Conscious and unconscious perception of errors in auditory feedback during vocalization: Behavioral functions and event-related potential correlates

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Abstract

During vocalization, errors in the auditory feedback are processed rapidly and automatically, suggesting that feedback control of vocalization operates unconsciously. Humans are also able to consciously detect errors in their auditory feedback during vocalization, but the question whether consciousness modulates speech feedback control remains little studied. To address this question, we concurrently measured behavioral vocal responses and electroencephalography (EEG) in 30 participants while their online auditory feedback was altered using individually calibrated threshold-level pitch-shift perturbations (i.e., errors). Following each vocalization trial, participants rated if they consciously detected pitch errors in their auditory feedback. We analyzed the data on a trial-by-trial basis to test if vocal responses to pitch perturbations are modulated by conscious perception. Our results revealed that even on trials where participants reported not noticing the perturbation at all, a vocal compensation to the altered auditory feedback was generated. Conscious error detection was associated with increased magnitude of vocal responses roughly 500-700 ms after the altered feedback compared to the unconscious trials. Conscious detection of the altered feedback correlated with early (Auditory awareness negativity) and late (Late positivity) neural activity responses as indexed by the modulation of event-related potentials (ERPs). Source localization of ERP responses suggested that conscious error detection was attributed to increased neural activity within the temporal, frontal and parietal cortical networks known to be involved in speech motor control. These findings emphasize the importance of investigating the role of higher-level conscious processing mechanisms in regulating speech feedback control, and their effect on the underlying neural and behavioral functions.

Keywords: Speech motor control; auditory feedback; sensorimotor integration; conscious perception; neural correlates of consciousness

1. Introduction

Speech is a complex task that requires coordination of cognitive, motor, and sensory programs. Even small changes in acoustical parameters of sound can lead to meaningful changes in communication. Therefore, the process of speech production needs to be

subjected to feedback monitoring that at the level of cortex involves frontal, temporal and parietal areas (Tourville & Guenther, 2011). Speech feedback control is often assumed to operate unconsciously, but the role of consciousness has rarely been probed in experimental studies. We studied if conscious perception modulates speech feedback control, and the brain mechanisms that correlate with conscious perception of errors during vocalization.

1.1. Speech feedback control

Current models of speech production (e.g., Houde & Nagarajan, 2011; Tourville & Guenther, 2011) do not distinguish between conscious and unconscious speech feedback control. Rather, the models are built around the idea that speech feedback control relies on an automatic comparison of how well the acoustic features of produced speech match the intended targets. Speech targets arise in the left-lateralized ventral premotor areas of the cortex and are executed by the motor areas. In addition to sending the feedforward motor commands, axons from the premotor cortex are assumed to relay information about the expected sensory outcome to areas such as the auditory cortex in the posterior superior temporal gyrus. This copy of the motor command is known as the efference copy (or corollary discharge). The consequence of the efference copy is that the sensory areas have an inhibited response to vocalizations that match the target of the motor program, but are excited by motor commands that result in vocalization errors (Behroozmand et al., 2022a; Behroozmand & Larson, 2011a; Chang et al., 2013; Eliades & Wang, 2008). In case of errors, the motor areas are recruited to initiate corrections to the motor commands (Burnett et al., 1997; Hain et al., 2000). We call the change in vocalization that follow errors in sensory feedback the *vocal response*.

Auditory feedback control of speech is measured behaviorally by “perturbing” auditory feedback in real-time with artificial vocalization errors. In a widely used version of the paradigm, participants hear a pitch-shifted version of their own voice during vocalization (Burnett et al., 1997; Elman, 1981; Hafke, 2008; Hain et al., 2000; Hawco et al., 2009). This so called “frequency-altered feedback paradigm” is often used to study suprasegmental features of speech such as prosody, stress, or rhythm, and in general, the stability of pitch regulation during vocalization. These features of vocalization are crucial for spoken language, and even relatively small changes in the pitch of vocalization can lead to meaningful changes in the

message conveyed (e.g., it might change the emphasis, or in tonal language it might change the meaning of the spoken word). Vocal responses to pitch perturbations are, on average, compensatory (i.e., if the perturbation increases the pitch of auditory feedback, participants typically react by lowering their voice). The vocal response is involuntary: Even when participants are asked to ignore the pitch perturbation, they still produce the vocal responses (Keough et al., 2013). Given that the onset of the vocal response is rapid (just over 100 ms), it can be assumed to be mediated by unconscious processes. However, as discussed next, previous studies that have tested the unconscious nature of vocal responding have significant methodological limitations, and consequently, the question to what extent conscious perception mediates vocal responses to perturbations remains open.

1.2. Does consciousness modulate vocal responses?

The study by Hafke (2008) is often cited as evidence that the speech feedback control system initiates vocal responses even when the individual remains unconscious of the perturbation. Hafke (2008) showed that in trained singers, perturbations as small as 9 cents evoked vocal responses, although the participants often reported not noticing perturbations of this size. However, to show that completely unconscious perturbations produce vocal responses, the analysis should *only* include trials where participants report that they did not notice the perturbations. Hafke's (2008) analysis also included trials where participants reported noticing the perturbation, which means that the vocal response might be contaminated by the trials where participants happen to consciously detect the errors. Another study replicated the finding of Hafke (2008) on a sample of participants without professional singing experience, but only assessed conscious perception of the perturbation by having the participants passively listen to recorded samples of perturbed or non-perturbed feedback (Xu et al., 2020). This is problematic because participants have increased ability to detect perturbations during "active" vocalization than during "passive" listening (Scheerer & Jones, 2018). The data by Scheerer & Jones (2018) shows that humans may be able to discriminate subtle perturbations as small as 10–15 cents, suggesting that 9 cent perturbations (observed to evoke vocal responses in Hafke, 2008) may not completely fall short of the capacity of conscious perceptual mechanisms. Scheerer and Jones (2018) found that the differences between the thresholds for vocal responses and for conscious perception are at best minimal (5 cents), and suggested that the supposedly unconscious vocal responses to very small perturbations are

instead biased by other factors such as vocal variability (i.e., participants may attribute the perturbation to the natural variability of their own voice).

Here, we aimed to test if participants initiate corrections to vocalization when they do not notice an auditory feedback error. If such analysis reveals that speech feedback control can be initiated solely based on unconscious perception, conscious perception could further modulate vocal responses to perturbations. In addition to the rapid vocal response component (called VR1), the vocal response may also contain a second, later component (VR2, typical onset after 300 ms). Asking participants to voluntarily control how they respond to a perturbation predominantly modifies the VR2 (Hain et al., 2000). For this reason, the VR2 is sometimes assumed to correspond to a conscious vocal response mode. The results by Franken et al. (2023) showed that when participants attributed pitch errors to themselves, they made larger corrective responses than when they attributed the pitch error to external factors, suggesting that conscious source monitoring of vocal errors modulates speech feedback control. In the present study we aimed to test the behavioral function of conscious perception on vocal responses by examining if consciously noticed perturbations produce different vocal responses than perturbations which participants report not noticing. To isolate the effect of conscious perception, one needs to compare trials that differ only with respect to consciousness while keeping physical stimulation (i.e., the perturbation) constant for each participant; otherwise, the difference between conscious vs. unconscious conditions could be solely due to physical differences between the conditions.

1.3. EEG correlates of conscious perception of errors in vocalization

In addition to testing if conscious perception modulates speech feedback control of pitch perturbations, the second aim of the present study was to elucidate the neural processes that underlie conscious perception of vocalization feedback errors by examining event-related potentials (ERPs). Due to efference copies, non-perturbed auditory feedback of self-produced vocalization triggers an inhibited auditory-evoked ERP compared to the same stimuli when heard through playback. This sensory suppression of self-produced speech is strongest around 100–200 ms after stimulus onset (Curio et al., 2000; Houde et al., 2002; Railo et al., 2022). When the auditory feedback the subject hears is perturbed, the amplitude of the ERPs increases, suggesting that the brain detects a vocalization error, and initiates corrections to

vocalization (Behroozmand et al., 2022b; Behroozmand & Larson, 2011b; Heinks-Maldonado et al., 2005; Scheerer & Jones, 2014, 2018c). This increase in ERP amplitude affects the ERP early (P1 wave, around 50–100 ms after stimulus onset), likely reflecting an initial unconscious detection of the vocalization error in the auditory cortex. Later processing phases (corresponding to N1–P2 waves around 100–300 ms) are assumed to correspond to more nuanced detection of the errors, and the control of subsequent corrections to vocalization.

While previous research has extensively studied the ERP correlates of speech feedback control, the studies have not isolated the correlates of conscious perception, but rather examined how, e.g. the size of the perturbation modulates ERPs. Here, while keeping physical stimulus constant, we contrast conscious vs unconscious perception with the aim of describing what neural processes underlie individuals' conscious perception of errors in their own voice. This type of contrastive approach is widely used in the search for "the neural correlates of conscious perception" which aims to find the neurobiological processes that enable subjective consciousness to emerge from brain activity (Crick & Koch, 1990; Dehaene, 2014). Given that physical stimulus features are kept constant for each participant, any differences between consciously noticed versus not-noticed conditions correlate with subjective conscious perception of the stimulus (Aru et al., 2012).

Previous research suggests that conscious perception of external sensory stimuli correlates with activity in sensory, frontal and parietal cortex (Dembski et al., 2021; Koch et al., 2016; Mashour et al., 2020), although the role of the "extrasensory" areas remains debated (Boly et al., 2017; Odegaard et al., 2017). ERP studies show that conscious perception of external auditory stimuli correlates with activity in two time-windows. An earlier correlate known as the Auditory Awareness Negativity (AAN) has a negative polarity, and takes place around 100-250 ms after stimulus onset (Dembski et al., 2021; Eklund et al., 2021; Eklund & Wiens, 2019; Filimonov et al., 2022). This neural correlate is assumed to reflect the subjective experience of the sensory stimulus. A later correlate known as the Late Positivity (LP)—which coincides with the P3b event-related potential (ERP) wave—is often argued to reflect higher-order conscious perception (Derda et al., 2019; Jimenez et al., 2021) or post-sensory processing (e.g., decision making or behaviorally responding to a stimulus; (Dembski et al., 2021;

Schlossmacher et al., 2020)). Other sensory modalities show similar correlates (Dembski et al., 2021).

1.4. Hypotheses of the present study

In order to vary conscious perception of the pitch perturbation while keeping its magnitude constant, we calibrate pitch perturbations for individual participants using a psychophysical staircase procedure. Whereas prior studies have often employed pitch shifts with brief duration (e.g., 200 ms; e.g., Scheerer & Jones, 2018; Behroozmand et al., 2022), following the procedure used by Hafke (2008), we here used a longer duration perturbation that lasted until the participants stopped their ongoing vocalization. We reasoned that if consciousness plays a role in speech feedback control, these effects might be best observed in situations where pitch-shift stimuli persist throughout the duration of vocalizations.

Following standard practice in consciousness studies, we measured conscious perception using a four-step scale commonly known as the Perceptual Awareness Scale (Overgaard & Sandberg, 2021; Ramsøy & Overgaard, 2004; Sandberg et al., 2010). The graded nature of the scale allows more stringent definition of the unconscious condition (the lowest alternative of the scale; (Koivisto et al., 2021; Overgaard et al., 2008; Phillips, 2021)), while still acknowledging the graded nature of conscious perception (the three higher response alternatives (Jimenez et al., 2018, 2020; Windey & Cleeremans, 2015).

To test three preregistered hypotheses in the subsequent EEG experiment, we contrast trials where participants reported conscious perception of the perturbation with trials where they failed to detect the perturbation. First, based on earlier research (Hafke, 2008; Xu et al., 2020), we hypothesize that vocal responses are initiated even when participants report not noticing the perturbation. In addition to this unconscious mode of feedback control, we hypothesize that speech feedback control can also operate at a conscious level, enabling additional corrections to speech. Second, based on studies examining the neural correlates of conscious perception of external sounds (Dembski et al., 2021; Eklund et al., 2021; Eklund & Wiens, 2019; Filimonov et al., 2022), we expected that conscious perception of the perturbation correlates with an early negative amplitude difference in central electrode locations (i.e., AAN). Finally, assuming that the ERPs in part reflect the initiation of vocal responses (e.g.,

Behroozmand et al., 2022), we expected to observe a correlation between ERP and vocal responses amplitudes.

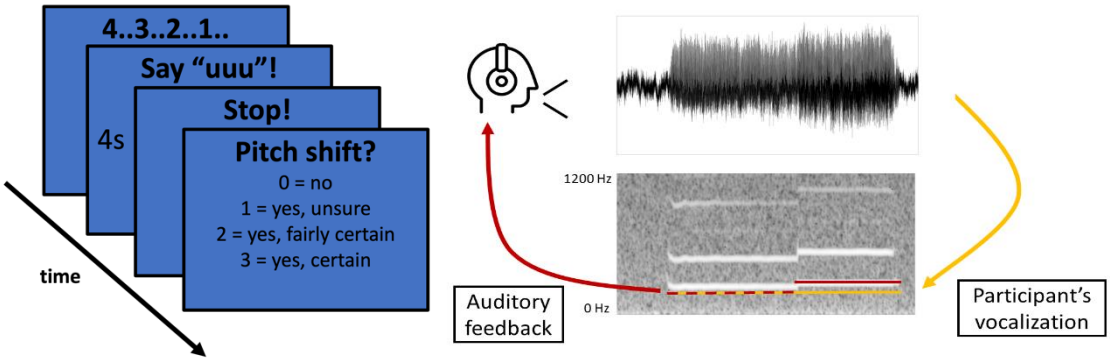

Figure 1: Graphical illustration of the experimental task. The participants heard their online auditory feedback through headphones while it was sometimes perturbed 1.5 seconds after the start of vocalization (upward pitch shift) and remained on until the end of the 4-second-long vocalization phase. In the panel on right, the yellow line denotes the true pitch of vocalization (i.e., unmodified auditory feedback), and the red line shows the perturbed (i.e., pitch-shifted) auditory feedback. After each vocalization, the participant reported if they detected the perturbation (on the right).

2. Methods

2.1. Pre-registration and data availability

The present study was preregistered prior to collecting data and running analyses (https://osf.io/am3rq/). All procedures described in this paper conform to the pre-registration, unless otherwise specified. All computer code used to run the experiment and analyze the results are publicly available at osf.io.

2.2. Participants

35 participants (Mage = 26, range: 20-36; 27 female) participated the study. All participants gave written informed consent. Sample size was determined based on previous studies, as described in the preregistration document. The participants were recruited using the university's participant recruitment website, by advertising among psychology, speech pathology, and biomedical students, and by word-of-mouth. The participants completed the experiment in exchange for course credit, or small financial reward. The exclusion criteria for

participating in the study included left-handedness, and self-reported presence of neurological, hearing, or voice disorders that would interfere with completing the experiment. A screening test of parcipants' hearing abilities was not conducted due to time constraints, and the fact that the experiment adjusts its difficulty to individual hearing abilities.

We excluded five participants from the analyses. Three of them did not complete the tasks as intended. One participant reported detecting the perturbation at every trial, one varied the pitch of their vocalization systematically over the course of every trial and one reported that they were unaware of any of the large-perturbation catch trials. Another two participants were excluded due to insufficient EEG quality. The research was approved by the ethics board of the Wellbeing services of the Southwest Finland and was carried out in accordance with the Declaration of Helsinki.

2.3. Procedure

The experimental procedure was completed in a single session, lasting up to two hours and 30 minutes. The perturbations were created using the Audapter package (Cai et al., 2008) using the phase vocoder option, and the experiment was run using the Psychtoolbox package (Brainard, 1997), both running in Matlab (version 2016B). Participants' vocalization was recorded using a Motu MicroBook IIc audio interface, and a microphone (Audio-technica AT2035) positioned at a 1-2 centimeters distance from the mouth. The participants heard their own voice through sound-isolating in-ear earphones. During each trial of all stages of the experiment, the auditory feedback was mixed with pink noise in order to reduce the participant's ability to hear their own voice due to insufficient headphone isolation, and bone conduction. We kept the sound level the same for all participants, except for a single participant, who considered the feedback to be too loud. Note that Audapter's phase vocoder pitch-shift function shifts not just the fundamental frequency but affects the whole spectrum (Figure 1). This is perceived as a change in pitch, with no noticeable change in vowel quality.

Before the experiment, we instructed the participant to produce the vowel */u:/* of sufficient length and loudness. The participant was not instructed about the pitch of the vocalization. We did not instruct the participant on how to respond to the perturbation, other than to keep

vocalizing until the preset time limit. The vowel choice was inspired by our replication of the experiment performed by Hafke (2008). We maintain that vowel choice is arbitrary, and that its graphical representation “uuuu” produced consistent vocalization in our international sample of participants. We chose to produce pitch perturbations rather than formant perturbations because pitch is the most frequently manipulated vocalization property in the perturbation paradigm studies (Hafke, 2008; Hain et al., 2000; Scheerer & Jones, 2018b; Villacorta et al., 2007), and researchers typically assume the the feedback control of pitch is based on unconscious processing.

At the beginning of the experiment, we first presented the participant with an interactive warm-up task, with the goal of exposing them to both unperturbed and highly perturbed feedback (+ 200 cents, present until the end of vocalization). During the warmup, the participants also practiced how to respond to the consciousness question that followed each trial. The warm-up continued until the desired quality of vocalization had been achieved and the participant was able to consistently identify the perturbed feedback.

After the warm-up, we presented the participant with a staircase calibration procedure, with a goal of estimating their perturbation perception threshold. The perturbation perception threshold represents a magnitude of pitch change (e.g., +20 cents) that the participant can consciously detect in a predefined proportion of trials (e.g., in 65 percent of the total trial count). We used the QUEST staircase algorithm (Watson & Pelli, 1983). The participant produced the /u/ phoneme for approximately 4 seconds. During the first 1.5 seconds of every trial, the participant was exposed to the unperturbed headphone feedback. Auditory feedback was perturbed 1.5 seconds after the beginning of vocalization, and the perturbation continued until the end of the trial. After each trial, the participant was asked to report on a 4-step scale whether they heard the change in the pitch (see below for details). The QUEST algorithm then placed the next perturbation at the value most likely to be near the specified threshold. A positive response (ratings 1-3, indicating a detection perturbation) lead to a decreased perturbation magnitude being used in the next trial of the experiment, while a negative response (lowest rating) lead to an increase of perturbation magnitude. Finally, we calculated the mean of the probability density function (as recommended by King-Smith et

al., 1994), and used this value as the individual perturbation perception threshold in the main phase of the experiment.

The calibration procedure had a fixed length of 50 trials, but it was re-run in case the results suggested an unreliable threshold estimate (e.g., unexpectedly high or low threshold value). All perturbations presented during the calibration as well as during the other phases of the experiment were upward, and the perturbation lasted until the end of vocalization. We initially estimated 75% perturbation detection thresholds, as it was considered an adequate trade-off between the amount of acquired unaware trials while maximizing perturbation size (to obtain clear ERPs). However, the 75% threshold resulted in a higher-than-expected amount of consciously perceived trials in the main experiment for the first participants, and therefore we lowered the threshold for later participants. In the participants included in the statistical analysis, the estimated thresholds were as follows: 75% threshold in 2 participants, 50% threshold in one participant, and 60% threshold in the remaining 27 participants. While this change is at odds with the pre-registration, it enabled us to maximize the number of aware and unaware trials per participant.

The main experiment, summarized in Figure 1, took place after the calibration session. We recorded the EEG signal only during this phase. This experiment contained 300 trials per participant, divided into blocks of 50 trials. Each block was followed by a short break. The participants were presented with perturbations for which the intensity was adjusted to the individual conscious pitch error detection threshold. Control trials without perturbations, and control trials with large perturbations (+200 cents) were presented as well. Trials without perturbations were included to verify that a participant typically reports not noticing a perturbation when it was not presented. Similarly, trials with large perturbations were used to exclude participants who systematically labelled them as 'unaware' (see Section Participants), and to make the task more enjoyable for the participants (by presenting, every now and then, trials where the perturbations was easily detectable). The control trials amounted to ~33% of all trials, and were equally divided into trials with no perturbations and trials with strong perturbations. These trials were randomly distributed across the whole session (i.e., different blocks did not necessarily contain the same distribution of different trial types). The participant was instructed that they will be able to hear their unmodified voice at

the beginning of each trial, and that this voice may then be modified as they continue vocalizing. After each trial, the participant was asked if they heard that the pitch of their vocalization was modified. The participant provided a response on a scale of 0 to 3, with higher numbers indicating clearer consciousness of the perturbation. The participants were told that the question concerns the auditory signal they hear from the headphones (e.g., not how they thought they vocalized), and that the numbers on the scale corresponded to these statements: 0) No, I did not hear any change in pitch; 1) I might have heard a change in pitch, but I am unsure: 2) I am fairly certain that I heard a change; and 3) I am very confident that I heard a change.

The difference between the options (0) and (1), in particular, was stressed to the participants. In the analysis the lowest alternative corresponds to the "unconscious" condition. This question measuring conscious perception of a stimulus is based on a widely used scale known as the Perceptual Awareness Scale (Ramsøy & Overgaard, 2004). Use of graded rating scale is important because previous studies in the visual modality suggest that the use of binary ratings scales may contaminate the "unconscious" category with stimuli the participants faintly consciously perceived, leading to confounded results regarding unconscious processing (Koivisto et al., 2021; Overgaard et al., 2008; Phillips, 2021).

2.4. Voice data processing and analysis

Participants' vocalization was processed in Matlab version R2022b with the perturbation onset data obtained from the voice-modulation software Audapter (Cai et al., 2008). During the preprocessing of vocalization data, we first lowpass filtered the data at 500 Hz and extracted the fundamental frequency (F0) from each vocalization using Matlab's *pitch* function. We removed the last 300 ms from the end of each trial as these contained unstable F0s. We removed trials which did not contain any vocalization, or contained vocalization that was too short, or too quiet to activate Audapter's perturbation algorithm. Next, we determined the start time of the perturbation relative to the start of each trial, and excluded trials which did not contain at least 800 ms of perturbed phonation. We used the 200 ms before the perturbation onset as a baseline period. For every sample from 200 ms before

perturbation onset until 800 ms after perturbation onset, we calculated the relative deviation of this sample from the baseline period, using the standard equation used in auditory perturbation research (Hafke, 2008; Hain et al., 2000):

$$cents = 100 * \left(\frac{10 * Log\left(\frac{F_s}{F_B}\right)}{log(2)} \right)$$

where F_s is the fundamental frequency of an individual audio sample, and F_B is the mean fundamental frequency during the 200 ms pre-perturbation period. This calculation takes absolute units of frequency (Hertz) and translates them to relative units (cents, 100 cents = 1 semitone), which enables comparing participants and trials with varying pitch. Lastly, we excluded trials which contained vocal responses larger than 200 cents at any time point during the trial.

2.5. EEG data acquisition and analysis

The EEG signal was be recorded from 32 scalp electrodes with NeurOne Tesla amplifier (Bittium, 2022), software version 1.5.0. Two additional electrodes were used during data collection. One was placed on the forehead (in-between the FP1 and FP2 electrodes) and served as the ground. The second one was placed on the nose and served as the reference during data collection. Sampling rate was 500 Hz. Markers that denoted participants' keyboard responses (conscious perception ratings), and trial type were added to the EEG signal during recording. The onset of the pitch perturbation was marked in the EEG signal during data preprocessing based on Audapter data. This was possible thanks to Audaper's ability to save timestamps of trial starts and perturbation onsets within the course of the experiment.

The EEG data was processed using EEGLAB, version 2022.1 (Delorme & Makeig, 2004) running in Matlab version R2022b. During preprocessing, channels containing a large proportion of noise and artifacts were rejected using the function pop_rejchan, using kurtosis and probability measures. The mean number of removed channels per participant was 6.83 (sd = 2.48). The signal was high pass filtered at 1 Hz using EEGLAB's function *pop_eegfiltnew*. Line

noise around 50 Hz was reduced using the *zapline* function (de Cheveigné, 2020). Other types of low pass filtering were not used. The data was re-referenced to average reference of all scalp electrodes. The data was epoched from 500 ms before the perturbation onset up to 1000 ms after the perturbation onset. Each trial was baseline corrected to the 500 ms time window before the perturbation onset. Next, we ran the Independent Component analysis (ICA), using the *pop_runica* function in 'extended' mode. After ICA, removed or missing channels were interpolated using function pop_interp with default parameters. Independent components were automatically labelled using ICLabel, and only those that were classified as being brain based with more than 70 percent probability were kept. Finally, we removed artifactual trials using the *pop_jointprob* function (local and global thresholds = 3). We excluded 903 trials during preprocessing (9.23 percent of the whole sample), leaving a total of 7432 trials left for the analysis described below.

2.6. Statistical analysis

2.6.1. Vocal responses

We analyzed the vocal responses using a mass univariate analysis, that is, the effect of consciousness on the vocal response is examined at every time point before and after the onset of the perturbation. While our preregistration did not specify a mass univariate analysis, its use here is justified because it allows comparisons at high temporal resolution while controlling family-wise statistical error rate. Second, the method is suitable to situations where prior information about the timing of effects is limited, as is the case here. To keep the vocal response distribution shapes normal, our analysis includes both "opposing" and "following" responses (Miller et al., 2023).

To run the mass univariate analysis of vocal responses, we have adopted a methodology typically used for mass univariate analysis of ERPs (Groppe et al., 2011; Pernet et al., 2015). First, we selected all critical trials, and ran a linear mixed effects regression model for each time point of the vocalization from 200 ms before the perturbation onset up to 800 ms after the perturbation onset. In the model, we treated the magnitude of the vocal response as the dependent variable, consciousness as a fixed-effect predictor, and the by-participant intercept as a random effect (pitch ~ consciousness + (1|participant)). This analysis resulted in a large

number of statistical tests. To account for multiple comparisons, we next ran the same series of tests with 1000 random permutations of the original trials. To do this, we randomly assigned trials to either in the aware or the unaware conditions, and repeatedly ran the previously described statistical model. To identify clusters with a significant effect of consciousness, we ran threshold-free cluster enhancement (TFCE; Smith & Nichols, 2009; Smith & Nichols, 2009) for both real regression results, and the results based on the random permutations using the *limo_tfce* function from the LIMO EEG toolbox (Pernet et al., 2011) . We selected the maximum TFCE-value (out of regression models for each time sample between -200-800 ms) for each of the random permutations, and saved these to form a null-distribution to which the TFCE values of the real (i.e., not randomized) data was compared to. TFCE-values of real data higher than 97.5 of randomly permuted TFCE-values were considered significant effect of consciousness (this is equal to two-tailed alpha level of 0.05).

2.6.2. ERPs

For the analysis of ERPs, we also used linear mixed-effects models on single-trial data. Unlike in the vocal response analysis, in the ERPs we expected to see two previously reported (Eklund et al., 2019, 2021; Eklund & Wiens, 2019; Filimonov et al., 2022; Schlossmacher et al., 2021) correlates: AAN (100-200 ms after stimulus onset), and LP (300-500 ms after stimulus onset). We analyzed these using two separate models, although only the analysis in the AAN time window was preregistered. In these models, we treated mean voltage during the time period (measured on a single-trial basis) as the dependent variable, consciousness as the fixed effect predictor, and the by-participant intercept as the random effect predictor (voltage ~ consciousness + (1|participant)). As specified in the preregistration, we only included the electrodes from the central electrode cluster (Cz, FC1, FC2, CP1, CP2) in this model (both AAN, and also LP are typically strongest in these electrodes (Eklund et al., 2019, 2021; Eklund & Wiens, 2019; Filimonov et al., 2022; Schlossmacher et al., 2021) . To visualize the scalp distribution of AAN and LP in terms of t values, we examined how consciousness influenced ERPs by running the model separately for each channel. We performed this analysis without differentiating between following and opposing vocal responses.

To model which brain sources contribute to AAN and LP, we performed source estimation using sLoreta (standardized low resolution brain electromagnetic tomography), which solves

the inverse problem of EEG source localization by generating a reference-free and polarity-independent single linear solution based on the linearly weighted sum of all scalp electrode potentials (Pascual-Marqui, 2002). Previous intracranial and brain imaging studies have validated the accuracy of the sLORETA (Mulert et al., 2004; Pizzagalli et al., 2004; Zumsteg et al., 2006). For each subject, sLORETA images of activation on cortical gray matter were generated using Montreal Neurological Institute's standardized template (MNI152). The resolution of the present reconstruction is limited by the small number of EEG electrodes, and the lack of individual MRIs (Song et al., 2015). Statistical analysis of source activations was performed separately for early (AAN; 100-200 ms) and late (LP; 300-500 ms) time windows by comparing the source density distributions in the conscious and unconscious conditions voxel-by-voxel using t tests. The results were corrected for multiple comparisons using permutation testing. Unlike the analysis on ERPs (which was performed on single-trial data), sLoreta analysis was based on average ERPs. This analysis was not preregistered.

3. Results

3.1. Behavioral results

Results showed that the participants greatly differed in their ability to consciously detect the perturbation (Figure 2). The mean perturbation magnitude determined by the staircase procedure was 23 cents (min 1 cent, max 71 cents). The mean proportion of critical trials (i.e., trials with a perturbation whose size was adjusted using the staircase) reported as aware during the experiment was 70%, but performance varied considerably between participants (min 16%, max 95%). The overall result is in line with that of Hafke (2008), who showed that perturbation magnitudes of 19 cents are, on average, below participants' 75% threshold of conscious perception.

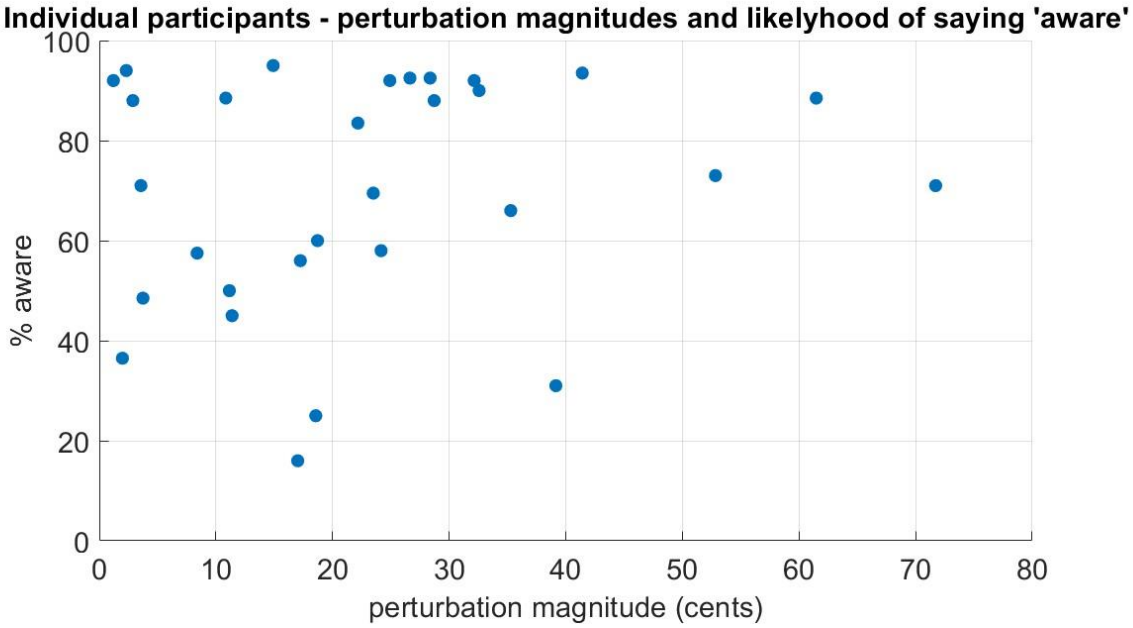

Figure 2: Individual participants' thresholds for conscious perception. X axis represents the perturbation magnitude played to each participant during the experiment, obtained by the staircase method. Y axis represents the likelihood of the participant labeling a trial with an 'aware' rating (i.e., rating scale alternatives 1–3).

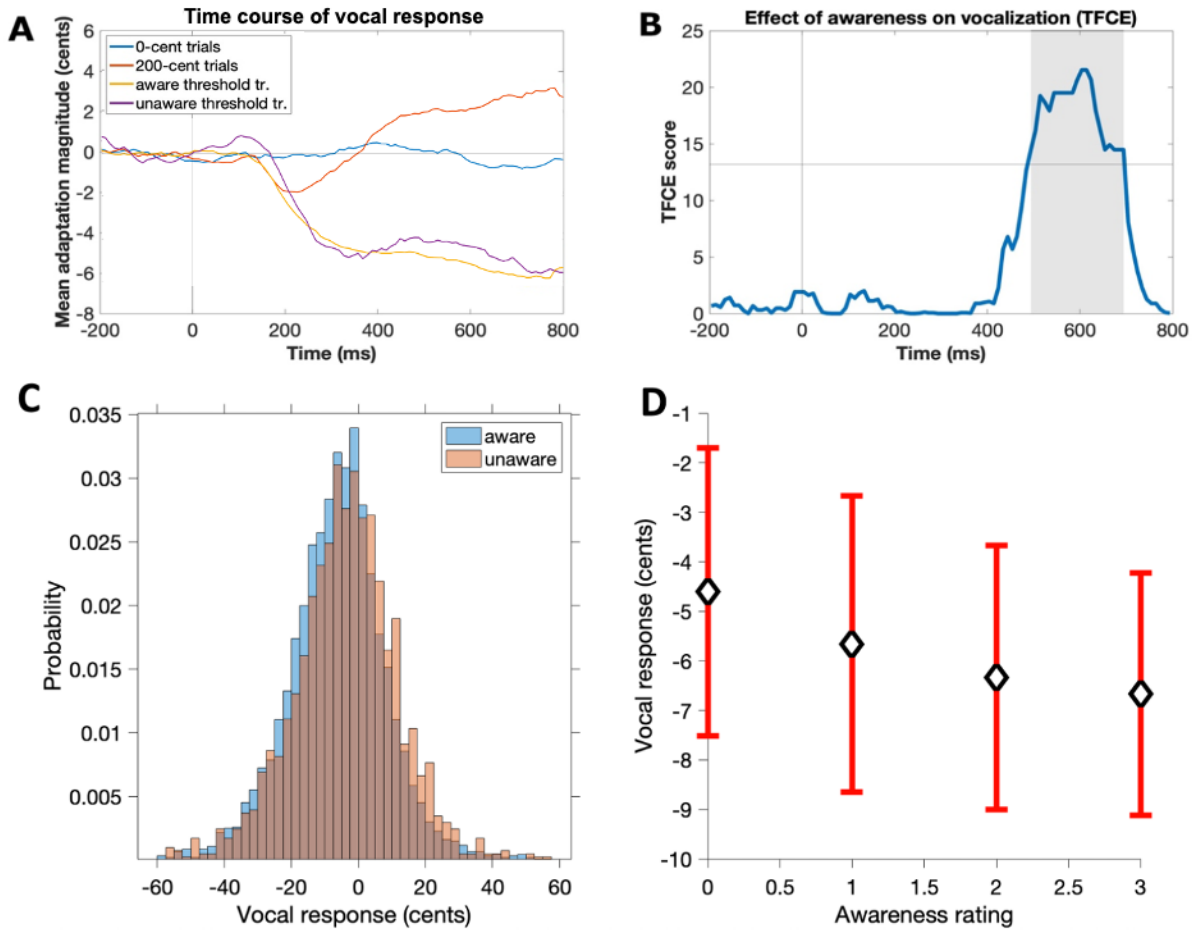

Figure 3: Vocal response results. (A) Mean vocal response. On the x axis, zero represents perturbation onset. On the Y axis, zero represents 200 ms pre-perturbation mean pitch. Consciousness ratings are here treated as binary for the ease of viewing (unaware = rating 0). (B) Results of the mass univariate analysis. Highlighted area represents the time interval with a statistically significant effect of consciousness, meaning that significant t-values cluster around this point. Horizontal line represents the statistical significance threshold (p < .05, corrected for multiple comparisons). (C) Histogram of the single-trial vocal responses (pooled across different participants) 494 to 694 ms after perturbation onset separately for unaware (rating 0), and aware (ratings 1-3) trials. (D) Mean vocal response magnitude 494 to 694 ms after perturbation onset as a function of consciousness rating (error bars represent the SEM).

3.2. Vocal responses

Mean time course of vocalization during each type of trial used in the experiment is visualized in Figure 3A. To simplify the visualization of the results, conscious vs. unconscious conditions have been dichotomized for Fig. 2A, although in the statistical analysis (Fig. 2B) the consciousness ratings were not dichotomized. Figure 2A shows that participants also performed vocal responses to threshold-level stimulus, both when they reported being conscious (ratings 1-3; yellow line) or unconscious (rating = 0; purple line) of it. Compared to the biphasic vocal response in high perturbation trials (red line; 200 cent perturbation), threshold level perturbations produced a longer duration vocal response. We quantified the statistical significance (p < .05, corrected for multiple comparisons) of the effect of conscious perception using mass univariate analysis whose result is visualized in Figure 3B. Permutation testing indicated that conscious perception of the perturbation increased vocal response magnitude in the time interval from 494 ms until 694 ms after perturbation onset (gray shaded area in Fig. 2B). As shown in Figure 2C, conscious perception equally modulated both compensatory (i.e., negative) and "following" (i.e., positive) vocal responses, and altogether the responses followed a normal distribution. Vocal response magnitude increased as a function of conscious perception rating in the 494-694 ms time-window (Fig. 2D) across the four rating scale steps.

3.3. ERPs

Graphical summary of the ERP results is shown in Figure 4. Trials rated as unconscious were associated with an oscillatory response (beginning before the perturbation) without clear ERP peaks, while conscious trials show early negative (100–200 ms) and late positive (300–

500 ms) ERP waves (Fig. 3A). We performed linear mixed effects regression tests in order to measure the effect of conscious perception on ERPs produced by the perturbation (Table 1). These analyses focused on two time-windows (AAN and LP) hypothesized to reflect conscious perception. The effect of conscious perception was significant for both the early component and the late time-window, reported in Table 1 (the intercept is the amplitude in unconscious trials, and the Consciousness Estimate indicates how ERP amplitude changes as rating increases one unit). As shown in Fig. 3B and Fig. 3C, the amplitude of the early and late responses increases as a function of consciousness rating, suggesting that these correspond to AAN and LP. The scalp distributions (Fig. 3D and Fig. 3E) of the early and late time window correlates are consistent with what has been previously reported for AAN and LP, although both time windows suggest somewhat a right-lateralized activation.

3.4. Vocal–ERP correlation

We tested for correlations between ERP and vocal response magnitudes. We selected the early and late ERP correlates as presented above, and tested if they correlate with vocal response amplitudes from (a) the same time interval, or (b) the time interval with a significant effect of consciousness (i.e., 464-694 ms), obtained from the mass univariate analysis of vocal responses (Figure 3). We used linear mixed effects regression to compare these variables on

a single-trial basis (pitch ~ erp_amplitude + (1|participant)). None of these 4 tests showed a near significant effect of ERP magnitude on vocal response magnitude.

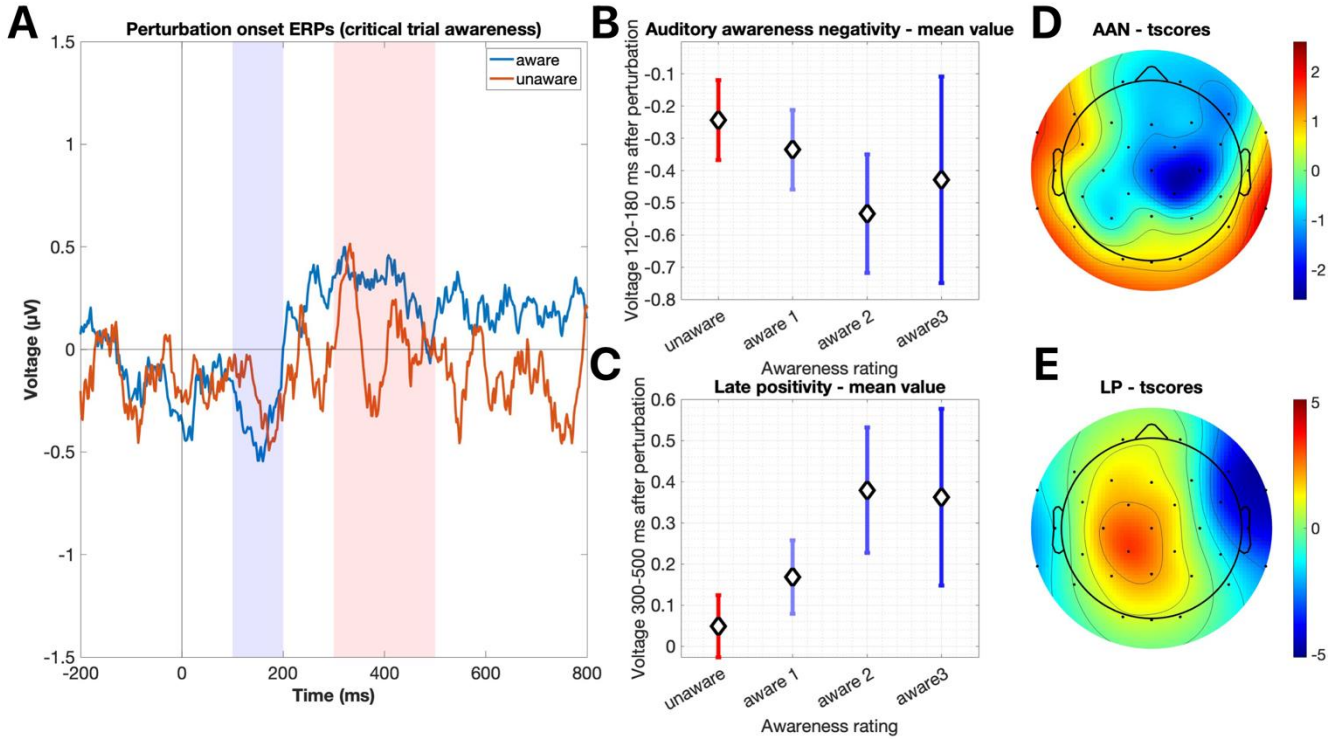

Figure 4: ERP results. (A) Mean ERP responses for trials rated as conscious and unconscious. Perturbation onset is at 0 ms. The consciousness rating is binarized for easier presentation (unaware = rating 0). (B) AAN amplitude as a function of consciousness. Error bars represent standard error of mean. (C) LP amplitude as a function of consciousness. Error bars represent standard error of mean. (D) Scalp distribution of AAN (map of t-values). (E) Scalp distribution of LP (map of t-values).

Table 1: Results of linear mixed effects regression on the effects of consciousness of early and late ERPs.					
Auditory Awareness Negativity, AAN (100-200 ms)					
Parameter	*Estimate*	*Lower 95% CI*	*Upper 95% CI*	*t*	*p*
Intercept	-0.19	-0.30	-0.08	-3.36	0.0008
Consciousness	-0.10	-0.17	-0.03	-2.98	0.0029
Late Positivity, LP (300-500 ms)					
Intercept	0.04	-0.16	0.25	0.39	0.69
Consciousness	0.18	0.11	0.25	4.96	< 0.0001

3.5. Source estimation

Figure 4 visualizes sources that were statistically significantly modulated by conscious perception of the perturbation during AAN (top panels), and LP (bottom panel) time-windows. This analysis was performed by contrasting dichotomized consciousness ratings (i.e., rating 0 vs. ratings 1–3). Table 2 and Table 3 lists the MNI coordinates of the (statistically significant) sources maximally modulated by conscious processing of vocal feedback pitch changes in the AAN, and LP time-windows, respectively. All local maxima are reported in the tables, but if multiple significant sources exist within a single structure, only the source with the highest effect of consciousness is presented in Tables 2 and 3.

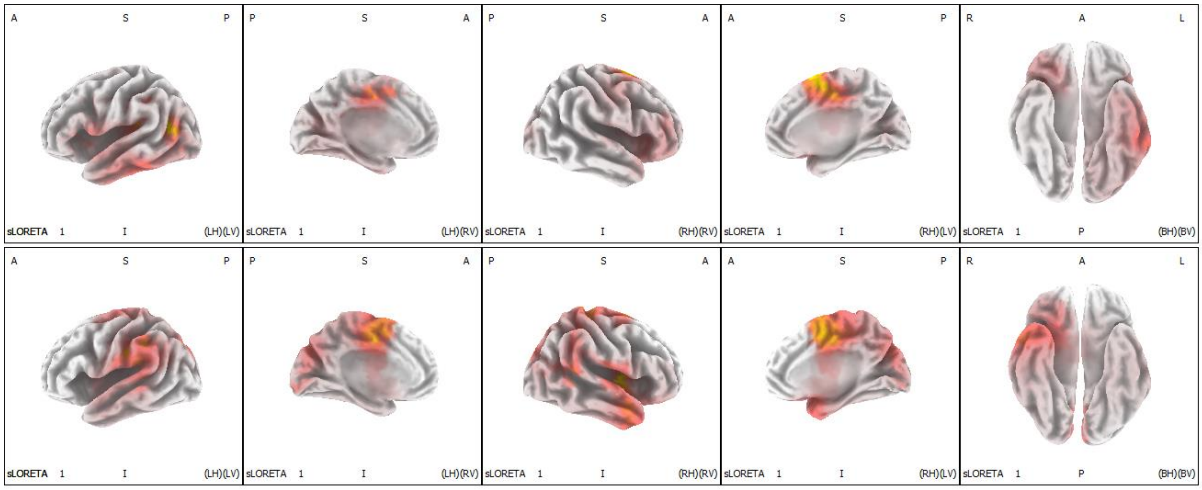

Figure 5: The estimated current source density maps of statistically significant ($p < .05$) modulation by consciousness (t test results, corrected for multiple comparisons). First row: AAN (100-200 ms post perturbation onset), second row: LP (300-500 ms post perturbation onset).

During the AAN time window, activity was modulated in distributed areas involving temporal, frontal, parietal, and even occipital cortex. In the temporal cortex, the effects of consciousness were strongest in the posterior part of left superior temporal gyrus and left inferior temporal cortex. Inferior frontal cortex and insula were activated bilaterally. Activations were also present in areas corresponding to motor and somatosensory areas, and strong activity was present especially in bilateral paracentral lobule and middle part of the cingulate cortex.

In the LP time window, bilateral paracentral lobule and middle cingulate cortex again showed strong modulation by conscious perception. Activity in the superior temporal gyrus was also modulated by conscious perception bilaterally. Conscious perception related activity is also present near the boundary of temporal and parietal cortex (this effect is somewhat left lateralized), in addition to more posterior parietal/occipital effects. Unlike in the AAN time window, the LP time-window showed considerably weaker effects in the frontal lobe.

Table 2. MNI coordinates of the maximum source activations in the AAN time window					
X	Y	Z	t-value	BA	Structure
-40	-55	20	-3.92	22	Superior Temporal Gyrus
10	10	70	-3.91	6	Superior Frontal Gyrus
10	0	60	-3.87	6	Medial Frontal Gyrus
15	10	65	-3.79	6	Middle Frontal Gyrus
-55	-65	15	-3.76	19	Middle Temporal Gyrus
-35	-40	20	-3.66	13	Insula
10	-10	50	-3.61	24	Cingulate Gyrus
5	-15	50	-3.55	31	Paracentral Lobule
20	0	60	-3.54	6	Sub-Gyral
-40	-30	30	-3.46	2	Postcentral Gyrus
-45	-30	30	-3.39	40	Inferior Parietal Lobule
-60	-35	-25	-3.23	20	Inferior Temporal Gyrus
-40	-45	35	-3.18	40	Supramarginal Gyrus
-55	10	10	-3.16	44	Precentral Gyrus
-55	-35	-25	-3.13	20	Fusiform Gyrus
-55	-70	5	-3.12	19	Middle Occipital Gyrus
-35	-35	10	-3.08	41	Transverse Temporal Gyrus
25	30	-5	-3.07	47	Inferior Frontal Gyrus
35	20	0	-2.93	47	Extra-Nuclear
-20	-45	30	-2.88	31	Precuneus
-40	-30	-15	-2.82	36	Parahippocampal Gyrus
-20	-65	15	-2.77	31	Posterior Cingulate
20	15	-15	-2.71	47	Subcallosal Gyrus
-15	-70	15	-2.67	18	Cuneus
20	30	-25	-2.65	47	Orbital Gyrus
-25	0	-45	-2.64	20	Uncus
-50	-70	30	-2.61	39	Angular Gyrus

Table 3. MNI coordinates of the maximum source activations in the LP time window					
X	Y	Z	t-value	BA	Structure
40	0	10	3.39	13	Insula
5	-5	55	3.25	6	Medial Frontal Gyrus
5	-5	50	3.24	24	Cingulate Gyrus
-45	-30	30	3.23	40	Inferior Parietal Lobule
5	5	60	3.20	6	Superior Frontal Gyrus
50	-5	10	3.19	6	Precentral Gyrus
-50	-25	30	3.17	2	Postcentral Gyrus
5	-15	50	3.08	31	Paracentral Lobule
65	-45	15	3.03	22	Superior Temporal Gyrus

As discussed further below, the results of the source localization should be interpreted cautiously. To try to validate the source reconstruction results, we ran control analyses where we contrasted the high-perturbation against no-perturbation (i.e., control) trials. While the number of trials included in these analyses are relatively low (because these control conditions were mainly included as behavioral controls), we reasoned that this contrast should reveal activation in cortical areas known to be involved in auditory feedback control of speech. The results revealed activations in frontal, temporal and parietal areas, largely overlapping with the source localization results reported above (see Supplementary Material).

4. Discussion

Using an experimental approach that allowed us to contrast instances where participants consciously perceive errors in their auditory feedback with trials where the same error goes unnoticed, we characterized the neural and behavioral correlates of conscious perception of errors in one's own voice. Our results showed that short latency vocal responses to pitch perturbations were elicited even when participants failed to consciously notice the error, but conscious perception of the error in auditory feedback correlated with stronger vocal responses at late time windows (around 500-700 ms after the error). That consciousness modulated vocal responses suggests that models of speech feedback control need to explain how unconscious and conscious modes of speech feedback control differ in terms of their function, and neural correlates. Our results indicate that conscious perception of an error in

one's own vocalization correlated with ERPs in early (AAN) and late (LP) time windows. Source reconstruction results suggest that during both these time windows, activity in distributed cortical areas correlated with conscious perception.

4.1. Effect of consciousness on vocal responses

The present results confirm the hypothesis that vocal responses to pitch perturbation are mediated by unconscious processes (Hafke, 2008; Keough et al., 2013; Xu et al., 2020). Because consciousness correlated with vocal responses only in relatively late time windows, our result is consistent with the proposal that the early vocal response component (VR1) is determined by unconscious processes, whereas the later component (VR2) can be modulated by consciousness (Hain et al., 2000).

That finding that consciousness only modulated late vocal responses aligns with current models of conscious perception. The early, unconscious part of vocal response is assumed to be mediated by a rapid, serial control circuit: mismatch between intended and produced vocalization activate error units in auditory cortex, which communicate the error to frontal cortex to rapidly initiate corrective movements. While this circuit compares auditory feedback to the learned, feedforward motor predictions (based on DIVA; e.g., Tourville & Guenther, 2011), the circuit itself is serial (i.e., "feedforward"), and does not involve the activation of recurrently activated cortical feedback loops. Theories of consciousness assume that this type of feedforward neural activity is not associated with conscious perception, although such activity can nevertheless trigger behavioral responses (Hurme et al., 2017; Lamme & Roelfsema, 2000). Consequently, consciousness likely only correlated with late vocal responses because conscious perception required the activation of feedback connections to trigger sustained, recurrent brain activity. This suggests that conscious perception of pitch errors in vocalization may enable more precise adjustments to speech motor commands (enabling, e.g., more precise control of prosody). Within the DIVA model, the more precise control of vocalization based on consciously perceived errors in auditory feedback could indicate that (the feedforward) motor targets are updated based on the consciously detected error, whereas the rapid, unconscious auditory speech feedback control is enabled by "adding" information about the error to the ongoing motor commands

(e.g., Guenther, 2016). As discussed in section *4.3. The role of consciousness in speech feedback control*, we emphasize that the present findings are correlative, and therefore do not demonstrate that the participants volitionally modified their vocalization based on the consciously detected errors.

In the present study, consciousness was associated with relatively minor changes in the vocal response magnitude. This is understandable, given that we did not instruct participants to modulate their vocalization. In our results, clearly consciously perceived perturbations (i.e., rating 3) were associated with almost 2 cents larger vocal responses than unconscious perturbation (i.e., rating 0; Fig. 2D), corresponding to over 10% increase in vocal response magnitude relative to (average) perturbation magnitude. The effect of consciousness on vocal response magnitude is more significant when one compares it to how much vocal responses change as a function of perturbation magnitude. In the study by Scheerer & Jones (2018) increasing the perturbation from 0 to 40 cents increased the early vocal response altogether about 10 cents, but the late response only little over 3 cents. Although direct comparisons between studies is difficult due to methodological differences, this comparison suggests that the effect size of the influence of conscious perception on vocal response magnitude may be meaningful. More generally, in the present study, the vocal response seems to have a somewhat longer duration when compared to previous studies. We attribute this difference to the fact that in our study the perturbation lasted longer than in many previous studies.

Our results are in line with previous research (Hafke, 2008; Scheerer & Jones, 2018), suggesting that participants can detect 20 cent pitch perturbations, on average, with roughly 75% accuracy. However, our results also suggest that there is a lot of individual variation the perceptual thresholds, and some participants had very small perceptual thresholds. It is possible that the large individual variation we observed here is due to methodological limitations. Measuring the thresholds turned out be challenging. We assume that a two-alternative forced-choice paradigm that minimizes the influence of criterion shifts in perceptual decisions would enable more precise measurement of detection thresholds when compared to the yes-no task employed in the present study. Because the perturbations had a long duration in the present study, it could also be argued that some

participants could detect the perturbation based on some confounding information such as beat tones (a vibration caused by the two simultaneous tones that differ slightly in frequency). We used sound-isolating in-ear earphones and embedded auditory feedback in background noise to eliminate the beat-tones. However, it is difficult to verify that we were able to eliminate beat tones completely. Finally, the difficulty in measuring perceptual threshold may be the fact that with low perceptual thresholds, detection of the perturbation is significantly influenced by the natural variation of pitch during vocalization (i.e., participant detects natural shifts in the pitch of their voice, but reports this as a "perturbation").

4.2. Neural correlates of consciously perceiving errors in auditory feedback

The ERP observed in the conscious condition in the present study resembles previously reported ERPs to pitch perturbations (Behroozmand & Larson, 2011a; Scheerer & Jones, 2018a). The ERPs we observed lack the classical P1-N1-P2 pattern often observed in perturbation studies likely due to the small size of the perturbations. Scheerer & Jones (2018) observed that only perturbation magnitudes larger than 20 cents displayed the P1-N1-P2 pattern.

The ERP correlates of conscious perception in the present study reveal a similar pattern of correlates as conscious perception of purely "external" auditory stimuli (i.e., stimuli not-related to the individual's own behavior), although, unlike in previous studies with "external" stimuli, the scalp distributions of AAN and LP are somewhat right lateralized (Dembski et al., 2021; Eklund et al., 2021; Eklund & Wiens, 2019; Filimonov et al., 2022). The primary sources of AAN have been in previous studies (that use external stimuli) localized to posterior superior temporal cortex (Dykstra et al., 2016; Eklund et al., 2019; Gärtner & Gutschalk, 2021; Wiegand & Gutschalk, 2012), although some results also report activity in frontal cortex (Dykstra et al., 2016; Eklund et al., 2019). Intriguingly, the present source localization results suggest that activity in distributed cortical areas contributed to AAN, in addition to sources in the left auditory cortex. Frontal activations were largely lacking in LP time window in the present study. This contrasts the typical interpretation that LP underlies

“accessing” conscious contents for task-relevant processing through mechanisms that involve the frontal cortex (Pitts et al., 2012; Schlossmacher et al., 2021).

The present source localization is limited in resolution due to the small number of electrodes whose locations were not digitized, and the use of template brain anatomy (Song et al., 2015). Confounds associated with speech (e.g., activity observed near the temple regions could be contaminated by vocalization) and oscillatory confounds in ERPs (see below for discussion) could also bias the results of source reconstruction. Yet, the observed sources are encouragingly consistent with the neural basis of speech production (Behroozmand et al., 2022a; Tourville et al., 2008; Toyomura et al., 2007). The control source reconstruction analyses are also largely consistent with the circuitry underlying speech production, although it should be noted that they are more widespread than the neural circuits assumed to underlie auditory feedback control of speech. Next, we first discuss the source activations in light of neural correlates of consciousness. After this, in the next chapter, we discuss how the observed sources activations may relate to neural mechanisms of speech motor control.

The widespread nature of the sources correlating with conscious perception of the perturbation in the AAN time window raises the possibility that conscious perception of errors in one’s own vocalization (and possibly the subsequent modifications to vocalization) is mediated by activity in frontal and parietal areas. Given that the sources in AAN time-window strongly overlapped with areas known to be involved in speech feedback control (Guenther, 2016), the present results suggest that that the same circuit that underlies speech motor control may also mediate conscious perception of the errors in vocalization. Put in terms frequently used in consciousness research, the present results suggest that participants may be able to consciously “access” information processed by the speech feedback control circuitry.

Based on theories of consciousness, conscious perception of error in vocalization could require, for example, that information about the detected error is integrated into a singular network with its own cause-effect power (often correlating with parietal activity; Tononi et al., 2016), that sensory activation “ignites” strong, sustained activation in distributed areas (Mashour et al., 2020), that higher-order frontal mechanisms take the auditory error

information as content (Brown et al., 2019), or that auditory cortex activates feedback connections to form recurrently communicating neural coalitions (Lamme, 2010; Lamme & Roelfsema, 2000). By and large, the present results are consistent with any of these theories, and future research is required to test which theories best capture the neural processes that correlates with the perception of errors in one's own auditory feedback.

The observed correlates of consciousness could reflect processes that do not directly produce conscious perception of pitch errors in vocalization, but rather "just correlate" with it (i.e., the correlates may reflect "prerequisites" or consequences of conscious perception; Aru et al., 2012). For example, the correlates observed in the present study likely include neural correlates of attention to one's vocalization as the participants closely attended to their voice to detect the perturbation. Attending the sound of one's own voice modulates ERPs (Hu et al., 2015a; Liu et al., 2018) in the same time-windows as consciousness in the present study, and additional research is needed to tease apart the overlap between consciousness and attention. Research suggests that attention and conscious perception interact but can also be dissociated from each other (Koivisto et al., 2005, 2006; Pitts et al., 2018).

In the present study, detecting the perturbations required participants also to separate the artificial pitch shift from normal variation in the pitch of their vocalization. This type of conscious monitoring of the source of the error is known to modulate vocal response amplitudes (Franken et al., 2023b; Subramaniam et al., 2018). The neural correlates of source monitoring of vocalization remain unknown, but based on studies in other modalities, it may be mediated by efference copy circuits similar to speech feedback control (David et al., 2008), and activate frontal and parietal regions such as the insula and temporoparietal junction (Kühn et al., 2013; Zito et al., 2020).

The ERPs observed in the present study contained an oscillation (roughly 10 Hz, i.e., alpha frequency) that was prominent especially when participants failed to consciously perceive the perturbation (Fig. 3A). The cause of this oscillation remains unclear. It could indicate that participants were more likely to not consciously notice the perturbation when it was presented at a specific phase of ongoing spontaneous neural activity. Prestimulus oscillations

have been shown to predict the perception of external auditory stimuli (C. Kayser et al., 2012; S. J. Kayser et al., 2016; Keil et al., 2012; Rahn & Basar, 1993). Secondly, because the perturbations were presented at a constant delay after vocalization onset in the present study, the oscillations could also reflect processes related to speech motor control, or to tracking the sensory consequences of speech (Cheung et al., 2016). Thirdly, the confound could also reflect e.g., muscular artifacts associated with vocalization.

4.3. The role of consciousness in speech feedback control

The sources that correlated with conscious perception overlap with the circuitry of speech feedback control. Vocalization errors are assumed to be detected in higher-order auditory cortex in posterior superior temporal gyrus (pSTG; which receive efferent copies from the motor cortex) (Hickok, 2022). Consistent with this, in the present study, left pSTG was activated during AAN and LP time windows. In the DIVA model, auditory errors are assumed to be translated to motor coordinates in the right inferior frontal gyrus (rIFG; Tourville et al., 2008; Toyomura et al., 2007). Activity in this area correlated with consciousness in the AAN time-window. Activity in the left IFG also correlated with consciousness during AAN. This area is an integral part of all models of speech production (Guenther, 2016), and it has been suggested to contribute to speech feedback control by regulating activity in sensorimotor areas (Behroozmand et al., 2022a). Activity in the left IFG has also previously been reported to correlate with AAN in (Dykstra et al., 2016). Also consistent with present results, brain imaging results suggest that right insular cortex activity correlates with errors in speech feedback (Toyomura et al., 2007). Bilateral paracentral activity (i.e., supplementary motor area), and the adjacent Cingular cortex correlated strongly with consciousness in both AAN and LP time windows. Both of these areas are activated during speaking (Guenther, 2016; Picard & Strick, 1996), and their stimulation or lesions results in speech-arrest or mutism (Filevich et al., 2012; Guenther, 2016). In the LP time-window, the area near the boundary between parietal and temporal areas correlated with consciousness. This corresponds to area referred to as spt in the dual-stream model, assumed to underlie sensory-to-motor transformations (Hickok, 2022). Activation in nearby areas during LP also includes the angular gyri, which have been reported to correlate with processing altered auditory feedback (Behroozmand et al., 2022a).

What is the relationship between the observed correlates of conscious perception of the perturbation and vocal control? There are at least two not mutually exclusive explanations. First, the observed correlates of consciousness may have causally modulated vocal responses. Given that both AAN and LP preceded the time-window when vocalization was modulated by consciousness, this conclusion is in line with the observed data. According to the standard interpretation, conscious control of behavior is mediated by processes taking place in the LP time window, although some evidence suggests that already early correlates of consciousness could mediate behavioral changes (Railo et al., 2015). Given that source reconstruction suggested that activity in frontal and parietal areas correlated with conscious perception in AAN time window, our findings are consistent with the interpretation that these processes are part of the neural mechanisms that initiated corrections to vocalization when the error was consciously noticed. However, neither AAN or LP amplitude predicted vocal response magnitudes, suggesting that the two ERP correlates of consciousness may not causally drive vocal responses.

The alternative explanation is that conscious perception of the perturbation (and therefore its neural correlates) did not causally influence the vocal responses. Based on this interpretation, a "third factor" explains the observed association between conscious perception and vocal responses. It could be, for example, argued that participants consciously detected the perturbations only on trials where they succeeded to selectively attend to the perturbation—and the same attentional selection possibly mediated amplified vocal responses. This interpretation is consistent with the fact that attention could modulate vocal responses (Hu et al., 2015a; Liu et al., 2018).

Even if consciousness may not necessarily causally influence the sensory feedback control of speech, it could play some other functional role in speech motor control and causally mediate adjustments to feedforward motor commands. For example, it is reasonable to assume that a person who consciously notices unwanted acoustic features in her own voice (e.g., a patient with speech deficits), might be able to learn optimal motor commands faster than a person who does not notice such features. If this is the case, consciousness might mediate changes that happen at longer time scales (e.g., across an experiment; (Hantzsch et al., 2022)) than

examined in the present study. Finally, while in the present study we examined a vary basic and automatic feature of speech motor control, future experiments with more complex speech tasks (e.g., spoken sentences where prosody has to be controlled deliberately to convey a precise meaning), might be better suited to uncover the functional role of consciousness in speech motor control.

4.4. Conclusion

Our results suggests that feedback control of speech functions in two different modes: A rapid unconscious mode, and a slower conscious mode that builds on the unconsciously determined vocal response. Activity in distributed cortical areas, including temporal, frontal and parietal cortices correlated with conscious perception of errors in vocalization, overlapping with circuits that underlie speech feedback motor control. Lack of understanding about how humans become conscious of their own voice, and how this enables them to voluntarily modulate their speech represents a significant gap in our understanding of the mechanisms of speech. Our results represent the first steps towards understanding this process, but significant questions remain open: What are the functional contributions of different cortical areas to conscious perception of errors in one's own vocalization? Through what mechanism does conscious perception modulate vocalization? Could biases in how one consciously perceives one's own voice lead to clinically meaningful speech deficits?

5. Author contributions

H.R. and D.S. designed the study. D.S. collected the data, and performed the statistical analysis, and visualizations. H.R. supervised data preprocessing and analysis, and R.B. supervised the source reconstruction and analysis. D.S. and H.R. wrote the first draft of the paper. All authors provided feedback and modifications to the manuscript, and approved the final version of the manuscript.

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