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Research Article

The influence of feature-based attention and response requirements on ERP correlates of auditory awareness

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Abstract

In search for the neural correlates of consciousness (NCCs), it is important to isolate the true NCCs from their prerequisites, consequences, and co-occurring processes. To date, little is known about how attention affects the event-related potential (ERP) correlates of auditory awareness and there is contradictory evidence on whether one of them, the late positivity (LP), is affected by response requirements. By implementing a GO-NOGO design with target and nontarget stimuli, we controlled for feature-based attention and response requirements in the same experiment, while participants rated their awareness using a perceptual awareness scale. The results showed a prolonged auditory awareness negativity (AAN) for aware trials, which was influenced neither by attention nor by response requirement. The LP was affected by both attention and response requirements. Consistent with the levels of processing hypothesis, the LP was related to consciousness as a correlate of the processing of higher-level stimulus features, likely requiring access to a "global workspace." Our findings further suggest that AAN is a proper ERP correlate of auditory consciousness and thus a true NCC in the auditory modality.

Keywords: consciousness; awareness; auditory; hearing; electroencephalography; threshold; auditory awareness negativity; late positivity; level of processing hypothesis; event-related potentials; global workspace theory; recurrent processing theory; phenomenal

Introduction

Over 30 years have passed since the search for the neural correlates of consciousness (NCCs) started in the early 1990s by Crick and Koch (1990). While vision remains the most explored perceptual modality (Crick and Koch 1998, Koivisto and Revonsuo 2010, Faivre et al. 2017, Förster et al. 2020), other modalities, especially hearing, have recently started to draw more attention in the NCC research (Gutschalk et al. 2008, Bekinschtein et al. 2009, Brancucci et al. 2016, Eklund and Wiens 2019, Dembski et al. 2021, Schlossmacher et al. 2021, Filimonov et al. 2022). Among the various types of NCCs and other available methods with different strengths, electrophysiological markers are especially suitable for studying perceptual consciousness because electroencephalography (EEG) is a reliable instrument to investigate cognitive processes that happen on a short time scale (Luck 2014).

In vision and hearing, the major electrophysiological NCCs are reflected in different waves of the event-related potentials (ERPs) between aware and unaware stimuli. They include early visual awareness negativity (VAN), appearing during the N1-N2 time window (Koivisto and Revonsuo 2010, Koivisto and Grassini 2016, Eklund and Wiens 2018), auditory awareness negativity (AAN) (Eklund and Wiens 2019, Schlossmacher et al. 2021, Filimonov et al. 2022), occurring in the similar time window as VAN, and the late positivity (LP), appearing in both modalities in the P3 time range. Recently, Dembski et al. (2021) have suggested an umbrella term for the awareness negativity family, called perceptual awareness negativity (PAN), which is found in vision, hearing, and somatosensory modalities. AAN typically appears over the occipital, temporal, or fronto-central areas, depending on the EEG reference, at ∼150–200 ms stimulus onset, while the LP appears at ∼300 ms post-stimulus (Eklund and Wiens, 2018, Eklund and Wiens 2019, Dembski et al. 2021, Eklund et al. 2019, 2021, Schlossmacher et al. 2021, Filimonov et al. 2022). However, depending on the task and stimulus complexity, these components can shift in time (Mathewson et al. 2009; Melloni et al. 2011, Leckey and Federmeier 2020, Schlossmacher et al. 2021).

It is important to isolate the true NCCs from their prerequisites, consequences, and co-occurring processes, for example

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from attention or response selection that might happen at the same time, before or after awareness (Aru et al. 2012, de Graaf et al., 2012, Tsuchiya et al., 2015, Koch et al. 2016). In addition to this technical limitation, modern theories of consciousness are based on different philosophical backgrounds and explanatory strategies (Signorelli et al. 2021), which makes conflicting interpretations possible for the same empirical findings. Theories and conceptual frameworks that acknowledge the existence of distinct phenomenal and access or reflective consciousness, such as the recurrent processing theory (RPT) (Lamme 2000), consider early components from the PAN family as the NCCs of phenomenal consciousness, while the contrasting view, held by proponents of the global neuronal workspace theory (GNWT), regards them as preconscious (Dehaene and Changeux 2011). According to the GNWT, only when a stimulus is selected by attention for further processing in a global neuronal workspace, involving higher-order cognitive functions in the fronto-parietal areas, conscious experience of the stimulus emerges (Dehaene and Naccache 2001; however, see recent modifications in Sergent et al. (2021).

As for the isolation of NCC proper from other cognitive processes, both PAN and LP have undergone substantial examination without concluding results. A significant body of literature in vision attributes task relevance (in particular, response requirement) not only to the LP (Pitts et al. 2012, Pitts et al. 2014a, Shafto and Pitts, 2015, Koivisto et al. 2016, Ye and Lyu 2019, Cohen et al. 2020, Dellert, et al. 2021, Dellert et al. 2022, Kronemer, 2022) but also to VAN (Pitts et al. 2012, Pitts et al. 2014a, Shafto and Pitts, 2015, Dellert et al. 2021). In the auditory modality, this relationship is less studied. To isolate NCCs in hearing, Eklund et al. (2019) manipulated response requirements in a tone detection task to dissociate response selection from awareness and found that both AAN and LP were unaffected by it. On the other hand, Schlossmacher et al. (2021) reported that the auditory LP was evoked only by task-relevant stimuli. In their study, AAN was modulated by both awareness and task relevance. Sergent et al. (2021) reported that enhanced P300, which constitutes the LP, was modulated by the task relevance or by the random sampling in the no-report condition and no such modulation was observed in the AAN time window. Taken together, the results are still inconclusive regarding the role of VAN/AAN and LP when it comes to separating the NCCs proper from other co-occurring processes.

Attention is another factor that may be confounded with awareness or may influence it. Whether attention is a prerequisite for awareness or whether attention and awareness can occur independently remains to be a highly debated topic. In the visual modality, evidence exists for both awareness requiring attention (Koivisto et al. 2009; Cohen et al. 2012) and not (Lamme, 2003; Koivisto and Revonsuo 2008; Koch and Tsuchiya, 2012; Maier and Tsuchiya, 2021). Furthermore, various types of attention, which are functionally distinct, can have different relations with awareness: in vision, Koivisto and Revonsuo (2008) found a dissociation between the ERP correlates of "feature-based" attention [selection negativity (SN)] and visual awareness (VAN), showing that they are independent processes, but in another study reported, by contrast, that "spatial" attention to visual stimuli is necessary for visual awareness and its neural correlate VAN to arise (Koivisto et al. 2009). The correlate of attention in the N2 time range (∼200 ms) in vision has been labeled SN (Hillyard and Anllo-Vento 1998). A functionally similar component in hearing, the processing negativity (PN), has been reported in the N1 time range (∼100 ms) and measured over fronto-central electrodes (Näätänen et al. 1978, Luck and Kappenman 2011). As for the NCCs, numerous studies have shown that PAN strongly correlates with awareness, whereas LP correlates with attention (Polich 2007, Koivisto and Revonsuo 2008, Koivisto et al. 2009, Pitts et al. 2012, Pitts et al. 2014a, Shafto and Pitts, 2015, Eklund et al. 2019, 2021, Förster et al. 2020, Dellert et al. 2021); however, debates regarding the relationship between PAN and attention remain (Bola and Doradzińska, 2021).

To date, little is known about how different forms of attention affect the recently discovered ERP components of auditory awareness. In the present study, we particularly focus on feature-based attention, which denotes an independent type of selection based on the stimulus-specific features and enhancement of their processing (Saenz et al. 2002, Koivisto et al. 2009, Cavanagh et al. 2023). Also, the evidence of whether LP in the auditory domain is affected by the response requirements is still contradictory and inconclusive; therefore, further research is required. To address these issues, we implemented a GO-NOGO experiment where both feature-based attention and response requirements were manipulated in a syllable discrimination task. Participants were asked to actively attend to one of the three syllables, which was different in each block and considered as a target stimulus. In the GO condition participants responded to the target stimuli with a button press, while in the NOGO condition, they withheld responding to targets and instead pressed a button when they did not hear target stimuli (yet heard all other stimuli). In this manner, the participants were selectively focusing processing resources on the features of the targets, as they were the task-relevant stimuli and the participants were asked to actively attend to the targets to carry out the task. In this case, activity associated with awareness in unattended trials without responding would reflect the direct correlate of consciousness. The subjective awareness of the stimuli was probed after each trial with a three-level perceptual awareness scale (PAS; Ramsøy and Overgaard 2004, Eklund et al. 2019). First, we implemented an exploratory mass-univariate factorial analysis to find the electrode clusters and time windows for further examination, contrasting aware targets with response vs unaware nontargets without response. Then we assessed the effects of awareness, attention, and response requirements on the auditory NCCs with linear mixed-effects models, using all the data. We also ran the Bayesian analysis to check for null effects of the critical interactions. Based on the previous electrophysiological studies using auditory and visual near-threshold stimulation (Koivisto and Revonsuo 2008, Koivisto et al. 2016, Ye and Lyu 2019, Förster et al. 2020, Schlossmacher et al. 2021), we expected awareness to be associated with AAN, while response requirement and attention to be associated with LP.

Methods

Participants

We did not predefine the sample size; however, we aimed at getting a minimum of 30 participants or more until we reached an 8-month time limit. Forty-eight healthy right-handed participants (age: $M = 25.15$years, SD = 3.98, 29 women and 19 men) were recruited from the Turku area. Before taking part in the experiment, participants gave their informed consent in accordance with the Declaration of Helsinki. The study was accepted by the Ethics Committee for Human Sciences at the University of Turku. All participants reported normal or corrected-to-normal vision and normal hearing. The exclusion criteria were failure in calibrating individual auditory thresholds within a 30%–70% detection rate, not following instructions, or noisy EEG data, meaning substantial noise over the majority of the electrodes before and after the preprocessing. Three participants were excluded from the study: one had touched the earphones during the experiment, and others failed to report awareness. Additionally, 13 participants had to be excluded from the EEG analysis because of noisy data or absence of trials in one of the eight main experimental conditions (Table 1). This resulted in a total sample of 45 participants for behavioral and 32 for the EEG analysis. Unaware targets in the NOGO condition accompanied by response were the stimulus type with the smallest number of trials ($M = 18.6$, $SD = 11.4$, $min = 3$, $max = 46$). In order to exclude the possibility that low trial count influenced our results, the ERPs were statistically analyzed with classical and Bayesian linear mixed-effects models, which included data from conditions with 10 or more trials.

Apparatus and stimuli presentation

Three near-threshold sound stimuli (syllables "du," "vi," and "me," spoken in a male voice) were downloaded from www.freesound.org and adjusted to approximately the same length (143 ± 17 ms) and volume (default normalization option) by Audacity software (v. 3.1.3). They were presented using PsychoPy (version 3.0.7) (Peirce et al. 2019) on a Windows 10–based computer. The stimuli were presented binaurally using in-ear earphones (Neuroscan, 10 ohm 1/4 stereo). Responses were recorded with an Xbox gaming control (model 1708). The three above-mentioned syllables were chosen because the participants were able to discriminate between them in our pilot experiment ($N = 9$) when they were presented near threshold. The syllables were used because it was easier to discriminate between them compared to simple tonal sounds according to the results from the pilot study.

Procedure

The study implemented a GO-NOGO design in which a total of six experimental blocks (100 trials/block) were performed by each participant. For half of the participants, the first three blocks were GO blocks, in which the targets were responded to with a button press, and the other three blocks were NOGO blocks, in which the participants responded to all other stimuli except the targets. For the other half of the participants, the order of GO and NOGO blocks was reversed. Each block consisted of 25 target stimuli, 50 non-target stimuli, and 25 catch (empty) trials. Catch trials were added to control the behavioral performance of the participants in assessing their own awareness: a high number of catch trials rated as aware would mean that participants are guessing rather than actually hearing the stimuli. For each participant, each of the auditory syllables served as targets in one GO and one NOGO block, while the other syllables were nontargets. The order in which the syllables were targets was counterbalanced across the participants.

Table 1. Experimental conditions used for statistical analysis in the GO and NOGO tasks with accounting for correct responses

Trial type	GO	NOGO
Aware target	Aware targets with button press	Aware targets without button press
Unaware targets	Unaware targets without button press	Unaware targets with button press
Aware nontargets	Aware nontargets without button press	Aware nontargets with button press
Unaware nontargets	Unaware nontargets without button press	Unaware nontargets with button press

The trial type shows a condition used in the analysis, and GO and NOGO tabs further specify the appropriate type of responding for that condition.

The trial structure is shown in Fig. 1. Each trial began with a blank grey screen presented for 900 ms, followed by a 500 ms prestimulus fixation cross in the center of the screen, a blank screen with a random period of 500–1000 ms, and a stimulus phase, where a sound or a catch trial was presented for 58 ms. Then, after a 900-ms blank screen, a second fixation cross (in the form of letter "x") was presented for 300 ms, followed by a 1020-ms blank screen when participants could respond with a button press. In the GO blocks, the participants were asked to press a button "A" on the joystick if they heard the target stimulus and otherwise to withhold responding; in the NOGO condition, they were asked to respond with the same button if they did not hear the target stimulus. After the response/withholding, the response participants were asked to rate their awareness on a modified version of the PAS (Ramsøy and Overgaard 2004; Sandberg, 2015), which had three levels corresponding to whether they heard the stimulus clearly, weakly, or not at all. We used the modified three-point version of PAS for consistency with similar AAN studies in hearing (Eklund et al. 2019, 2021, Eklund and Wiens 2019). In the current design, the second fixation cross was helpful for participants to localize the time window of the sound presentation (which was discovered in a pilot study); without it, they would have had to guess when the stimulus presentation ended and whether the response phase began.

Before the actual experiment, participants performed a practice task with 10 audible stimuli at normal volume to better understand the procedure. The practice task implemented a GO condition. After the practice task and when the instructions were understood, participants performed a calibration procedure to indicate their individual awareness thresholds for each syllable: during the calibration, participants rated their awareness for all three sounds. The calibration of syllables' volume level consisted of one or two blocks having 160 and 120 trials, respectively: each of the three sounds were calibrated individually with the "two-down one-up" staircase procedure. If any of the three thresholds could not be calculated after the first block, a calibration continued with the second block. After the calibration, participants performed a validation task, including PAS and a stimulus discrimination task, where they were asked to identify a sound if they heard it. The inclusion criteria were 30%–70% of aware trials and at least 20% of correct recognition for each syllable. A trial was scored as aware when the syllable was heard either weakly or clearly.

EEG recording

EEG signals were recorded using active 64 Ag/AgCl sintered ring electrodes attached to a recording cap (Easycap GmbH, Germany) and NeurOne system (Mega Electronics Ltd) amplifier using a bandpass of 0.05–100 Hz, with a 500-Hz sampling rate. EEG was processed using EEGLAB (Delorme and Makeig 2004) (version, 2021.1) and MATLAB (2018), 2018 (version, R2021b).

Data analysis

Behavioral data were analyzed with R (R Development Core Team 2019) software, using lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017) packages. We implemented a number of aware trials with correct responses $\sim$ attention $*$ responding $+ (1|id)$ linear mixed-effects model with responding and feature-based attention as fixed effects and random intercept as a random effect. The trial types, representing experimental conditions, are shown in Table 1, and aware–unaware contrasts for specific conditions are demonstrated in Table 2. R's ANOVA function, using Satterthwaite's method, was performed on the models to obtain

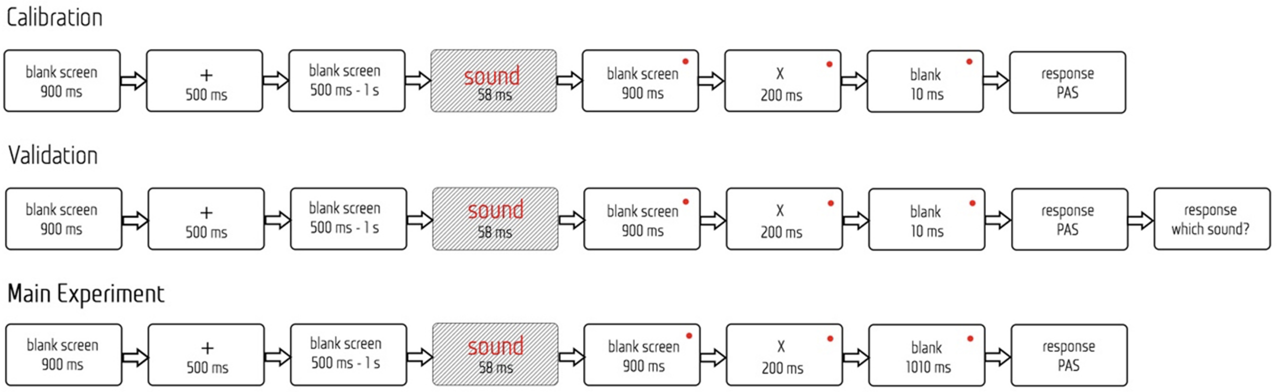

Figure 1 Trial structure. Trials in calibration, validation, and experiment started with a blank screen, followed by a fixation cross, a random 500–1000 ms interval before stimulus presentation, blank screen, followed by a fixation cross. Each trial ended with an awareness rating. In the validation trial, a stimulus discrimination question ("which sound did you hear?") was presented after the awareness rating. The red dot indicates the moment from when the participants could respond with a button press on a joystick

Table 2. Aware–unaware differences for different conditions

Differences	Aware	Unaware
Nontargets without response	Aware nontargets from GO	Unaware nontargets from GO
Nontargets with response	Aware nontargets from NOGO-	Unaware nontargets from NOGO
Targets without response	Aware targets from NOGO	Unaware targets from GO
Targets with response	Aware targets from GO	Unaware targets from NOGO

ANOVA tables. A separate model was implemented on awareness ratings without accounting for the correctness of responding, in which case pressing/not pressing a button was not considered. Both "weakly" and "clearly" heard trials were counted as aware trials, since participants rarely report hearing (Eklund and Wiens, 2018, Eklund and Wiens 2019) or seeing (Koivisto and Grassini 2016) the near-threshold stimuli clearly. To exclude any order effects, we compared the results of two participant groups who first performed either the GO or NOGO condition by adding a random effect of order in the model on awareness ratings with accounting for correct responses. The significance level was set to 0.05.

The EEG was re-referenced to linked mastoids (average of electrodes TP9 and TP10). The EEGLAB function "pop_rejchan" was used to remove bad channels, with the options kurtosis, joint probability, and spectrum checked using an absolute threshold of 4 SD. Additional visual inspection was performed before applying a 0.5-Hz high-pass filter finite impulse response, Hamming windowed; transition bandwidth, 1 Hz; filter order, 1650). The high-pass filter parameter was chosen due to the latest recommendations for improving data quality in similar ERP components or time windows (Zhang et al. 2024). The number of removed electrodes per participant ranged from 0 to 11 electrodes (M = 4.156, SD = 3.303). The EEGLAB function "pop_cleanline" was performed to filter out line noise at 50 Hz. Interpolation was performed on the removed electrode using the built-in spherical interpolation function in EEGLAB "pop_interp." Low-pass filtering at 45 Hz was performed using the "eeg_filtnew" function in EEGLAB. Independent component analysis was performed, and artifactual components were removed by manual inspection (M = 20.4, SD = 10.5, min = 0, max = 35), visualized by the ICLabel plugin (Pion-Tonachini et al. 2019) (version 1.3.). The IC was removed if a substantial noise was present in the IC scalp distribution, power spectrum, and trial-to-trial variability chart. A baseline was corrected to activity from –200 to 0 ms preceding the onset of the auditory stimulus. The remaining bad trials were rejected via EEGLAB function pop_jointprob, using joint probability on the recorded electrodes (local activity probability limit: 4 SD, global limit: 2 SD).

In order to extract the AAN and LP time windows, we have applied a Factorial Mass Univariate ERP Toolbox, FMUT (Fields and Kuperberg 2020), which is an extension of the Mass Univariate ERP Toolbox, MUT (Groppe et al. 2011). FMUT implements factorial ANOVA in a mass-univariate setup. To avoid circularity (Kriegeskorte et al. 2009), we used only one contrast, aware targets with response vs unaware nontargets without response, which contained all the effects of interest. We analyzed trials with accounting for correct responding (Table 1), using all channels and time points in a 0–800 ms time window. To test for statistical significance, a non-parametric permutation approach with 1000 repetitions (Maris and Oostenveld 2007) was selected, and to take into account clustering of effects, correcting for multiple comparisons, permutation-based cluster mass correction (Groppe et al. 2011b) was performed. We choose the family-wise alpha of the test to be 0.05. This resulted in two clusters of statistically significant activity in the AAN and LP time windows.

Since cluster-based methods have lower statistical power and could miss some effects of interest (Kallionpää et al. 2019), especially with few trials in some conditions, we have conducted linear mixed-effects models using lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017) packages in R (R Development Core Team 2019) on the mean amplitudes of time windows and electrode clusters of AAN and LP obtained from FMUT. Awareness, feature-based attention, responding, and their interactions were introduced as fixed effects, and random intercept as a random effect [amplitude ~ awareness × feature-based attention × responding + (1|id)]. R's ANOVA function, using Satterthwaite's method, was performed on the models to obtain ANOVA tables. To confirm the absence of the interactions in the AAN time window and the absence of the effect of awareness in the LP time windows, we ran follow-up Bayesian analyses using rstanarm (Goodrich et al. 2022), bayestestR (Makowski et al. 2019), and emmeans (Lenth 2021) packages. In the Bayesian analyses,

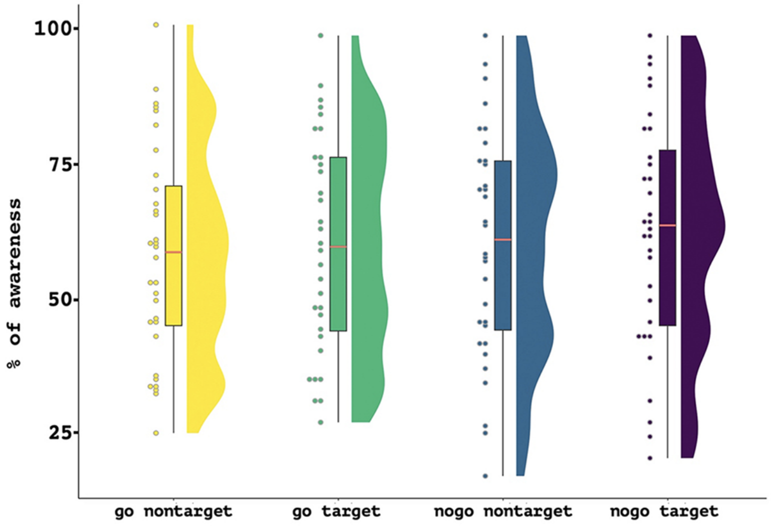

Figure 2 Percentage of aware targets and non-targets as a function of response requirements with accounting for correct responding. The rainclouds show the data distribution, while dots show individual participant's results. In addition, boxplots show standard measure of central tendencies

Bayes factors (BFs) were calculated for the effects and to interpret the interactions we calculated the BFinclusion (BFIncl) factor. The interpretations for BF followed conventional evidence categories (Jeffreys, 1961), where BF between 3 and 0.33 was considered inconclusive evidence and BF of <0.33 supports the absence of the effect of interest. Only the trial types with 10 or more trials per participant were included in the models. In order to get the omnibus influence of the effects of interest, we used a contrast coding scheme for fixed effects in the Bayesian analysis (assigning –0.5 and 0.5 to the factor levels). For assessing the effect of awareness in the LP time window, we ran an additional amplitude ∼ awareness + (1|id) model on a subset of nontarget trials without responding.

Results

Behavior

The number of aware trials with correct responses ∼ attention * responding + (1|id) linear mixed-effects model was calculated for $N = 32$ (results for the full sample, $N = 45$, are available in the Supplementary material) to assess the influence of different factors on the proportion of awareness, without accounting for the accuracy of responses. The analysis shows a significant effect of attention, $F(1,31) = 196.576$, $P < .001$, $M = –33.312$, 95% confidence interval (CI) [–39.372, –27.253] on awareness, showing that targets ($M = 121.792$, $SD = 38.436$) were rated more often as aware than nontargets ($M = 117.667$, $SD = 38.763$). Significant effect of responding, $F(1,31) = 9.821$, $P = .002$, $M = –9.375$, 95% CI [–15.434, –3.316], was also present. The percentages of aware targets and non-targets in GO and NOGO conditions with accounting for correct responses are shown in Fig. 2. When the correct responding was taken into account, the analysis shows significant effects of responding on awareness, $F(1, 31) = 23.467$, $P < .001$, $M = –11.754$, 95% CI [–17.886, –5.623]: the number of aware trials was lower in the conditions requiring responding than in the conditions not requiring responding. No effect of attention or order was present, suggesting that the results were not affected by the order of GO and NOGO conditions.

Catch trials were rarely rated as aware both without (percent of aware catch trials: $M = 3.438$, $SD = 8.704$ in the GO condition and $M = 5.979$, $SD = 4.673$ in the NOGO condition) and with a button response (percent of aware catch trials: $M = 0.708$, $SD = 1.160$ in the GO condition and $M = 3.750$, $SD = 6.998$ in the NOGO condition). In the NOGO condition, catch trials were more often rated as aware than in the GO condition, both with response, $M = –3.042$, 95% CI [–5.567, –0.513], $t = –2.454$, $df = 31$, $P = .02$, and without it, $t = –1.653$, $df = 31$, $P = .047$.

Electroencephalography

ERPs were calculated for 32 participants. Grand averages from Cz electrode are represented in Fig. 3. Scalp topographies for the different conditions show aware–unaware differences in Fig. 4 (Table 2 contains conditions selected for calculating difference waves). Results of mass univariate factorial analyses are represented in Fig. 5.

The results of the scalp topographies of the different conditions in Fig. 4 show mainly negative awareness-related ERP over occipital, temporal, and parietal regions in the AAN time window of ∼250 ms and onward. Targets with responses also demonstrate increased positive activity in the LP time window starting from ∼500 ms onward, similar to the grand averages of the same condition in Fig. 3.

FMUT revealed two statistically significant clusters in to AAN and LP time windows. The AAN cluster (cluster mass = 23 257, P-value = .002) included frontal-central, central, parietal, and occipital channels (Cz, FC1, FC2, C3, C4, CP5, CP6, P7, P8, CPz, Pz, POz, Oz, Iz, C1, CP1, P1, PO3, O1, CP3, P3, P5, PO7, C2, CP2, P2, PO4, O2, CP4, P4, P6, and PO8), and the LP cluster (cluster mass = 19 744, P-value = .006) included frontal, frontal-central, central-parietal, parietal and parieto-occipital channels (Fp1, FPz, Fp2, AF3, AF4, F5, F6, F3, F1, Fz, F2, F4, FC5, FC3, FC1, FC2, FC4, FC6, C5, C3, C1, Cz, C2, C4, C6, CP5, CP3, CP1, CPz, CP2, CP4, CP6, P5, P3, P1, Pz, P2, P4, P6, PO3, POz, and PO4). F-values indicate a significant cluster beginning at ∼220–250 ms over the temporal-parietal and occipital-parietal regions, moving to the central and parietal-temporal region at ∼320 ms and then to the left temporal area at ∼500 ms. A second cluster starts at ∼660 ms in the central, frontal, and parietal areas and spreads further toward temporal and posterior areas.

As the figures indicate, AAN emerges over the posterior and temporal region at ∼220–300 ms after stimulus onset and spreads

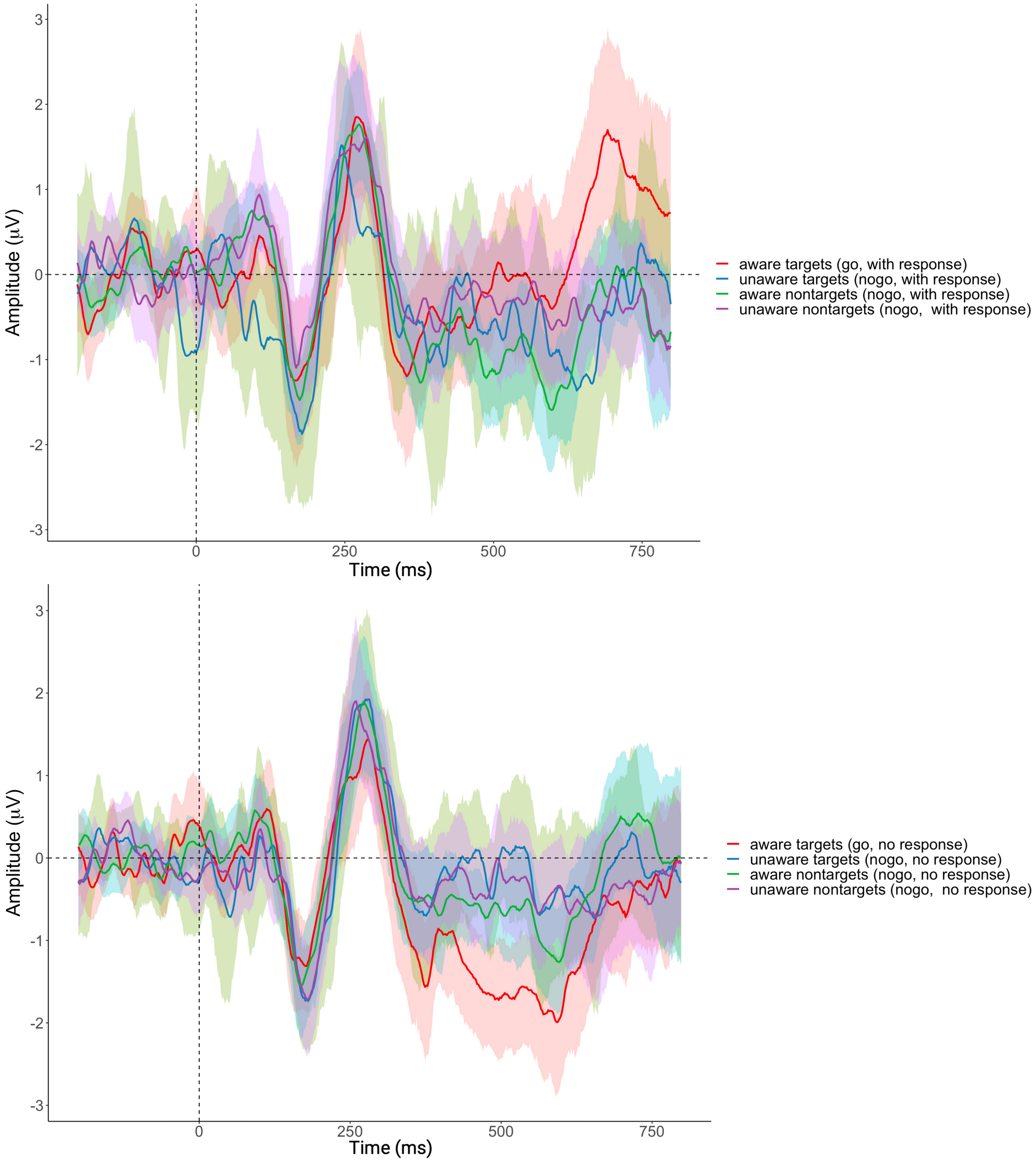

Figure 3 Grand average ERPs of different conditions in Cz electrode. The upper part shows aware and unaware conditions with button response, and the lower part shows these conditions without response

to the central, parietal, and temporal electrodes at least up to 450–550 ms post-stimulus. The LP starts at ∼660 ms after stimulus onset and spreads up to 800 ms post-stimulus. Additionally, the scalp distribution of AAN in its middle and late phases shows some left lateralization.

Taking FMUT results into consideration, we have defined time windows for AAN (220–550 ms stimulus onset) and LP (660–800 ms). The R's ANOVA function on the linear mixed-effects model in the AAN time window showed significant effects of awareness, $F(1, 31) = 29.981$, $P < .001$, and attention, $F(1, 31) = 6.656$, $P = .011$. Follow-up Bayesian analysis concluded the absence of critical interactions (BF = 0.098 and BFincl < 0.001 for Awareness × Attention, BF = 0.020 and BFincl < 0.001 for Attention × Responding, BF = 0.015 and BFincl < 0.001 for Awareness × Responding, BF = 0.011 and BFincl < 0.001 for Awareness × Attention × Responding interactions) in the AAN time window. The amplitude differences in the AAN time window are shown in Fig. 6 (upper panel): aware trials are more negative than unaware in both conditions with and without responding, which indicate AAN. In addition, a more widespread, but less strong negativity between aware targets and nontargets in the condition with responding can indicate PN, which occurs in auditory GO/NOGO studies.

In the LP time window (Fig. 6, lower panel), significant effect of awareness, $F(1, 31) = 18.458$, $P < .001$, Responding × Awareness, $F(1, 31) = 4.282$, $P = .039$, and Responding × Attention interactions, $F(1, 31) = 4.029$, $P = .046$, were present. The two-way interactions suggest that attention and responding increased the positivity of

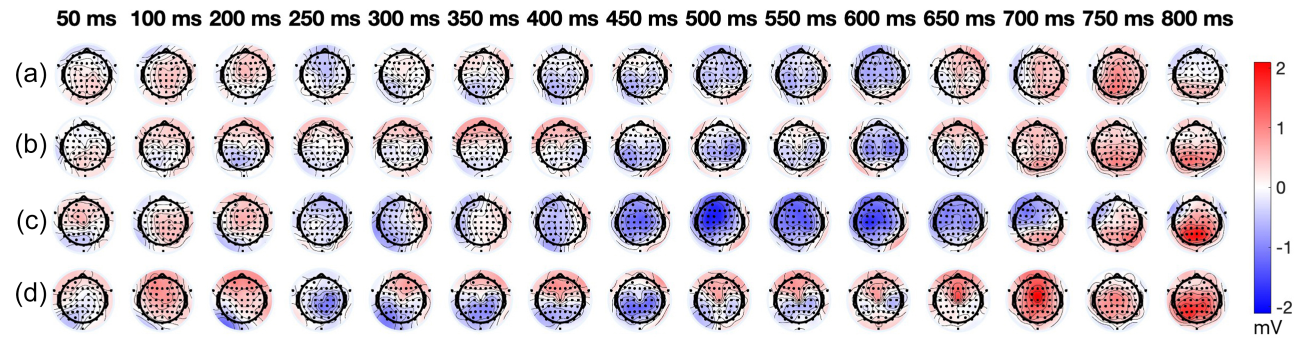

Figure 4 Scalp topographies of the aware–unaware differences in different conditions. (a) nontargets without response, (b) nontargets with response, (c) targets without response, and (d) targets with response

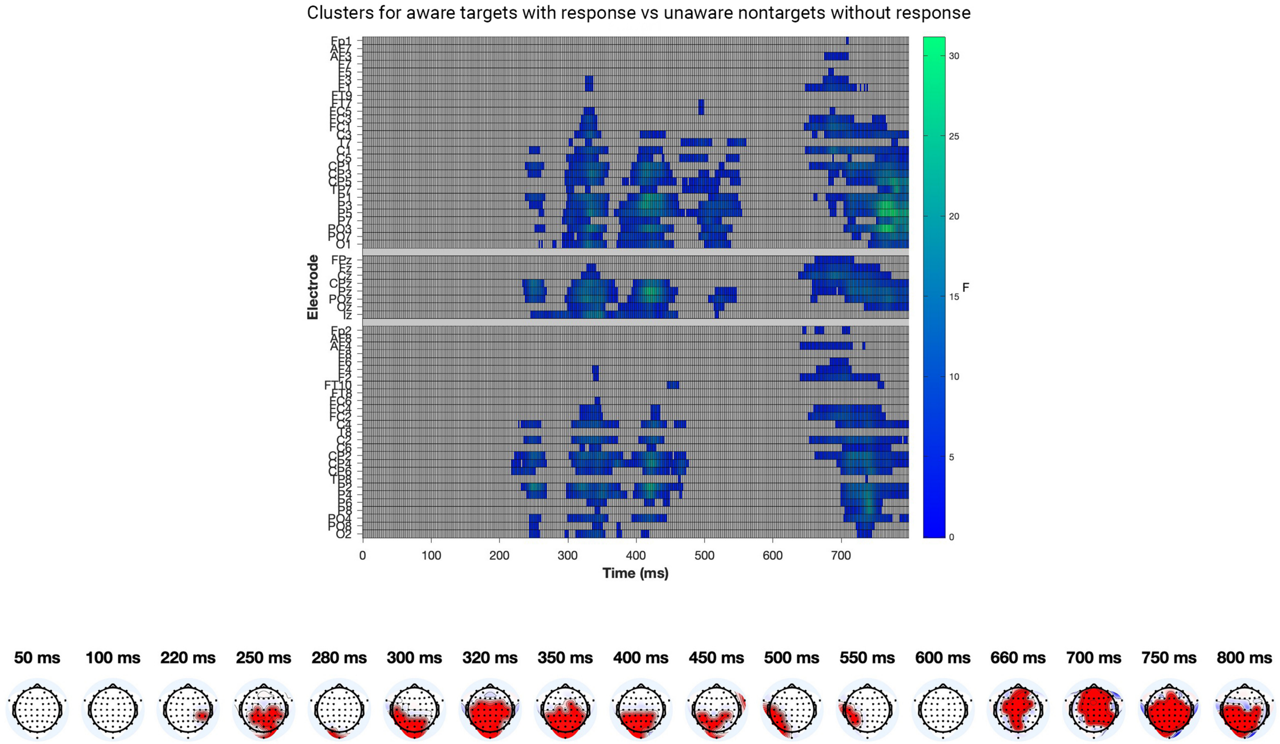

Figure 5 Results of factorial mass univariate analysis. The upper panels show statistically significant contributions of each factor on the ERP amplitudes at each time point and electrode; color denotes *F*-value. The lower panel shows the corresponding statistically significant effects on scalp topographic maps

the amplitudes particularly in aware trials. For responded to targets, the effect of awareness was not significant, 95% CI [−0.063, 1.334], $t = 1.857$, $P = .073$. A follow-up Bayesian analysis separately assesing the effect of awareness [amplitude ∼ awareness + (1|id)] in unattended (i.e. nontarget) trials without response did not support any effect of awareness (BF = 0.132) in the LP, showing that the LP is not a direct correlate of awareness, but rather reflects Eklund et al. 2020 attention or later processes required in responding.

Discussion

The aim of the present study was to examine how feature-based attention and response requirements affect ERP correlates of auditory consciousness. Unlike research in vision, previous studies in the auditory modality have mainly focused on awareness without assessing the effects of attention and responding (Eklund and Wiens 2019; Eklund et al. 2020, Filimonov et al. 2022). A recent study by Eklund et al. (2019) reported that both AAN and early LP were present in trials with and without response requirement. Recently, Schlossmacher et al. (2021) reported that both AAN and LP amplitudes were modulated by task-relevance of the stimuli. It should be also noted that Eklund et al. (2019) and Schlossmacher et al. (2021) studies varied in paradigm and stimuli, which was the most likely cause of controversial results: for instance, in the Eklund et al. (2019) study participants always attended to the same and simpler stimuli. Another study by Sergent et al. (2021) also reported that P300 (an ERP component in the LP time window) was enhanced by the task relevance, while in the no-report condition, a bifurcation in brain dynamics, possibly marking consciousness, started in the AAN time window (250–500 ms). However, the authors did not explicitly mention AAN, describing the ERPs in that time window as a central positive waveform associated with posterior negativity.

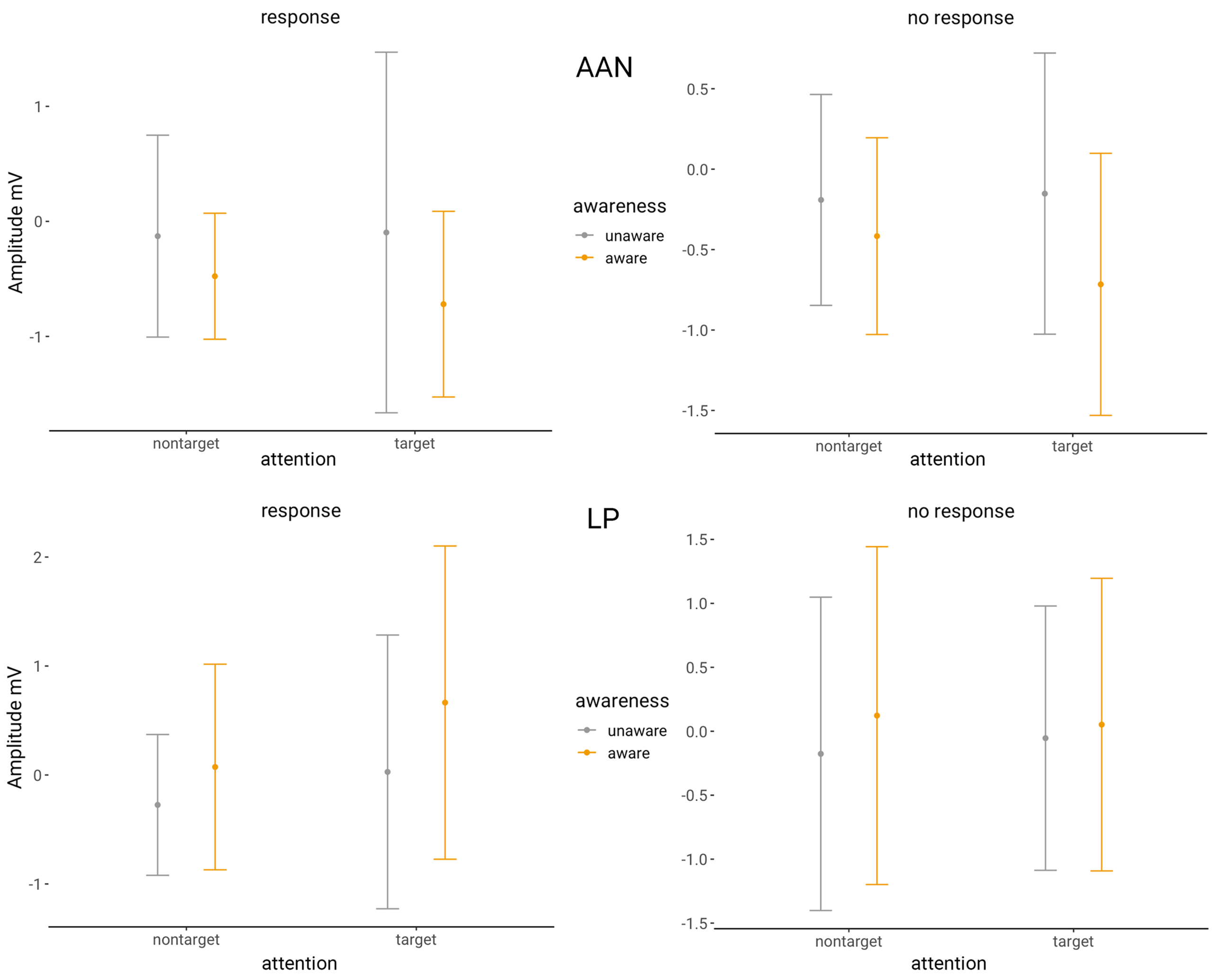

Figure 6 The modeled results from the linear mixed-effects models. Mean amplitudes for aware and unaware trials under different attention and responding conditions in AAN and LP time windows. The error bars represent 95% CI

We studied the effects of feature-based attention and response requirements on auditory awareness and its neurophysiological correlates in the same experiment, implementing a GO-NOGO design. Our results showed prolonged AAN for aware trials, which started at ∼220 ms post-stimulus. A relatively late LP started at ∼660 ms post-stimulus when attention and responding interacted with awareness. Our results suggest that AAN reflected awareness, not feature-based attention or response requirements. The absence of interactions between attention, awareness, and responding in the AAN time window was supported by a follow-up Bayesian analysis. Attention did not have an effect on AAN per se as there was no Awareness × Attention interaction. However, one should note that other types of attention were not examined in the present study; therefore, the results can be generalized only to the specific type of feature-based attention. In feature-based attention, observers selectively focus processing resources (i.e. attend) to the features of the target stimuli in order to carry out the given task that only applies to them. Our study shows that AAN reflects auditory awareness of the stimuli independently of their selection for further processing.

The scalp topography of AAN showed some left lateralization possibly because the sound stimuli were syllables and thus activated left-hemispheric language and speech recognition processes. The AAN was prolonged possibly due to the task and stimulus complexity. It showed significant negative activity over temporo-parietal and posterior electrodes from ∼220–300 ms up to ∼450–550 ms. It showed significant negative activity over temporal, parietal, and central electrodes from ∼220–300 ms up to ∼450–550 ms. A similar pattern for AAN has also been reported in studies using complex auditory stimuli (Schlossmacher et al. 2021) or longer tones (Gutschalk et al. 2008). Similarly, a prolonged VAN was reported in vision when no responding was required in an experiment with a rather complex design (Dellert et al. 2022). While the syllables used in the present study were relatively short in duration (58 ms), they were more complex than the simple tones both physically and as components of spoken language, which could have led to a prolonged AAN time window. It should also be noted that the ERPs were calculated in trials in which target vs nontarget discrimination was made correctly, meaning that the syllables were properly recognized. The latency of AAN could also be explained by the level of processing hypothesis (LoP), where early electrophysiological correlates are associated with the low-level stimulus processing, such as color recognition in vision (Windey and Cleeremans 2015, Jimenez et al. 2021). Jimenez et al. (2021) reported a delayed VAN in a color recognition task and we expect that similar mechanisms could influence AAN delay.

Whether LoP propositions regarding the NCCs are correct or not, it is generally known that different experimental paradigms influence latencies of different ERP components (Mathewson et al. 2009, Melloni et al. 2011).

The scalp topography of AAN demonstrated some left lateralization, which contradicts with the previous findings (Eklund et al. 2019; Eklund and Wiens 2019, Eklund, et al., 2020, Filimonov et al. 2022; however, see Eklund et al. 2021). A possible explanation for the left lateralization is that syllables were processed as speech and speech processing has been found to be left-lateralized in the majority of the population (Mazoyer et al. 2014). Earlier research had also found evidence for pre-attentive speech processing in the left hemisphere (Näätänen et al. 1997, Alho et al. 1998, Rinne et al. 1999); therefore, a tentative conclusion with regard to our results could be that the direct neural correlates of the auditory awareness of speech could be left-lateralized. However, as we did not perform a source reconstruction, it is difficult to say with certainty whether the present activity that showed up over the temporal electrodes actually took place in the left auditory cortex. Additionally, we used only one contrast in FMUT, which could lower the precision of components topography. The results are, nevertheless, consistent with studies which located the sources of AAN to the bilateral auditory cortices (Eklund et al. 2019). While we mainly found activity in the left hemisphere, Eklund et al. (2019) used simple tones instead of syllables, which could have led to bilateral activation observed in their study.

The LP was modulated over frontal, central, temporal, and parietal electrode sites at ~660–800 ms by responding and attention. Similar conclusions were reached by Schlossmacher et al. (2021), who reported no LP for the task irrelevant conditions; however, when task relevancy was factored in, both mid- and late-latency LPs were enhanced, suggesting that the LP is not an NCC proper and mainly indexes some form of post-perceptual processing (Pitts et al. 2014a, Koivisto et al. 2016, Ye and Lyu 2019; Förster et al. 2020), which is in harmony with the RPT (Lamme 2000). It should be noted that our study did not show any positive aware–unaware differences for nontargets with or without responding in the LP time windows, and thus no LP was observed for nontargets. In addition, our Bayesian analysis on nontarget trials without responding did not find any effect of awareness in the LP time window, supporting the null hypothesis and further indicating that the LP is not a correlate of awareness per se.

Although LP appeared later than in most of the previous experiments (Koivisto et al. 2016, Eklund et al. 2019, Filimonov et al. 2022), a plausible explanation for its delayed latency could be the complexity of our task (Leckey and Federmeier 2020), requiring participants to both detect and discriminate between stimuli, as well as to some extent inhibit their responses in the NOGO condition. Furthermore, research in vision has shown that LP is sensitive to stimulus identification and semantics as well as to the response selection (Koivisto et al. 2016, Jimenez et al. 2018, Derda et al. 2019). Delay in LP onset could also be caused by the task-specific inhibition of response after processes of stimulus detection and discrimination. Evidence suggests that a P3 ERP component, which underlines LP, is related to the response inhibition in GO-NOGO tasks (Bruin et al. 2001, Dimoska et al. 2006, Vallesi 2011, Gonzalez-Rosa et al. 2013, Pires et al. 2014) and that its latency is usually delayed in the NOGO condition (Tian and Yao 2008, Barry et al. 2018).

Many studies have linked LP to the task-relevant cognitive processing (Koivisto et al. 2005, Koivisto and Revonsuo 2008, Pitts et al. 2014a). In general, our results may also fit with the LoP predictions (Jimenez et al. 2018, 2021, Derda et al. 2019), which state that NCCs of the PAN family are associated with awareness of lower-level stimulus features, whereas the LP is related to the higher-level properties such as categorization. Our results agree with this statement, suggesting that the LP might be related to awareness of such higher-level features, which also require conscious access and attention.

The association of feature-based attention and AAN does not seem plausible as there were no interactions between attention and awareness. Having simultaneous processes and ERP components, we suggest that feature-based attention could be associated with the PN (Hillyard and Anllo-Vento 1998, Koivisto and Revonsuo 2008, Luck and Kappenman 2011, Näätänen et al. 1978, but see Fogarty, 2020 for objection). There are, however, many factors that may have influenced attention in the way the experiment was conducted: if attention works as a gain control (Hillyard et al. 1973) at an early stage of processing, presenting auditory stimuli that vary greatly in pitch and location makes it likely that attentional effects begin already in the cochlea. If the stimuli, however, are similar in both pitch and location, it is less likely to see early attentional effects since both attended and ignored stimuli are coded by the same pools of neurons until a later stage of processing (Luck and Kappenman 2011). It is possible that the syllables used in our study failed to elicit more negative activity in fronto-central electrodes during the early stage of processing because they were too similar in pitch and appeared bilaterally. Earlier ERP research has also found that early attentional effects are diminished when differences between attended and unattended stimuli are reduced (Hansen and Hillyard 1983). In addition to that, there is evidence pointing to attentional modulation at both early and late stages of perceptual processing depending, for example, on stimulus and task parameters (Vogel et al. 2005).

A substantial body of literature from the visual modality presents inconsistent evidence on whether attention and task relevancy affect VAN. Pitts et al. (2012) found that both VAN (named Nd2 in their study) and SN were enlarged for attended stimuli; however, one cannot exclude a possibility that these components were superimposed and SN has started later: for instance, Koivisto et al. (2009) reported that only the late part of VAN was influenced by attention. In the Shafto and Pitts, (2015) study, whose paradigm and EEG results were reproduced by Dellert et al. 2021, VAN and N170 were both enhanced in the task-relevant condition; however, the authors argued that this could also be caused by a higher inter-trial variability, rather than response magnitude, which could potentially be the case for the Pitts et al., (2012) study as well. Alternatively, attention affects VAN. On the other hand, a study by Kronemer, 2022, using fMRI, scalp- and high-density intracranial EEG, reported that VAN was not influenced by the task relevance. In another study by Dellert et al. 2022, VAN was not affected by attention when the relevance of the target stimulus was uncertain. Also, depending on the type of attention, it could either be associated with awareness or not (Koivisto and Revonsuo 2008, Koivisto et al. 2009). Taken together, results on relation between VAN (PAN) and various types of attention are still divergent.

We found significant effects of feature-based attention and task interactions both with and without awareness at a later stage, and this could be taken to index later attentional processing plus other task-related cognitive operations (Koivisto et al. 2017, Jimenez et al. 2018, Derda et al. 2019). One of the other factors that may have influenced our results is the speed of the stimulus presentation rate. Previous studies have shown that a rapid presentation rate (typically, two to four stimuli per second) is more suitable if the aim is to test attention effects on early sensory processing (Lavie 1995). Conversely, if the stimulus is presented with a slow rate (as in the present study), there is ample time for the brain to process the stimulus and early attentional modulation is not needed (Hansen and Hillyard 1980, Woldorff and Hillyard 1991).

Behavioral findings indicated that responding influenced awareness in conditions with accounting for correct responses. When correct responses were not accounted for, reported awareness was influenced only by attention. The finding that responding did not have a statistically significant effect in the latter condition is not surprising, because the responding variable was confounded with incorrect GO and NOGO responses as, by definition, the accuracy of responses was not considered and the analysis focused only on the awareness ratings. Responding behavior was represented in the analysis by accounting for correct responses and had direct influence on the results. One could argue that responding, when it is performed correctly, already required selective attention and that since our GO-NOGO design contained conflicting responding instructions for targets and non-targets in the GO-NOGO blocks, attention as a factor (2: targets and nontargets) was not statistically significant in the second analysis. However, in overall awareness ratings attention played a significant role, as participants were more often aware of targets vs non-targets. Since target stimuli were more frequently aware than nontarget stimuli in the NOGO condition, responding was associated with lower awareness ratings, which we consider as a limitation of our study design. Therefore, both attention and response requirements influenced awareness. As our ERP results suggest, these effects took place at relatively late stage of processing, indicating that phenomenal consciousness, in case it arises earlier, is not influenced by them.

A possible difference between awareness ratings corresponding to either detection or identification of a stimulus should also be considered. In our experiment, awareness ratings implied detection; however it is possible that some of the "weakly" and most of the "clearly" aware trials reached identification as it was reported in Koivisto et al. (2017). We did not focus on this as few trials were heard clearly; however, since participants were able to discriminate between targets and nontargets by correct responding, the identification probably took place in a considerable amount of "weakly" heard trials.

It is worth mentioning that the present study differed from previous studies in various ways. First and foremost, instead of preselecting electrodes or time windows for measuring AAN and LP, which has been the case in most previous studies (e.g. Eklund et al. 2019; Eklund et al. 2020), we chose to perform factorial mass univariate analysis in order to get a more nuanced picture of how the electrophysiological correlates of awareness are affected by response requirements and attention. By not having preselected time windows, we were able to measure effects related to AAN and LP outside the conventional time windows and electrodes. Our results show that AAN is prolonged, possibly due to stimulus complexity. Instead of mid-latency LP at 350–550 ms, we observed negative awareness-related activation possibly related to stimulus evaluation. As for the LP, the results show a clear effect of attention as well as response requirements at ∼660–700 ms. The downside of using mass univariate analysis is that unexpected effects can be found when having such a broad time window for the analysis while at the same time using all electrodes. Simulation studies have also found that, compared to conventional approaches, mass univariate analysis can yield more false negatives as the control for multiple comparisons is more rigorous. However, a decrease in power is not usually found for large components like the P3 that make up the LP (Groppe et al. 2011). In order to avoid such situation and to prove lack of effects, we implemented linear mixed-effects models and a follow-up Bayesian analyses on these time windows. Secondly, in order to avoid circular analysis, also referred as "double dipping" (Kriegeskorte et al. 2009), we used only one contrast in FMUT, which could possibly reveal the clusters with less precision. A major limitation of our study is a low number of trials in some of the experimental conditions for some participants, resulting from the several conditions needed to manipulate both responding and attention at the same time. Also, while response requirements were controlled, both target and nontarget stimuli were still task relevant, which inevitably adds post-perceptual processing. In contrast, no-report paradigms do not have such caveat; however, they lack trial-by-trial precision leaving degree of awareness unknown. Finally, the effect of the one subtype of attention that was manipulated could have to some extent been swamped by other forms of attention, which were not manipulated.

Implications for further research

Our results support the view that early electrophysiological correlates belonging to the PAN family are the most direct markers of phenomenal consciousness and are not dependent on selective attention or response requirements. As to event-related brain potentials, AAN is the NCC in hearing and the LP is closely related to access or reflective consciousness and other cognitive processes, such as attention and response selection.

We see several implications for future research on the NCCs in hearing. First direction is to further investigate the possible dissociation between AAN and the attention-related PN, utilizing different experimental designs and different types of stimulus materials as well as studying different types of attention. In the present study we did not find an effect of feature-based attention in AAN/PN time window; however, as discussed, there are factors related to the current study that might have influenced present results. Therefore, additional research on dissociating attention and consciousness in the early N1-N2 time window is required.

Another line of further investigation could be related to the lateralization of auditory NCCs for different types of sounds as contents of phenomenal consciousness: it is known that in the majority of the population speech and music are processed asymmetrically by different hemispheres. One could hypothesize that if the basic feature processing modules are lateralized on the cortex, then also the NCCs associated with them would be asymmetrically lateralized. This line of investigation would link lateralized auditory NCCs to the specific sound features and theories of auditory lateralization. Such studies would require EEG source reconstruction and special type of bistable stimulation.

Conclusion

We have controlled for both feature-based attention and response requirements in the same experiment using a GO-NOGO paradigm. Our results show a prolonged AAN for aware trials. AAN is not associated with feature-based attention and response. The LP started at a ∼660 ms post-stimulus time window is present for attended aware stimuli with response requirement. The scalp topography of AAN is left lateralized probably because the sound stimuli were syllables. Our findings indicate that AAN is an electrophysiological correlate of awareness and LP is affected by both feature-based attention and response requirements. LP could be related to the processing of the higher and more abstract features of the stimuli, such as their semantic or conceptual properties, as well as to response selection. This processing requires access to a "global workspace" and thus refers to "access consciousness" or "reflective consciousness" rather than purely "phenomenal" consciousness.

Author contributions

Dmitri Filimonov (Conceptualization, Methodology, Software, Investigation, Formal analysis, Writing—original draft, Writing—review & editing), Andreas Krabbe (Investigation, Formal analysis, Writing—original draft), Antti Revonsuo (Conceptualization, Writing—review & editing, Supervision), and Mika Koivisto (Conceptualization, Methodology, Writing—review & editing, Supervision)

Supplementary data

Supplementary data is available at *Neuroscience of Consciousness* online.

Conflict of interest

None declared.

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Data availability

The data and materials for all experiments and analyses are available at OSF: https://osf.io/u2etp/.

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