

Breathing and sense of self: Visuo–respiratory conflicts alter body self-consciousness

Dan Adler^{a,*}, Bruno Herbelin^b, Thomas Similowski^{c,d,e,1}, Olaf Blanke^{b,f,1}

^a Division of Pulmonary Diseases, Geneva University Hospital, Geneva, Switzerland

^b Center for Neuroprosthetics, Ecole Polytechnique de Lausanne, 1015 Lausanne, Switzerland

^c Sorbonne Universités, UPMC Univ Paris 06, UMR.S 1158 “Neurophysiologie Respiratoire Expérimentale et Clinique”, F-75005 Paris, France

^d INSERM, UMR.S 1158 “Neurophysiologie Respiratoire Expérimentale et Clinique”, F-75005 Paris, France

^e AP-HP, Groupe Hospitalier Pitié-Salpêtrière Charles Foix, Service de Pneumologie et Réanimation Médicale (Département “R3S”), F-75013 Paris, France

^f Department of Neurology, Geneva University Hospital, Geneva, Switzerland

ARTICLE INFO

Article history:

Accepted 8 August 2014

Available online 4 September 2014

Keywords:

Breathing

Cerebral cortex

Bodily self-consciousness

Respiratory gating

Dyspnea

ABSTRACT

Bodily self-consciousness depends on the processing of interoceptive and exteroceptive signals. It can be disrupted by inducing signal conflicts. Breathing, at the crossroad between interoception and exteroception, should contribute to bodily self-consciousness. We induced visuo–respiratory conflicts in 17 subjects presented with a virtual body or a parallelepipedal object flashing synchronously or asynchronously with their breathing. A questionnaire detected illusory changes in bodily self-consciousness and breathing agency (the feeling of sensing one’s breathing command). Changes in self-location were tested by measuring reaction time during mental ball drop (MBD). Synchronous illumination changed the perceived location of breathing (body: $p=0.008$ vs. asynchronous; object: $p=0.013$). It resulted in a significant change in breathing agency, but no changes in self-identification. This was corroborated by prolonged MBD reaction time (body: $+0.045$ s, 95%CI [0.013; 0.08], $p=0.007$). We conclude that breathing modulates bodily self-consciousness. We also conclude that one can induce the irruption of unattended breathing into consciousness without modifying respiratory mechanics or gas exchange.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Self-consciousness is a complex phenomenon involving the feeling that experiences and thoughts are bound to the self and are experienced by a unique entity: the “I” of conscious experience (Blanke, 2012; Damasio, 1999). Self-consciousness depends on the brain dynamical processing of various bodily signals (Frith, 2005; Jeannerod, 2006). Bodily self-consciousness can be experimentally modulated by inducing multisensory exteroceptive conflicts, e.g. between vision and touch (Botvinick and Cohen, 1998; Ehrsson, 2007; Fournier and Jeannerod, 1998; Lenggenhager et al., 2007; Sforza et al., 2010). For example, during the “full body illusion experiment”, participants view their own “virtual” body from behind through a head-mounted display while the investigator strokes their back (Lenggenhager et al., 2007). When the “felt” and the “seen” stroking are synchronous, participants mislocalize the touch to the virtual body, self-identify with it, and describe

their self to be shifted toward it (Lenggenhager et al., 2007). This does not occur when the “felt” and “seen” stimuli are asynchronous (Lenggenhager et al., 2007). Inducing conflict between an interoceptive signal (heartbeat) and an exteroceptive signal (visual feedback) also modulates bodily self-consciousness (Aspell et al., 2013; see also Suzuki et al., 2013). Likewise, changes in illusory touch, self-identification and self-location can be induced by cardio-visual illumination synchronous to the heartbeat, but not by asynchronous illumination (Aspell et al., 2013). This supports the hypothesis that signals from inside and outside the human body are integrated by cortical systems devoted to bodily self-consciousness (Aspell et al., 2013; Suzuki et al., 2013).

Breathing is at the crossroad of interoception and exteroception. From the interoceptive point of view, the act of breathing generates an intense afferent traffic from the rib cage, respiratory muscles, bronchopulmonary mechanoreceptors and the upper airways (Davenport and Vovk, 2009). From the exteroceptive point of view, breathing establishes a link between the body and the environment, e.g. by contributing to the perception of temperature and odours. Breathing is also “caught midway between the conscious and the unconscious, and peculiarly sensitive to both” (Richards, 1953). Indeed, while the continuously fluctuating

* Corresponding author. Tel.: +41 795534070.

E-mail address: dan.adler@hcuge.ch (D. Adler).

¹ The last two authors contributed equally to this work.

respiratory neurosensory traffic is normally gated out and does not result in conscious breathing sensations (Chan and Davenport, 2008; Davenport and Vovk, 2009), minor environmental, bodily or emotional changes can induce the encroachment of breathing into consciousness (cognitive breathing awareness). Breathing is also under significantly more conscious control than most other vegetative functions, automatic ventilation being subject to major sources of disruption from cortical origin. For instance, breathing is heavily involved in interhuman communication, as one of the markers of emotion and through the implication of the respiratory system in speech production. Finally, noxious respiratory sensations strongly involve the insular cortex (Banzett et al., 2000; Evans et al., 2002; Peiffer et al., 2001; Raux et al., 2013) that is otherwise known for its role in bodily self-consciousness (Craig, 2003; Critchley et al., 2004; Damasio, 1999).

For all these reasons, breathing is highly likely to contribute to bodily self-consciousness. To test this hypothesis, we used a full body illusion paradigm to present subjects with a visual stimulus that was either synchronous or asynchronous with their breathing. We then tested the effects of conflicting visuo-respiratory signals on the perceived location of breathing, self-identification, self-location, and other conscious breathing sensations related to the virtual body.

2. Methods

2.1. Participants

Seventeen healthy subjects ($F: 11$; age: 21.6 ± 1.4) participated in the experiment. They received detailed information about the methods used and gave their written consent to participate. However, to keep them fully naive, they were initially not informed about the actual “respiratory” purpose of the study, which was revealed post hoc with the possibility to withdraw consent. The study was approved by the local ethics committee – *La Commission d'éthique de la recherche Clinique de la Faculté de Biologie et de Médecine* – at University of Lausanne, Switzerland and was performed in accordance with the Declaration of Helsinki.

2.2. Experimental setting

We used an experimental setup similar to those used to study bodily self-consciousness based on visuo-tactile and cardio-visual

integration (Aspell et al., 2013; Ionta et al., 2011). To eliminate any contribution of the respiratory-related postural sway to the results, participants were studied lying on their back and wore a head-mounted display (HMD) showing either a picture of their own body standing two meters in front of them (body condition) or a human-sized white parallelepipedal object (object condition) (Fig. 1). Inspiratory movements were monitored using a belt-mounted linear transducer (Pneumotrace™, Morro Bay, California) fitted at the level of the umbilicus. A flashing silhouette of waxing and waning intensity was generated with an in-house software according to inspiratory movements in such a way as to make its luminosity maximal at the end of inspiration and minimal at the end of expiration. This silhouette could be flashing in synchrony with breathing (synchronous condition) or asynchronously by replaying a prerecorded breathing pattern out of phase and by continuously adjusting replay speed in real time to ensure that the frequency of the signal was never the same as the subject's breathing frequency (80% or 120% of the measured frequency; as in Aspell et al., 2013). Participants were not informed that the visual flashing was related to their breathing.

The various conditions were combined in a two by two factorial design: (1) SyncBody, where the virtual body was displayed by the HMD and the flashing silhouette was in synchrony with breathing; (2) AsyncBody: virtual body, asynchronous flashing silhouette; (3) SyncObject, where the human sized parallelepipedal object was displayed by the HMD and the flashing silhouette was in synchrony with breathing; (4) AsyncObject: virtual object, asynchronous flashing. Each condition consisted in 60 s of visual stimulation followed by a measurement of self-location or subjective responses.

2.3. Subjective responses

Subjective responses were assessed using questionnaires during an experimental section of four blocks, one for each condition in a random order. At the end of each experimental block, the participants answered 8 questions (in random order, according to a 7-point Likert scale from $-3 =$ totally disagree to $+3 =$ totally agree), derived from questionnaires previously used during visuo-tactile and cardio-visual experiments (Aspell et al., 2013; Lenggenhager et al., 2007). Question 1 pertained to perceived location of breathing (Q1, Table 1). Question 2 pertained to awareness of the visuo-respiratory experimental manipulation (Q2, Table 1). Questions 3

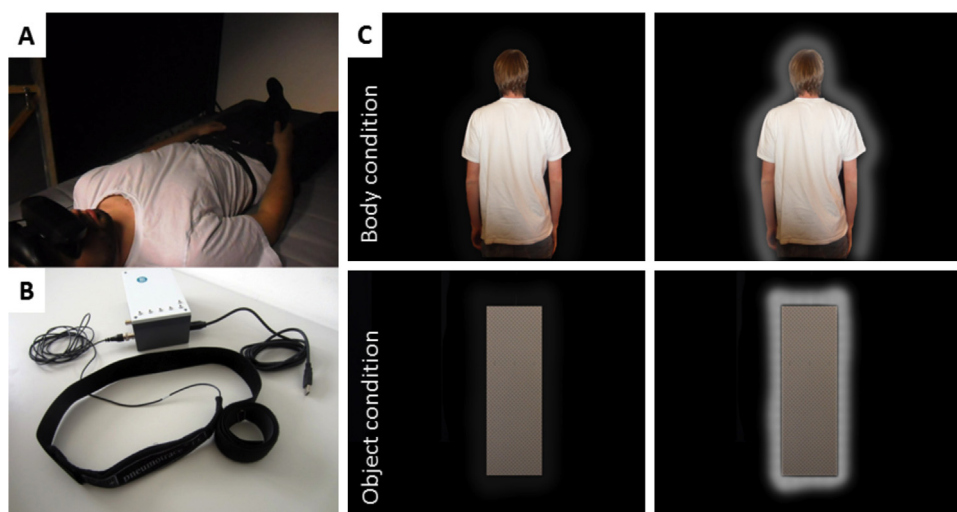


Fig. 1. Setup and equipment for the experiment. The subjects wearing head-mounted displays (A) and a linear transducer mounted on respiration belt (B). In the Body condition, participants were shown their own back illuminated synchronously (or asynchronously) with respect to their respiratory movements. In the Object condition, the video showed an illuminated human-sized square instead of the participant's back (C).

Table 1a
Answers to self-identification questionnaire for body condition.

		SyncBody median (IQR)	AsyncBody, median (IQR)	<i>p</i>
Q1	It seemed as if I was feeling my respiration in the virtual body	0 (-3; +2)	-3 (-3; -1)	0.008
Q2	It seemed as if the flashing was my respiration	+3 (+2; +3)	-3 (-3; +1)	0.0004
Q3	It seemed as if the virtual body was using my lungs to breathe	-1 (-3; +1)	-3 (-3; -3)	0.0088
Q4	I felt as if the virtual body was breathing with me	+2 (+1; +3)	-3 (-3; -2)	0.0006
Q5	I felt as if the virtual body was my body	-2 (-3; 0)	-3 (-3; 1)	0.9
Q6	I felt as if my real body was drifting towards the virtual body	-3 (-3; -2)	-3 (-3; -2)	0.56
Q7	I felt as if the virtual body was drifting towards my real body	-3 (-3; -2)	-3 (-3; -3)	0.79
Q8	It seemed as if I had two bodies	-3 (-3; -3)	-3 (-3; -2)	0.25

“-3” indicates total disagreement with the proposal whereas “+3” indicates total agreement. Results are expressed as median and interquartile ranges. *p* Value < 0.05 account for statistical difference between Sync and Async conditions using Wilcoxon matched pairs signed-rank test.

Table 1b
Answers to self-identification questionnaire for object condition.

		SyncObject, median (IQR)	AsyncObject median (IQR)	<i>p</i>
Q1	It seemed as if I was feeling my respiration in the virtual object	0 (-3; +1)	-3 (-3; -2)	0.013
Q2	It seemed as if the flashing was my respiration	+3 (+2; +3)	-3 (-3; -1)	0.0004
Q3	It seemed as if the object was using my lungs to breathe	-2 (-3; 0)	-3 (-3; -3)	0.04
Q4	I felt as if the object was breathing with me	+3 (+2; +3)	-3 (-3; -1)	0.0004
Q5	I felt as if the virtual object was my body	-3 (-3; -2)	-3 (-3; -3)	0.9
Q6	I felt as if my real body was drifting towards the virtual object	-3 (-3; -3)	-3 (-3; -3)	0.52
Q7	I felt as if the virtual object was drifting towards my real body	-3 (-3; -2)	-3 (-3; -1)	0.97
Q8	It seemed as if I had two bodies	-3 (-3; -3)	-3 (-3; -3)	0.6

“-3” indicates total disagreement with the proposal whereas “+3” indicates total agreement. Results are expressed as median and interquartile ranges. *p* Value < 0.05 account for statistical difference between Sync and Async conditions using Wilcoxon matched pairs signed-rank test.

and 4 pertained to breathing agency, namely the feeling of sensing one's breathing command and the sensation that the motor act of breathing was related to the virtual body or object (Q3, Q4, Table 1). Question 5 pertained to self-identification with the virtual body (Q5, Table 1). Questions 6 to 8 were intended as control.

2.4. Self-location

Self-location was assessed using the mental ball drop task (MBD) (Ionta et al., 2011; Pfeiffer et al., 2013). Each experimental condition

was tested 6 times in random order. At the end of each experimental block, the participants were asked to imagine dropping a ball from their dominant hand held at the level of their supine body. They pressed a button with their index finger when they imagined dropping the ball, held the button pressed during the imagined duration of ball dropping, and released the button when they imagined that the ball hit the floor. The response time (RT) from pressing the button to releasing it has been shown to be a sensitive marker of self-location above the floor (Lenggenhager et al., 2009): in full body illusion experiments where the subject is supine and the virtual

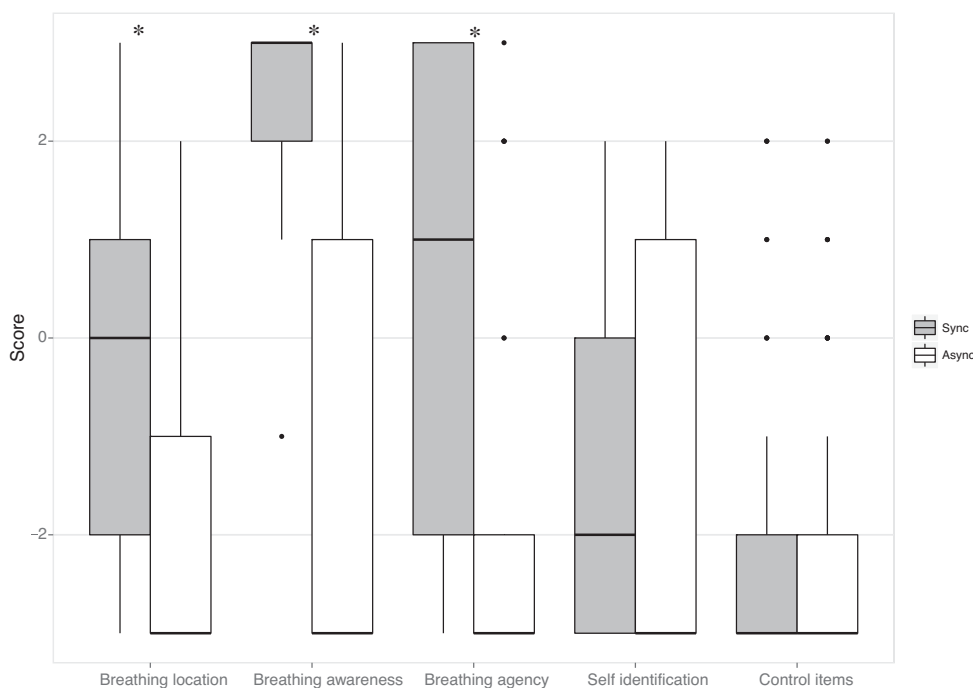


Fig. 2. Perceived location of breathing in the virtual body (Q1) and Breathing agency (Q3 and Q4) are stronger when the body outline is illuminated synchronously with respiratory movements. Synchronous illumination had no effect on illusory self-identification (Q5). Median, interquartile range and range are displayed for both illumination processes (sync/async) in the body condition. Asterisks indicate significant differences.

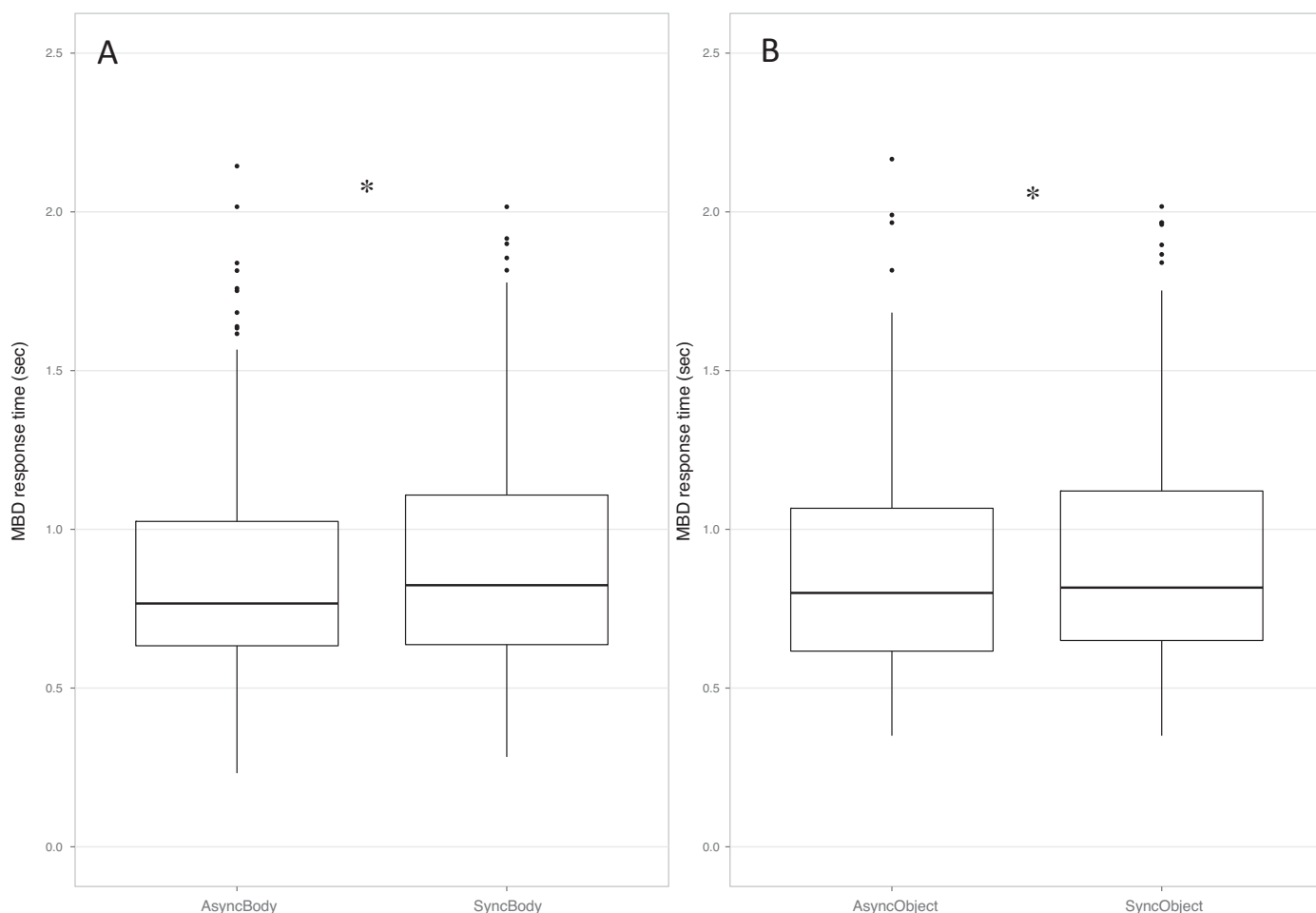


Fig. 3. Mental ball drop response time (RT) measured in seconds during synchronous and asynchronous illumination for body (panel A) and object (panel B) conditions. Participants showed a significantly stronger drift in self-location towards the virtual body/object with synchronous illumination. Asterisks indicate significant differences.

body/object is displayed above him/her, longer RTs are associated to drift towards the virtual body/object. Three repeated MBDs were performed for each condition. Of note, the participants performed a non-recorded training session comprising at least 20 trials before entering the experimental protocol itself.

2.5. Statistical analysis

Because of a skewed distribution, self-identification data are summarized by their median and interquartile range (IQR). MBD data were normally distributed and are summarized as mean \pm SD. The Wilcoxon matched-pairs signed-rank test was used to compare the effects of the Sync/Async conditions on items of the self-identification questionnaire under body and object conditions. A mixed effects linear model was used to analyse MBD-RT data, using three MBD-RT per subject and computing mean MBD-RT in each condition by taking into account the dependence of repeated data in the same subject. All analyses were performed with Stata 12.0 for Windows. Differences were considered significant for $p < 0.05$.

3. Results

3.1. Subjective responses (Table 1, Fig. 2)

The perceived location of breathing (Q1) was displaced towards the virtual body or object when they were illuminated

synchronously to breathing (SyncBody and SyncObject). This did not occur during AsyncBody and AsyncObject.

Visuo-respiratory inputs did not result in illusory self-identification with the virtual body or the virtual object, with consistently low scores for Q5 regardless of the condition.

In contrast, SyncBody and SyncObject induced the sensation that breathing agency was related to the virtual body/object (Q3 and Q4).

Of note, participants became aware of the visuo-respiratory manipulation (Q2) during SyncBody and SyncObject, but not during AsyncBody and AsyncObject.

There were no significant differences between conditions regarding the control questions Q6 to Q8.

3.2. Self-location (Fig. 3)

The mental ball drop task reaction times were significantly longer after SyncBody than after AsyncBody (+0.045 s, 95%CI [0.013; 0.08], $p = 0.007$), indicating a drift in self-location towards the virtual body (panel A). Similar findings were observed after SyncObject and AsyncObject (+0.037 s, 95%CI [0.007; 0.067], $p = 0.016$) (panel B). The subjective changes were therefore corroborated by behavioural measurement of self-location. Of note, mental ball drop task reaction times did not differ between body and object conditions within the same flashing conditions (SyncBody vs SyncObject, $p = 0.96$; AsyncObject vs AsyncBody, $p = 0.603$).

4. Discussion

This study provides arguments for a respiratory-related modulation of bodily self-consciousness. Indeed, visuo-respiratory synchronization caused the participants to perceive their breathing as displaced towards a virtual body or even a mere geometrical object. It also interfered with breathing agency.

4.1. Bodily self-consciousness during visuo-respiratory conflicts

First of all, synchronous visuo-respiratory stimulations induced cognitive awareness of respiration. Our subjects became aware of their breathing activity without having received any intrinsic respiratory stimulation, indicating that visual inputs are able to capture respiratory cues that are normally gated out and do not give rise to conscious perceptions. Cognitive awareness of respiration did not occur during asynchronous visuo-respiratory stimulations (which rules out a putative role of the abdominal belt used to monitor breathing as an “ungating” trigger, see Section 4.3). These observations resemble those made during cardio-visual experiments (Aspell et al., 2013).

In addition, synchronous visuo-respiratory stimulations also induced our subjects to “locate their breathing” somewhere between them and in the virtual body (or object) (Q3 and Q4). Mislocalization of a stimulus or of a sensation has previously been reported after visuo-tactile synchronization (Botvinick and Cohen, 1998; Ehrsson, 2007; Lenggenhager et al., 2007; Sforza et al., 2010) and cardio-visual synchronization (Aspell et al., 2013). In our subjects, the subjective modification of the perceived location of breathing was corroborated by a lengthening of the mental ball drop test reaction time, indicative of a “behavioural drift” in self-location towards the virtual body or object. These observations provide strong support to our working hypothesis that breathing contributes to bodily self-consciousness. They also support current proposals that exteroceptive (Blanke et al., 2004; Blanke and Metzinger, 2009) and interoceptive signals (Craig, 2002; Damasio, 2000; Tsakiris et al., 2011) are both important for representation of self in the brain.

The subjective and behavioural changes observed in our subjects were synchrony-dependent, but were similar in the “body” and “object” conditions. Body-specificity has been a frequent finding of previous studies using exteroceptive conflicts although not a consistent finding (Hansel et al., 2011; Ionta et al., 2011; Lenggenhager et al., 2007). Body specificity lacked in cardio-visual experiments (Aspell et al., 2013). Our findings with respiration strengthen the notion that the modulation of bodily self-consciousness induced by visuo-interoceptive conflicts is not, or less, body-specific than the corresponding modulation induced by visuo-tactile conflicts.

4.2. Body ownership, agency, and breathing

Visuo-respiratory stimulations did not increase levels of body ownership in our subjects: they answered Q5 (“I felt as if the virtual body was my body”) with very low ratings and did so consistently across conditions (Table 1). This contrasts with visuotactile experiments (Botvinick and Cohen, 1998; Ehrsson, 2007; Lenggenhager et al., 2007; Sforza et al., 2010) and cardio-visual experiments (Aspell et al., 2013). However, our subjects described a synchrony-dependent modulation of the feeling that the motor act of breathing was related to the virtual body (Q3 and Q4). Previous work on the sense of agency has revealed that sensorimotor conflicts between motor signals and their sensory feedback (vision, auditory, tactile) are of key relevance for experimental manipulations of agency for movements of hands (Franck et al., 2001; Frith, 2005), or whole bodies (Kannape and Blanke, 2013; Kannape et al., 2010). The ribcage and respiratory muscle

somatosensory systems have the general features of the skeletal locomotor system. The synchrony-dependent changes in breathing agency that we observed could therefore relate to sensorimotor conflicts induced by visuo-respiratory manipulation. It could also relate to the involvement of respiratory-related cortical networks during the experiments. Indeed, in contrast to cardiac control that is purely neurovegetative, breathing control has both vegetative and behavioural determinants. Several cortical networks allow for voluntary breathing (Gandevia et al., 1990; Gandevia and Rothwell, 1987; Macefield and Gandevia, 1991; Similowski et al., 1996) and other non-homeostatic disruptions of ventilation such as speech production (Loucks et al., 2007; Murphy et al., 1997), and are engaged during inspiratory load compensation (Raux et al., 2007). In our subjects, it could thus be hypothesized that visuo-respiratory stimulation, by ungating respiratory sensations, resulted in a cortical motor response and the corresponding perception. This would be similar to the description of a respiratory-related cortical activity occurring during normal, unloaded breathing in certain healthy subjects participating to inspiratory loading experiments (Raux et al., 2007; Tremoureaux et al., 2014). This phenomenon has been interpreted as the result of respiratory ungating following the mere institution of breathing measurements.

4.3. Ungating

During quiet breathing in healthy individuals, a refined sensorimotor network permanently monitors the state of the respiratory system, but this information is gated out and quiet breathing normally does not give rise to any conscious perception (Chan and Davenport, 2008; Davenport et al., 2007; Davenport and Vovk, 2009). Increases in respiratory-related afferent traffic above the gating threshold generate respiratory sensations. The gating threshold can also be manipulated irrespective of physiological changes. For example, respiratory ungating can be easily induced by asking a subject to concentrate on breathing. It can also be induced by changes in the external environment with which breathing is intimately connected (e.g. air temperature, odours), or emotional state (Chan et al., 2012). It could be argued that our subjects wore a thoracic device and were exposed to experimental conditions that might have induced some degree of stress, which may have interfered with their perception of breathing and biased our results. However, the effects of synchronous visuo-respiratory stimulations that we observed lacked during asynchronous visuo-respiratory stimulation. We therefore posit that, in addition to unveiling the role of breathing in bodily self-consciousness, our data seemingly provide the first experimental documentation of respiratory ungating obtained independently of any change in respiratory mechanics or blood gases, without asking the subjects to consciously attend to their breathing, and without purposely manipulating their emotional state.

4.4. Perspectives and conclusions

We believe that our observations open new avenues to the understanding of the pathophysiology of dyspnoea. Indeed, dyspnoea is currently considered to occur when the perception of respiratory signals (by definition “ungated” and giving rise to “somatic awareness”) generates negative emotions (“affective awareness”) (Parshall et al., 2012). From a therapeutic point of view, dyspnea can be alleviated by interventions that reduce the intensity of a respiratory stimulus (e.g. bronchodilators reducing dynamic hyperinflation in chronic obstructive pulmonary disease). It can also be alleviated by pharmacological and nonpharmacological interventions targeting its affective dimension (Banzett et al., 2011; Donesky et al., 2014; von Leupoldt et al., 2010; Wadell et al., 2013) and by attention diverting strategies (Thornby

et al., 1995; von Leupoldt et al., 2007). A third approach to alleviate dyspnoea is to “fool the brain” about the respiratory sensorimotor balance, for example by generating “pseudo-respiratory” stimuli (e.g. trigeminal stimulation or furosemide inhalation) (Nishino et al., 2000; Schwartzstein et al., 1987). Whether or not virtual reality and visuo-respiratory paradigms will provide useful adjuncts to this arsenal of dyspnea-modulating interventions will have to be determined by future studies. It has already been demonstrated that experimental modulation of bodily self-consciousness interferes with tactile perception and pain processing (Aspell et al., 2009; Hansel et al., 2011; Romano et al., 2014). These effects have been associated with increased brain activity in the temporoparietal cortex, the insula and the premotor and posterior parietal cortex (Ionta et al., 2011; Petkova et al., 2011), all brain areas that are known to be involved, to various extents, in the pathophysiology of dyspnea.

Funding

TS is supported by the program “Investissement d’Avenir ANR-10-AIHU-06” of the French Government. OB is supported by the Bertarelli Foundation and the Swiss National Science Foundation. The funding sources had no role in study design; in the collection, analysis and interpretation of data; in the writing of the report; and in the decision to submit the article for publication. This study does not involve any conflict of interest, financial or otherwise.

Acknowledgements

The authors thank Lionel Renaud and Audrey Schenker for their valuable contribution during the experimental work. They would also like to acknowledge the assistance of Angèle Gayet-Ageron and Elise Dupuis-Lozeron with data analysis as well as Anthony Saul for help with English style and grammar.

References

- Aspell, J.E., Heydrich, L., Blanke, O., 2013. Turning body and self inside out: visualized heartbeats alter bodily self-consciousness and tactile perception. *Psychol. Sci.* 24, 2445–2453.
- Aspell, J.E., Lenggenhager, B., Blanke, O., 2009. Keeping in touch with one's self: multisensory mechanisms of self-consciousness. *PLoS One* 4, e6488.
- Banzett, R.B., Adams, L., O'Donnell, C.R., Gilman, S.A., Lansing, R.W., Schwartzstein, R.M., 2011. Using laboratory models to test treatment: morphine reduces dyspnea and hypercapnic ventilatory response. *Am. J. Respir. Crit. Care Med.* 184, 920–927.
- Banzett, R.B., Mulnier, H.E., Murphy, K., Rosen, S.D., Wise, R.J., Adams, L., 2000. Breathlessness in humans activates insular cortex. *NeuroReport* 11, 2117–2120.
- Blanke, O., 2012. Multisensory brain mechanisms of bodily self-consciousness. *Nat. Rev. Neurosci.* 13, 556–571.
- Blanke, O., Landis, T., Spinelli, L., Seeck, M., 2004. Out-of-body experience and autoscopia of neurological origin. *Brain* 127, 243–258.
- Blanke, O., Metzinger, T., 2009. Full-body illusions and minimal phenomenal selfhood. *Trends Cogn. Sci.* 13, 7–13.
- Botvinick, M., Cohen, J., 1998. Rubber hands ‘feel’ touch that eyes see. *Nature* 391, 756.
- Chan, P.Y., Davenport, P.W., 2008. Respiratory-related evoked potential measures of respiratory sensory gating. *J. Appl. Physiol.* 105, 1106–1113.
- Chan, P.Y., von Leupoldt, A., Bradley, M.M., Lang, P.J., Davenport, P.W., 2012. The effect of anxiety on respiratory sensory gating measured by respiratory-related evoked potentials. *Biol. Psychol.* 91, 185–189.
- Craig, A.D., 2002. How do you feel? Interoception: the sense of the physiological condition of the body. *Nat. Rev. Neurosci.* 3, 655–666.
- Craig, A.D., 2003. Interoception: the sense of the physiological condition of the body. *Curr. Opin. Neurobiol.* 13, 500–505.
- Critchley, H.D., Wiens, S., Rotshtein, P., Ohman, A., Dolan, R.J., 2004. Neural systems supporting interoceptive awareness. *Nat. Neurosci.* 7, 189–195.
- Damasio, A., 1999. *The Feeling of What Happens*. Random House, London.
- Damasio, A.R., 2000. *The Feeling of What Happens: Body and Emotion in the Making of Consciousness*. Harcourt Brace, New York, NY.
- Davenport, P.W., Chan, P.Y., Zhang, W., Chou, Y.L., 2007. Detection threshold for inspiratory resistive loads and respiratory-related evoked potentials. *J. Appl. Physiol.* 102, 276–285.
- Davenport, P.W., Vovk, A., 2009. Cortical and subcortical central neural pathways in respiratory sensations. *Respir. Physiol. Neurobiol.* 167, 72–86.
- Donesky, D., Nguyen, H.Q., Paul, S.M., Carrieri-Kohlman, V., 2014. The affective dimension of dyspnea improves in a dyspnea self-management program with exercise training. *J. Pain Symptom Manage.* 47, 757–771.
- Ehrsson, H.H., 2007. The experimental induction of out-of-body experiences. *Science* 317, 1048.
- Evans, K.C., Banzett, R.B., Adams, L., McKay, L., Frackowiak, R.S., Corfield, D.R., 2002. BOLD fMRI identifies limbic, paralimbic, and cerebellar activation during air hunger. *J. Neurophysiol.* 88, 1500–1511.
- Fourneret, P., Jeannerod, M., 1998. Limited conscious monitoring of motor performance in normal subjects. *Neuropsychologia* 36, 1133–1140.
- Franck, N., Farrer, C., Georgieff, N., Marie-Cardine, M., Dalery, J., d'Amato, T., Jeannerod, M., 2001. Defective recognition of one's own actions in patients with schizophrenia. *Am. J. Psychiatry* 158, 454–459.
- Frith, C., 2005. The self in action: lessons from delusions of control. *Conscious Cogn.* 14, 752–770.
- Gandevia, S.C., McKenzie, D.K., Plassman, B.L., 1990. Activation of human respiratory muscles during different voluntary manoeuvres. *J. Physiol.* 428, 387–403.
- Gandevia, S.C., Rothwell, J.C., 1987. Activation of the human diaphragm from the motor cortex. *J. Physiol.* 384, 109–118.
- Hansel, A., Lenggenhager, B., von Kanel, R., Curatolo, M., Blanke, O., 2011. Seeing and identifying with a virtual body decreases pain perception. *Eur. J. Pain* 15, 874–879.
- Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., Gassert, R., Blanke, O., 2011. Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron* 70, 363–374.
- Jeannerod, M., 2006. The origin of voluntary action: history of a physiological concept. *C. R. Biol.* 329, 354–362.
- Kannape, O.A., Blanke, O., 2013. Self in motion: sensorimotor and cognitive mechanisms in gait agency. *J. Neurophysiol.* 110, 1837–1847.
- Kannape, O.A., Schwabe, L., Tadi, T., Blanke, O., 2010. The limits of agency in walking humans. *Neuropsychologia* 48, 1628–1636.
- Lenggenhager, B., Mouthon, M., Blanke, O., 2009. Spatial aspects of bodily self-consciousness. *Conscious Cogn.* 18, 110–117.
- Lenggenhager, B., Tadi, T., Metzinger, T., Blanke, O., 2007. Video ergo sum: manipulating bodily self-consciousness. *Science* 317, 1096–1099.
- Loucks, T.M., Poletto, C.J., Simonyan, K., Reynolds, C.L., Ludlow, C.L., 2007. Human brain activation during phonation and exhalation: common volitional control for two upper airway functions. *NeuroImage* 36, 131–143.
- Macefield, G., Gandevia, S.C., 1991. The cortical drive to human respiratory muscles in the awake state assessed by premotor cerebral potentials. *J. Physiol.* 439, 545–558.
- Murphy, K., Corfield, D.R., Guz, A., Fink, G.R., Wise, R.J., Harrison, J., Adams, L., 1997. Cerebral areas associated with motor control of speech in humans. *J. Appl. Physiol.* 83, 1438–1447.
- Nishino, T., Ide, T., Sudo, T., Sato, J., 2000. Inhaled furosemide greatly alleviates the sensation of experimentally induced dyspnea. *Am. J. Respir. Crit. Care Med.* 161, 1963–1967.
- Parshall, M.B., Schwartzstein, R.M., Adams, L., Banzett, R.B., Manning, H.L., Bourbeau, J., Calverley, P.M., Gift, A.G., Harver, A., Lareau, S.C., Mahler, D.A., Meek, P.M., O'Donnell, D.E., 2012. An official American Thoracic Society statement: update on the mechanisms, assessment, and management of dyspnea. *Am. J. Respir. Crit. Care Med.* 185, 435–452.
- Peiffer, C., Poline, J.B., Thivard, L., Aubier, M., Samson, Y., 2001. Neural substrates for the perception of acutely induced dyspnea. *Am. J. Respir. Crit. Care Med.* 163, 951–957.
- Petkova, V.I., Bjornsdotter, M., Gentile, G., Jonsson, T., Li, T.Q., Ehrsson, H.H., 2011. From part- to whole-body ownership in the multisensory brain. *Curr. Biol.* 21, 1118–1122.
- Pfeiffer, C., Lopez, C., Schmutz, V., Duenas, J.A., Martuzzi, R., Blanke, O., 2013. Multisensory origin of the subjective first-person perspective: visual, tactile, and vestibular mechanisms. *PLoS One* 8, e61751.
- Raux, M., Straus, C., Redolfi, S., Morelot-Panzini, C., Couturier, A., Hug, F., Similowski, T., 2007. Electroencephalographic evidence for pre-motor cortex activation during inspiratory loading in humans. *J. Physiol.* 578, 569–578.
- Raux, M., Tyvaert, L., Ferreira, M., Kindler, F., Bardinet, E., Karachi, C., Morelot-Panzini, C., Gotman, J., Pike, G.B., Koski, L., Similowski, T., 2013. Functional magnetic resonance imaging suggests automatization of the cortical response to inspiratory threshold loading in humans. *Respir. Physiol. Neurobiol.* 189, 571–580.
- Richards Jr., D.W., 1953. The Lewis A. Conner memorial lecture, the nature of cardiac and of pulmonary dyspnea. *Circulation* 7, 15–29.
- Romano, D., Pfeiffer, C., Maravita, A., Blanke, O., 2014. Illusory self-identification with an avatar reduces arousal responses to painful stimuli. *Behav. Brain Res.* 261, 275–281.
- Schwartzstein, R.M., Lahive, K., Pope, A., Weinberger, S.E., Weiss, J.W., 1987. Cold facial stimulation reduces breathlessness induced in normal subjects. *Am. Rev. Respir. Dis.* 136, 58–61.
- Sforza, A., Bufalari, I., Haggard, P., Aglioti, S.M., 2010. My face in yours: visuo-tactile facial stimulation influences sense of identity. *Soc. Neurosci.* 5, 148–162.
- Similowski, T., Catala, M., Rancurel, G., Derenne, J.P., 1996. Impairment of central motor conduction to the diaphragm in stroke. *Am. J. Respir. Crit. Care Med.* 154, 436–441.
- Suzuki, K., Garfinkel, S.N., Critchley, H.D., Seth, A.K., 2013. Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubber-hand illusion. *Neuropsychologia* 51, 2909–2917.

- Thornby, M.A., Haas, F., Axen, K., 1995. [Effect of distractive auditory stimuli on exercise tolerance in patients with COPD.](#) *Chest* 107, 1213–1217.
- Tremoureux, L., Raux, M., Hudson, A.L., Ranohavimparany, A., Straus, C., Similowski, T., 2014. [Does the supplementary motor area keep patients with Ondine's curse syndrome breathing while awake?](#) *PLoS One* 9, e84534.
- Tsakiris, M., Tajadura-Jimenez, A., Costantini, M., 2011. [Just a heartbeat away from one's body: interoceptive sensitivity predicts malleability of body-representations.](#) *Proc. Biol. Sci.* 278, 2470–2476.
- von Leupoldt, A., Taube, K., Henkhus, M., Dahme, B., Magnussen, H., 2010. [The impact of affective states on the perception of dyspnea in patients with chronic obstructive pulmonary disease.](#) *Biol. Psychol.* 84, 129–134.
- von Leupoldt, A., Taube, K., Schubert-Heukeshoven, S., Magnussen, H., Dahme, B., 2007. [Distractive auditory stimuli reduce the unpleasantness of dyspnea during exercise in patients with COPD.](#) *Chest* 132, 1506–1512.
- Wadell, K., Webb, K.A., Preston, M.E., Amornputtisathaporn, N., Samis, L., Patelli, J., Guenette, J.A., O'Donnell, D.E., 2013. [Impact of pulmonary rehabilitation on the major dimensions of dyspnea in COPD.](#) *COPD* 10, 425–435.