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Inhalation boosts perceptual awareness and decision speed

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Abstract

The emergence of consciousness is one of biology's biggest mysteries. During the past two decades, a major effort has been made to identify the neural correlates of consciousness, but in comparison, little is known about the physiological mechanisms underlying first-person subjective experience. Attention is considered the gateway of information to consciousness. Recent work suggests that the breathing phase (i.e., inhalation vs. exhalation) modulates attention, in such a way that attention directed toward exteroceptive information would increase during inhalation. One key hypothesis emerging from this work is that inhalation would improve perceptual awareness and near-threshold decision-making. The present study directly tested this hypothesis. We recorded the breathing rhythms of 30 humans performing a near-threshold decision-making task, in which they had to decide whether a liminal Gabor was tilted to the right or the left (objective decision task) and then to rate their perceptual awareness of the Gabor orientation (subjective decision task). In line with our hypothesis, the data revealed that, relative to exhalation, inhalation improves perceptual awareness and speeds up objective decision-making, without impairing accuracy. Overall, the present study builds on timely questions regarding the physiological mechanisms underlying consciousness and shows that breathing shapes the emergence of subjective experience and decision-making.

NEW & NOTEWORTHY Breathing is a ubiquitous biological rhythm in animal life. However, little is known about its effect on consciousness and decision-making. Here, we measured the respiratory rhythm of humans performing a near-threshold discrimination experiment. We show that inhalation, compared with exhalation, improves perceptual awareness and accelerates decision-making while leaving accuracy unaffected.

attention; consciousness; decision-making; respiration

INTRODUCTION

Understanding the neural and physiological mechanisms underlying consciousness is an intricate challenge for cognitive scientists. Although much research has focused on the neural correlates of consciousness (1), less is known about the influence of key physiological rhythms, such as breathing, on the emergence of subjective experience, and near-threshold decision-making. Given the ubiquity of breathing in the animal realm, and its disruption in major human diseases such as asthma or chronic

obstructive pulmonary disease, extensive research is now required to understand its influence on consciousness.

In our daily lives, we often have to make decisions under time pressure and uncertainty (2–5), where perceptual awareness plays a central role. Imagine that you are cycling to work in the morning with a colleague. A fog leaves you with little visibility, but since you are very late and know the way well, you pedal quickly. Suddenly, at full speed on a downhill road, you briefly see an unusual detour sign. You would have to decide quickly and accurately about the orientation of the sign. This process can

be called objective decision-making because it involves making a choice about an objective state of reality (i.e., the orientation of the sign). Now, imagine that, after a few seconds, your friend who is following you asks you if you had clearly seen the orientation of the sign or not (and thus, whether you are confident about your objective decision), considering the speed and the lack of visibility. You would have to make a choice based on your perceptual awareness of the sign. This process can be called subjective decision-making because it requires making a choice about a subjective state of reality (i.e., “seen” or “unseen”).

Studies on consciousness traditionally investigate both objective and subjective decision-making using a contrastive paradigm (6, 7, see Ref. 8 for review), in which subjects first have to decide about a physical property of a near-threshold stimulus (i.e., its objective state, such as its orientation to the left or the right) and are then required to determine their perceptual awareness of the stimulus (i.e., their subjective state of perception, such as the visibility and confidence in their objective decision).

Interestingly, in such experiments, a stimulus with identical properties presented in different trials may or may not access consciousness (9, 10), ultimately influencing perceptual awareness and decision-making. This trial-to-trial variability is believed to emerge from time-varying modulations in attention (11, 12), where attention would act as a “gateway” to perceptual awareness (13–15). The physiological determinants of such trial-to-trial variability in conscious access remain poorly understood.

Recent work suggests that the breathing phase may modulate attention over time, by balancing exteroceptive and interoceptive information processing (16). In this line, cardiac interoception is impaired during the inhalation relative to the exhalation phase (17), suggesting that inhalation may facilitate exteroception at the expense of interoception. One key hypothesis emerging from this work is that inhalation would improve perceptual awareness and near-threshold decision-making.

The present study directly tested this hypothesis. We recorded the breathing phases of 30 humans performing a classical near-threshold orientation discrimination task. Subjects were asked to decide whether a liminal Gabor was tilted to the right or to the left (objective decision) and then to rate their subjective visibility (subjective decision). In line with our hypothesis, the data revealed that inhalation improves perceptual awareness and speeds up objective decision-making, without impairing accuracy.

MATERIALS AND METHODS

Participants

Thirty participants (9 women, 21.9 ± 3.5 yr old, 5 left-handed) took part in the experiment after detailed information and written consent. The protocol was approved ethically by the institutional review board (Number IRB 1810B) of the Euromov Center (University of Montpellier, Montpellier, France). All subjects had normal or corrected to normal vision. None of the participants had any neurological disorder, history of psychiatric illness, substance abuse, or were on any pharmacological treatments that could influence their performance.

Setup

The experimental setup is depicted in Fig. 1A. Experiments were conducted in an acoustically attenuated and electrically shielded room with a steady dim light. Subjects were seated facing a 23 in. LED monitor (Dell P2314Hc) with a spatial resolution of $1,920 \times 1,080$ pixels and a vertical refresh rate of 60 Hz, placed 90 cm in front of them. A chin rest was used to maintain a constant viewing distance and head position. Behavioral responses were collected with a computer keyboard (Dell Keyboard KB4021).

We measured respiratory parameters (phase, frequency) using a Nox respiratory inductance plethysmograph (RIP) belt placed on the participants’ thorax. An Arduino board processed the signals from this belt and transmitted the diaphragm motion data to a computer.

To control the breathing mode (nasal or oral) without causing discomfort to participants, we developed lightweight, ergonomic breathing sensors based on fast-response thermistors (Biopac Model TSD202A) and flexible PVC cannulas (Castorama Model 8011963703855) with an external diameter of 9 mm and an internal diameter of 6 mm. Exhalation increased the temperature of the nasal/oral airflow (air from inside the body), whereas inhalation cooled it (air from outside the body). The thermistors of the sensors thus measured the heat changes induced by the back-and-forth flow of nasal/oral air at the entrance of the nostril/mouth. During oral breathing, participants were asked to remove the nasal cannula, place the oral cannula between their lips, and put on a nose clip to prevent the natural tendency to breathe through the nose.

Subjects wore headphones playing white noise (presented as a waterfall sound) to mask the sound generated by their own breathing. Before the start of the experiment, the sound level of the white noise was adjusted for each participant to determine the appropriate level needed to mask the sound of breathing. This allowed us to control for a possible perceptual bias induced by a difference in auditory afference between the inhale and exhale phase of breathing, in both nasal and oral conditions.

The acquisition of the respiratory signal, the visual stimuli, and the behavioral responses were synchronized using triggers (voltage peaks) generated by the MATLAB code and sent to the TMSI Refa amplifier via a National Instruments USB-6002 multifunction digital acquisition card.

Task

Our experimental paradigm was inspired by the study by Gelbard-Sagiv et al. (10) which was adapted to the present research question. Subjects performed a delayed near-threshold Gabor orientation discrimination task (Fig. 1C), where the liminal visual stimulus was tilted to the left or to the right in a randomized fashion. Following the appearance of a liminal Gabor, subjects were first asked to make a two-forced-choice objective decision. The qualifier “objective” reflects the fact that this decision relates to the objective nature of the presented Gabor (objectively left- or right-oriented). Subjects were asked to choose as accurately and quickly as possible which was the orientation of the presented near-threshold stimulus of a contrastive paradigm. Then a subjective decision was requested from

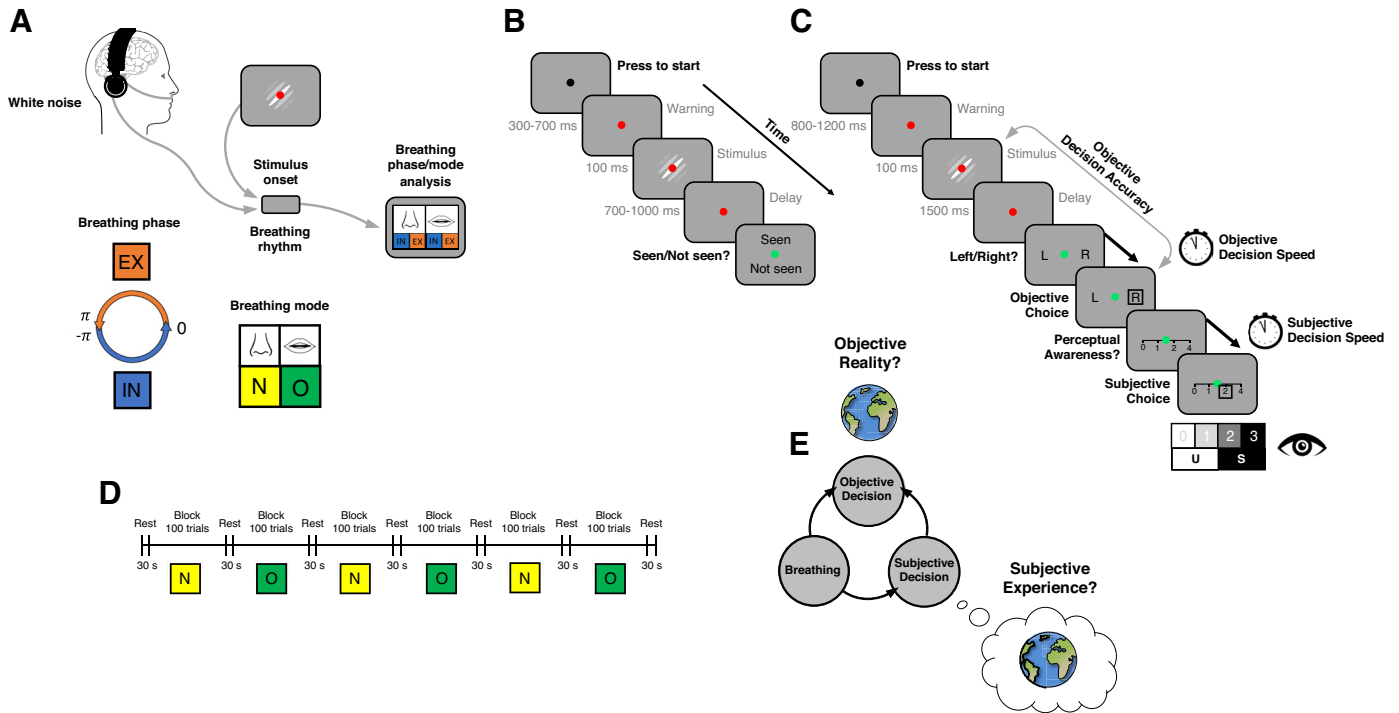


Figure 1. Experimental design and procedure. **A:** experimental setup. Participants performed the experimental task while breathing through their nose (nasal mode, N) or mouth (oral mode, O) depending on the experimental block. Breathing rhythm and behavioral responses were recorded and synchronized with the occurrence of Gabor on the screen. The analysis of the signals determined a posteriori, for each trial, if the Gabor had appeared during an inspiratory (IN) or expiratory (EX) phase. A headset controlled participants' auditory afference with white noise (presented as the sound of a waterfall). In the illustrated example, the participant performs the task in nasal mode (i.e., breathing through the nose). **B:** staircase paradigm. At the beginning of each block, subjects performed a fine-grained version of this classic procedure to determine their perceptual threshold as precisely as possible. **C:** delayed near-threshold Gabor orientation discrimination task. A 100-ms liminal Gabor tilted randomly to the left or right was presented to subjects who then had to choose (or guess) the Gabor orientation (objective decision), and evaluate their conscious experience (subjective decision) on the Perceptual Awareness Scale as follows: 0: no perception, "I saw nothing, I guessed the orientation of the Gabor"; 1: brief overview, "I have the impression that something was presented on the screen, but I did not see the orientation of the Gabor"; 2: almost clear perception, "I saw the orientation of the Gabor, I am almost sure of my answer but a doubt persists"; 3: clear perception, "I have seen the orientation of the Gabor, I am certain of my answer, I have no doubt". A green dot indicated the time during which the Gabor was presented. A red dot indicated the time when the subjects had to make a decision, as quickly and accurately as possible. Objective decision accuracy (i.e., mean percentage of correct objective choices) was determined by comparing, for each trial, the actual Gabor orientation with the objective response (if equal, correct). Subjective and objective decision speed (i.e., mean subjective and objective RT, respectively) was calculated by subtracting the time of appearance of the green dot from the time of the subject's response. **D:** experimental block design. Participants performed six blocks of 100 trials: three blocks in nasal mode, three blocks in oral mode. Nasal and oral blocks alternated one after the other, starting with either a nasal or an oral block depending on the participants' order of arrival (the 15 odd participants started with a nasal block, while the 15 peers started with an oral block). In the example shown, the task begins with a nasal block. Blocks lasted about 5 min each and were separated by 30 s of rest. In addition to the main task, participants also reported the occasional appearance of supraliminal white dots (10% of trials). When a white dot appeared, participants were instructed to press a button as quickly as possible. Response time (RT)_{control} on this parallel attention task controlled for attentional resources during the experiment, without changing any other aspect of the paradigm. **E:** synthesis of the experimental design. S, seen; U, unseen.

the subjects for perceptual awareness, where they had to evaluate the subjective visibility and related confidence of the Gabor orientation on the Perceptual Awareness Scale (PAS), a 4-point Likert scale classically used to evaluate conscious experience (18).

Gabor stimuli (4° of visual angle, 2 cycles per visual degree) were created and presented using the Psychtoolbox3 package for MATLAB (19, 20). The stimulus presentation duration was fixed at 100 ms throughout the experiment.

In addition to the main task, participants also reported the occasional appearance of supraliminal white dots (10% of trials). When a white dot appeared, participants were instructed to press a button as quickly as possible. Response time (RT)_{control} on this parallel attention task controlled for attentional resources during the experiment (21–23), without changing any other aspect of the paradigm.

Time Course of a Session

Each experimental block began with a staircase paradigm task (Fig. 1B). This classic procedure is commonly used to identify the stimulus contrast threshold (SCT) associated with each individual's stimulus-conscious access. Below the SCT, the contrast was too weak for the Gabor patch to access consciousness, leading to only "unseen" reports. Conversely, when the contrast was above SCT, subjects consciously perceived all the stimuli, resulting in only "seen" reports. The SCT was defined as the level of contrast at which $\sim 50\%$ of the Gabors reached consciousness, (the other 50% being perceived nonconsciously). This staircase procedure was repeated at the start of each new block to maintain the Gabor at the perceptual threshold throughout the experiment.

Before the main acquisition, the experimental instructions were explained to the subjects who performed a familiarization

task. This preliminary habituation step allowed us to confirm that the instructions were well understood and respected.

To emphasize, for both the objective and subjective decisions, subjects were asked to respond as quickly and accurately as possible. They were also warned that if they exceeded the maximum allowed response time of 5 s, a “Too late” message was displayed on the screen, indicating that the trial was lost and unusable for data analysis. In accordance with the methodological recommendations (18), the subjects were encouraged to exploit all four possible responses on the PAS (i.e., 0, 1, 2, and 3) according to their subjective experience scaled as follows: 0: no perception, “I saw nothing, I guessed the orientation of the Gabor”; 1: brief overview, “I have the impression that something was presented on the screen, but I did not see the orientation of the Gabor”; 2: almost clear perception, “I saw the orientation of the Gabor, I am almost sure of my answer but a doubt persists”; 3: clear perception, “I have seen the orientation of the Gabor, I am certain of my answer, I have no doubt.” Of note, the start position of the slider used for the subjective decision was randomized on the PAS to control spatial priming bias in subjects’ responses.

To promote a homogeneous distribution of stimuli over the entire respiratory cycle, we took into account the results of Perl et al. (24) showing a tendency of subjects to trigger stimuli on the inhalation phase. To counteract this effect, we asked subjects to directly trigger the beginning of each trial as soon as the black center dot appeared, immediately after the subjective response of the previous trial (10). The task was thus speeded both by the limited response time of the objective and subjective decisions requested, but also by the high rhythm imposed to trigger the successive trials.

All subjects performed a series of six blocks of 100 trials with a forced 30-s break between each block. Because it has been shown that breathing mode (nasal vs. oral) can influence the effect of breathing phase on cognition (25), we controlled for a potential mode effect by alternating each condition in the block design. The blocks started either with the nasal mode (odd subjects) or with the oral mode (even subjects), then alternated the two modes from one block to the other (Fig. 1D). A trial lasted an average of 4.6 ± 0.08 s and a block an average of 7 min 42 ± 8 s.

Data Analyses

Data were collected and analyzed using MATLAB software (MathWorks, Natick, MA) and the Psychophysics Toolbox extensions (19, 26).

Respiratory Phase

To determine the instantaneous respiration phase, the respiratory time series were first bandpass filtered between 0.2 and 0.8 Hz (27). All trials were then categorized by respiratory phase, determined by estimating the angle of the Hilbert transform of the respiratory signal at the time of stimulus presentation. Gabors presented within respiratory phases of $-\pi$ and 0 were categorized as inhale trials, and those presented within respiratory phases of 0 and π were categorized as exhale trials (25).

Perceptual Awareness, Decision Speed, Accuracy

Perceptual awareness (i.e., average number of subjective choices), was compiled for each subject, each subjective experience (“unseen,” “seen”), each phase (inhale, exhale), and each mode (nasal, oral). For clarity and in accordance with the instructions for the subjective decision task, subjective choices 0 and 1 were pooled together as “unseen” and subjective choices 2 and 3 as “seen” (e.g., see Refs. 28 and 29). Decision speed [i.e., mean subjective response time (RT) and objective RT during subjective and objective decision, respectively], and accuracy (i.e., mean percentage of correct objective choices) were compiled for each subject, each phase (inhale, exhale), and each mode (nasal, oral). RT_{control} (i.e., mean reaction time in the parallel attentional task) was compiled for each subject and each experimental block.

Statistical Analyses

Perceptual awareness data were analyzed using a three-way repeated-measures analysis of variance (rmANOVA) with SUBJECTIVE EXPERIENCE (“unseen” [0 1], “seen” [2 3]), respiratory PHASE (Inhale, Exhale) and MODE (Nasal, Oral) as within-subject factors. Decision speed and accuracy data were analyzed using a two-way rmANOVA with respiratory PHASE (Inhale, Exhale) and MODE (Nasal, Oral) as within-subject factors. Statistical analyses were performed using Jamovi software (v.1.1.9.0, The jamovi project). The significance level was set at $P < 0.05$. When performing rmANOVA, Mauchly’s test was exploited systematically to check for data sphericity and Greenhouse–Geisser (GG) correction was used to correct for any deviation from sphericity. Effect sizes were estimated for each main effect and interaction by calculating partial eta squared (η_p^2). In accordance with the conventional interpretation of η_p^2 , a value of 0.01 is interpreted as indicating a small effect size, a value of 0.06 a medium effect size, and a value of 0.14 or more as a large effect size (30). Post hoc comparisons were conducted using Tukey’s honestly significant difference (HSD) procedure. Results are presented as means \pm standard errors (SE).

RESULTS

Inhalation Improves Perceptual Awareness, without Affecting Subjective Decision Speed

First, we tested the effect of breathing on perceptual awareness and subjective decision speed (Fig. 2A). The rmANOVA revealed that the effect of the breathing PHASE on perceptual awareness (i.e., the average number of subjective choices) depended on SUBJECTIVE EXPERIENCE, as evidenced by the significant PHASE \times SUBJECTIVE EXPERIENCE interaction ($F_{1,29} = 7.88$, $P = 0.009$, $\eta_p^2 = 0.214$, Fig. 2B). Tukey’s HSD post hoc tests showed that the effect of PHASE on perceptual awareness was significant for “unseen” trials when the Gabor orientation was not consciously perceived ($unseen_{\text{inhale}} < unseen_{\text{exhale}}$, $P_{\text{Tukey}} = 0.003$, black asterisks), but not for “seen” trials ($seen_{\text{inhale}} \sim seen_{\text{exhale}}$, $P_{\text{Tukey}} = 0.365$). This indicates that subjects were less likely to report the Gabor orientation as “unseen” when the stimuli were presented on inhalation than on exhalation. Moreover, the average number of subjective choices was higher for “unseen” than for “seen” trials when the stimuli

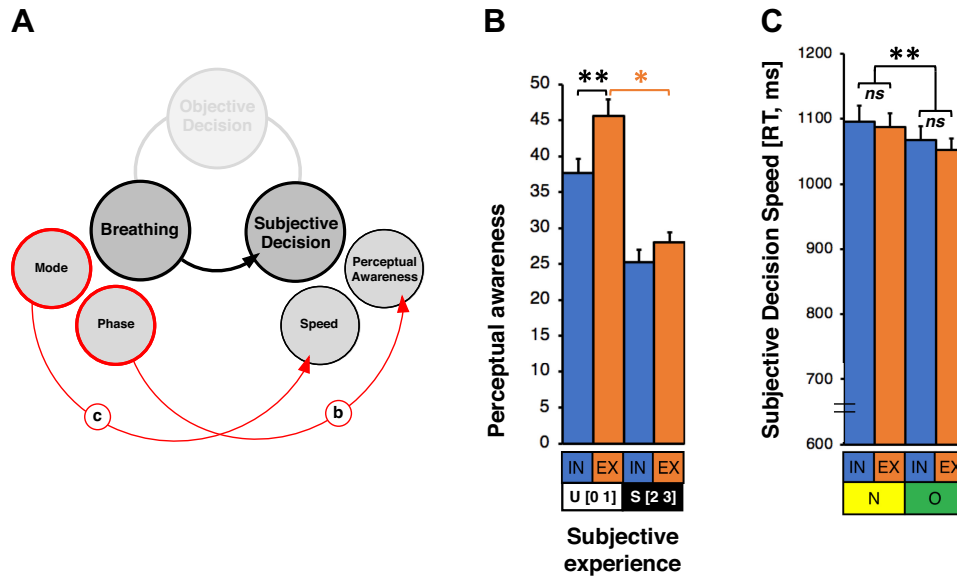


Figure 2. Inhalation improves perceptual awareness, without affecting subjective decision speed. **A:** the effect of breathing mode and phase on perceptual awareness and subjective decision speed. Red arrows indicate the significant effects observed. **B:** perceptual awareness (i.e., average number of subjective choices) as a function of breathing phase by subjective experience. The black asterisks indicate a significant difference in the occurrence of “unseen” following stimuli presented during inhalation vs. exhalation. The orange asterisk indicates a significant difference between the occurrence of “unseen” and “seen” following stimuli presented during exhalation. For clarity, as we found no significant effect of breathing mode on perceptual awareness, we pooled nasal and oral modes together on the figure. **C:** subjective decision speed [i.e., mean subjective response time (RT)] as a function of breathing mode and phase. EX, exhale; IN, inhale; N, nasal; *ns*, not significant; O, oral; S, seen; U, unseen. * $P < 0.05$, ** $P < 0.01$. Error bars represent standard errors (SE) of the means.

were presented on exhalation ($unseen_{exhale} > seen_{exhale}$, $P_{Tukey} = 0.026$, orange asterisk). This indicates that subjects were more likely to report the Gabor orientation as “unseen” than “seen” when the stimuli were presented on exhalation. This effect was absent when the stimuli were presented on inhalation, where the average number of subjective choices was comparable for “unseen” and “seen” trials ($unseen_{inhale} \sim seen_{inhale}$, $P_{Tukey} = 0.321$). Hence, subjects were less likely to report the Gabor orientation as “unseen” when the stimuli were presented on inhalation than on exhalation. Altogether, these data suggest that, relative to exhalation, inhalation improves perceptual awareness of near-threshold exteroceptive stimuli.

The rmANOVA also revealed a significant main effect of MODE on subjective decision speed ($F_{1,29} = 10.65$, $P = 0.003$, $\eta_p^2 = 0.269$). Subjective RT was faster when participants breathed through the mouth than through the nose (Fig. 2C). Conversely, the main effect of PHASE on subjective decision speed was not significant ($F_{1,29} = 2.66$, $P = 0.114$, $\eta_p^2 = 0.084$). Hence, our data provide evidence that inhalation, compared with exhalation, significantly improves perceptual awareness while leaving subjective decision speed unaffected.

Inhalation Speeds up Objective Decision-Making, without Affecting Accuracy

Second, we tested the effect of breathing on objective decision speed and accuracy (Fig. 3A). The rmANOVA revealed a significant main effect of PHASE on objective decision speed. Objective RT was faster following a Gabor presented on inhalation compared with exhalation ($F_{1,29} = 49.97$, $P < 0.001$, $\eta_p^2 = 0.633$, Fig. 3B), but this effect was not influenced by the MODE condition, as evidenced by the nonsignificant

MODE \times PHASE interaction ($F_{1,29} = 0.040$, $P = 0.843$, $\eta_p^2 = 0.001$).

Surprisingly however, the rmANOVA on objective decision accuracy revealed no significant main effect of PHASE ($F_{1,29} = 0.58$, $P = 0.452$, $\eta_p^2 = 0.020$), nor any significant MODE \times PHASE interaction ($F_{1,29} = 0.040$, $P = 0.844$, $\eta_p^2 = 0.001$) (Fig. 3C). Hence, our data provide evidence that inhalation, compared with exhalation, significantly accelerates objective decision-making while leaving accuracy unaffected.

Control of Attentional Resources during the Experiment

Finally, the rmANOVA on $RT_{control}$ of the parallel attention task (used to control for attentional resources during the experiment) revealed no significant main effect of BLOCK_{ORDER} (GG-corrected $F_{1,29} = 1.29$, $P = 0.274$, $\eta_p^2 = 0.043$). Overall, these experimental control analyses suggest that attentional resources were statistically comparable over the course of the experiment.

DISCUSSION

The purpose of this study was to investigate the potential influence of breathing on perceptual awareness and near-threshold decision-making. Altogether, our results show that 1) inhalation improves perceptual awareness, without affecting subjective decision speed, and 2) inhalation speeds up objective decision-making, without affecting accuracy.

As a main finding, we confirmed our hypothesis that inhalation improves perceptual awareness. Specifically, we found that subjects were less likely to choose the “unseen” subjective state after perceiving a stimulus presented on inhalation,

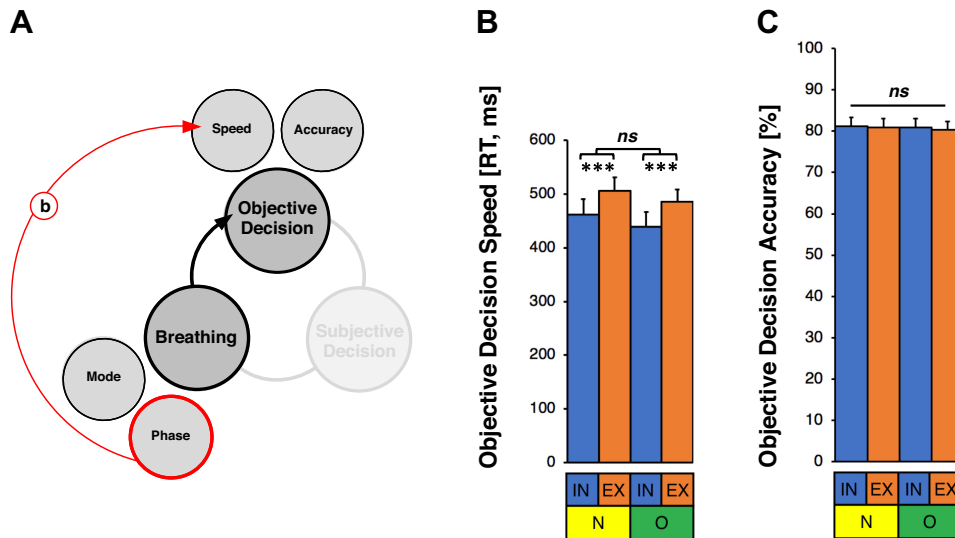


Figure 3. Inhalation speeds up objective decision-making, without affecting accuracy. **A:** the effect of breathing mode and phase on objective decision speed and accuracy. The red arrow indicates the significant effect observed. **B:** objective decision speed [i.e., mean objective response time (RT)] as a function of breathing mode and phase. **C:** objective decision accuracy (mean percentage of correct objective choices) as a function of breathing mode and phase. EX, exhale; IN, inhale; N, nasal; *ns*, not significant; O, oral. $***P < 0.001$. Error bars represent standard errors (SE) of the means.

compared with exhalation. This result echoes the recent hypothesis of respiratory modulation of exteroceptive and interoceptive attention, according to which inhalation would enhance exteroceptive attention at the expense of interoception (16). In line with this idea, a study has shown recently that exhalation improves cardiac interoception at both the behavioral and neural levels (17). Our study corroborates and complements these findings and highlights the positive impact of inhalation on the perceptual awareness of exteroceptive stimuli.

At the neural level, the positive influence of inhalation on perceptual awareness could reflect an excitation of noradrenergic neurons of the locus coeruleus (LC), a small nucleus located in the brainstem that controls most noradrenergic neurons in the brain. In mice, the brainstem neurons located in the preBötzinger complex are known to be the inspiratory rhythmogenesis center in mammals and project directly to the LC, which modulates its activity (31). Thus, with each inhalation and in respect to their level of activation, LC neurons are excited by this subset of neurons. In humans, LC activity is also known to be modulated by the respiratory phase (32–35). Through its effect on arousal, neural gain, and attention, inspiratory-induced phasic excitation of the LC could promote exteroception (36, 37). Conversely, an expiratory LC release of excitation could limit the chances of an exteroceptive stimulus being consciously perceived.

Another neural correlate of our behavioral results could be the α waves, a prominent type of brain activity whose spontaneous fluctuations are known to modulate attention (38, 39). Indeed, a recent study has shown that the breathing phase modulates the power of the α band and related perceptual threshold psychometric function (40). States of decreased prestimulus α -band power are associated with enhanced neural excitability, resulting in improved visual awareness through a more liberal detection criterion (41–45). Conversely, higher prestimulus α -band power is related to a more conservative response criterion (i.e., more “unseen” reports; 46, 47).

Altogether, the influence of the respiratory phase on α waves represents a strong neurophysiological argument for the hypothesis of respiratory modulation of exteroceptive

and interoceptive attention (16). We propose that inhalation promotes conscious processing of exteroceptive information through an upregulation of LC activity and a decrease in α waves power.

A secondary aim of the present study was to investigate the effect of breathing on near-threshold decision-making. Interestingly, we found that mouth breathing accelerates subjective decisions. One possible explanation is an elevation of arousal in the oral condition. Arousal has been shown to modulate urgency in decision-making (48, 49). In infants, forced oral breathing can lead to elevated arousal (50, 51).

Finally, we found that inhalation accelerates objective decision-making. Subjects responded faster when the stimulus was presented on inhalation, an effect independent from the respiratory mode. This effect of the breathing phase on objective decision speed suggests a faster processing of exteroceptive information during inhalation. This echoes the results of the seminal study by Zelano et al. (25) that showed an acceleration of the detection of fearful faces during inhalation versus exhalation. Moreover, the difference between the reaction time during inhalation and exhalation is of the same order of magnitude (i.e., less than 50 ms, see Ref. 52). However, it is important to mention that in the study by Zelano et al. (25), this effect was only observed in the nasal condition. Considering the wide respiratory modulations of brain activity observed during nasal breathing (e.g., olfactory cortex, amygdala, hippocampus), the authors interpreted this as an effect driven by the neurophysiological modulation of the olfactory system. Indeed, during nasal (but not oral) breathing, the back and forth movement of the air in the nasal cavity mobilizes the mechanoreceptors of the olfactory sensory neurons. These transmit an electrical signal to the olfactory bulb, which then propagates to the cortex and subcortical areas (53, 54).

In our study, the experimental task is very different from that of Zelano et al. (25) in terms of design. Nevertheless, the closeness in the scale of the observed effects suggests a common mechanism. Moreover, an amodal influence (i.e., in both nasal and oral mode) of the respiratory phase on cognitive performance has already been reported (24). Overall, contrary to what the results of the Zelano et al.’s seminal

study suggested, namely the nasal specificity of the phasic breathing effect, our results show, like those of Perl et al. (24), that phasic breathing modulation can be observed in oral condition.

Unlike objective decision speed, our data showed no effect of breathing on objective decision accuracy. This result may seem surprising at first, but it is in line with a recent extensive study grouping several experimental tasks spanning pitch discrimination, visual motion discrimination, visual memory, emotion discrimination, and sound detection (52). As in our study, the results revealed that participants' response times, but not so much their accuracy, consistently and significantly covary with the respiratory cycle, differing between inhalation and exhalation. Moreover, the authors report a respiratory modulation of the reaction times inducing effects between 20 and 50 ms, which is comparable with the scale of our results (i.e., less than 50 ms) and those of Zelano et al. (25). This lack of effect on accuracy is also consistent with a recent review on the influence of spontaneous brain oscillations on perceptual decision-making showing that α -band power fluctuations modulate perceptual awareness, visibility, and confidence but not, surprisingly, objective decision accuracy (44). This is precisely what our data demonstrate, adding an argument for respiratory modulation of α waves as a neurophysiological occurrence in line with our results.

A few methodological considerations should be noted when interpreting these data. A potential bias could be induced by the effect of breathing on the motor execution of the decision choice. Recently, it has been shown that the respiratory phase modulates the initiation of a voluntary movement as well as the associated readiness potential, the drift of neural activity known to precede a self-initiated movement (27). This study reveals that humans tend to initiate a movement on exhalation, rather than on inhalation. However, we believe that this is not the case in our study for two reasons. First, this breathing-action coupling disappears when the action is triggered by an exteroceptive stimulus, which is the case in our experimental paradigm. Second, this potential motor bias is unlikely because in our study subjects were making delayed perceptual decisions. This delay between stimulus and decision response rules out the possibility that the reported effects are due to the influence of breathing on motor actions (55).

To conclude, the present study aimed at investigating the effect of breathing rhythm on perceptual awareness and near-threshold decision-making. In line with recent findings in the interoceptive domain, our data confirmed our main hypothesis that inhalation improves perceptual awareness, without affecting subjective decision speed. Moreover, we found that inhalation speeds up objective decision-making, without impairing accuracy. We propose that breathing rhythm drives fluctuations in brain excitability through the modulation of both the noradrenalin-LC system and α -band oscillations. In consciousness research, this respiratory-induced attention modulation would influence the trial-to-trial variability of perceptual awareness and decision-making commonly observed in near-threshold experiments. Overall, these results are consistent with the emerging notion of an olfaction-based template in the evolution of human brain function (24), and extend the respiratory modulation of

cognition to perceptual awareness and decision-making under time pressure and uncertainty.

DATA AVAILABILITY

Data will be made available upon reasonable request.

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GRANTS

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

L.M., A.C., C.-E.B., S.P., and A.D. conceived and designed research; L.M. performed experiments; L.M., A.C., G.D., and S.J. analyzed data; L.M., A.C., C.-E.B., G.D., S.J., S.P., and A.D. interpreted results of experiments; L.M. and A.C. prepared figures; L.M. drafted manuscript; L.M., A.C., C.-E.B., G.D., S.P., and A.D. edited and revised manuscript; L.M., A.C., C.-E.B., G.D., S.J., S.P., and A.D. approved final version of manuscript.

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