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RAPID REPORT | *Higher Neural Functions and Behavior*

The "embreathment" illusion highlights the role of breathing in corporeal awareness

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Monti A, Porciello G, Tieri G, Aglioti SM. The "embreathment" illusion highlights the role of breathing in corporeal awareness. *J Neurophysiol* 123: 420–427, 2020. First published December 4, 2019; doi:10.1152/jn.00617.2019.—Recent theories posit that physiological signals contribute to corporeal awareness, the basic feeling that one has a body (body ownership) that acts according to one's will (body agency) and occupies a specific position (body location). Combining physiological recordings with immersive virtual reality, we found that an ecological mapping of real respiratory patterns onto a virtual body illusorily changes corporeal awareness. This new way of inducing a respiratory bodily illusion, called "embreathment," revealed that breathing is almost as important as visual appearance for inducing body ownership and more important than any other cue for body agency. These effects were moderated by individual levels of interoception, as assessed through a standard heartbeat-counting task and a new "pneumoception" task. By showing that respiratory, visual, and spatial signals exert a specific and weighted influence on the fundamental feeling that one is an embodied agent, we pave the way for a comprehensive hierarchical model of corporeal awareness.

NEW & NOTEWORTHY Our body is the only object we sense from the inside; however, it is unclear how much inner physiology contributes to the global sensation of having a body and controlling it. We combine respiration recordings with immersive virtual reality and find that making a virtual body breathe like the real body gives an illusory sense of ownership and agency over the avatar, elucidating the role of a key physiological process like breathing in corporeal awareness.

corporeal awareness; embodiment; interoception; respiration; virtual reality

INTRODUCTION

Humans are uniquely aware of having a body, controlling its actions, and dwelling in it, a form of self-consciousness that goes under the name of corporeal awareness (Berlucchi and Aglioti 2010) or embodiment (Longo et al. 2008). Bodily illusions and neurological disorders imply that one becomes aware of one's body when different cues, from the appearance of the body to the position of its parts, are aligned in space and time and integrated at the neural level (Blanke et al. 2015). Among these bodily cues, breathing has an intuitive appeal as a factor inducing a sense of embodiment. Indeed, breaths enable bodily survival and continuously provide the brain with vital information about physiology (Del Negro et al. 2018), emotion (Boiten 1998), and cognition (Perl et al. 2019; Zelano et al. 2016). Furthermore, contrary to other bodily signals, breaths are easily accessible to consciousness and partially amenable to voluntary control. For the same reasons, however, the impact of breathing on corporeal awareness is difficult to gauge in a safe, ecological, and experimentally controlled fashion. Thus here we sought to measure how much breaths influence the awareness of one's body through a new way of inducing a respiratory bodily illusion that we call "embreathment," a real-time ecological mapping of the respiratory frequency and amplitude of each participant onto a virtual body (avatar), using a custom-made immersive virtual reality setup (Fig. 1 and Supplemental Video S1; see MATERIALS AND METHODS). We expected that participants would feel more embodied in a "congruent" avatar matching the respiratory, spatial, or visual features of their real body than in an "incongruent" avatar in which such a matching did not occur. Furthermore, we hypothesized that breathing had a specific influence on corporeal awareness over and above other sensory channels. Finally, we thought that the influence of bodily signals on explicit and implicit markers of embodiment would be moderated by interoceptive sensibility and accuracy (as defined by Garfinkel et al. 2015).

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MATERIALS AND METHODS

A detailed description of the experimental methods (including Supplemental Video S1 and Supplemental Tables S1–S6), some minor supplemental results, and all recorded data are available at https://osf.io/g92ur/.

Participants

Thirty-two healthy male volunteers took part in the study (mean = 22.31 yr, range = 19–33 yr) after providing their written informed consent. The local ethics committee at the Fondazione Santa Lucia Research Hospital reviewed and approved the experimental protocol. Participants were recruited outside the laboratory from a subject pool of local university students. All of them were naïve to the purpose of the research and received monetary compensation.

Procedure

Participants completed the Italian Multidimensional Assessment of Interoceptive Awareness (MAIA) questionnaire (Calì et al. 2015) and

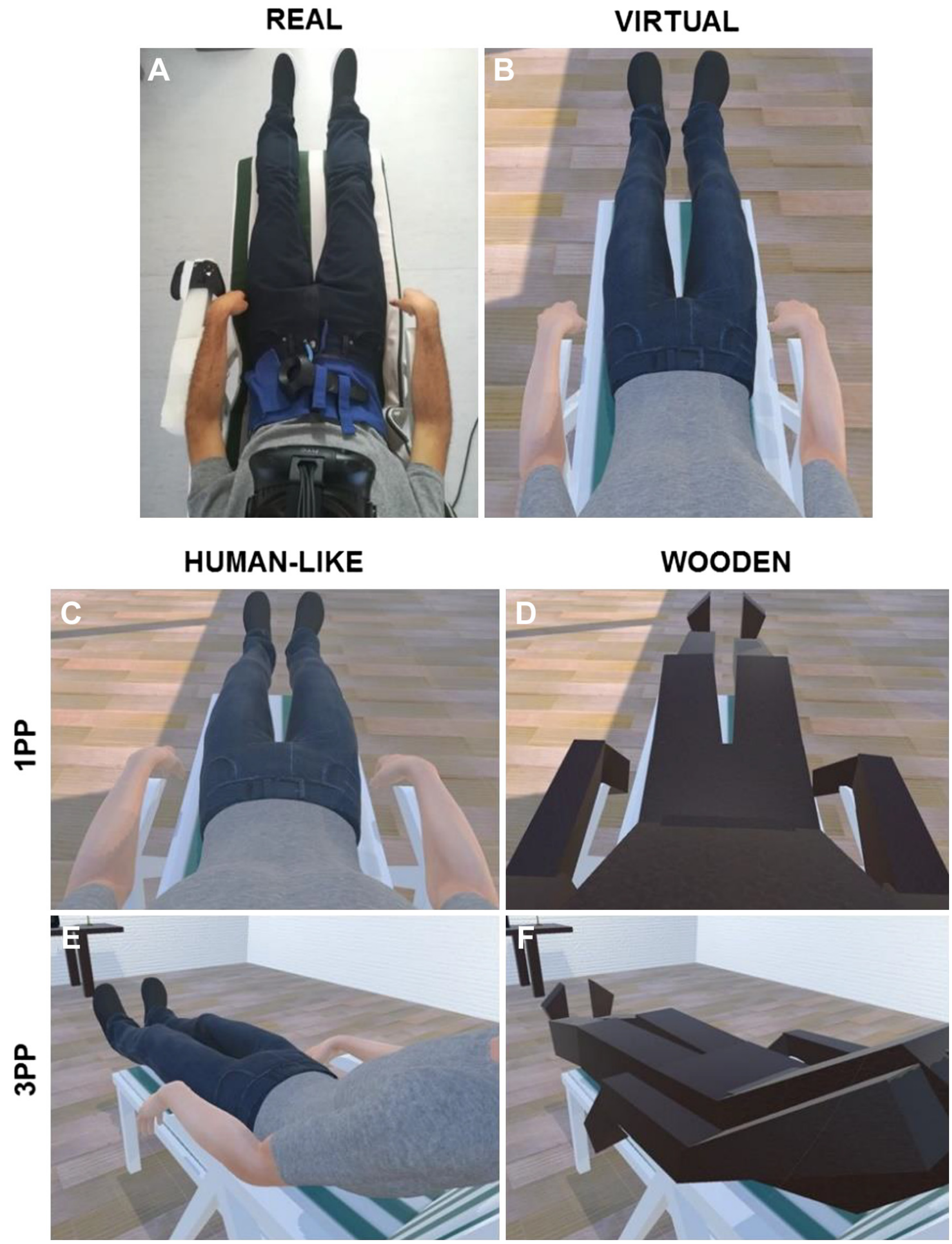


Fig. 1. Experimental setup. *Top*: experimental apparatus, consisting of a head-mounted display and a breathing belt sensor (*A*), used to map the real breathing pattern of a participant onto a virtual body (avatar) in an immersive virtual reality environment (*B*) (see Supplemental Video S1). *Bottom*: besides mapping breathing in a synchronous or asynchronous fashion, the apparatus allowed us to manipulate the visual appearance and the spatial perspective of the avatar, which could combine a “human-like” or “wooden” appearance with a first-person or third-person perspective (1PP or 3PP) (*C–F*).

then underwent an immersive virtual reality experience consisting of eight counterbalanced experimental conditions. In condition 1, participants saw an avatar that looked, lay, and breathed like their real body, i.e., it had a “human-like” appearance, was seen from a first-person perspective, and breathed as the participant, in real time, thanks to a custom-made immersive virtual reality setup (Fig. 1 and Supplemental Video S1). In condition 8, appearance, location, and breathing were all incongruent, i.e., the avatar was a “wooden” virtual character, was seen from a third-person perspective, and breathed with an opposite pattern, i.e., it inhaled when the participant exhaled, and vice versa (Fig. 1 and Supplemental Video S1). Conditions 2–7 presented all possible intermediate combinations of congruent and incongruent bodily signals (Table S1). At the end of each scenario, participants answered a five-item questionnaire on feelings of body ownership, agency, and location (Table S2) using a visual analog scale (VAS) ranging from 0 (“I did not have that feeling of that sort at all”) to 100 (“I perceived a strong feeling of that sort”). Finally, participants completed a heartbeat-counting task and a “pneumoception” task. In the counting task, subjects counted their heartbeats during four different randomized time intervals (25 s, 35 s, 45 s, 100 s) while undergoing a bipolar lead II ECG. In the pneumoception task, each subject listened to a series of 26 unlabeled breathing sound tracks and classified them as “self tracks” or “nonself tracks” (unbeknown to the participant, half of the tracks contained his own breathing sounds, whereas the other half were taken from a frequency- and amplitude-matched control subject).

Data Analysis

Explicit self-reported markers of embodiment. We built three linear mixed-effects models to assess how much ratings of perceived body ownership, agency, and location changed when respiratory, visual, and spatial features of the virtual body were either congruent or incongruent with those of the real body. Each model had VAS ratings of a specific facet of corporeal awareness (ownership, agency, or location) as its dependent variable. As fixed effects, all models had appearance (two levels: human-like and wooden), perspective (two levels: first- and third-person perspective), and breathing (two levels: phase and antiphase). These fixed effects were tested for interactions with each other, as well as with the interoceptive sensibility (*isen*) and accuracy (*iacc*) scores. *Isen* and *iacc* were based on MAIA ratings (*isen*) and performance in heartbeat counting and pneumoception tasks, respectively. As random effects, the models included by-subject intercepts as well as by-subject slopes for the effects of appearance, perspective, and breathing. The relative importance of each effect was gauged comparing its standardized regression coefficient with the others' (Darlington 1990; Johnson and LeBreton 2004).

Implicit physiological markers of embodiment. Breathing signals were downsampled to 43 Hz with a Hamming window-designed finite impulse response antialiasing filter of order 30, detrended, and baseline-corrected to get phase peaks, amplitudes, and frequencies of each participant in each experimental condition. Values outside the median plus or minus 2.5 times the median absolute deviation were classified as outliers and subsequently excluded from further analysis. To measure how much the participants' baseline-corrected breathing amplitude varied as a function of human-avatar sensory congruency, we built a linear mixed-effects model that featured amplitude as a dependent variable and appearance (two levels: human-like and wooden), perspective (two levels: first- and third-person perspective), and breathing (two levels: phase and antiphase) as fixed effects. Random effects and interactions were specified as above.

RESULTS

Perspective, Appearance, and Breathing Contribute to the Sensation of Owning a Body

The linear mixed-effects model run on subjective ratings of body ownership (see MATERIALS AND METHODS) showed a main effect of respiratory congruency; when the avatar breathed in phase with the real body, participants' feeling that the virtual body was theirs increased by ~7.86 ± 4.54 points on a 0–100 VAS compared with when the avatar breathed in antiphase with the real body, $\chi^2(1, N = 255) = 16.72$, $P < 0.001$ (Fig. 2*B*). This main effect interacted with the individual level of interoceptive accuracy (*iacc*); for each one-unit decrease in *iacc*, the effect of congruent breathing on perceived body ownership increased by ~40.99 ± 23.21 points, $\chi^2(1, N = 255) = 7.85$, $P = 0.005$ (Fig. 3*D*).

Also the two other factors that were manipulated during the experiment, i.e., appearance and perspective, modified the sensation of owning the virtual body. Ratings of body ownership for the congruent, human-like avatar were 9.46 ± 4.66 VAS points higher than for the incongruent, wooden avatar, $\chi^2(1, N = 255) = 11.68$, $P < 0.001$. Likewise, when the avatar was seen from a congruent, first-person perspective, perceived body ownership was 37.55 ± 4.78 points higher than when the avatar was observed from an incongruent, third-person perspective, $\chi^2(1, N = 255) = 151.29$, $P < 0.001$ (Fig. 2*B*). The main effect of perspective was further qualified by an interaction with the interoceptive sensibility index (*isen*), $\chi^2(1, N = 255) = 12.22$, $P < 0.001$; for each one-unit decrease in *isen*, the effect of congruent perspective on perceived body ownership went up by ~11.86 ± 7.97 points (Fig. 3*A*). A further interaction between perspective and the interoceptive accuracy index (*iacc*), $\chi^2(1, N = 255) = 5.41$, $P = 0.02$, entailed that the effect of perspective went up by ~53.3 ± 24.47 points whenever *iacc* decreased by one unit (Fig. 3*C*). Overall, the model had a marginal R^2 of 0.39 and a conditional R^2 of 0.75.

Perspective and Appearance Contribute to the Sensation of Dwelling in a Body

The linear mixed-effects model run on subjective ratings of body location indicated that the sensation of dwelling in the human-like avatar was 3.24 ± 2.58 VAS points higher than in the wooden avatar, $\chi^2(1, N = 255) = 12.42$, $P < 0.001$ (Fig. 2*D*). In addition to this main effect of appearance, spatial perspective also influenced perceived body location; participants' feeling of occupying the place of the first-person avatar was 58.41 ± 5.66 points higher than the corresponding feeling for the third-person avatar, $\chi^2(1, N = 255) = 135.58$, $P < 0.001$ (Fig. 2*D*).

Furthermore, perspective interacted with the interoceptive sensibility index (*isen*), $\chi^2(1, N = 255) = 4.37$, $P = 0.036$; whenever *isen* values went down by one unit, the effect of perspective on perceived body location went up by 14.56 ± 9.43 points (Fig. 3*B*). The model had a marginal R^2 of 0.64 and a conditional R^2 of 0.94.

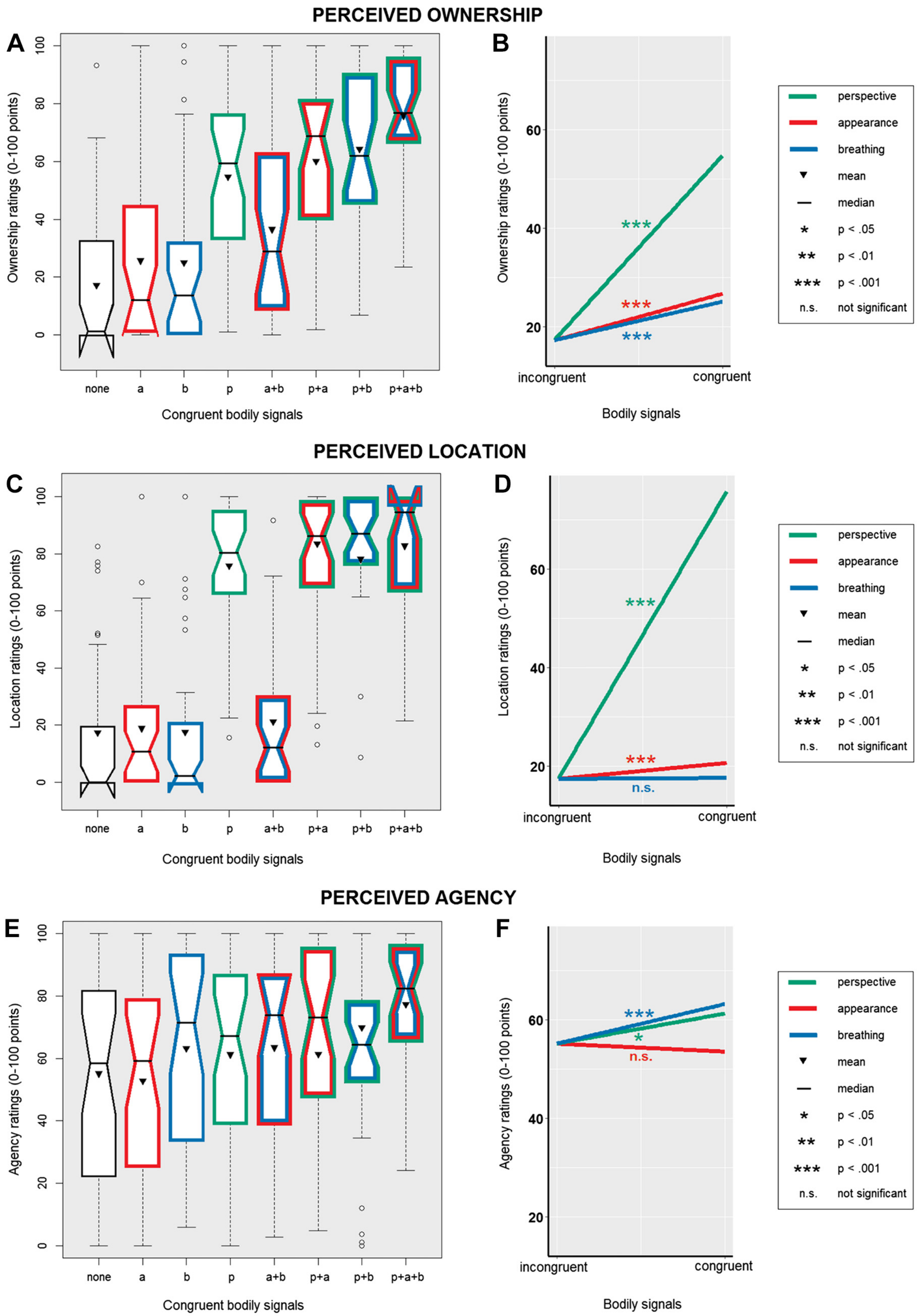
Breathing and Perspective Contribute to the Sensation of Controlling the Movements of the Body

The mixed-effects model run on subjective ratings of body agency showed that participants felt 8.05 ± 4.93 VAS points more in control of the avatar that breathed in phase with them than of the avatar that breathed in antiphase with them, $\chi^2(1, N = 255) = 13.63$, $P < 0.001$ (Fig. 2*F*). This main effect was qualified by an interaction with the interoceptive accuracy (*iacc*) index, $\chi^2(1, N = 255) = 4.36$, $P = 0.037$; for each one-unit decrease in *iacc*, the effect of congruent (in phase) breathing increased by 15.62 ± 25.22 points (Fig. 3*E*). Also, the sensation of controlling the movements of the first-person avatar was 6.11 ± 5.36 points higher than for the third-person avatar, $\chi^2(1, N = 255) = 5.82$, $P = 0.016$. The marginal R^2 of the model was 0.11, whereas the conditional R^2 of the model was 0.62.

Breathing Amplitude Changes as a Function of Human-Avatar Congruency

The linear mixed-effects model run on participants' breathing wave amplitude showed a main effect of breathing, $\chi^2(1, N = 255) = 4.80$, $P = 0.028$; when the avatar breathed in phase with the real body, the amplitude of breathing waves had an ~2.1-mm decrease (Fig. 4*B*). This latter main effect was moderated by visual appearance, which interacted with breathing, $\chi^2(1, N = 255) = 16.82$, $P < 0.001$; hence, the amplitude

Fig. 2. Congruency between real and virtual bodily signals impacts on feelings of body ownership (*A* and *B*), location (*C* and *D*), and agency (*E* and *F*). *Left*: boxplots of perceived ownership (*A*), location (*C*), and agency (*E*) ratings as a function of type of congruent bodily signals, including appearance (a), breathing (b), perspective (p), and their combinations. *Right*: estimated effects of each bodily signal on the ratings of perceived ownership (*B*), location (*D*), and agency (*F*). Effects are expressed as standardized regression coefficients (slopes) of the underlying linear mixed models. The steeper the slope, the greater the relative importance of a predictor (Darlington 1990; Johnson and LeBreton 2004), i.e., the importance of a given bodily signal.


PERCEIVED OWNERSHIP
A
Ownership ratings (0-100 points)
0
20
40
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Congruent bodily signals
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Ownership ratings (0-100 points)
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incongruent
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PERCEIVED LOCATION
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Location ratings (0-100 points)
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PERCEIVED AGENCY
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Agency ratings (0-100 points)
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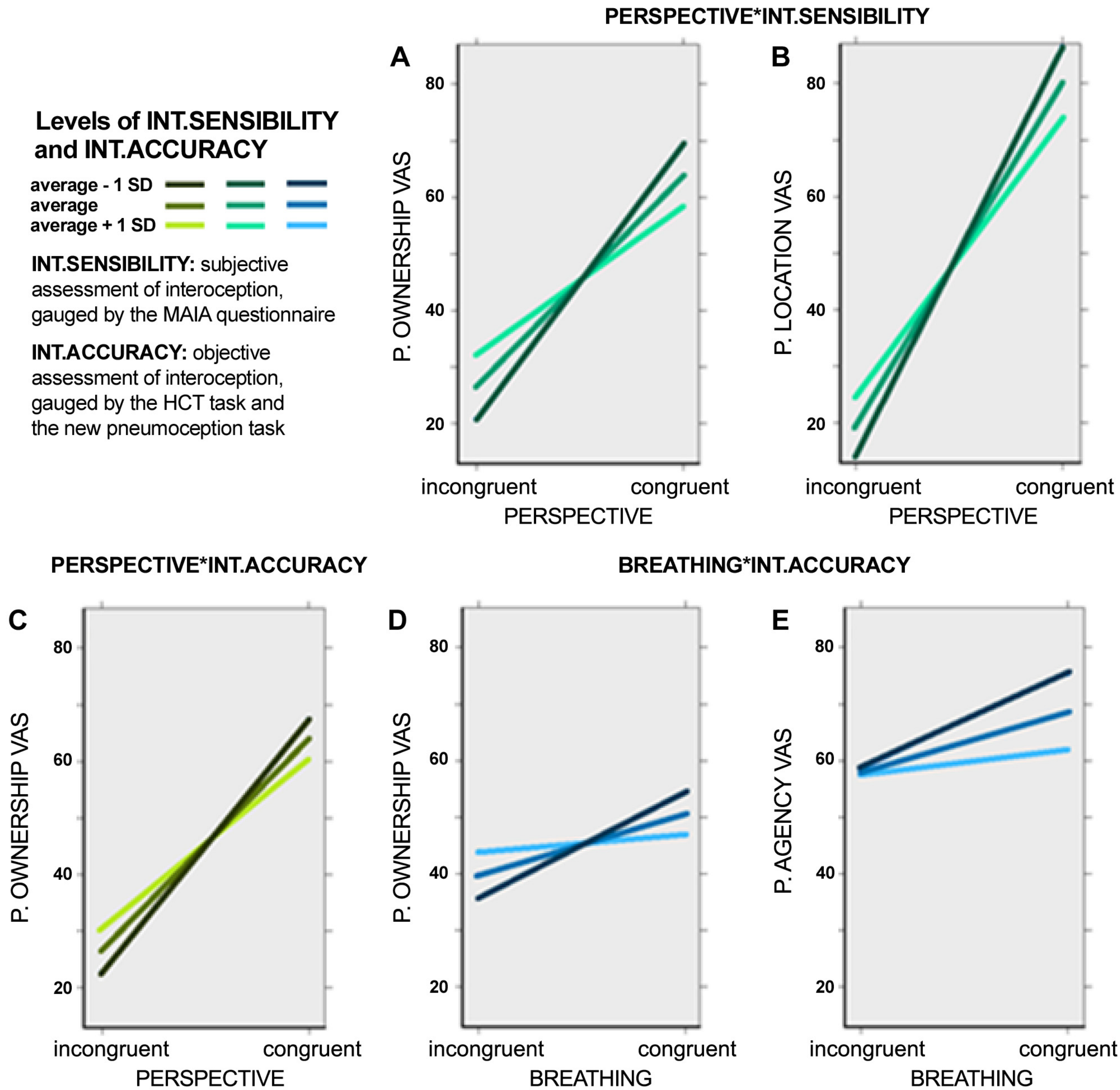

Fig. 3. Interoceptive sensibility moderates the effects of perspective on ratings of perceived body ownership (*A*) and location (*B*). Interoceptive accuracy moderates the effects of perspective (*C*) and breathing (*D*) on perceived ownership and the effect of breathing (*E*) on perceived agency. Overall, participants with lower interoception scores are more susceptible to the experimental manipulations. HCT, heartbeat-counting task; Int., interoceptive; MAIA, Multidimensional Assessment of Interoceptive Awareness; P., perceived; VAS, visual analog scale.

increased by ~0.2 mm when the observed in-phase avatar had a human-like appearance and decreased by ~1.7 mm when participants observed a wooden in-phase avatar (Fig. 4*C*). Furthermore, appearance interacted with perspective, $\chi^2(1, N = 255) = 9.16$, $P = 0.002$; thus breathing amplitude increased by ~0.7 mm if both appearance and perspective were congruent and decreased by ~0.6 mm if there was a combination of congruent perspective and incongruent appearance (Fig. 4*D*). Finally, there was a main effect of interoceptive accuracy, $\chi^2(1, N = 255) = 6.21$, $P = 0.013$; for each one-point decrease in interoceptive accuracy, breathing wave amplitudes had an average ~5.9-mm increase. The model had a marginal R^2 of 0.15, whereas its conditional R^2 was 0.56. All results are summarized in Tables S3–36 (see MATERIALS AND METHODS).

DISCUSSION

In this study, we manipulated breathing signals in an ecological fashion and measured their impact on the sense of having a body, controlling its movements, and dwelling in it. We confirmed the hypothesis that breathing specifically impacts on the subjective feelings of body ownership and agency that are core to subjective experience of self-consciousness. Furthermore, we found that objective breathing patterns change as a function of the degree of congruency between real and virtual bodies. Finally, we showed that the effects of both breathing and spatial perspective on embodiment depend on the interoceptive ability to perceive respiratory and cardiac signals.

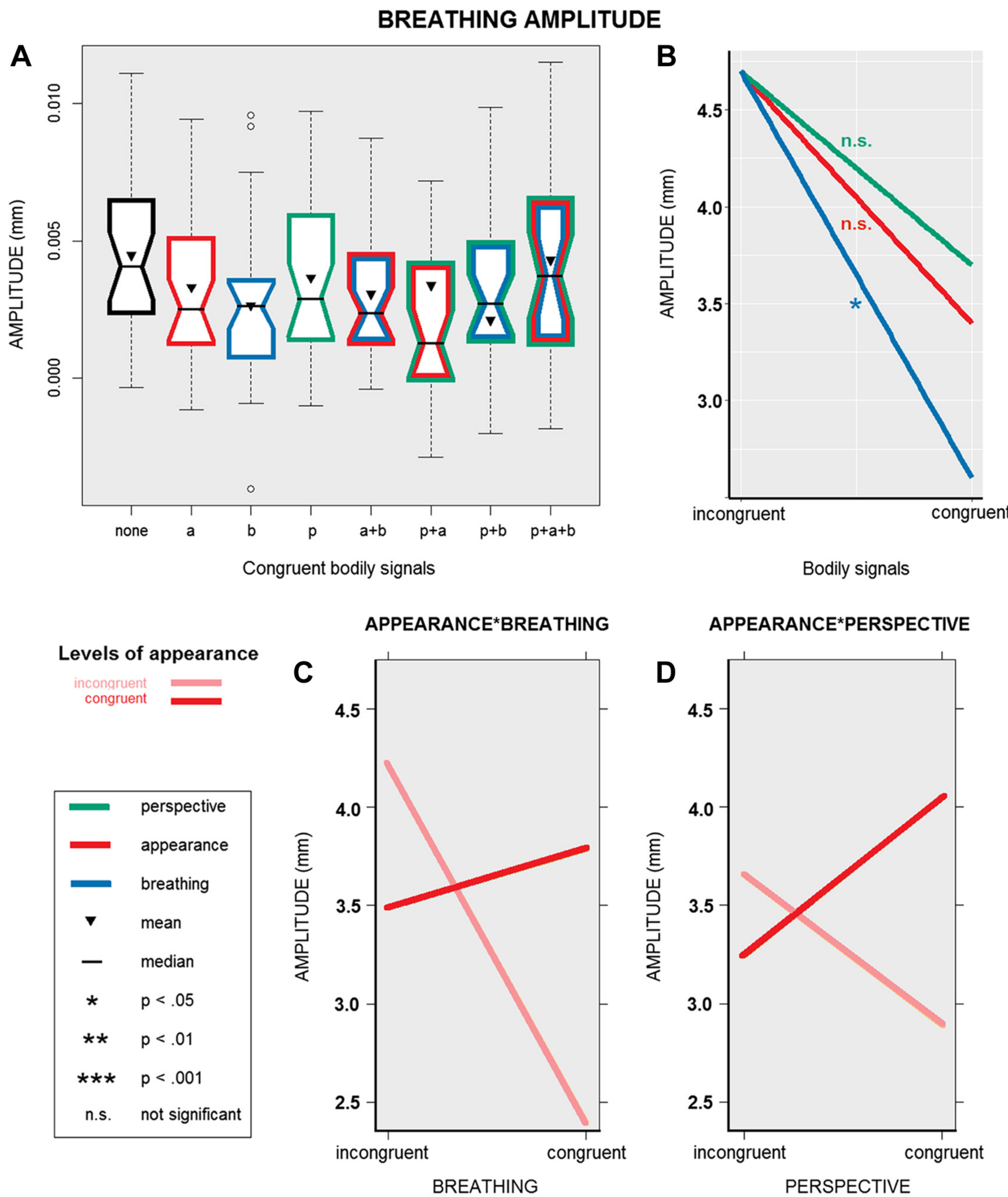

Fig. 4. Boxplots representing the amplitude of participants' real breathing waves recorded in conditions 1–8 (*A*). Estimated effect of perspective (p), appearance (a), and breathing (b) on the amplitude of participants' breathing waves (*B*) is shown; interaction plots show how appearance (congruent vs. incongruent) moderates the estimated effects of breathing (*C*) and perspective (*D*) on the amplitude of breathing waves.

Our data indicate that congruent breathing increases the sensation of owning the virtual body, controlling for the larger effects of perspective and appearance. This fits well with theories that posit that physiological signals play a crucial role in giving rise to human self-consciousness (Craig 2009; Critchley and Harrison 2013; Herbert and Pollatos 2012; Park and Tallon-Baudry 2014), especially when they are manipulated in an ecological fashion (Porciello et al. 2018). This result extends what was previously known from a study by Allard and colleagues (2017), who found that participants were more likely to display self-identification with a picture of a body seen from the back when this image artificially flashed in sync with their breathing (although flashing does not consistently increase self-identification; see Adler et al. 2014 and Porciello et al. 2016). Here, we determined that real breaths ecologically mapped onto a virtual body observed from a first-person perspective also increase perceived body ownership. Other studies used nose breathing (Watanabe et al. 2004) or a tension sensor (Czub and Kowal 2019) to inflate and deflate avatars but did not estimate the effect of breathing on corporeal awareness.

Congruent breathing also increases the sensation of controlling the movements of the avatar. The observed boost in agency ratings extends the finding that, when the outcome of a voluntary, occasional action is consistent with expectations, the sense of agency goes up (Sato and Yasuda 2005; Villa et al. 2018). Here, we demonstrate that the same link between agency and outcome holds true even when dealing with breathing, a continuous homeostatic action that can be altered by emotions and volition. Our data imply that spontaneous actions, which are under limited voluntary control and serve a built-in purpose, induce a strong feeling of agency if appropriately mapped onto a virtual body. Of note, breathing also had an impact on the sense of body agency and ownership when the virtual body did not have a human-like appearance, confirming that respiratory signals are strong enough to induce changes in bodily self-consciousness even when visual features are not realistic (Allard et al. 2017).

In contrast with the transient visuo-tactile stimulation protocols that have been traditionally employed in bodily illusion studies so far, breathing can be conceived as a form of natural, continuous multisensory self-stimulation. Indeed, breathing simultaneously provides the brain with exteroceptive, proprioceptive, and interoceptive feedback. Besides visibly inflating or deflating the trunk, breaths produce a peculiar sound and can trigger a cascade of afferent cues (Davenport and Vovk 2009; Del Negro et al. 2018), coming from respiratory tract/muscle mechanoreceptors (Yu 2005), carotid body chemoreceptors (Kumar and Prabhakar 2012), lung nociceptors (Adriaensen and Timmermans 2011), and nasal airflow thermoreceptors (Sozansky and Houser 2014). Because the embreathment illusion manipulates the live mapping of real breathing patterns onto a visible avatar, it chiefly taps into the (mis)alignment of the exteroceptive and proprioceptive components of breathing. However, the interoceptive component of respiration also plays a key role. Here, in keeping with the influential work of Craig (2002), we construe interoception as a broad feeling of the physiological condition of the body, implemented by small-diameter Aδ and C primary afferents. In this sense, the embreathment illusion also taps into the (mis)alignment between what is seen in the virtual world and what is felt through interoceptive small-fiber afferents, i.e., breath-related chemoreceptors and thermoreceptors.

The importance of interoception in the embreathment illusion is further underscored by the finding that interoceptive accuracy and sensibility moderate the impact of breathing and perspective on specific facets of corporeal awareness (Fig. 3). This suggests that someone who has a sharper sense of internal states also has a more stable corporeal awareness and thus becomes less susceptible to bodily illusions, extending previous findings limited to the rubber hand illusion and to cardiac interoception (Tsakiris et al. 2011). Of note, we assessed interoceptive accuracy combining a standard heartbeat-tracking measure (Schandry 1981) with a new pneumoception task (see MATERIALS AND METHODS). Given that cardiac interoception alone does not predict performance across other interoceptive domains like breathing (Garfinkel et al. 2016), our new method provides a more comprehensive assessment of interoceptive accuracy.

Human-avatar sensory congruency was also mirrored by implicit physiological markers of embodiment. In particular, when the avatar combined a congruent breathing or perspective with a human-like appearance, the average breath amplitude increased. This result is consistent with the fact that embodiment procedures boost physiological activity in other domains also, from skin conductance (Armel and Ramachandran 2003; Tieri et al. 2015), to midterm temperature (Tieri et al. 2017) and histamine reactivity (Barnsley et al. 2011). Symmetrically, when congruent breathing or perspective was paired with a wooden avatar, the average breath amplitude decreased. However, this may be due also to the fact that an incongruent appearance elicits a higher autonomic arousal (Tieri et al. 2017), which in turn increases the respiratory frequency (Boiten et al. 1994) and thus makes it harder to breathe deeply. More research is needed to clarify this issue. Also individuals who were more accurate in perceiving breaths and heartbeats had shallower breathing, possibly because superior interoceptive abilities allow them to fine tune the respiratory cycle without resorting to deep inspiration.

Capitalizing on these results, future studies may test whether human-avatar congruency correlates with the number and amplitude of sighs, which were excluded from the present analytical framework, and investigate how the impact of breathing on embodiment generalizes to females, who should display an even stronger influence of respiratory signals due to sex differences in interoceptive accuracy (Grabauskaitė et al. 2017; Harver et al. 1993). Follow-up experiments may also modulate the influence of breathing on corporeal awareness through voluntary control of respiration, possibly with the help of embreathment-based biofeedback or mindful meditation protocols. This goal could also be achieved stimulating the main afferent pathway carrying respiratory information, i.e., the vagus nerve, both in healthy people and in patients who need to improve their control of breathing, like those suffering from panic disorder (Nardi et al. 2009), anxiety (Jerath et al. 2015), depression (Neuman et al. 2006), or depersonalization (Michal et al. 2014).

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

A.M., G.P., G.T., and S.M.A. conceived and designed research; A.M. and G.P. performed experiments; A.M. and G.P. analyzed data; A.M., G.P., and S.M.A. interpreted results of experiments; A.M. prepared figures; A.M. drafted manuscript; A.M., G.P., G.T., and S.M.A. edited and revised manuscript; A.M., G.P., G.T., and S.M.A. approved final version of manuscript.

REFERENCES

Adler D, Herbelin B, Similowski T, Blanke O. Breathing and sense of self: visuo-respiratory conflicts alter body self-consciousness. *Respir Physiol Neurobiol* 203: 68–74, 2014. doi:10.1016/j.resp.2014.08.003.

Adriaensen D, Timmermans J-P. Breath-taking complexity of vagal C-fibre nociceptors: implications for inflammatory pulmonary disease, dyspnoea and cough. *J Physiol* 589: 3–4, 2011. doi:10.1113/jphysiol.2010.201434.

Allard E, Canzoneri E, Adler D, Morélot-Panzini C, Bello-Ruiz J, Herbelin B, Blanke O, Similowski T. Interferences between breathing, experimental dyspnoea and bodily self-consciousness. *Sci Rep* 7: 9990, 2017. doi:10.1038/s41598-017-11045-y.

Armel KC, Ramachandran VS. Projecting sensations to external objects: evidence from skin conductance response. *Proc Biol Sci* 270: 1499–1506, 2003. doi:10.1098/rspb.2003.2364.

Barnsley N, McAuley JH, Mohan R, Dey A, Thomas P, Moseley GL. The rubber hand illusion increases histamine reactivity in the real arm. *Curr Biol* 21: R945–R946, 2011. doi:10.1016/j.cub.2011.10.039.

Berlucchi G, Aglioti SM. The body in the brain revisited. *Exp Brain Res* 200: 25–35, 2010. doi:10.1007/s00221-009-1970-7.

Blanke O, Slater M, Serino A. Behavioral, neural, and computational principles of bodily self-consciousness. *Neuron* 88: 145–166, 2015. doi:10.1016/j.neuron.2015.09.029.

Boiten FA. The effects of emotional behaviour on components of the respiratory cycle. *Biol Psychol* 49: 29–51, 1998. doi:10.1016/S0301-0511(98)00025-8.

Boiten FA, Frijda NH, Wientjes CJ. Emotions and respiratory patterns: review and critical analysis. *Int J Psychophysiol* 17: 103–128, 1994. doi:10.1016/0167-8760(94)90027-2.

Calì G, Ambrosini E, Picconi L, Mehling WE, Committeri G. Investigating the relationship between interoceptive accuracy, interoceptive awareness, and emotional susceptibility. *Front Psychol* 6: 1202, 2015. doi:10.3389/fpsyg.2015.01202.

Craig AD. How do you feel? Interoception: the sense of the physiological condition of the body. *Nat Rev Neurosci* 3: 655–666, 2002. doi:10.1038/nrn894.

Craig AD. How do you feel—now? The anterior insula and human awareness. *Nat Rev Neurosci* 10: 59–70, 2009. doi:10.1038/nrn2555.

Critchley HD, Harrison NA. Visceral influences on brain and behavior. *Neuron* 77: 624–638, 2013. doi:10.1016/j.neuron.2013.02.008.

Czub M, Kowal M. Respiration entrainment in virtual reality by using a breathing avatar. *Cyberpsychol Behav Soc Netw* 22: 494–499, 2019. doi:10.1089/cyber.2018.0700.

Darlington RB. *Regression and Linear Models*. Philadelphia, PA: McGraw-Hill, 1990.

Davenport PW, Vovk A. Cortical and subcortical central neural pathways in respiratory sensations. *Respir Physiol Neurobiol* 167: 72–86, 2009. doi:10.1016/j.resp.2008.10.001.

Del Negro CA, Funk GD, Feldman JL. Breathing matters. *Nat Rev Neurosci* 19: 351–367, 2018. doi:10.1038/s41583-018-0003-6.

Garfinkel SN, Seth AK, Barrett AB, Suzuki K, Critchley HD. Knowing your own heart: distinguishing interoceptive accuracy from interoceptive awareness. *Biol Psychol* 104: 65–74, 2015. doi:10.1016/j.biopsycho.2014.11.004.

Garfinkel SN, Manassei MF, Hamilton-Fletcher G, In den Bosch Y, Critchley HD, Engels M. Interoceptive dimensions across cardiac and respiratory axes. *Philos Trans R Soc Lond B Biol Sci* 371: 20160014, 2016. doi:10.1098/rstb.2016.0014.

Grabauskaitė A, Baranauskas M, Griškova-Bulanova I. Interoception and gender: what aspects should we pay attention to? *Conscious Cogn* 48: 129–137, 2017. doi:10.1016/j.concog.2016.11.002.

Harver A, Katkin ES, Bloch E. Signal-detection outcomes on heartbeat and respiratory resistance detection tasks in male and female subjects. *Psychophysiology* 30: 223–230, 1993. doi:10.1111/j.1469-8986.1993.tb03347.x.

Herbert BM, Pollatos O. The body in the mind: on the relationship between interoception and embodiment. *Top Cogn Sci* 4: 692–704, 2012. doi:10.1111/j.1756-8765.2012.01189.x.

Jerath R, Crawford MW, Barnes VA, Harden K. Self-regulation of breathing as a primary treatment for anxiety. *Appl Psychophysiol Biofeedback* 40: 107–115, 2015. doi:10.1007/s10484-015-9279-8.

Johnson JW, LeBreton JM. History and use of relative importance indices in organizational research. *Organ Res Methods* 7: 238–257, 2004. doi:10.1177/1094428104266510.

Kumar P, Prabhakar NR. Peripheral chemoreceptors: function and plasticity of the carotid body. *Compr Physiol* 2: 141–219, 2012. doi:10.1002/cphy.c100069.

Longo MR, Schüür F, Kammers MPM, Tsakiris M, Haggard P. What is embodiment? A psychometric approach. *Cognition* 107: 978–998, 2008. doi:10.1016/j.cognition.2007.12.004.

Michal M, Reuchlein B, Adler J, Reiner I, Beutel ME, Vögele C, Schächinger H, Schulz A. Striking discrepancy of anomalous body experiences with normal interoceptive accuracy in depersonalization-derealization disorder. *PLoS One* 9: e89823, 2014. doi:10.1371/journal.pone.0089823.

Nardi AE, Freire RC, Zin WA. Panic disorder and control of breathing. *Respir Physiol Neurobiol* 167: 133–143, 2009. doi:10.1016/j.resp.2008.07.011.

Neuman Å, Gunnbjörnsdottir M, Tunsäter A, Nyström L, Franklin KA, Norrman E, Janson C. Dyspnea in relation to symptoms of anxiety and depression: a prospective population study. *Respir Med* 100: 1843–1849, 2006. doi:10.1016/j.rmed.2006.01.016.

Park H-D, Tallon-Baudry C. The neural subjective frame: from bodily signals to perceptual consciousness. *Philos Trans R Soc Lond B Biol Sci* 369: 20130208, 2014. doi:10.1098/rstb.2013.0208.

Perl O, Ravia A, Rubinson M, Eisen A, Soroka T, Mor N, Secundo L, Sobel N. Human non-olfactory cognition phase-locked with inhalation. *Nat Hum Behav* 3: 501–512, 2019. doi:10.1038/s41562-019-0556-z.

Porciello G, Daum MM, Menghini C, Brugger P, Lenggenhager B. Not that heart-stopping after all: visuo-cardiac synchrony does not boost self-face attribution. *PLoS One* 11: e0160498, 2016. doi:10.1371/journal.pone.0160498.

Porciello G, Bufalari I, Minio-Paluello I, Di Pace E, Aglioti SM. The ‘Enfacement’ illusion: a window on the plasticity of the self. *Cortex* 104: 261–275, 2018. doi:10.1016/j.cortex.2018.01.007.

Sato A, Yasuda A. Illusion of sense of self-agency: discrepancy between the predicted and actual sensory consequences of actions modulates the sense of self-agency, but not the sense of self-ownership. *Cognition* 94: 241–255, 2005. doi:10.1016/j.cognition.2004.04.003.

Schandry R. Heart beat perception and emotional experience. *Psychophysiology* 18: 483–488, 1981. doi:10.1111/j.1469-8986.1981.tb02486.x.

Sozansky J, Houser SM. The physiological mechanism for sensing nasal airflow: a literature review. *Int Forum Allergy Rhinol* 4: 834–838, 2014. doi:10.1002/alr.21368.

Tieri G, Tidoni E, Pavone EF, Aglioti SM. Body visual discontinuity affects feeling of ownership and skin conductance responses. *Sci Rep* 5: 17139, 2015. doi:10.1038/srep17139.

Tieri G, Gioia A, Scandola M, Pavone EF, Aglioti SM. Visual appearance of a virtual upper limb modulates the temperature of the real hand: a thermal imaging study in immersive virtual reality. *Eur J Neurosci* 45: 1141–1151, 2017. doi:10.1111/ejn.13545.

Tsakiris M, Tajadura-Jiménez A, Costantini M. Just a heartbeat away from one’s body: interoceptive sensitivity predicts malleability of body-representations. *Proc Biol Sci* 278: 2470–2476, 2011. doi:10.1098/rspb.2010.2547.

Villa R, Tidoni E, Porciello G, Aglioti SM. Violation of expectations about movement and goal achievement leads to sense of agency reduction. *Exp Brain Res* 236: 2123–2135, 2018. doi:10.1007/s00221-018-5286-3.

Watanabe T, Ogikubo M, Ishii Y. Visualization of respiration in the embodied virtual communication system and its evaluation. *Int J Hum Comput Interact* 17: 89–102, 2004. doi:10.1207/s15327590ijhc1701_7.

Yu J. Airway mechanosensors. *Respir Physiol Neurobiol* 148: 217–243, 2005. doi:10.1016/j.resp.2004.12.007.

Zelano C, Jiang H, Zhou G, Arora N, Schuele S, Rosenow J, Gottfried JA. Nasal respiration entrains human limbic oscillations and modulates cognitive function. *J Neurosci* 36: 12448–12467, 2016. doi:10.1523/JNEUROSCI.2586-16.2016.