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ORIGINAL ARTICLE

Breathing affects self-other voice discrimination in a bodily state associated with somatic passivity

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Abstract

A growing number of studies have focused on identifying cognitive processes that are modulated by interoceptive signals, particularly in relation to the respiratory or cardiac cycle. Considering the fundamental role of interoception in bodily self-consciousness, we here investigated whether interoceptive signals also impact self-voice perception. We applied an interactive, robotic paradigm associated with somatic passivity (a bodily state characterized by illusory misattribution of self-generated touches to someone else) to investigate whether somatic passivity impacts self-voice perception as a function of concurrent interoceptive signals. Participants' breathing and heartbeat signals were recorded while they performed two self-voice tasks (self-other voice discrimination and loudness perception) and while simultaneously experiencing two robotic conditions (somatic passivity condition; control condition). Our data reveal that respiration, but not cardiac activity, affects self-voice perception: participants were better at discriminating self-voice from another person's voice during the inspiration phase of the respiration cycle. Moreover, breathing effects were prominent in participants experiencing somatic passivity and a different task with the same stimuli (i.e., judging the loudness and not identity of the voices) was unaffected by breathing. Combining interoception and voice perception with self-monitoring framework, these data extend findings on breathing-dependent changes in perception and cognition to self-related processing.

Nathan Faivre and Olaf Blanke contributed equally to this study.

1 | INTRODUCTION

Interoception refers to the processing of afferent sensory signals originating from the inside of the body, such as signals from the heart, lungs, or intestines. Although traditionally considered as mostly unconscious signals of the autonomic nervous system, recent research has shown that heartbeat and respiration signals can also affect many perceptual and cognitive processes. For instance, there is consistent evidence showing that external sensory stimuli (visual, tactile or auditory) are perceived differently when presented in different phases of the cardiac cycle (Birren et al., 1963; Motyka et al., 2019; Sandman et al., 1977). Cardiac phase dependency has also been observed for pain perception (Wilkinson et al., 2013) and emotional processing (Garfinkel et al., 2014), as well as cognitive functions such as memory (Pfeifer et al., 2017) or social cognition (Azevedo et al., 2017). By comparison, only few recent studies demonstrated respiratory phase dependency in emotion distinction and memory recall (Zelano et al., 2016), as well as visuospatial perception (Perl et al., 2019), and visual pattern recognition (Nakamura et al., 2018). Interestingly, all studies investigating the impact of respiration on cognitive functions reported enhanced performance during inspiration as compared to the expiration phase, arguably due to inspiration-driven neural synchronization of task-relevant cortical and subcortical regions (Heck et al., 2019; Perl et al., 2019; Zelano et al., 2016).

The impact of interoceptive processes on the perception of self-related stimuli (such as perception of one's own voice or face) has only rarely been investigated (Ambrosini et al., 2019). Accordingly, it is not known whether inspiration-enhanced performance extends to the perception of self-related stimuli (such as perception of one's own face or voice). Here, we investigated cardiac and respiratory phase dependency of self-voice perception. We recorded heartbeat and respiration signals of healthy participants performing two self-related auditory tasks (self-other voice discrimination; loudness judgment) (Iannotti et al., 2021; Orepic et al., 2021). We investigated whether self-voice perception would differ in trials occurring during different phases of respiratory (inspiration, expiration) and heartbeat (systole, diastole) cycles. Following previously reported breathing effects on cognition (Nakamura et al., 2018; Perl et al., 2019; Zelano et al., 2016) and heartbeat effects on self-face perception (Ambrosini et al., 2019), we predicted better performance in auditory tasks during inspiration and during systole.

The processing of interoceptive signals is also relevant for bodily self-consciousness (BSC) (Blanke et al., 2015; Park & Blanke, 2019a, 2019b), a low-level perceptual account of self-consciousness based on the integrated processing of multisensory, sensorimotor, and interoceptive bodily signals. Key components of BSC are self-identification, self-location, first-person perspective (Blanke et al., 2015; Blanke & Metzinger, 2009). Experimental evidence has demonstrated that exposure to conflicting interoceptive and exteroceptive signals (afferent sensory signals encompassing vision, audition, somatosensation, gustation and olfaction) can lead to altered states of BSC (Adler et al., 2014; Aspell et al., 2013; Suzuki et al., 2013). Alterations of BSC have also been reported by using a robotic device (Hara et al., 2011), which creates sensorimotor conflicts between a participant's upper limb movements and touch sensations on the back. Namely, poking movements performed with the front part of the robotic device (placed in front of participants) are replicated by the back part of the device (Figure 1), resulting in the corresponding tactile stimuli on participants' back (synchronous stimulation). Moreover, adding a temporal delay between the participants' movements and the tactile stimulation delivered on the back (asynchronous stimulation) induces an alteration of BSC characterized by differences in self-location (Blanke et al., 2014) and in self-monitoring (Faivre et al., 2020). Importantly, these and related stimulations also induce the feeling that another person is in the room (Bernasconi et al., 2021; Blanke et al., 2014; Salomon et al., 2020; Serino et al., 2021), a loss of self-agency (Sato & Yasuda, 2005; Tsakiris et al., 2005), and somatic passivity (i.e., the impression that someone else is applying tactile sensations on our body), compatible with an altered state of BSC, characterized by misperceiving self as other (Blanke et al., 2014; Salomon et al., 2020). Based on our previous findings (Blanke et al., 2014; Salomon et al., 2020), here we also investigated whether conflicting sensorimotor stimulation (able to induce systematic changes in conscious self-other experience) would additionally modulate potential interoceptive effects on self-other voice discrimination. Extending our previous findings that have linked BSC with self-voice perception (Orepic et al., 2021) we here reanalyzed the latter data in the light of two physiological signals (respiration and heartbeat).

2 | METHOD

2.1 | Participants

The study involved 30 right-handed participants (9 male, mean age ± *SD*: 21.8 ± 2.4 years old), chosen from the general population, fluent in French and naïve to the purpose of the study. All participants reported no hearing deficits and no history of psychiatric or neurological disorders. Participants gave informed consent in accordance with institutional guidelines (protocol 2015–00092, approved by the Comité Cantonal d'Ethique de la Recherche of Geneva)

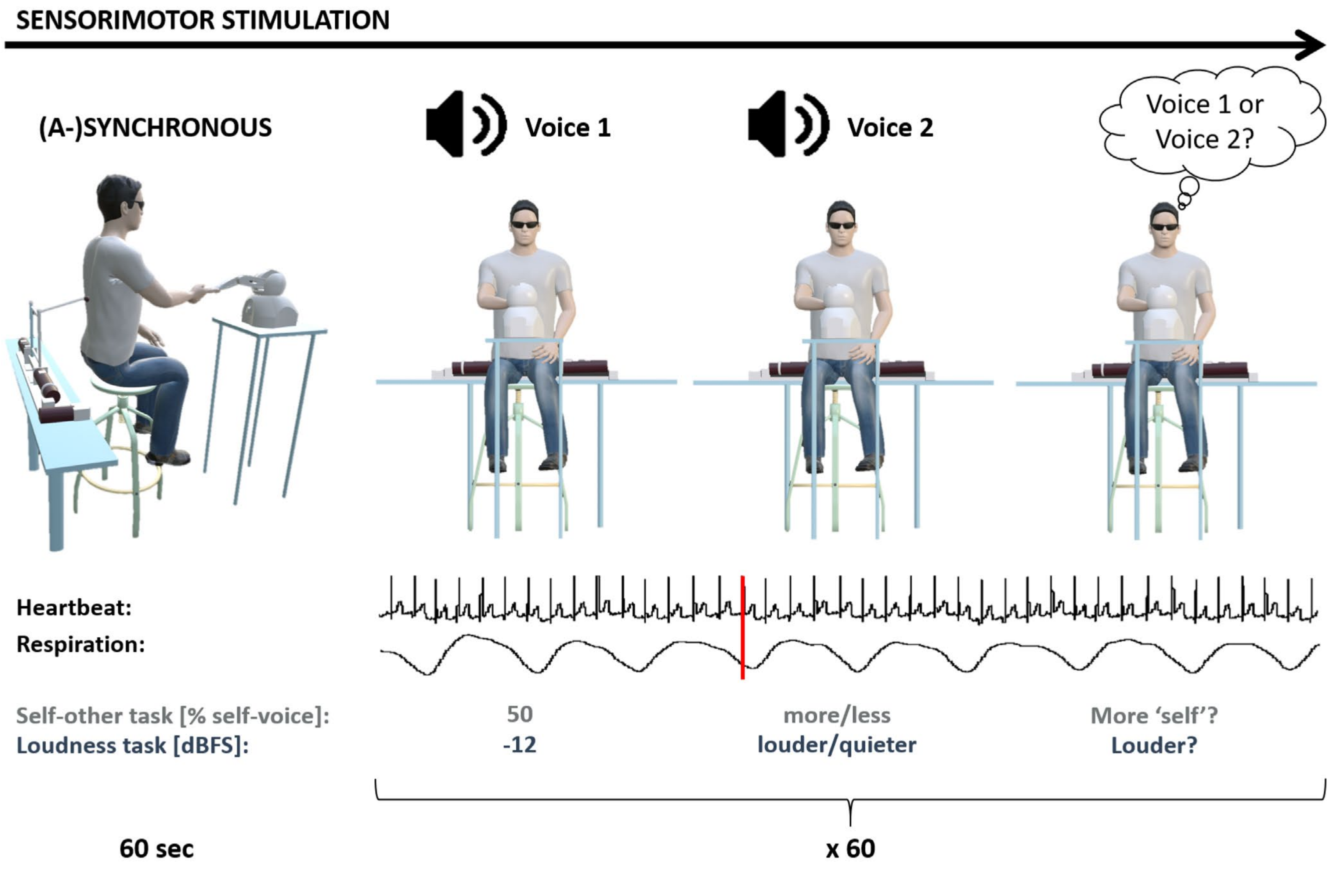

FIGURE 1 Experimental block design. Heartbeat and respiration signals were continuously recorded during sensorimotor stimulation and auditory tasks (see main text for description). The cardiac and respiratory phase was extracted at the onset of the second vocal stimulus (red line). Adapted from (Orepic et al., 2021)

and the Declaration of Helsinki, and received monetary compensation (CHF 20/h). Two participants were excluded from the analysis due to noisy ECG and respiration signals. The analysis reported here was done on the sample from experiment 1 of our previous study (Orepic et al., 2021).

2.2 | Auditory tasks

Pairs of gender-matched acquaintances participated in this study. Participants' voices were recorded while saying 10 words in French (Zoom H6 Handy recorder; see Supporting Information for an overview). Background noise removal and normalization of the recordings for average intensity (−12 dBFS) and duration (500 milliseconds) was done in Audacity software. These recordings were used to generate voice morphs spanning a voice identity continuum between two participants (acquaintances) by using TANDEM-STRAIGHT (Kawahara et al., 2013) (e.g., a voice morph can be generated such that it contains 30% of person A's, 70% of person B's voice). Finally, the generated voice morphs were recreated six times, such that each copy contained different sound intensity. Participants heard the recordings through a speaker (JBL Control 1 Pro) placed 1 meter behind them. The experimental design was created in MATLAB 2017b with Psychtoolbox library (Kleiner et al., 2007). The other voice was the voice of an acquaintance. This was done in order to ascertain that the participants were familiar with both tested voices (i.e., contrasting self-voice to the voice of an unfamiliar other would potentially indicate a familiarity effect (Stevenage, 2018), similar to self-face and biological motion research (Alzueta et al., 2019; Bortolon & Raffard, 2018; Loula et al., 2005). The level and the duration of acquaintance was not measured.

Participants performed two auditory tasks—self-other task and loudness task. During both tasks, blindfolded participants repeatedly heard the same word twice, while the first word in each word-pair always sounded the same (50% self-voice, −12 dBFS). In the self-other task, the second word was always equally loud as the first word (−12 dBFS), but varied in participants' self-voice percentage (% self-voice: 15, 30, 45, 55, 70, 85). In each trial, participants were instructed to indicate which of the two words sounded more like their own voice by clicking on a button. In the loudness task, the second word always contained the same ratio of the two voices (50% of both participants), but varied in sound intensity (dBFS: −14, −13, −12.5, −11.5, −11, −10). Accordingly, participants were instructed to choose the louder of the two words. Six sound intensity levels and six voice ratios were chosen based on extensive pilot testing.

2.3 | Robotic system

The robotic system consisted of two integrated units: the front part—a commercial haptic interface (Phantom Omni, SensAble Technologies)—and the back part—a three degree-of-freedom robot (Hara et al., 2011) (Figure 1). Participants were seated between the front and back robot and were asked to perform repeated poking movements with their right index finger using the front robot. Participants' pokes were replicated by the back robot, thus applying corresponding touches on participants' backs. The touches were mediated by the robot either in synchronous (without delay) or asynchronous (with 500 milliseconds delay) fashion, creating different degrees of sensorimotor conflict between the upper limb movement and somatosensory feedback on the back (Blanke et al., 2014; Faivre et al., 2020; Salomon et al., 2020). Participants carried out a familiarization session, after which they were asked to perform poking movements in any direction (touches could be applied on their backs in a region with a 200 mm × 250 mm surface).

2.4 | Experimental design

The study consisted of two experimental sessions. For the first session, participants came with an acquaintance (a friend), who also participated in the study. Both of them were screened for eligibility criteria, after which their voices were recorded. For the second session, each participant came individually and performed the auditory tasks. Respiration and heartbeat signals were recorded throughout the entire second session.

The second session comprised two blocks of each auditory task (loudness and self-other)—one block with the synchronous and another block with the asynchronous stimulation (Figure 1). The order of blocks (loudness synchronous, loudness asynchronous, self-other synchronous, self-other asynchronous) was counterbalanced across participants. Each block started with 60 s of robot manipulation, without auditory stimulation, after which an auditory cue indicated the beginning of the actual auditory task. Throughout the auditory tasks, participants continued moving the robot and auditory stimuli were not time-locked to participants' movements. Each block contained 60 randomly ordered trials (10 word pairs, each presented with 6 stimulus intensities). The words within a pair were separated by 500 milliseconds and an inter-trial interval of 1 to 1.5 s (randomly jittered) was added to avoid predictability of the stimuli.

At the end of the second session, participants performed two additional blocks (synchronous and asynchronous) in which they passively listened to the same voice morphs while manipulating the robot. Instead of performing an auditory task during these blocks, participants were asked to fill out a short questionnaire after each block (Likert scale from 0 (not at all) to 6 (very strong), adapted from Blanke et al., 2014) to assess illusory self-touch ("I felt as if I was touching my back by myself"), somatic passivity ("I felt as if someone else was touching my back") and the feeling of a presence ("I felt as if someone was standing close to me"). The questionnaire contained five additional items related to the perception of vocal stimuli, which are reported in the Supporting Information.

2.5 | Respiration and heartbeat

Respiration and heartbeat signals were collected using a respiration belt and bipolar ECG electrodes (Biopac MP36R system), respectively, at a sampling rate of 2000 Hz, following our previous work (Park et al., 2020). Respiration belt was placed about 5 cm below participants' armpits, whereas the bipolar electrodes were placed on the 2 clavicles and lower left rib. A trigger was sent at the onset of the second word in each word pair (Figure 1), in order to determine, for each trial, in which part of the heartbeat and respiration cycle the auditory stimulus occurred.

Cycle of the continuous respiration signal was divided into inspiration and expiration periods (Park et al., 2020). We first obtained signal phase values by applying Hilbert transform to the bandpass-filtered signal between 0.2 and 0.8 Hz. Phase values belonging to the interval $(-\pi, 0)$ were classified as expiration (54.1% trials), whereas those in the interval $(0, \pi)$ as inspiration (45.9% trials). Systole and diastole of a heartbeat signal were defined as parts of a heartbeat cycle with previously defined onsets and durations relative to R peak (Kunzendorf et al., 2019), specifically 65–329 ms for systole (36.5% trials), and 379–805 ms for the diastole (45% trials). Preprocessing of both physiological signals was conducted using the FieldTrip toolbox (Oostenveld et al., 2011).

2.6 | Statistical analysis

The effect of respiration on performance in both auditory tasks was analyzed with mixed-effects binomial regressions with Response as dependent variable and Respiration (inspiration, expiration), Condition (synchronous, asynchronous) and Stimulus (levels: 1–6), together with a three-way interaction, as fixed effects. The Response-variable indicates whether participants perceived a stimulus as sounding more like their own voice (self-other task) or as louder (loudness task) compared to the reference stimulus. Random effects included a by-subject random intercept. By-subject random slopes for the main effects were added following model selection based on maximum likelihood. Trials with reaction times greater or smaller than two interquartile ranges from the median for each subject were considered as outliers and excluded.

The same mixed-effects binomial regression was applied to investigate the effect of heartbeat on auditory task performance, except that instead of the Respiration variable, the model contained Heartbeat variable with two levels: systole and diastole. A linear mixed-effects regression with Reaction Times as a dependent variable and the same fixed and random effects was also performed for both auditory tasks (self-other, loudness) and both physiological signals (respiration, heartbeat). Additionally, all the mixed-effects regressions were performed time-locked to the button press (i.e., at reaction time), instead of the sound onset.

Following our previous work (Blanke et al., 2014; Faivre et al., 2020; Salomon et al., 2020; Serino et al., 2021), we also assessed the changes in the subjective experience evoked by the robotic stimulation—e.g., passivity and self-touch sensations measured by a Likert-scale. The effect of Condition (synchronous, asynchronous) on ratings in questionnaire items was assessed by one-tailed t-tests, as the direction of the effect has been previously established (Bernasconi et al. 2021; Blanke et al. 2014; Salomon et al. 2020; Serino et al., 2021). For the questionnaire items that significantly differed between the two sensorimotor conditions (synchronous, asynchronous) on the group level, we further created a variable (e.g., Passivity variable), indicating whether individual participants experienced the illusion assessed by the corresponding question. Thus, participants were divided in two groups—those with a positive asynchronous-synchronous rating difference (e.g., Passivity+) and those with a negative or zero difference (e.g., Passivity-). Such variables were added as an additional fixed factor in the mixed-effects logistic regression assessing auditory task performance. Therefore, these regressions contained dependent variable Response and fixed effects of Respiration (inspiration, expiration), Stimulus (levels 1–6) and Illusion (+, −). Having already established a link between the experimental manipulation and interoceptive signals in previous analyses, the purpose of this analysis was to extend those findings to the subjective experience related to the experimental manipulation.

Finally, to control for the effects of sensorimotor stimulation and the auditory tasks on the measured physiological signals, we computed each participant's respiration and heartbeat rate and rate variability and for all four parameters performed a two-way ANOVA with Condition (synchronous, asynchronous) and Task (self-other, loudness) as fixed effects with an interaction term and by-subject random effects. Heart rate variability was represented as root mean square of successive RR interval differences (RMSSD) (Shaffer & Ginsberg, 2017), and respiration rate variability as a coefficient of variation (CV) (Noto et al., 2018).

To investigate potential confounds due to gender (there were more female participants), we repeated the main mixed-effects regressions with an additional main effect of Gender. However, there was no effect of Gender nor an interaction with other main effects (Supporting Information) and no differences to the main results. Respiration parameters were computed using BreathMetrics (Noto et al., 2018) and heartbeat using BioSig (Schölgl et al., 2011) toolbox. Statistical tests were performed with R, using notably the lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2018), and afex (Singmann et al., 2019). The results were illustrated in R using sjplot (Lüdecke, 2018) and ggplot2 (Wickham, 2016) packages.

3 | RESULTS

3.1 | Respiratory phase

3.1.1 | Self-other discrimination

A mixed-effects binomial regression assessing the dependence of Response to the effects of Respiration, Condition and Stimulus in the self-other discrimination task revealed a main effect of Respiration (estimate $= -1.02$, $Z = -3.49$, $p < .001$), indicating a lower rate of 'self' response during inspiration, compared to expiration. We further observed a main effect of Stimulus (estimate $= 0.53$, $Z = 4.84$, $p < .001$), showing that 'self' responses were more frequent when voice-morphs contained more self-features. The effect of Respiration significantly interacted with the effect of Stimulus (estimate $= 0.24$, $Z = 3.17$, $p = .002$), revealing a steeper slope for the curve fitted for the inspiration phase. This indicates that participants were better in discriminating their own voice from another person's voice during inspiration compared to expiration (Figure 2). By fitting four-parameter psychometric curves, we additionally showed that respiration did not introduce a bias in self-other voice discrimination and did not significantly

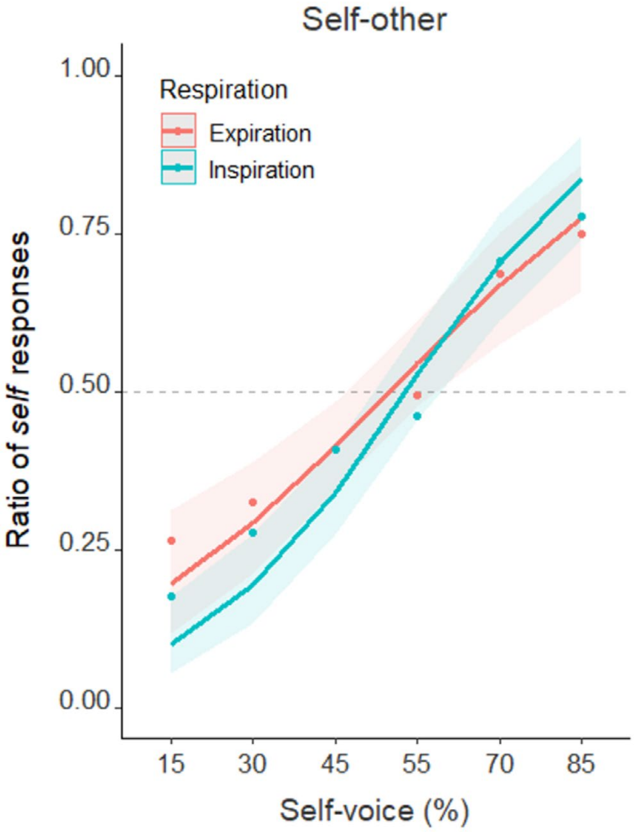

FIGURE 2 Psychometric curves fitted for two respiration phases (expiration, inspiration) during the self-other task. Six stimulus levels on the abscissa represent six self-voice ratios and the ordinate indicates the rate at which the corresponding stimulus level was perceived as more resembling the 'self' than the baseline (50% self-voice). The dots represent grand average response. The shaded areas around each curve represent the 95% confidence intervals. A steeper curve fitting the perception during inspiration indicates that participants were better at discriminating between their own and someone else's voice during inspiration compared to expiration periods. This was especially prominent for other-dominant voice morphs

improve recognition of self-dominant stimuli (Supporting Information).

The mixed-effects binomial regression also revealed a two-way interaction between the effects of Respiration and Condition (estimate = 0.89, $Z = 2.17$, $p = .03$) and a three-way interaction between the effects of Respiration, Condition and Stimulus (estimate = −0.21, $Z = -1.97$, $p = .048$). To further investigate the nature of these interactions, we performed separate mixed-effects logistic regression for the two levels of Condition (synchronous and asynchronous). For the dataset containing the asynchronous experimental blocks, the effect of Respiration was significant (estimate = −0.98, $Z = -3.30$, $p < .001$) and it significantly interacted with the effect of Stimulus (estimate = 0.22, $Z = 2.92$, $p = .004$), again indicating a lower intercept and a steeper slope for the inspiration phase (Figure 3, left). On the contrary, such an effect of Respiration did not occur during synchronous sensorimotor stimulation (estimate = −0.08, $Z = -0.27$, $p = .79$) nor did it interact with the effect of Stimulus (estimate = 0.02, $Z = 0.22$, $p = .83$) (Figure 3, right). This analysis shows that the observed effects of the respiration on the self-other discrimination (Figure 2) were only found during asynchronous sensorimotor stimulation (Figure 3, left)—i.e., participants were better in discriminating their own from another person's voice during the asynchronous sensorimotor stimulation, but not during the synchronous stimulation. Equivalent models relying on the Bayesian framework revealed evidence in favor of the null hypothesis according to which breathing did not affect self-other discrimination in the synchronous condition (Bayes factor = 0.17, see Supporting Information).

3.1.2 | Bodily self-consciousness

As we reported previously (Orepic et al., 2021), the analysis of subjective ratings revealed that participants experienced stronger somatic passivity in the asynchronous (mean rating = 3.21, 95% CI = [2.34, 4.09]) versus synchronous (2.43, [1.57, 3.28]) condition (t[27] = 2.05, $p = .025$, Cohen's $d = 0.35$). Participants rated illusory self-touch significantly stronger in the synchronous (2.39, [1.58, 3.21]) versus asynchronous (1.39, [0.61, 2.18]) condition (t[27] = 2.58, $p = .008$, $d = 0.49$). There were no significant differences between conditions in other questionnaire items (all $p > .05$).

To further assess the relationship between the observed differences in subjective experience and in auditory perception, we ran the same mixed-effects logistic regression on self-other task performance with an additional binary independent variable reflecting whether participants experienced somatic passivity and self-touch (see Method). Thus, participants were divided in two groups—those with a positive asynchronous-synchronous rating difference (Passivity+, $N = 16$; Self-touch+, $N = 14$) and those with a negative or zero difference (Passivity-, $N = 12$; Self-touch-, $N = 14$). We observed a significant interaction between Passivity and Respiration (estimate = −1.08, $Z = -2.76$, $p = .006$) and a three-way interaction between Respiration, Stimulus and Passivity borderlined with significance (estimate = 0.17, $Z = 1.73$, $p = .084$; other details of the model in the Supporting Information). Investigation of these interactions revealed a steeper curve for the inspiration phase only in the Passivity+ group (Figure 4, left) (Respiration: estimate = −1.18, $Z = -4.15$, $p < .001$; Stimulus: estimate = 0.54, $Z = 3.94$, $p < .001$; Respiration-Stimulus

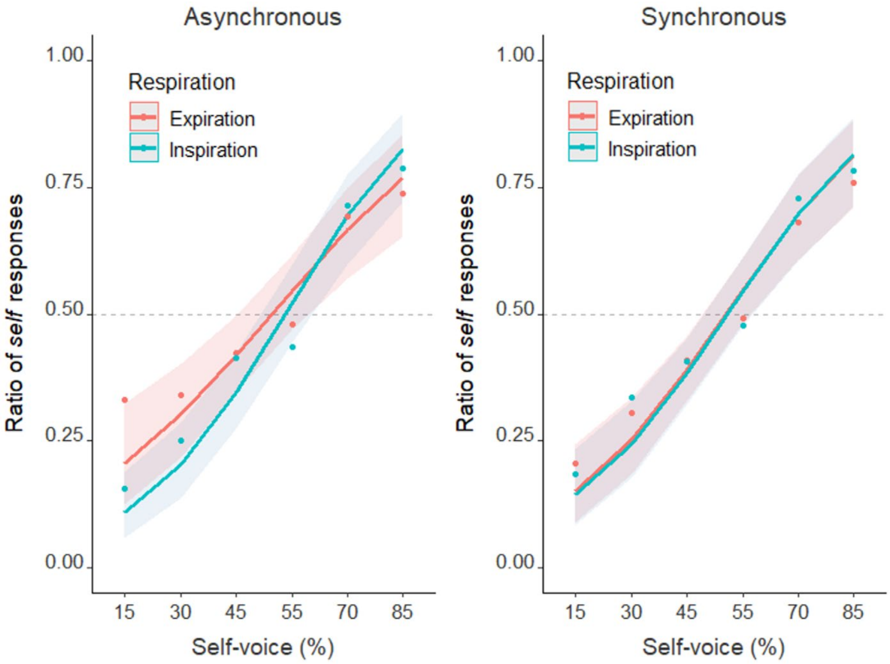

FIGURE 3 Psychometric curves fitted for respiration phases for the two sensorimotor conditions of the self-other task. Inspiration was advantageous for self-other voice discrimination only during the asynchronous stimulation

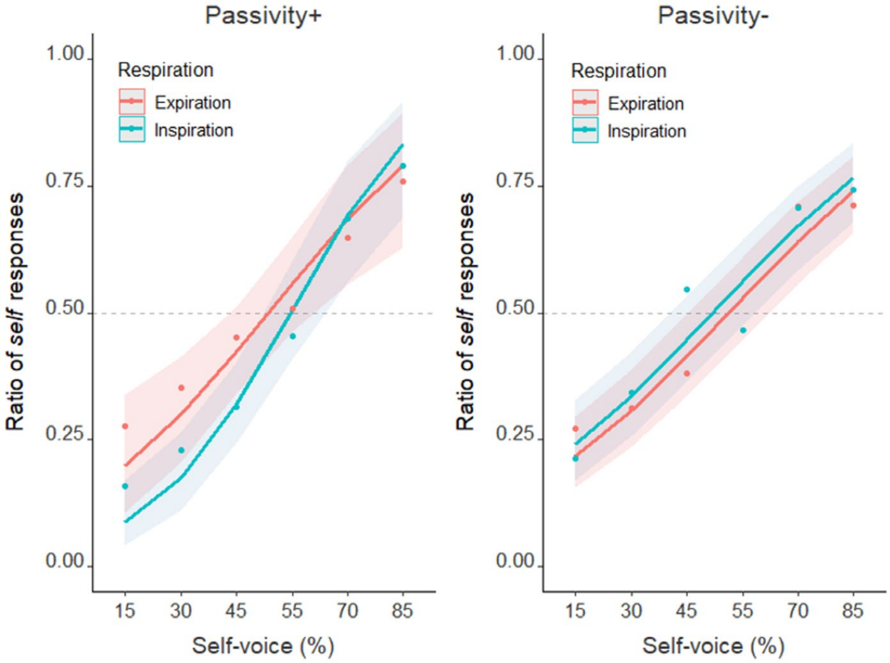

FIGURE 4 Only participants experiencing somatic passivity (Passivity+, left) were better in discriminating between self and other voices during inspiration compared to expiration. Respiration did not affect voice perception in the Passivity- group (right)

interaction: estimate = 0.24, $Z = 3.32$, $p < .001$). No such effects were found in the Passivity- group (Figure 4, right) (Respiration: estimate = 0.13, $Z = 0.46$, $p = .646$; Stimulus: estimate = 0.47, $Z = 9.65$, $p < .001$; Respiration-Stimulus interaction: estimate = 0, $Z = 0.02$, $p = .984$). There were no significant interactions between Self-touch and Respiration (Supporting Information).

3.1.3 | Loudness perception

Mixed-effects binomial regression on loudness perception with Response as a dependent variable and Respiration, Condition and Stimulus as fixed effects revealed only a main effect of Stimulus (estimate = 0.56, $Z = 11.73$, $p < .001$). Respiration did not affect loudness judgment (estimate = 0.07, Z = 0.28, p = .780), nor did it interact with any of the other fixed effects (Condition: estimate = −0.25, Z = −0.68, p = .497; Stimulus: estimate = 0, Z = 0.03, p = .977). There was no main effect of Condition (estimate = −0.19, Z = −0.74, p = .460), no two-way interaction between Condition and Stimulus (estimate = 0.07, Z = 1.01, p = .310), nor a three-way interaction between Respiration, Condition and Stimulus (estimate = 0.02, Z = 0.22, p = .825). These results suggest that loudness judgment does not depend on the respiration phase (Figure 5). Equivalent Bayesian models revealed evidence in favor of the null hypothesis according to which breathing did not affect loudness judgments (BF = 0.15, see Supporting Information).

3.2 | Cardiac phase

Heartbeat phase did not affect task performance in either of the auditory tasks—there were no main effects of Heartbeat either on self-other (estimate = 0.26, Z = 0.79, p = .428), nor on loudness judgment (estimate = −0.27, Z = −0.92, p = .359). Both models indicated a main effect of Stimulus (self-other: estimate = 0.56, Z = 10.08, p < .001; loudness: estimate = 0.53, Z = 10.12, p < .001) and no effect of Condition (self-other: estimate = 0.21, Z = 0.69, p = .488; loudness: estimate = −0.49, Z = −1.73, p = .083). There were no significant interactions between the fixed effects in either task (for a detailed report see Supporting Information). Equivalent Bayesian models revealed evidence in favor of the null hypothesis according to which heartbeat did not affect self-other discrimination (BF = 0.17) nor loudness judgments (BF = 0.26, Supporting Information).

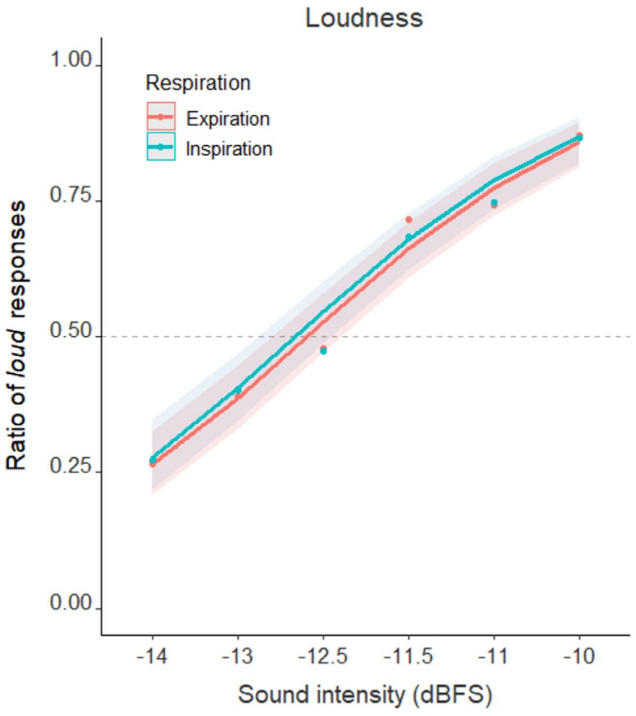

FIGURE 5 Psychometric curves fitted for two respiration phases (expiration, inspiration) during the loudness task. Six stimulus levels on the abscissa represent six sound intensity levels and the ordinate indicates the rate at which the corresponding stimulus level was perceived louder than the baseline (12 dBFS). The dots represent grand averages and the shaded areas around each curve represent the 95% confidence intervals. Respiration did not affect loudness judgment

3.3 | Reaction times

There were no significant effects of Respiration on reaction times in either auditory task (loudness: estimate = 0, t(105.1) = −0.2, p = .839; self-other: estimate = 0.01, t(3194) = 0.79, p = .432). Similarly, we observed no main effect of Hearbeat in either auditory task (loudness: estimate = 0, t(2491) = −0.03, p = .976; self-other: estimate = 0.02, t(2423) = 0.92, p = .358). Finally, neither of the two effects (Respiration, Heartbeat) showed a significant interaction with other fixed effects (Supporting Information).

Similarly, mixed-effects binomial regressions assessing the dependence of Response to the effects of Respiration time-locked to the button press (i.e., reaction time) did not yield any significant results in either auditory task (Supporting Information). Thus, we observed a significant effect of Respiration (Figure 2) and a significant interaction between Respiration and Condition (Figure 3) only with the respiration signal time-locked to the sound onset (Figure 1) and not to the button press (i.e., reaction time).

3.4 | Physiological analysis

Neither robotic stimulation nor the auditory tasks modulated parameters of respiratory or cardiac physiological signals. ANOVA did not indicate significant differences between respiration rate during asynchronous (mean = 0.35 Hz, 95% CI [0.33, 0.37] Hz) and synchronous (0.35, [0.33, 0.37] Hz) conditions (F[1, 26] = 0.06, p = .813) and respiration rate also did not differ during loudness (0.35, [0.33, 0.37] Hz) and self-other (0.35, [0.33, 0.37] Hz) tasks (F[1, 26] = 0.12, p = .733). Similarly, respiration rate variability did not differ between these conditions (asynchronous (0.37, [0.31, 0.43] Hz) vs. synchronous (0.36, [0.30, 0.42] Hz) conditions (F[1, 26] = 0.21, p = .649); loudness (0.36, [0.30, 0.42] Hz) vs. self-other (0.37, [0.31, 0.44] Hz) tasks (F[1, 26] = 0, p = .964)). This was also found for heart rate (asynchronous (80.95, [77.36, 84.55] bpm) vs. synchronous (81.16, [77.81, 84.51] bpm) conditions (F[1, 26] = 0, $p = .945$); loudness (80.59, [77.20, 83.99] bpm) vs. self-other (81.53, [77.98, 85.07] bpm) tasks (F[1, 26] = 1.81, $p = .190$)) and heart rate variability (asynchronous (36.55, [30.53, 42.57] bpm) vs. synchronous (35.09, [28.44, 41.73] bpm) (F[1, 26] = 0.12, $p = .731$); loudness (36.18, [29.25, 43.12] bpm) vs. self-other: 35.43, [29.75, 41.11] bpm) (F[1, 26] = 0.13, $p = .717$)). Finally, there were no significant interactions between the effects of Condition and Task for any of the parameters (breathing rate: F(1, 26) = 0.62, $p = .437$; breathing rate variability: F(1, 26) = 0.02, $p = .894$; heart rate: F(1, 26) = 0, $p = .999$; heart rate variability: F(1, 26) = 0.22, $p = .645$).

4 | DISCUSSION

We report that participants were better in discriminating their own from someone else's voice during the inspiration phase compared to the expiration phase. Moreover, this inspiratory advantage for self-voice processing was stronger during the asynchronous sensorimotor stimulation and was thus more pronounced in the condition inducing illusory misattribution of self-generated sensations to someone else. Moreover, breathing did not affect auditory perception when participants made loudness judgments of the same self-related vocal stimuli and the cardiac phase did not modulate the performance in either of the two auditory tasks.

An advantage of inspiration over expiration in self-other discrimination has not been reported before and extends previous respiratory phase dependency data to self-related cognition. Thus, other cognitive processes have been shown to be improved during inspiration and included memory retrieval (Zelano et al., 2016), spatial perception (Perl et al., 2019), visual pattern recognition (Nakamura et al., 2018), and emotion discrimination (Zelano et al., 2016). It has been argued that the inspiratory phase of the respiratory cycle drives neural synchronization of cortical and sub-cortical regions, thereby affecting the corresponding task-related neural activations (Heck et al., 2019; Zelano et al., 2016). Based on differences in resting-state functional connectivity between inspiration and expiration phases, it has also been proposed that inspiration-driven patterns of neural activity may improve the processing of incoming stimuli (Perl et al., 2019). Our results associate breathing with self-related processing by demonstrating a solid inspiratory-phase advantage in self-voice perception. We observed that inspiration led to systematic sensitivity changes, without a perceptual bias, in self-other voice discrimination (i.e., steeper psychometric curve, Figure 2) and that these sensitivity changes were driven by differences in other-dominant voice morphs (left asymptote; Figure 2). We also note that the present effect on self-other voice discrimination was independent of more basic breathing parameters such as breathing rate and variability, which were equal in both auditory tasks.

Another important finding was that the improvement in self-other discrimination during inspiration was further modulated by changes related to online sensorimotor stimulation, and, in particular, to asynchronous sensorimotor stimulation. Thus, the observed increase in sensitivity for self-other discrimination during the inspiration phase (as indicated by a steeper psychometric curve) was only found during asynchronous sensorimotor stimulation. As this inspiration-dependent effect on self-voice perception was absent in the synchronous condition, the present data show that only the stronger sensorimotor conflict impacts the effect of the breathing cycle on self-other discrimination. Asynchronous stimulation contains a stronger sensorimotor conflict, as there is an additional temporal conflict between poking movements in the front and tactile sensations on participants' back, in addition to the spatial conflict, which is also present during synchronous stimulation. Such robotically-applied sensorimotor conflicts during asynchronous stimulation have been related to changes in BSC, especially to the feeling of a presence and to somatic passivity (Bernasconi et al., 2021; Blanke et al., 2014; Orepic et al., 2021; Salomon et al., 2020), and have also been shown to modulate source monitoring, characterized by perceiving own thoughts as generated by another person (Serino et al., 2021). In a final analysis we showed that the inspiration-driven advantage for self-other voice discrimination is not only dependent on asynchronous sensorimotor simulation, but also to the altered BSC state associated with it. This final analysis revealed that the inspiration-driven effect was observed only in the participants reporting somatic passivity—i.e., in those participants susceptible to misattributing self-generated tactile sensations to someone else. Therefore, the present breathing effect in self-other discrimination is not only associated with the online respiratory cycle and the sensorimotor state of the participant, but also to an alteration of BSC (i.e., somatic passivity). Interestingly, the advantage of inspiration in self-other voice discrimination was again most pronounced for other-dominant voice morphs, indicating that in an other-oriented BSC state (i.e., otherness associated during asynchronous stimulation with somatic passivity) participants were more sensitive to recognizing self-other morphs as another person (see (Serino et al., 2021) for a similar finding using another paradigm).

There are several methodological differences between the present study and previous work exploring the effect of breathing on cognitive functions. First, in our study we did not control whether our participants employed nasal or oral breathing. Even though in the literature some tasks were modulated by nasal breathing only (Arshamian et al., 2018; Zelano et al., 2016), there is evidence indicating that some cognitive and perceptual functions are modulated by respiratory phase independent of nasal airflow (Perl et al., 2019). It thus remains unclear whether nasal breathing is necessary to observe the present effects on self-voice perception. Secondly, in the study of Nakamura et al. (2018) the effect of respiration on the task performance was present when stimuli were phase-locked to respiration and disappeared with stimuli being randomly presented throughout the respiration cycle. In the present study, however, we observed a differential effect on self-voice perception without explicit phase-locking of the stimuli to the respiration signal. Our stimuli were randomly distributed throughout the respiration cycle, but divided based on the phase (inspiration, expiration) of the stimulus onset. Moreover, when stimuli were divided based on the phase of the button press (i.e., at the reaction time), the main effects disappeared. There were also no significant effects of breathing on reaction times. This suggests that breathing (and its relationship with sensorimotor processing) interacts with the perceptual (i.e., input) pathways, as opposed to the output pathways related to self-voice processing. Thirdly, the lack of an effect of the breathing cycle on loudness perception in the present study might be due to the fact that it is not an explicitly self-related task. It is also possible that loudness perception simply does not depend on perceptual changes related to the inspiration versus expiration phase. Similarly, Perl et al. (2019) did not observe respiratory modulation of performance during a lexical decision task, as they did for a visuospatial perception task (neither of the two was self-related). Further behavioral and neuroimaging investigations are needed to unveil the impact of these parameters (e.g., mouth-vs-nasal breathing, stimulus phase-locking) on breathing-dependent self-processing as well as to identify the underlying mechanisms mediating the observed effects (e.g., synchronization of neuronal activity or changes in brain connectivity in self-processing networks).

One could have also expected that self-voice perception would be improved during the expiration phase, as, under natural conditions, we only hear our voice when we speak, i.e., when we exhale. It is possible that an experimental paradigm involving an active self-voice perception task (i.e., involving speaking), as opposed to a passive task (listening) would yield different results than observed here (e.g., improved performance for the expiration phase for self-dominant voice stimuli). Such an effect would thus differ from passive effects in previous work relating respiration to cognitive processes (Heck et al., 2019; Perl et al., 2019; Zelano et al., 2016) and showing that the inspiratory phase is associated with enhancements in cognitive performance (and potentially related to neural synchronization of task-relevant networks). Finally, recent work has doubted the validity and reliability of some measures used in interoception research (see (Desmedt et al., 2018; Zamariola et al., 2018)), especially those assessing the capacity to perceive internal bodily states (e.g., heartbeat counting task). However, we did not use such measures and were primarily interested in the dependency of self-voice perception on the phase of interoceptive signals. Thus, our participants were not instructed to pay attention to the recorded respiratory or cardiac signals and we did not test interoceptive awareness, but investigated the performance in auditory voice perception tasks (Orepic et al., 2021) with respect to the cardiac and respiratory cycle.

To summarize, we demonstrate (1) a relationship between breathing and self-other voice discrimination, which is (2) dependent on sensorimotor integration and (3) related to feelings of otherness in the form of somatic passivity. From the two tested interoceptive functions, only the respiratory cycle, but not the cardiac cycle, affected self-voice perception. Breathing is fundamentally related to speech and voice production (thus to the sound of our own voice) (Von Euler, 2011) and with voluntary action (Park et al., 2020). We argue that the present findings about the coupling between inspiration and self-other voice discrimination may reflect that voice perception and the voluntary action of speaking are coupled with the basic physiological function of breathing, which are absent (or less pronounced) for cardiac physiology. We also did not observe cardiac-dependent differences in reaction times as it has been reported for self-face perception (Ambrosini et al., 2019), arguing that different physiological signals (e.g., respiration and heartbeat) might affect self-related processes differently, depending on their intrinsic cyclic differences, their specific functional associations, and likely the investigated sensory modality.

CONFLICT OF INTEREST

O.B. and G.R. are inventors on patent US 10,286,555 B2 (Title: Robot-controlled induction of the feeling of a presence) held by the École Polytechnique Fédérale de Lausanne (EPFL) that covers the robot-controlled induction of the presence hallucination (PH). O.B. and G.R. are inventors on patent US 10,349,899 B2 (Title: System and method for predicting hallucinations) held by the École Polytechnique Fédérale de Lausanne (EPFL) that covers a robotic system for the prediction of hallucinations for diagnostic and therapeutic purposes. O.B. and G.R. are cofounders, board members and shareholders of Metaphysiks Engineering SA, a company that develops immersive technologies, including applications of the robotic induction of PHs that are not related to the diagnosis, prognosis, or treatment in medicine. O.B. is member of the board and shareholder of Mindmaze SA.

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AUTHOR CONTRIBUTIONS

Pavo Orepic: Conceptualization; data curation; formal analysis; investigation; methodology; software; validation; visualization; writing – original draft. **Hyeong-Dong Park:** Investigation; methodology; writing – original draft. **Giulio Rognini:** Conceptualization; methodology; project administration. **Nathan Faivre:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; software; supervision; validation; writing – original draft. **Olaf Blanke:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing – original draft.

DATA AVAILABILITY STATEMENT

Anonymized data and analysis scripts are available on the open science frameworkAUTHOR: Please check all website addresses and the functionality of the underlying links and confirm that they are correct. (Please note that it is the responsibility of the author(s) to ensure that all URLs given in this article are correct and usable.) (https://osf.io/kvqrn/).

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