken as a behavioral proxy for the size of PPS – the location of the PPS boundary (see Canzoneri, Magosso, & Serino, 2012; Serino et al. 2015a, 2017, for a similar approach), while the slope of the function (inversely proportional to b), represents the steepness or sensitivity with which the near (peri-personal) and far (extra-personal) space are divided. That is, this procedure allowed for estimating two elemental characteristics of the function describing visuo-tactile integration as a function of distance: its central point (i.e., the spatial distance at which visual stimulation significantly modulates tactile processing, which can be taken as a proxy of the spatial location of the PPS boundary) and its slope (i.e., the gradient of the transition between far and near space, which can be taken as a proxy of the sensitivity of the PPS boundary; Noel, Grivaz, et al., 2015, Noel, Pfeiffer, et al., 2015; Canzoneri et al., 2012).

3. Results

3.1. Peripersonal space

A 2 (audio-visual deprivation: deprived vs. non-deprived) \times 2 (body part: trunk vs. face) repeated-measures ANOVA was carried out both on the central point and slope parameters of the PPS data after subjecting this data to sigmoid fitting. With regard to the central point, results revealed a significant main effect of body part ($F(1, 19) = 11.35$, $p = 0.0032$, partial $\eta^2 = 0.37$), indicating that the boundary of peri-face space is closer to the body ($M = 3.65$, $SD = 0.75$) than is the boundary of peri-trunk space ($M = 4.36$, $SD = 0.92$). This result replicates prior findings (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013; Noel, Grivaz, et al., 2015, Noel, Pfeiffer, et al., 2015; Galli et al., 2015; Serino et al., 2015). No significant main effect of audio-visual deprivation ($F(1, 19) = 1.05$, $p = 0.31$), nor a significant interaction ($F(1, 19) = 2.18$, $p = 0.15$), were found. Thus, it appears that audio-visual deprivation plays no role in altering the overall size of peripersonal space.

We then compared the slope of the function as a measure of the gradient of change between near and far space. A 2 (audio-visual deprivation) \times 2 (body part) repeated-measures ANOVA indicated that audio-visual deprivation significantly alters the PPS gradient ($F(1, 19) = 4.88$, $p = 0.039$, partial $\eta^2 = 0.27$; Fig. 2). The gradient between near and far space was diminished after audio-visual deprivation (audio-visual deprivation; $M = 1.77$, $SD = 0.50$; no audio-visual deprivation; $M = 1.11$, $SD = 0.52$). It is important to note here that the larger the parameter governing the slope of the function, the shallower the slope. No significant main effect for body part ($F(1, 19) = 2.39$, $p = 0.13$), nor a significant interaction ($F(1, 19) = 2.98$, $p = 0.10$), were found. These results suggest that after a short period of audio-visual deprivation the representation of visuo-tactile peripersonal space (around the face and trunk) is of similar size, but that the transition between what is coded as ‘near’ space and what is coded as ‘far’ space becomes less well defined.

3.2. Interoceptive accuracy

A one-sample t -test comparing the mean change in interoceptive accuracy (IAcc) to zero was performed. Contrary to the hypothesis, results demonstrated no systematic change in interoceptive accuracy inside and outside the anechoic room when examined at the group level ($t(19) = 1.12$, $p = 0.27$). Thus, seemingly audio-visual deprivation did not alter interoceptive accuracy as assessed in the present study. We then run a series of exploratory analyses to investigate whether audio-visual deprivation might induce more subtle effects at an individual level. While there was a strong trend, heart rates did not differ statistically between sensory environments (standard environment; $M = 70.1$, $SD = 11.9$, deprived environment; $M = 62.49$, $SD = 11.5$; $t(19) = 2.00$, $p = 0.052$), and heart rate was seemingly not correlated with IAcc (standard environment, $r = -.10$, $p = 0.56$; sensory deprived environment, $r = 0.03$, $p = 0.89$). Similarly, there was seemingly no order effect (1st session, $M = 0.72$, $SD = 0.15$; 2nd session, $M = 0.66$, $SD = 0.22$, $t(19) = 1.03$, $p = 0.31$) and further, Cronbach’s alpha across trials (reliability of the heartbeat count) was high both within the standard ($\alpha = 0.85$) and sensory deprived ($\alpha = 0.86$) environments. Inspection of the data showed that 11 participants (55%; 3 female, 23 years old) improved IAcc after audio-visual deprivation, while the remaining 9 (45%; 3 female, 24 years old) had worsened at the task. For both groups, the change in IAcc was significant, as shown by a one-sample t -test relative to zero for both the improved ($t(10) = 5.59$, $p = 0.0002$, Cohen’s $d = 3.5$) and poorer performing ($t(8) = -3.50$, $p = 0.008$, Cohen’s $d = 2.21$) groups. Importantly, no correlation between interoceptive accuracy inside and outside the anechoic room was found (Spearman’s rho; $r = -0.09$, $p = 0.70$), indicating that participants did not improve or worsen at the heartbeat accuracy task simply as a consequence of regression to the mean phenomenon. Further, eleven additional participants (3 female, mean age 22 years old), who did not participate in the main experiment were recruited in order to assure test-retest reliability of the heartbeat monitoring task under standard sensory conditions. These participants performed the task on two occasions separated by 7–10 days, always in standard sensory conditions. Results indicate that, contrarily to the case when the interoceptive accuracy task was performed in two distinct sensory environments, when performing the task in the same standard sensory environment, performance within subjects is positively correlated ($r = 0.78$, $p = 0.042$). Taken together, these findings suggest that audio-visual deprivation may not systematically affect interoceptive accuracy throughout the entirety of the population, but may do so on an individual-by-individual basis. Hence, in subsequent analyses, this factor was taken into account by separating the sample of participants into two groups: those who had better interoceptive accuracy inside the anechoic room (Better IAcc), and those who had poorer (Worse IAcc) interoceptive accuracy

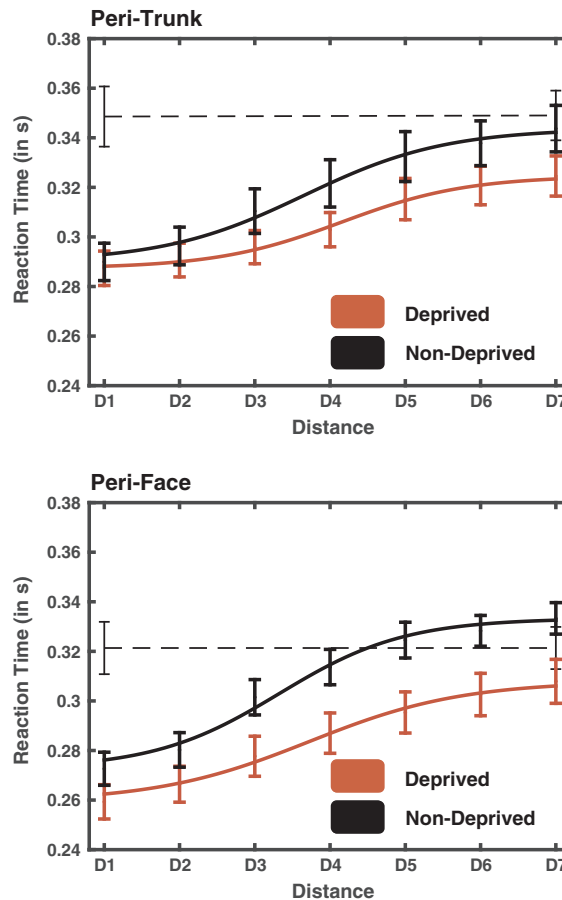


Fig. 2. PPS Results. Reaction time to tactile stimulation (y-axis, in seconds) is plotted as a function of distance between the location of touch and visual stimuli (x-axis, D1 = closest, D7 = farthest, see text for further detail). Participants' RT decreased the closer the visual and tactile stimulation were provided one from another – both inside (red) and outside (black) the anechoic room, and both for when tactile stimulation was applied on the trunk (upper panel) and the face (lower panel). The dashed line represents the fastest RT to unimodal tactile stimuli (baseline condition). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

inside the sensory deprived environment (see Tsakiris et al., 2011 for a similar approach where participants are divided via median split according to interoceptive accuracy). It must be clearly acknowledged here, however, that the initial hypothesis was that participant's interoception generally would improve after audio-visual deprivation and that this would allow us to scrutinize the interplay between interoception and PPS. As detailed above, this was not the case and hence the following reported effects are data-driven as opposed to hypotheses-driven, and thus must be taken as such. Further, while the initially amassed sample yielded a statistical power of 0.90, assuming the same effect size with half the sample size yields a statistical power of 0.57.

3.3. Modulation of PPS after audio-visual deprivation depending on changes in IAcc

We asked whether and how the changes in the PPS were related to group specific changes in interoceptive accuracy as a function of audio-visual deprivation. A 2 (audio-visual deprivation: deprived vs. non-deprived) \times 2 (body part: trunk vs. face) \times 2 (IAcc Group: better vs. worse) mixed ANOVA was carried out, both on the central point and on the slope of the sigmoidal function. In terms of the central point, results revealed a main effect of body part ($F(1, 19) = 11.35, p = 0.0032, \text{partial } \eta^2 = 0.37$). The rest of analyses were non-significant (all $p > 0.12$). More interestingly, with regard to the slope and as illustrated in Fig. 3, in addition to the main effect of audio-visual deprivation ($F(1, 19) = 4.88, p = 0.03, \text{partial } \eta^2 = 0.27$), analysis showed a significant body part \times audio-visual deprivation \times IAcc group interaction ($F(1, 19) = 4.94, p = 0.03, \text{partial } \eta^2 = 0.20$). In order to elucidate the root of this interaction, two separate 2 (audio-visual deprivation) \times 2 (IAcc group) mixed ANOVAs were carried out, one for each body-part. For the face PPS, results showed a main effect of audio-visual deprivation ($F(1, 19) = 4.23, p = 0.05, \text{partial } \eta^2 = 0.18$), yet no main effect for IAcc group ($F(1, 19) = 0.13, p = 0.72$), and no significant interaction ($F(1, 19) = 0.22, p = 0.64$). That is, the gradient between 'near' and 'far' PPS around the face was shallower after audio-visual deprivation for all participants, regardless of their interoceptive accuracy. On the other hand, analysis performed on trunk PPS, in addition to the main effect of audio-visual deprivation showed a significant audio-visual deprivation \times IAcc group interaction ($F(1, 19) = 6.16, p = 0.02, \text{partial } \eta^2 = 0.24$), with no main effect of IAcc Group (F

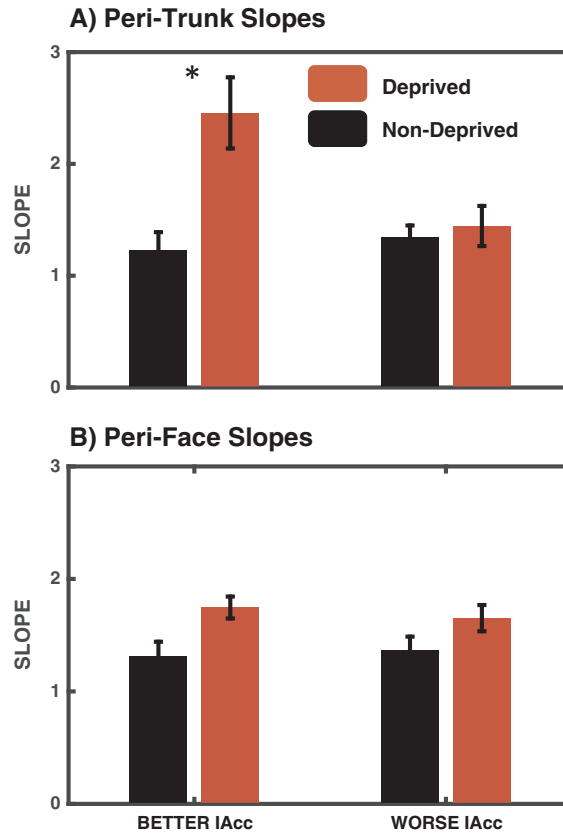


Fig. 3. PPS slopes by interoceptive accuracy during audio-visual deprivation. Gradient of PPS is indicated by the value governing the sigmoidal function (higher value indicates a less steep gradient) as a function of sensory environment (red, inside the anechoic room – black, outside the anechoic room). Slope data are presented based on whether participants' were better (left) or worse (right) interoceptors in the anechoic room. Results indicate that the flattening of PPS representation inside the anechoic room is driven by the better interoceptors for the peri-trunk representation (A, top panel) but not for the peri-face representation (B, bottom panel). Means are represented, error bars indicate ± 1 S.E.M, and * indicates $p < 0.05$ (inside vs. outside peri-trunk representation for better interoceptors inside the anechoic room). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(1, 19) = 3.109, $p = 0.09$). Paired-sample t-tests showed a significant difference between deprivation and no deprivation ($t(10) = 2.73$, $p = 0.02$, Cohen's $d = 1.73$; audio-visual deprivation; $M = 2.4$, S.E.M = 0.39; no audio-visual deprivation, $M = 1.2$, S.E.M = 0.20) for the better IAcc group, but not for the worse IAcc group ($t(9) = 0.616$, $p = 0.55$). These results, therefore, seem to indicate a selective blurring of 'near' and 'far' space under audio-visual deprivation around the trunk specific to those participants whose interoceptive performance improved under conditions of audio-visual deprivation.

3.4. Questionnaires results as a function of audio-visual deprivation

Next, we investigated whether audio-visual deprivation induced changes in specific experiences or personality traits, and how these effects were related to changes in IAcc and PPS representation. A Wilcoxon signed-rank test was run comparing average responses between audio-visual deprivation conditions for each item in the BSC questionnaire, each subscale of the O-LIFE, and for the RHS. As illustrated in Fig. 4a, results revealed that following audio-visual deprivation subjects reported significantly higher scores for three items in the BSC questionnaire: (i) 'How strong was the feeling that you were lost in space' ($z = 2.56$, $p = 0.01$), (ii) 'How strong was the feeling that you were floating in the air?' ($z = 2.30$, $p = 0.02$), and (iii) 'How strong was the feeling that you could hear yourself blink' ($z = 1.99$, $p = 0.04$). In terms of hallucinatory behavior and schizotypy tendency, results revealed (respectively Fig. 4b and 4c) a significantly higher tendency toward hallucinatory experience inside, as compared to outside, the anechoic room ($z = 1.70$, one-tailed $p = 0.044$), as well as a trend indicating a proneness to 'unusual experience' inside the anechoic room as compared to outside ($z = 1.40$, $p = 0.07$, one-tailed). Overall, phenomenological experience after a session of audio-visual deprivation were reminiscent of schizotypal behavior (see Rosenzweig, 1959, for a similar observation), in that we found a higher tendency toward hallucinations and a loss of self-environment boundary (Nelson, Fornito, Harrison, Yücel, & Sass, 2009; Noel et al., 2017).

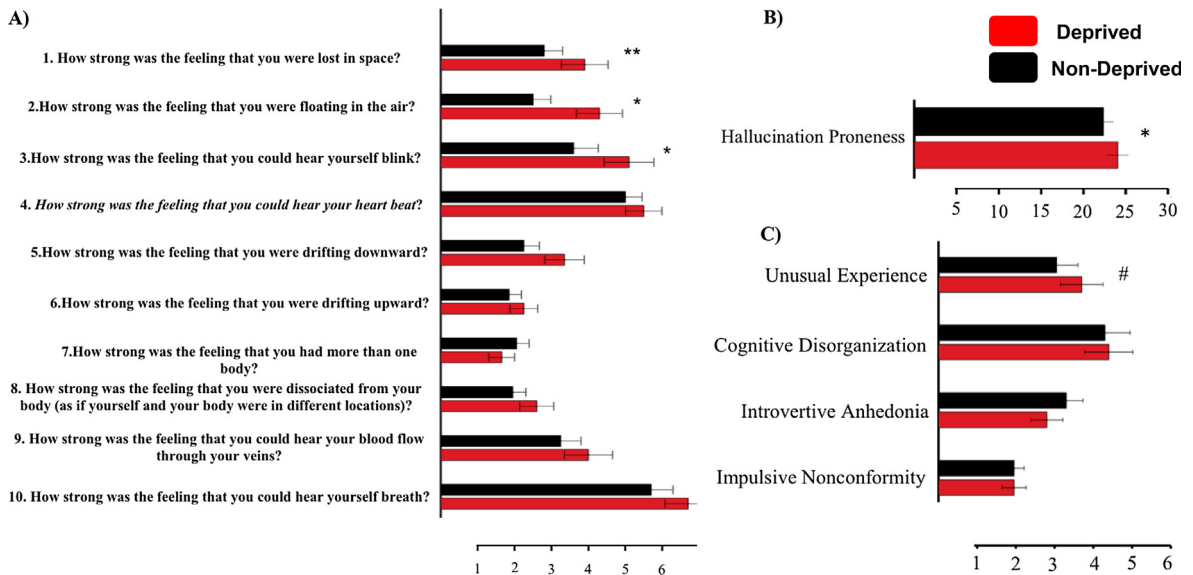


Fig. 4. Questionnaires results. (A) Self-Attribution; Participants reported a stronger tendency to feel (1) lost in space, (2) floating in the air, and to (3) hear themselves blink inside as opposed to outside the anechoic room. (B) RHS; Participants scored higher in proneness to hallucinations inside of the anechoic room. (C) O-LIFE; Participants scored higher in reporting ‘Unusual Experience’ inside when compared with outside the anechoic room (statistical trend at $p = 0.07$). Means are depicted, error bars represent ± 1 S.E.M., and * indicates $p < 0.05$, ** < 0.01 , and # $p = 0.07$.

3.5. Questionnaires results depending on changes in interoceptive accuracy

Separate Mann–Whitney U tests were run on the difference between questionnaire responses (to either item, subscale, or whole questionnaire) inside and outside the anechoic room (i.e., after or not a session of audio-visual deprivation), and across the two IAcc groups. For the RHS, results revealed no significant difference between groups ($z = 0.539$, $p = 0.58$). With regard to the O-LIFE subscales, Mann–Whitney U test showed that the better and worse IAcc groups did not show significantly different alterations in Schizotypy subscale responses inside and outside the anechoic room (Unusual Experience; $z = 0.308$, $p = 0.75$; Cognitive Disorganization; $z = 1.109$, $p = 0.26$; Introvertive Anhedonia; $z = 0.078$, $p = 0.93$; Impulsive Nonconformity; $z = 1.329$, $p = 0.16$). Lastly, Mann–Whitney U tests revealed significant interactions across IAcc groups for two items in the BSC questionnaire. Participants with better IAcc showed a larger increase in their responses to items 2 (‘How strong was the feeling that you were floating in the air?’ $p = 0.031$) and 8 (‘How strong was the feeling that you were dissociated from your body – as if yourself and your body were in different locations.’ $p = 0.039$) when compared with participants in the worse IAcc group.

3.6. Correlation between interoceptive accuracy, peripersonal Space, and phenomenology

Finally, in order to elucidate the relationship between the malleability of PPS representation, interoceptive accuracy, and the proneness to atypical phenomenology under the framework of audio-visual deprivation, we tested for correlations between the variables demonstrating significant alterations as a function of audio-visual deprivation (see above; correlations were not executed among variables that did not show a significant modulation in the above analyses in order to preclude from increasing Type I error). We first calculated the amount of change (as the difference between values inside and outside the anechoic room; i.e., sensory deprived minus not sensory deprived) in each of the variables of interest (i.e., slope of peri-trunk space, report of ‘unusual experiences’ and interoceptive accuracy) as a consequence of audio-visual deprivation. Subsequently, we drew Spearman rho correlations among these variables. Results demonstrated significant positive correlations between the change in peri-trunk gradient and the change in interoceptive accuracy as a consequence of audio-visual deprivation ($r = 0.46$, $p = 0.03$; Fig. 5a). Similarly, findings revealed a significant positive correlation between the change in peri-trunk gradient after audio-visual deprivation and the change in self-reported ‘Unusual Experiences’ inside the anechoic room ($r = 0.44$, $p = 0.041$; Fig. 5b). That is, participants with degraded peri-trunk space representation following audio-visual deprivation (i.e., shallower in slope) were also those participants who improve in interoceptive accuracy after audio-visual deprivation, and whom more likely reported ‘Unusual Experiences’ following audio-visual deprivation. No significant correlation was found between the change in interoceptive accuracy after audio-visual deprivation, and the change in ‘Unusual Experience’ self-report ($r = -0.0049$, $p = 0.87$). Mediation analysis between the change in interoceptive accuracy and the change in proneness to ‘Unusual Experience’ after audio-visual deprivation with the degradation of peri-trunk representation as mediator revealed that this later variable boosted the relation between interoceptive accuracy and ‘Unusual Experience’ (from $r = -0.0049$ to $r = 0.20$, $p < 0.01$), however the relationship between ‘Unusual Experience’ and interoceptive accuracy nonetheless remained non-significant ($p = 0.58$, bootstrapped from 1000 iterations), and thus other variables apart from peri-trunk representation likely impacts the latter relationship.

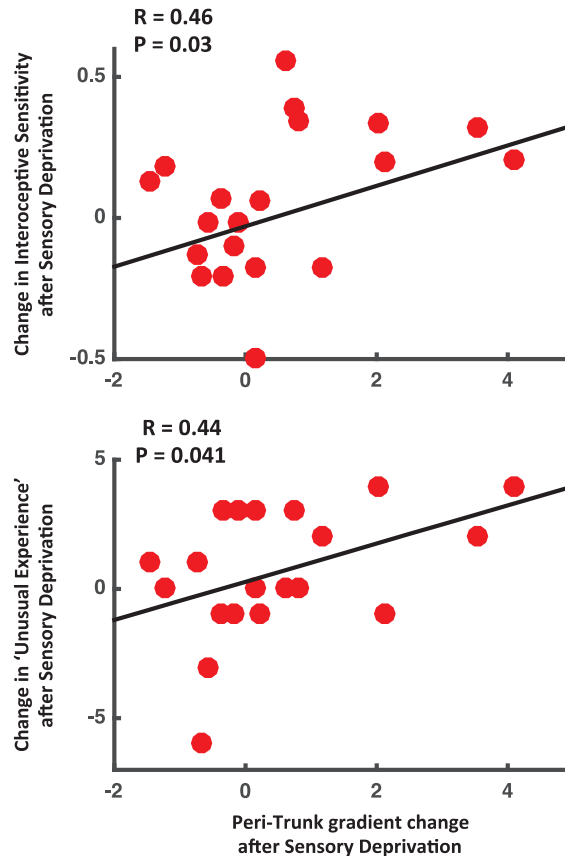


Fig. 5. Relationship between changes on PPS representation, interoceptive accuracy and phenomenology as induced by audio-visual deprivation. The magnitude of changes in the gradient (slope) of participants' PPS representation around the trunk after audio-visual deprivation (x-axis) was positively correlated with the amount of change in their interoceptive accuracy (upper panel) and their proneness to agree with the occurrence of 'unusual experiences' (lower panel) after audio-visual deprivation.

4. Discussion

Overall, the present results indicate that after a brief period of audio-visual deprivation – and while still in the sensory deprived environment - the size of participant's peri-face and peri-trunk peripersonal space representation was not changed, although interestingly, the boundary between the peri- and extra-personal spaces became more poorly defined. More precisely, the main observation of the current study is that the slope of the function describing how the location of an external visual stimulus affects tactile processing became less steep, indicating that the division between the near and far space becomes shallower after a brief period of audio-visual deprivation. Quite intriguingly, this behaviorally defined effect on the “spatial self” (Blanke et al., 2015; Serino et al., 2016; Noel et al., 2017) was associated at the phenomenological level to the reports of ‘being lost in space’, and to a lesser extent, of ‘floating in the air’. Further, replicating prior findings (Mason & Brady, 2009), the present data suggest that after audio-visual deprivation, subjects experienced an increased tendency toward reporting hallucinatory and other unusual experiences. Contrary to our initial hypothesis, audio-visual deprivation did not induce specific changes in interoceptive accuracy at the group level, at least with the heat-beat counting task used in the present study.

The fact that the gradient separating the near and the far space became shallow upon audio-visual deprivation illustrated that the sensitivity of the PPS boundary in separating between the peri- and extra-personal space is reduced after audio-visual deprivation. It has been proposed that the main role of PPS is to predict what can potentially interact with the body and what cannot, by integrating external stimuli from the environment with tactile information on the body (Cléry, Guipponi, Odouard, Wardak, Ben Hamed, 2015; Cléry et al., 2017). This integration mechanism might have a fundamental role in the implementation of both defensive (Graziano & Cooke, 2006) and approaching (Rizzolatti et al., 1997) behaviors. Most previous studies detailing PPS representations report changes in PPS size (the central point of the function in the present paradigm) as a function of a host of factors, such as after tool use (Iriki, Tanaka, & Iwamura, 1996; Canzoneri, Ubaldi, et al., 2013), hours of immobilization (Bassolino, Serino, Ubaldi, & Ladavas, 2014), or following amputation and prosthesis implantation (Canzoneri, Marzolla, et al., 2013). More recently PPS representation has been shown to be related to individual differences (Ferri et al., 2015) and to possess a relationships to personality traits (Sambo et al., 2013; Fossataro et al., 2016). However, to the best of our knowledge, no previous study has investigated factors affecting the gradient of the PPS (the slope of the function in our paradigm). A possible explanation for the change in PPS slope after audio-visual

deprivation is that the definition of one's own PPS is dependent on the integration of exteroceptive cues with bodily cues and thus, when exteroceptive signals are degraded, the boundaries of PPS representation become less well-defined. Indeed, Noel & Wallace (2016) have demonstrated that the process of multisensory integration itself is atypical after a short period of audio-visual deprivation.

After the removal of exteroceptive cues, it is conceivable that individuals will rely on other sources of body-related information in order to define a representation of their body and space (see Van der Stoep, Serino, Farnè, Di Luca, & Spence, 2016, Van der Stoep, Postma, & Nijboer, 2017) for a review of multisensory spatial coding). In the current study, we hypothesize that this information could come from interoceptive signals. Surprisingly, however, contrary to what we anticipated, the removal of exteroceptive signals did not translate into an unequivocal enhanced monitoring of interoceptive events for all participants. Enhanced interoceptive accuracy was only observed for a subsample of the tested cohort, while the rest of participants actually exhibited poorer interoceptive accuracy after audio-visual deprivation. This pattern cannot be attributed to a regression to the mean phenomenon, as there was no correlation between performance on the interoceptive task (heartbeat mental tracking) inside and outside the anechoic room. That is, if this effect were a result of regression to the mean and independent of audio-visual deprivation, we would predict that those participants performing well during a first interoceptive test would generally perform worse the second time, and vice-versa, thus giving rise to a negative correlation. Likewise, the fact that some participants showed improved interoceptive accuracy, while others showed a decline in accuracy, is unlikely to be a result of the noisiness of the measure, as both previous literature (Ehlers & Breuer, 1992; Werner et al., 2013; Knoll & Hoddap, 1992) and our own data demonstrate good test-retest reliability for interoceptive accuracy under non-deprived conditions. Thus, as previous literature has indicated (see Hebert & Pollatos, 2012, for a review), it appears that individuals' accuracy to their heartbeat may be a trait-like characteristic, and similarly the current study seemingly suggest that the manner in which interoceptive accuracy is modulated in deprived sensory environments is idiosyncratic to the individual. In addition to the potential association with the manner in which peri-trunk space is represented, in future work it will be interesting to determine a mechanistic explanation as to why certain individuals perform worse in an interoceptive detection task even when exteroceptive cues are impoverished, as in the current experiment. A putative explanation may lie in Khalsa, Rudrauf, Feinstein, and Tranel (2009) observation that there are seemingly two pathways of interoception; one involving visceral afferents projecting to the insula and another involving skin afferents projecting to the somatosensory cortex. Perhaps individual's whose interoceptive accuracy increased/decreased after audio-visual deprivation rely on different pathways. Similarly, while here a causal manipulation was attempted (i.e., "impoverished exteroceptive environment will result in increased interoceptive accuracy which will allow us to examine the interplay between interoception and PPS"), the fact that only about half of the participants actually improved in interoceptive accuracy (contrary to what was hypothesized), forced the analyses to be correlational and not causal in nature. In turn, in the future it will be interesting to explore other putative causal manipulations of interoception.

Interestingly, the external environmental dependence of interoceptive ability (i.e., become better or worse under audio-visual deprivation conditions) may represent an important and stable intra-individual trait, as highlighted by the close relationship between this variable and the subjective experience of the self in space and PPS. That is, although there was no general effect of the sensory environment on interoceptive ability, the manner in which audio-visual deprivation impacted interoceptive accuracy was associated with particular phenomenological and PPS effects on an individual. Specifically, results demonstrated that individuals who showed greater accuracy to interoceptive signals after audio-visual deprivation, as opposed to those who did not, also showed a greater predisposition toward agreeing with statements such as 'I felt as I was floating in the air', and 'I felt as I were dissociated from my body'. Further, changes in subjective experience mirrored those in multisensory processing of PPS, as participants who became better interoceptors inside the anechoic room, and only those participants, also showed a less spatially defined gradient in the way looming stimuli close to their body affected tactile processing at the trunk (i.e., exhibited a less clearly defined boundary for the trunk-centered PPS). This was not the case for the face, where both better and worse interoceptors exhibited a less fine-grained change between the near and far space after audio-visual deprivation. Importantly, however, it must be noted that the directionality of these effects (interoception, peri-trunk representation, and phenomenology) may not be determined with the current experimental design and dataset.

In terms of the specificity observed with regard the change in interoceptive accuracy after audio-visual deprivation and the representation of peri-trunk space, it may be that, as interoceptive accuracy was measured by means of a heartbeat-counting task, and as the heart is located in the trunk, perhaps our interoceptive measure was most sensitive and closely related to trunk-centered representations. This possibility raises the question of whether different body-part (e.g., head) centered interoceptive sensitivities exist (e.g., salivation), and prompts future research to develop measures relating interoception at different body-parts. The second possibility is that the peri-trunk PPS is most sensitive to individual variability in interoceptive accuracy - or perhaps peri-trunk representation is further associated with the somatosensory than the visceral interoceptive pathways (Khalsa et al., 2009), although this is but a speculation and remains to be tested. This prospect fits nicely with the recent postulation that different body-part centered peripersonal space representations exist, yet are not entirely independent from each other (Serino et al., 2015; Blanke et al., 2015). In particular, it is hypothesized that the peri-trunk representation is a more general representation of PPS, referencing the rest of body-part centered peripersonal space representations, and reflecting changes in the perceived position of oneself in space (Noel, Grivaz, et al., 2015, Noel, Pfeiffer, et al., 2015; Salomon et al., 2017). Thus, trait-specific individual differences, such as for interoceptive accuracy, might be more closely related to the peri-trunk PPS, as a more general self-related representation, than to other body-parts specific representations.

The last finding of the current study is that the reciprocal interplay exhibited between interoceptive accuracy and exteroceptive representations at the trunk appears to also relate to personality traits, above and beyond the experience of the self in space. Specifically, there was a positive correlation between a particular individual's peri-trunk PPS gradient change as a consequence of

audio-visual deprivation and the change in interoceptive accuracy following audio-visual deprivation, as well as between the former variable and participant's score on the 'Unusual Experiences' subscale of the O-LIFE questionnaire. Importantly, the fact that these latter two (interoceptive accuracy and 'Unusual Experiences' subscale) did not correlate among each other, but solely with the degradation in peri-trunk representation after audio-visual deprivation, seemingly implies that the manner in which an individual processes exteroceptive multisensory stimuli plays the functional link between bodily interoceptive ability and mental disorder, or at least a particular subcategory of schizotypy, as assessed here. It must be noted, however, that (1) these correlational analyses do not permit to establish neither directionality nor causality, and (2) the association between interoception and self-report of "unusual experiences" remained non-significant even when mediated by their respective association with peri-trunk gradient.

A number of limitations of the current work must be mentioned. First, the degree of audio-visual deprivation in the named condition was fairly limited. That is, this deprivation included solely the auditory and visual modalities modality, while tactile, proprioceptive, and vestibular modalities all remained. Further, the auditory deprivation achieved is better characterized as a reduction in environmental noise than a complete absence of auditory input. Similarly related to the audio-visual deprivation manipulation, while psychophysical testing and self-reports were executed within the anechoic chamber, during testing visual signals were provided, and hence it is unclear whether, and for how long, does audio-visual deprivation effects on perception persist following the improvised exposure phase (although see Noel & Wallace, 2016, for another psychophysical effect persisting for approximately 15 min following 15 min of audio-visual deprivation). A second class of limitation regards to the interoceptive task utilized and the degree to which test-retest reliability was tested within the framework of the current study. While, as above-mentioned, the Schandry task is known to have good test-retest reliability under standard sensor environments (e.g., Werner et al., 2013), it does not correlate with all other heartbeat discrimination tasks (see Garfinkel et al., 2015), and most importantly, as highlighted by Ring and Brener (1996), performance on this task is influenced by beliefs about heart rate (but also the processing of cardiac sensations). Further, it is unknown whether this task is equally reliable under sensory deprived conditions. That is, in the current study test-retest reliability was not performed in the sensory deprived environment, and hence this remains an interesting question for future research. Lastly, we must reinforce that while our sample size was determined for appropriate statistical power given prior published effect sizes, and that while the majority of the reported effects are indeed found when utilizing the entire cohort, the specific degradation of peri-trunk space following audio-visual deprivation was solely found after separating the groups with improved and worsened interoceptive accuracy following audio-visual deprivation. In turn, the effects and interpretation reliant on the division of good and poor interoceptors count with solely about 10 subjects per group – a sample size with poor statistical power.

Recent work has focused on the contributions of lower-level multisensory processes to the schizophrenia pathology (Parnas et al., 2001; Sass & Parnas, 2003; Williams et al., 2010; de Jong et al., 2009; Noel, Cascio, et al., 2017; Noel, Lytle, et al., 2017; , Noel, Stevenson, & Wallace, 2018; Stevenson et al., 2014, 2017). In particular, experimental evidence has indicated disturbances in the processing of far exteroceptive signals in schizophrenic populations (Pearl et al., 2009). These findings, and the related concept that schizophrenia reflects a disturbance in the relative weight attributed to exteroceptive vs. interoceptive sensory signals, fits well within the present results, and may explain why a relationship was found between the change in peri-trunk representation before and after audio-visual deprivation and schizotypic traits (also see Noel et al., 2017). The present results, thus, contribute to the emerging framework of embodied psychopathology (Fuchs, 2005; Matthews, 2007) and propose a putative intermediary step (namely, peripersonal space representation) between interoceptive abilities and psychopathologies such as schizophrenia.

Acknowledgments

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References

- Adler, D., Herbelin, B., Similowski, T., & Blanke, O. (2014). Breathing and sense of self: Visuo-respiratory conflicts alter body self-consciousness. *Respiratory Physiology & Neurobiology*, 203, 68–74.
- Ainley, V., Maister, L., Brokfeld, J., Farmer, H., & Tsakiris, M. (2013). More of myself: Manipulating interoceptive awareness by heightened attention to bodily and narrative aspects of the self. *Consciousness and Cognition*, 2(4), 1231–1238.
- Ainley, V., Tajadura-Jiménez, A., Fotopoulou, A., & Tsakiris, M. (2012). Looking into myself: The effect of self-focused attention on interoceptive sensitivity. *Psychophysiology*, 49(11), 1672–1676.
- Aspell, J. E., et al. (2013). Turning body and self inside out: visualized heartbeats alter bodily self-consciousness and tactile perception. *Psychological Science*. <http://dx.doi.org/10.1177/0956797613498395>.
- Barnsley, N., Mcauley, J. H., Mohan, R., Dey, A., Thomas, P., & Mosley, G. (2012). The rubber hand illusion increases histamine reactivity in the real arm. *Current Biology*, 21(23), R945–R946. <http://dx.doi.org/10.1016/j.neubiorev.2011.03.013>.
- Bassolino, M., Serino, A., Ubaldi, S., & Ladavas, E. (2014). Everyday use of the computer mouse extends peripersonal space representation. *Neuropsychologia*, 48(3), 803–811.
- Bernasconi, F., Noel, J. P., Park, H. D., Favier, N., Seeck, M., Spinelli, L., ..., Serino, A. (2018). Audio-tactile and peripersonal space processing around the trunk in human parietal and temporal cortex: An intracranial EEG study. [bioRxiv](https://arxiv.org/abs/1808.08881).
- Berlucchi, G., & Aglioti, S. M. (2010). The body in the brain revisited. *Experimental Brain Research*, 200(1), 25–35.
- Bermudez, J. L., Marcel, A. J., & Eilan, N. (Eds.). (1995). *The body and the self*. Cambridge, MA: MIT Press.
- Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal self-hood. *Trends in Cognitive Sciences*, 13, 7–13.
- Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, neural, and computational principles of bodily self-consciousness. *Neuron*, 88, 145–166. <http://dx.doi.org/10.1016/j.neuron.2015.09.029>.
- Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, 13, 556–571.

- Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature*, 391, 756.
- Bultitude, J. H., Walker, I., & Spence, C. (2017). Space-based bias of covert visual attention in complex regional pain syndrome. *Brain*, 140, 2306–2321.
- Canzoneri, E., Magosso, E., & Serino, A. (2012). Dynamic sounds capture the boundaries of peripersonal space representation in humans. *PLoS One*, 7, e44306.
- Canzoneri, E., Marzolla, M., Amoresano, A., Verni, G., & Serino, A. (2013). Amputation and prosthesis implantation shape body and peripersonal space representations. *Scientific Reports*, 3, 2844. <http://dx.doi.org/10.1038/srep02844>.
- Canzoneri, E., di Pellegrino, G., Herbelin, B., Blanke, O., & Serino, A. (2016). Conceptual processing is referenced to the experienced location of the self, not the location of the physical body. *Cognition*, 154, 182–192.
- Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., & Serino, A. (2013). Tool use reshapes the boundaries of body and peripersonal space representations. *Experimental Brain Research*, 228(1), 25–42.
- Claridge, G., McCreery, C., Mason, O., Bentall, R., Boyle, G., Slade, P., et al. (1996). The factor structure of schizotypal traits: A large replication study. *British Journal of Clinical Psychology*, 35, 103–115.
- Cléry, J., Guipponi, O., Odoouard, S., Wardak, C., & Ben Hamed, S. (2015). Impact prediction by looming visual stimuli enhances tactile detection. *Journal of Neuroscience*, 35, 4179–4189. <http://dx.doi.org/10.1523/JNEUROSCI.3031-14.2015>.
- Cléry, J., Guipponi, O., Odoouard, S., Pinède, S., Wardak, C., & Hamed, S. B. (2017). The prediction of impact of a looming stimulus onto the body is subserved by multisensory integration mechanisms. *Journal of Neuroscience*, 37, 10656–10670. <http://dx.doi.org/10.1523/JNEUROSCI.0610-17.2017>.
- Craig, A. D. (2009). How do you feel — now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, 10, 59–70.
- Craig, A. D. (2002). How do you feel? Interoception: The sense of the physiological condition of the body. *Nature Reviews Neuroscience*, 3, 655–666.
- Critchley, H., & Seth, A. (2012). Will studies of macaque insula reveal the neural mechanisms of self-awareness? *Neuron*, 74, 423–426.
- Critchley, H., Hamm, A., & Harmon-Jones, E. (2011). Interoception and emotion: The return of peripheralism? *Psychophysiology*, 48, S16–S17.
- Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, 7, 189–195.
- Damasio, A. R. (2000). *The feeling of what happens: Body and emotion in the making of consciousness*. New York, NY: Harcourt Brace.
- Damasio, A. R. (2010). *Self comes to mind. Constructing the conscious brain*. London: Heineman.
- de Jong, J. J., Hodiadmont, P. P., Van den Stock, J., & de, G. B. (2009). Audiovisual emotion recognition in schizophrenia: reduced integration of facial and vocal affect. *Schizophrenia Research*, 107(2–3), 286–293.
- de Haan, A. M., Van Stralen, H. E., Smit, M., Keizer, A., Van der Stigchel, S., & Dijkerman, H. C. (2017). No consistent cooling of the real hand in the rubber hand illusion. *Acta Psychologica*, 179, 68–77.
- de Haan, A., Smit, M., Miranda, S., Van der Stigchel, S., & Dijkerman, H. C. (2016). Approaching threat modulates visuotactile interactions in peripersonal space. *Experimental Brain Research*, 234(7), 1875–1884.
- De Paep, A. L., Crombez, G., & Legrain, V. (2017). Remapping nociceptive stimuli into a peripersonal reference frame is spatially locked to the stimulated limb. *Neuropsychologia*, 101, 121–131.
- De Paep, A. L., Crombez, G., Spence, C., & Legrain, V. (2014). Mapping nociceptive stimuli in a peripersonal frame of reference: Evidence from a temporal order judgment task. *Neuropsychologia*, 56(1), 219–228. <http://dx.doi.org/10.1016/j.neuropsychologia.2014.01.016>.
- Di Pellegrino, G., Ladavas, E., & Farnè, A. (1997). Seeing where your hands are. *Nature*, 388, 730.
- Domschke, K., Stevens, S., Pfleiderer, B., & Gerlach, A. L. (2010). Interoceptive sensitivity in anxiety and anxiety disorders: An overview and integration of neurobiological findings. *Clinical Psychology Review*, 30(1), 1–11. <http://dx.doi.org/10.1016/j.cpr.2009.08.008>.
- Dunn, B. D., Dalgleish, T., Ogilvie, A. D., & Lawrence, A. D. (2007). Heartbeat perception in depression. *Behaviour Research and Therapy*, 45(8), 1921–1930. <http://dx.doi.org/10.1016/j.brat.2006.09.008>.
- Durlik, C., & Tsakiris, M. (2015). Decreased interoceptive accuracy following social exclusion. *International Journal of Psychophysiology*, 96(1), 57–63. <http://dx.doi.org/10.1016/j.ijpsycho.2015.02.020>.
- Ehlers, A., & Breuer, P. (1992). Increased cardiac awareness in panic disorder. *Journal of abnormal psychology*, 101(3), 371–382.
- Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science*, 317, 1048 doi:317/5841/1048.
- Ehrsson, H. H., Wieck, K., Weiskopf, N., Dolan, R. J., & Passingham, R. E. (2007). Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. *Proceedings of the National Academy of Sciences of the United States of America*, 104(23), 9828–9833. <http://dx.doi.org/10.1073/pnas.0610011104>.
- Fairclough, S. H., & Goodwin, L. (2007). The effect of psychological stress and relaxation on interoceptive accuracy: Implications for symptom perception. *Journal of Psychosomatic Research*, 62(3), 289–295. <http://dx.doi.org/10.1016/j.jpsychores.2006.10.017>.
- Ferri, F., Ardizzi, M., Ambrosecchia, M., & Gallese, V. (2013). Closing the gap between the inside and the outside: interoceptive sensitivity and social distances. *PLoS One*, 8(10), e75758. <http://dx.doi.org/10.1371/journal.pone.0075758>.
- Ferri, F., Costantini, M., Huang, Z., Perrucci, M. G., Ferretti, A., Romani, G. L., et al. (2015). Intertrial variability in the premotor cortex accounts for individual differences in peripersonal space. *Journal of Neuroscience*, 35, 16328–16339.
- Filbrich, L., Alamia, A., Verfaillie, C., Berquin, A., Barbier, O., Libouton, X., et al. (2017). Biased visuospatial perception in complex regional pain syndrome. *Scientific Reports*, 7, 9712.
- Fossataro, C., Sambo, C. F., Garbarini, F., & Iannetti, G. D. (2016). Interpersonal interactions and empathy modulate perception of threat and defensive responses. *Scientific Reports*, 6, 19353.
- Fuchs, T. (2005). Corporealized and disembodied minds. A phenomenological view of the body in melancholia and schizophrenia. *Philosophy, Psychiatry, & Psychology*, 12, 95–107.
- Galli, G., Noel, J. P., Canzoneri, E., Blanke, O., & Serino, A. (2015). The wheelchair as a full-body tool extending the peripersonal space. *Frontiers in Psychology*, 6, 639. <http://dx.doi.org/10.3389/fpsyg.2015.00639>.
- Garfinkel, S. N., Seth, A. K., Barrett, A. B., Suzuki, K., & Critchley, H. D. (2015). Knowing your own heart: distinguishing interoceptive accuracy from interoceptive awareness. *Biological Psychology*, 104, 65–74. <http://dx.doi.org/10.1016/j.biopsycho.2014.11.004> S0301-0511(14) 00229-4 [pii].
- Graziano, M. S., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, 44(6), 845–859.
- Haggard, P., Iannetti, G. D., & Longo, M. R. (2013). Spatial sensory organization and body representation in pain perception. *Current Biology*, 23(4), R164–R176. <http://dx.doi.org/10.1016/j.cub.2013.01.047>.
- Herbert, B. M., & Pollatos, O. (2012). The body in the mind: on the relationship between interoception and embodiment. *Topics in Cognitive Science*. Available: <http://www.ncbi.nlm.nih.gov/pubmed/22389201>.
- Iachini, T., Ruggiero, G., Ruotolo, F., Schiano di Cola, A., & Senese, V. P. (2015). The influence of anxiety and personality factors on comfort and reachability space: A correlational study. *Cognitive Processing*. <http://dx.doi.org/10.1007/s10339-015-0717-6>.
- Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., et al. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron*, 70, 363–374.
- Iriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport*, 7, 2325–2330.
- James, W. (1890). *The principles of psychology*. New York: Dover.
- Kandula, M., van der Stoep, N., Hofman, D., & Dijkerman, H. C. (2017). On the contribution of overt tactile expectations to visuo-tactile interactions within the peripersonal space. *Experimental Brain Research*. <http://dx.doi.org/10.1007/s00221-017-4965-9>.
- Khalsa, S. S., Rudrauf, D., Feinstein, J. S., & Tranel, D. (2009). The pathways of interoceptive awareness. *Nature Neuroscience*, 12, 1494–1496.
- Khalsa, S. S., Rudrauf, D., Damasio, A. R., Davidson, R. J., Lutz, A., & Tranel, D. (2008). Interoceptive awareness in experienced meditators. *Psychophysiology*, 45(4), 671–677. <http://dx.doi.org/10.1111/j.1469-8986.2008.00666.x>.
- Knoll, J. F., & Hodapp, V. (1992). A comparison between two methods for assessing heartbeat perception. *Psychophysiology*, 29, 218–222. <http://dx.doi.org/10.1111/j.1469-8986.1992.tb01689.x>.
- Launay, G., & Slade, P. (1981). The measurement of hallucinatory predisposition in male and female prisoners. *Personality and Individual Differences*, 2, 221–234.
- Legrain, V. (2017). Lost in space. Do somatic symptoms affect the perception of extra-somatic stimuli? *Brain*, 140(9), 2254–2256.

- Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video ergo sum: Manipulating bodily self-consciousness. *Science*, 317(5841), 1096.
- Maister, L., & Tsakiris, M. (2013). My face, myself: Cultural differences in integrated bodily self-awareness. *Cognitive Neuroscience*. <http://dx.doi.org/10.1080/17588928.2013.808613>.
- Mason, O., & Claridge, G. (2006). The Oxford-Liverpool Inventory of Feelings and Experiences (O-LIFE): Further description and extended norms. *Schizophrenia Research*, 82, 203–211.
- Mason, O. J., & Brady, F. (2009). The psychotomimetic effects of short-term sensory deprivation. *Journal of Nervous and Mental Disease*, 197(10), 783–785.
- Mason, O., Claridge, G., & Jackson, M. (1995). New scales for the assessment of schizotypy. *Personality and Individual Differences*, 18, 7–13.
- Matthews, E. (2007). *Body-subjects and disordered minds. Treating the whole person in psychiatry*. Oxford: Oxford University Press.
- Morrison, A. P., Wells, A., & Nothard, S. (2002). Cognitive and emotional predictors of predisposition to hallucinations in non-patients. *British Journal of Clinical Psychology*, 41, 67–78.
- Moseley, G. L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., et al. (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 13169–13173. <http://dx.doi.org/10.1073/pnas.0803768105>.
- Mussgay, L., Klinkenberg, N., & Rüdell, H. (1999). Heartbeat perception in patients with depressive, somatoform, and personality disorders. *Journal of Psychophysiology*, 13, 27–36.
- Nelson, N., Fornito, A., Harrison, B. J., Yücel, M., Sass, L. A., et al. (2009). A disturbed sense of self in the psychosis prodrome: Linking phenomenology and neurobiology. *Neuroscience & Biobehavioral Reviews*, 33, 807–817.
- Noel, J.-P., Blanke, O., Serino, A., & Salomon, R. (2017). Interplay between narrative and bodily self in access to consciousness: No difference between self- and non-self attributes. *Frontiers in Psychology*, 8, 72. <http://dx.doi.org/10.3389/fpsyg.2017.00072>.
- Noel, J.-P., De Niar, M. A., Stevenson, R., Alais, D., & Wallace, M. T. (2016). Atypical rapid audio-visual temporal recalibration in autism spectrum disorders. *Autism Research*. <http://dx.doi.org/10.1002/aur.1633>.
- Noel, J.-P., Cascio, C., Wallace, M., & Park, S. (2017). The spatial self in schizophrenia and autism spectrum disorder. *Schizophrenia Research*, 179, 8–12. <http://dx.doi.org/10.1016/j.schres.2016.09.021>.
- Noel, J.-P., Lytle, M., Cascio, C., & Wallace, M. T. (2017). Disrupted integration of exteroceptive and interoceptive signaling in autism spectrum disorder. *Autism Research*. <http://dx.doi.org/10.1002/aur.1880>.
- Noel, J., Grivaz, D., Marmaroli, P., Lissek, H., Blanke, O., & Serino, A. (2015). Full body action remapping of peripersonal space: The case of walking. *Neuropsychologia*, 70, 375–384. <http://dx.doi.org/10.1016/j.neuropsychologia.2014.08.030>.
- Noel, J. P., Pfeiffer, C., Blanke, O., & Serino, A. (2015). Full body peripersonal space as the space of the bodily self. *Cognition*, 144, 49–57.
- Noel, J. P., & Wallace, M. (2016). Relative contribution of visual and auditory spatial representations to tactile localization. *Neuropsychologia*, 82, 84–90.
- Noel, J. P., De Niar, M., Lazzara, N., & Wallace, M. (2017). Uncoupling between multisensory temporal function and non-verbal turn-taking in Autism Spectrum Disorder. *IEEE Transactions on cognitive and developmental systems*, 99. <http://dx.doi.org/10.1109/TCDS.2017.2778141>.
- Noel, J. P., Stevenson, R. A., Wallace, M. T., et al. (2018). Atypical audiovisual temporal function in autism and schizophrenia: similar phenotype, different cause. *European Journal of Neuroscience*, 1–12. <http://dx.doi.org/10.1111/ejn.13911>.
- Park, H. D., Bernasconi, F., Bello-Ruiz, J., Pfeiffer, C., Salomon, R., & Blanke, O. (2016). Transient modulations of neural responses to heartbeats covary with bodily self-consciousness. *Journal of Neuroscience*, 36, 8453–8460.
- Parnas, J., & Sass, L. A. (2001). Solipsism, self, and schizophrenic delusions. *Philos Psychiatry Psychol*, 8, 101–120.
- Pearl, D., Yodashtkin-Porat, D., Katz, N., Valevski, A., Aizenberg, D., Sigler, M., et al. (2009 Mar). Differences in audiovisual integration, as measured by McGurk phenomenon, among adult and adolescent patients with schizophrenia and age-matched healthy control groups. *Comprehensive Psychiatry*, 50(2), 186–192.
- Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: Perceptual illusion of body swapping. *PLoS One*, 3(12), e3832.
- Pfeiffer, C., Noel, J. P., Serino, A., & Blanke, O. (2018). Vestibular modulation of peri-personal space boundaries. *European Journal of Neuroscience*. <http://dx.doi.org/10.1111/ejn.13872>.
- Pollatos, O., Traut-Mattausch, E., Schroeder, H., & Schandry, R. (2007). Interoceptive awareness mediates the relationship between anxiety and the intensity of unpleasant feelings. *Journal of Anxiety Disorders*, 21(7), 931–943. <http://dx.doi.org/10.1016/j.janxdis.2006.12.004>.
- Postmes, L., Sno, H. N., Goehard, S., van der Stel, J., Heering, H. D., & de Haan, L. (2014). Schizophrenia as a self-disorder due to perceptual incoherence. *Schizophrenia Research*, 152, 41–50. <http://dx.doi.org/10.1016/j.schres.2013.07.027>.
- Ring, C., & Brener, J. (1996). Influence of beliefs about heart rate and actual heart rate on heartbeat counting. *Psychophysiology*, 33, 541–546.
- Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1997). The space around us. *Science*, 11, 190–191.
- Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981). Afferent properties of periarculate neurons in macaque monkeys. II. Visual responses. *Behavioural Brain Research*, 2, 147–163.
- Ronchi, R., Bernasconi, F., Pfeiffer, C., Bello-Ruiz, J., Kaliuzhna, M., & Blanke, O. (2017). Interoceptive signals impact visual processing: Cardiac modulation of visual body perception. *NeuroImage*, 158, 176–185.
- Rosenzweig, N. (1959). Sensory deprivation and schizophrenia: Some clinical and theoretical similarities. *American Journal of Psychiatry*, 116, 326–329.
- Salomon, R., Lim, M., Pfeiffer, C., Gassert, R., & Blanke, B. (2013). Full body illusion is associated with widespread skin temperature reduction. *Frontiers in Behavioral Neuroscience*, 7, 65.
- Salomon, R., Noel, J. P., Lukowska, M., Favier, N., Metzinger, T., Serino, A., et al. (2017). Unconscious of multisensory bodily inputs in the peripersonal space shapes bodily self-consciousness. *Cognition*.
- Sambo, C. F., & Iannetti, G. D. (2013). Better safe than sorry? The safety margin surrounding the body is increased by anxiety. *Journal of Neuroscience*, 33, 14225–14230.
- Sass, L. A., & Parnas, J. (2003). Schizophrenia, consciousness, and the self. *Schizophrenia Bulletin*, 29, 427–444.
- Schandry, R. (1981). Heart beat perception and emotional experience. *Psychophysiology*, 18, 483–488. <http://dx.doi.org/10.1111/j.1469-8986.1981.tb02486.x>.
- Serino, A. (2016). Variability in multisensory responses predicts the self-space. *Trends in Cognitive Science*, 20(3), 169–170.
- Serino, A., Noel, J. P., Galli, G., Canzoneri, E., Marmaroli, P., Lissek, H., et al. (2015). Body part-centered and full body-centered peripersonal space representations. *Science Reports*, 5, 18603. <http://dx.doi.org/10.1038/srep18603>.
- Serino, A., Noel, J. P., Mange, R., Canzoneri, E., Pellencin, E., Bello-Ruiz, J., ..., Herbelin, B. (2017). Peri-personal space: an index of multisensory body-environment interactions in real, virtual, and mixed realities. *Frontiers in ICT*; doi: 10.3389/fict.2017.00031.
- Seth, A. K. (2013). Interoceptive inference, emotion, and the embodied self. *Trends in Cognitive Sciences*, 17(11), 656–663.
- Seth, A. K., et al. (2011). An interoceptive predictive coding model of conscious presence. *Frontiers in Psychology*, 2, 395.
- Stevens, S., Gerlach, A. L., Cludius, B., Silkens, A., Craske, M. G., & Hermann, C. (2011). Heartbeat perception in social anxiety before and during speech anticipation. *Behaviour Research and Therapy*, 49(2), 138–143. <http://dx.doi.org/10.1016/j.brat.2010.11.009>.
- Stevenson, R. A., Siemann, J. K., Schneider, B. C., Eberly, H. E., Woynaroski, T. G., Camarata, S. M., et al. (2014). Multisensory temporal integration in autism spectrum disorders. *Journal of Neuroscience*, 34, 691–697.
- Stevenson, R. A., Park, S., Cochran, C., McIntosh, L. G., Noel, J.-P., Barense, M. D., et al. (2017). The associations between multisensory temporal processing and symptoms of schizophrenia. *Schizophrenia Research*.
- Suzuki, K., et al. (2013). Multisensory integration across interoceptive and exteroceptive domains modulates self-experience in the rubber-hand illusion. *Neuropsychologia*. <http://dx.doi.org/10.1016/j.neuropsychologia.2013.08.014>.
- Tajadura-Jiménez, A., & Tsakiris, M. (2013). Balancing the “inner” and the “outer” self: Interoceptive sensitivity modulates self-other boundaries. *Journal of Experimental Psychology: General*. <http://dx.doi.org/10.1037/a0033171>.
- Tajadura-Jiménez, A., Longo, M., Coleman, R., & Tsakiris, M. (2012). The person in the mirror: Using the enfacement illusion to investigate the experiential structure of self-identification. *Consciousness & Cognition*, 21(4), 1725–1738.

- Teneggi, C., Canzoneri, E., di Pellegrino, G., & Serino, A. (2013). Social modulation of peripersonal space boundaries. *Current Biology*, 23, 406–411. <http://dx.doi.org/10.1016/j.cub.2013.01.043>.
- Tsakiris, M. (2008). Looking for myself: Current multisensory input alters self-face recognition. *PLoS One*, 3, e4040.
- Tsakiris, M., Tajadura-Jimenez, A., & Costantini, M. (2011). Just a heart-beat away from one's body: Interoceptive sensitivity predicts malleability of body-representations. *Proceedings of the Royal Society of London B: Biological Sciences*, 278, 2470–2476.
- Van der Stoep, N., Postma, A., & Nijboer, T. C. W. (2017). Multisensory perception and the coding of space. In *Neuropsychology of space* (pp. 123–158). San Diego, CA: Elsevier Inc., doi.org/10.1016/B978-0-12-801638-1.00004-5.
- Van der Stoep, N., Serino, A., Farnè, A., Di Luca, M., & Spence, C. (2016). Depth: The forgotten dimension in multisensory research. *Multisensory Research*, 29, 493–524. <http://dx.doi.org/10.1163/22134808-00002525>.
- Werner, N. S., Kerschreiter, R., Kindermann, N. K., & Duschek, S. (2013). Interoceptive awareness as a moderator of affective responses to social exclusion. *Journal of Psychophysiology*, 27(1), 39–50.
- Williams, L. E., Light, G. A., Braff, D. L., & Ramachandran, V. S. (2010 Aug). Reduced multisensory integration inpatients with schizophrenia on a target detection task. *Neuropsychologia*, 48(10), 3128–3136.