NeuroImage 310 (2025) 121168

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Event-related potential correlates of consciousness in simple auditory hallucinations[☆]

Dmitri Filimonov [a,c,d,*], Saana Lenkkeri [b,c], Mika Koivisto [a,c], Antti Revonsuo [a,c,d]

[a] Department of Psychology, University of Turku, Finland
[b] Faculty of Medicine, University of Turku, Finland
[c] Turku Brain and Mind Centre, University of Turku, Finland
[d] Division of Cognitive Neuroscience and Philosophy, University of Skövde, Sweden

ARTICLE INFO

Keywords:
Consciousness
Awareness
Auditory
Hearing
Electroencephalography
Threshold
Auditory awareness negativity
Hallucinations
Auditory hallucinations
Event-related potentials
Global workspace theory
Recurrent processing theory
Phenomenal

ABSTRACT

Neural correlates of consciousness (NCC) have been proposed for perceptual awareness in various sensory modalities. To date, perceptual awareness negativity (PAN) and late positivity (LP) are considered the main NCC candidates, and the question remains which one is the NCC proper. Investigating states where the content of consciousness is independent of the physical stimulus, may provide additional theoretical and empirical value. We studied the event-related potential (ERP) markers of auditory awareness in simple auditory hallucinations using a Pavlovian conditioning paradigm, where participants listened to the near-threshold tones and stimulus-absent trials, rating subjective clarity with the perceptual awareness scale (PAS). The results showed auditory awareness negativity (AAN) — an early event-related potential difference between aware and unaware stimuli — in the hallucinatory condition, suggesting that AAN is an NCC proper in auditory consciousness. Late positivity was absent in simple auditory hallucinations.

1. Introduction

Neural correlates of consciousness (NCC) have been proposed for perceptual awareness in various sensory modalities. To date, the main event-related potential (ERP) NCC candidates are perceptual awareness negativity (PAN) and late positivity (LP) (Dembski et al., 2021). PAN is an umbrella term, highlighting a family of components that share temporal, locational, and functional similarities. They arise over the primary sensory areas in similar temporal windows and are present even when the participants are not required to attend to the stimuli or report them. PAN includes the visual awareness negativity (VAN) (Förster et al., 2020; Filimonov et al., 2022; Koivisto and Grassini, 2016a; Koivisto and Revonsuo, 2010; Jimenez et al., 2018; 2021; Railo et al., 2015; Wiens et al., 2023), the auditory awareness negativity (AAN) (Eklund et al., 2019a, 2019b, 2020; Filimonov et al., 2022, 2024a, 2024b; Zhu et al., 2024) and the somatosensory awareness negativity (SAN) (Dembski et al., 2021; Auksztulewicz and Blankenburg, 2013; Schröder et al., 2021). LP is often observed after PAN for aware task-related or attended stimuli and is thought to be the correlate of conscious access, when the content of consciousness enters subsequent cognitive operations (Jimenez et al., 2018; 2021; Koivisto et al., 2016a, 2016b, 2017; Eklund et al., 2019b, 2020; Eklund and Wiens, 2018; D. Filimonov et al., 2024a, D. 2024b; Pitts et al., 2014a; Cohen et al., 2020; Schlossmacher et al., 2020, 2021; Wiens et al., 2023).

In addition to the experimental evidence, various theories of consciousness interpret and advocate for different NCCs based on their predictions. For instance, LP — an aware-unaware difference in the time window of the P3b component and the component itself — is proposed by the Global Neuronal Workspace Theory (GNWT) as the NCC proper, since, according to the theory, one can only be conscious of what one can report (Dehaene and Changeux, 2011; Dehaene and Naccache, 2001; Mashour et al., 2020). However, recent work on the GNWT theoretical extension, the Global Playground, accommodates recent findings and postulates that LP is not always required for consciousness (Sergent

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[☆] This research has received a grant from Signe and Ane Gyllenbergs Foundation.

[*] Corresponding author.
E-mail address: dmitri.d.filimonov@utu.fi (D. Filimonov).

https://doi.org/10.1016/j.neuroimage.2025.121168
Received 11 November 2024; Received in revised form 19 March 2025; Accepted 21 March 2025

et al., 2021). PAN, on the other hand, can be accommodated by Recurrent Processing Theory (RPT), which postulates that phenomenal consciousness arises before cognitive access and is correlated with localized recurrent processes between higher and lower areas (Lamme, 2000, 2010). Other theories that predict perceptual awareness in the earlier time window free of subjective reports can also interpret PAN as supportive or neutral evidence, depending on their predictions (Seth and Bayne, 2022): for instance, IIT attributes consciousness to integrated information and predicts that it is associated with posterior cortical regions, where PAN generators are based.

The evidence for PAN has been found in experiments that utilize no-report paradigms, where participants passively perceive stimuli, and in a combination of report and non-report paradigms (Cohen et al., 2020; I. Schlossmacher et al., 2021; Zhu et al., 2024; Dellert et al., 2021). It has also been observed in studies that introduce different tasks, levels of stimulus processing, and manipulate attention and task relevance (Koivisto et al., 2017; M. Jimenez et al., 2021; D. Filimonov et al., 2024a; D. 2024b; Eklund et al., 2019b, 2020; Eklund and Wiens, 2018; Shafto and Pitts, 2015; Wiens et al., 2023; Dellert et al., 2022). The main limitations of no-report paradigms are the uncertainty of whether and when the participants are aware of the stimuli, the possible inclusion of non-conscious processing, and that such paradigms do not prevent post-perceptual stimulus related mentation (Pitts et al., 2018; Block, 2019; Duman et al., 2022; Tsuchiya et al., 2016).

We propose a complementary approach to further understand perceptual awareness and the NCC: additional evidence could be provided from states where the content of consciousness arises without any physical stimulation, such as dreaming and hallucinations. The current paradigm is not a no-report paradigm; however, it avoids physical stimulus-related activity and, therefore, NCC will reflect consciousness in purer form (closer to dreaming).

The present study investigated the NCC in simple auditory hallucinations of pure tones. Auditory hallucinations refer to a phenomenologically rich group of endogenously mediated percepts that are common in clinical but also occur in healthy populations (Blom, 2015). The most common type is verbal hallucinations (Blom, 2015). One previous study on a related topic examined auditory illusions (Faramarzi et al., 2021) and reported electrophysiological patterns resembling AAN and LP. The study utilized a continuous paradigm, where illusions were caused by speech-in-noise detection. Therefore, the ERPs were response-locked and the onsets of illusory perceptions were statistically estimated. Unlike hallucinations, which occur without physical stimulation, illusions are based on sensory input, which was a continuous background noise in the Faramarzi et al. (2021) study. Their design also included response requirements, which could serve as a potential confounding factor if the aim had been to dissociate the NCC proper from preceding or co-occurring cognitive processes (Aru et al., 2012; de Graaf et al., 2012; Koch et al., 2016; Tsuchiya et al., 2015). Nevertheless, the Framarzi et al. (2021) study provided converging evidence that the main NCC candidates seem to be robust across different states of perceptual awareness, leading to the suggestion of a similar mechanism.

Theory-specific predictions on hallucinations vary in detail and relate to predictions regarding perceptual awareness. According to RPT, local recurrent activity in modality-specific sensory areas is required for phenomenal consciousness (Lamme, 2010); therefore, hallucinations would also involve corresponding recurrent processing. In RPT, hallucinations could be indexed by PAN. In GNWT, hallucinations involve activation in the modality-specific sensory areas, coordinated by the prefrontal cortex, ACC, and parietal areas (Naccache and Munoz-Musat, 2024). GNWT-related studies report the absence of LP under hypnotically induced perceptual deficits (negative hallucinations) (Naccache and Munoz-Musat, 2024), but the theory does not make explicit predictions regarding the NCC of hallucinations per se. IIT could interpret hallucinations as differences in the causal structure of primary sensory regions, in accordance with the composition axiom (Albantakis et al., 2023). In that case, IIT would treat PAN (or AAN) as an electrophysiological index of hallucinations, similar to perceptual awareness (Boly et al., 2017; Koch et al., 2016). According to predictive processing theory, hallucinations arise from disruptions in predictive mechanisms, wherein top-down priors shape bottom-up sensory signals (Seth et al., 2012). However, predictive processing theory does not position itself as a theory of consciousness but rather as a conceptual framework and, therefore, does not make specific predictions regarding specific hallucinatory NCC (Hohwy and Seth, 2020). According to the Temporospatial theory of consciousness, hallucinations are caused by reduced anticorrelations between the cortical default mode network and the central executive network (Robinson et al., 2016), which undermines the distinction between internally and externally generated stimuli (Stefanelli, 2023). This theory explains awareness and hallucinations in terms of non-additive pre-stimulus and post-stimulus interaction, remaining neutral regarding NCC candidates: if the NCC appear to be a visible result of that interaction, it might support the theory or, otherwise, contradict it.

In the present study, we focused on auditory hallucinations and used a stimulus-locked design to investigate the timing of the ERP components precisely with high temporal resolution. We utilized a Pavlovian conditioning paradigm (Powers et al., 2017) to induce simple auditory hallucinations of tones in silence. For auditory hallucinations, we expected to find auditory awareness negativity in an approximately similar time window and over a similar location as in perceptual awareness: approximately from 200 ms to 300 ms post stimulus onset and over the fronto-central, temporal and parietal areas, which is common to linked mastoid reference (Filimonov et al., 2022; 2024a, 2024b). We did not make any specific predictions about the LP component.

2. Methods

2.1. Participants

Thirty-three healthy right-handed participants were recruited from the Turku area. Before participating in the study, they gave their informed consent in accordance with the Declaration of Helsinki. The study was approved 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 to calibrate individual auditory thresholds within 45 %−65 % detection rate, absence of hallucinations (< 10 trials), or noisy EEG data in any of the conditions, meaning substantial noise over the majority of the electrodes before and after preprocessing. Ten participants were excluded from the study: two had noisy EEG data, for two participants the EEG files could not be retrieved, one participant reported awareness in all trials, while others lack hallucinatory experiences (reporting fewer than 10 trials). The remaining sample size consisted of 23 participants. Fig. 1 demonstrates signal detection theory sensitivity values for both included and excluded participants.

2.2. Stimuli

Near-threshold beep stimuli (tone A, 440 Hz, 5 ms Hamming window) were presented using PsychoPy (version 3.0.7) (Pierce et al., 2019) on a Windows 10–based computer. The stimuli were presented binaurally using in-ear earphones (Etymotic ER2 Tubal Insert Earphones, 10 ohm ¼ stereo). Responses were recorded with an Xbox gaming control (model 1708).

2.3. Procedure

The study contained six blocks with 25 near-threshold sounds and 75 stimulus-absent trials (100 trials in each block, 600 trials in total). To trigger auditory hallucinations, we implemented a Pavlovian paradigm: before each block a conditioning sequence with 20 consecutive near-threshold sound trials was presented, after which the block started.

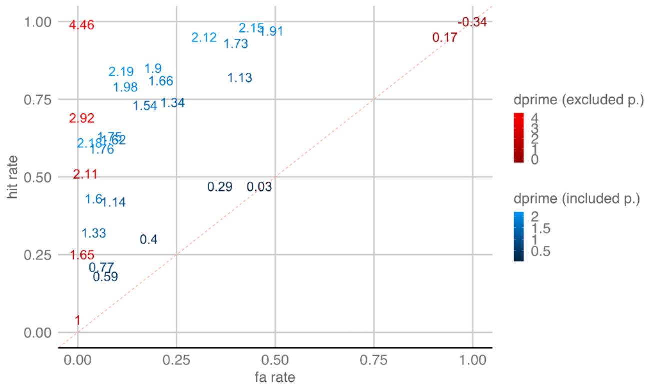

Fig. 1. d' values of the participants included in the analysis (blue gradient, $n =$ 23) and excluded (red gradient, $n = 7$). The y-axis denotes the proportion of aware trials when the near-threshold sound stimulus was presented, while the x-axis denotes the proportion of false alarm trials associated with the hallucinatory experience: when trials without a stimulus were rated as aware. One excluded participant's behavioral data could not be retrieved.

Experimental blocks contained few stimulus-present trials; a sound was always played at a fixed interval after the dot, increasing the probability of hallucinations. Predictive fixation dot and sound occurrence relationship were conditioned. Participants were asked to assess the subjective clarity of the sound. The task was not an objective forced-choice discrimination between the presence or absence of a sound and the participants were informed that sometimes the sounds would be presented and sometimes would not.

The trial structure is shown in Fig. 2. The time course of conditioning and experimental trials was identical. Each block began with a conditioning sequence of 20 stimulus-present near-threshold trials, after which the regular block started. Each trial began with a blank grey screen presented for 300 ms, followed by a 350 ms pre-stimulus fixation dot in the center of the screen, a blank 450 ms blank screen and a stimulus period, where sound was played or no sound was presented for 350 ms. Then, after a 600 ms blank screen, participants were asked to rate their awareness on a modified version of the perceptual awareness scale (PAS) (Ramsøy and Overgaard, 2004; Sandberg and Overgaard, 2015), which had three levels corresponding to whether they heard the stimulus clearly, weakly or not at all. We implemented the modified three-point version of PAS for consistency with similar AAN studies in hearing (Eklund et al., 2019a; Eklund et al., 2019b; R. Eklund et al., 2021; Filimonov et al., 2022; D. 2024a, D. 2024b). Both stimulus-present aware and hallucinatory trials corresponded to a PAS rating of "weakly" or "clearly" heard to stimulus/no-stimulus.

Before the actual experiment, participants performed a calibration procedure to find their individual awareness threshold. Calibration consisted of three interleaved 1-up 1-down staircases with 3,3,2,2,2,2,1,1,1,0.5,0.5,0.5,0.1,0.1,0.01 step sizes in db. Each staircase had 5 reversals and started with 0.0001 (0.8 dB), 0.005 (40 dB) and 0.0008 (6 dB) value of initial computers volume. If one of the staircases finished seven trials earlier or more than the others, the data was taken from the last two staircases. After the calibration, a binomial psychometric function with a probit link was fitted to the data from staircases (Wichmann and Hill, 2001) to estimate a 50 % detection threshold. In addition, the threshold was estimated by averaging the last five reversal intensities from each staircase. Finally, a third threshold was estimated as the average of the first two. To assess if the calibration was successful, participants performed a 40-trial validation task with PAS that included 20 sounds and 20 stimulus-absent trials. The first threshold obtained by the function was used. The validation was successful if the false alarm rate fell within the 30 % – 70 % range. Otherwise, a psychometric function plot displaying the three thresholds was shown to the experimenter to choose another threshold, after which a new validation block started. If the second validation failed, a new calibration with a single 1-up 2-down staircase was performed, using a previously estimated threshold as a starting value.

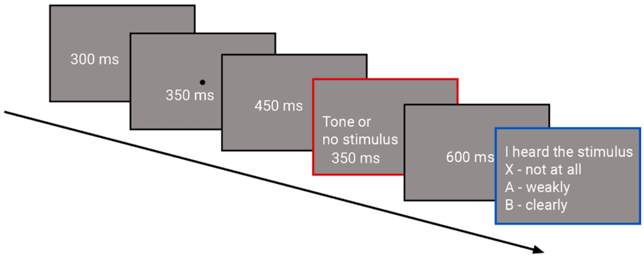

Fig. 2. Trial structure. Every trial started with a 300 ms blank screen, followed by a 350 ms fixation dot, a 450 ms blank screen, followed by a 350 ms period during which either a near-threshold tone or no stimulus was presented. Then, after a 600 ms blank screen, participants saw a response screen.

2.4. *EEG recording*

The EEG data was recorded using active 64 Ag/AgCl sintered ring electrodes attached to a recording cap (EASYCAP GmbH, Germany) and NeurOne (Mega Electronics ltd) amplifier using a bandpass filter of 0.05–100 Hz, with a 500 Hz sampling rate. The EEG was recorded with the Fz electrode reference and then converted to a common average reference during preprocessing.

2.5. *Analysis*

Descriptive statistics (M and SD) on the number of trials and signal detection measures (sensitivity, d' and response bias, beta) for hallucinatory trials were calculated. Two-tailed *t*-tests were used to compare d' to 0 and beta to 1 to test whether the presence of sounds was subjectively discriminated better than expected by chance and whether any response bias was present. The EEG data was processed with EEGLAB (Delorme and Makeig, 2004) (version, 2024.0) and Matlab (version, R2022b). The EEGLAB function "pop_rejchan" was used to remove bad channels using kurtosis, joint probability and spectrum options, with an absolute threshold of 4 SD. After applying a 0.5 Hz high-pass filter (FIR, Hamming windowed; transition bandwidth, 1 Hz; filter order, 1650), additional visual inspection was performed to detect and remove any remaining bad channels. The high-pass filter parameter was chosen based on the latest recommendations for improving data quality for similar ERP components or time windows (Zhang et al., 2023). The EEGLAB function "pop_cleanline" was used to filter out line noise at 50 Hz. The number of removed electrodes per participant ranged from 0 to 12 electrodes ($M = 5.609$, $SD = 2.904$). Low-pass filtering was performed at 30 Hz (FIR, Hamming windowed; transition bandwidth, 6.7 Hz; filter order, 247) after which the continuous EEG was epoched. Artefactual components detected by the independent component analysis were removed by manual inspection ($M = 22.826$, $SD = 8.590$, min $= 0$, max $= 38$), visualized with the ICLabel plugin (Pion-Tonachini et al., 2019) (version 1.4.). An IC was removed if substantial noise was present in both the IC scalp distribution, power spectrum and in the trial-to-trial variability chart. A baseline correction was performed using the interval from −200 to 0 ms of the onset of the stimulus or blank in stimulus-absent trials, and removed electrodes were interpolated using EEGLAB's built-in spherical interpolation function, "pop_interp". The data was re-referenced to the linked mastoids.

The ERPs were analyzed with the LIMO MEEG package (Pernet et al., 2011, 2021), which is an EEGLAB extension that implements a General Linear Model (GLM) to compute within-subject variance across trials and integrates parameter estimates across subjects, performing a statistical test on every data point. We used LIMO to avoid the a priori selection of channels and time windows while preserving statistical power (Fields and Kuperberg, 2020). To test for statistical significance and account for the clustering of effects, correcting for multiple comparisons, a non-parametric permutation approach with 1000 repetitions (Maris and Oostenveld, 2007) and cluster-mass correction for multiple comparisons (Groppe et al., 2011a) were selected. The threshold for significance was set to 0.05. We ran two separate analyses on hallucinatory vs unaware stimulus absent trials and aware vs unaware stimulus present trials.

3. Results

Fig. 3 shows the number and proportion of hallucinatory trials as well as aware trials with sound per participant. The number of hallucinatory ranged from 12 to 220 trials (*M* = 90.913, SD = 69.869), while the aware trial with sound ranged from 27 to 147 trials (*M* = 95.652, SD = 37.350). For the participants who reported hallucinatory experience, there were many hallucinatory trials in general. The number of unaware stimulus-absent trials ranged from 230 to 438 trials (*M* = 359.087, SD = 69.869), while the number of unaware stimulus-present trials ranged from 3 to 123 trials (*M* = 54.348, SD = 37.349). Only 11 participants rated aware stimulus-present trials (*M* = 24.0, SD = 41.030) and only 8 participants rated aware stimulus-absent trials (*M* = 3.696, SD = 9.012) as “clear”. For the signal detection theory (SDT) measures, aware trials were treated as hits, while hallucinatory trials were treated as false alarms. The SDT measures showed an average d’ = 1.440 (SD = 0.639) and beta = 1.832 (SD = 1.544). d’ differed from zero ($t = 10.804$, $p < 0.001$) and beta from 1 ($t = 2.583$, $p = 0.017$), which underline good discrimination and conservative bias.

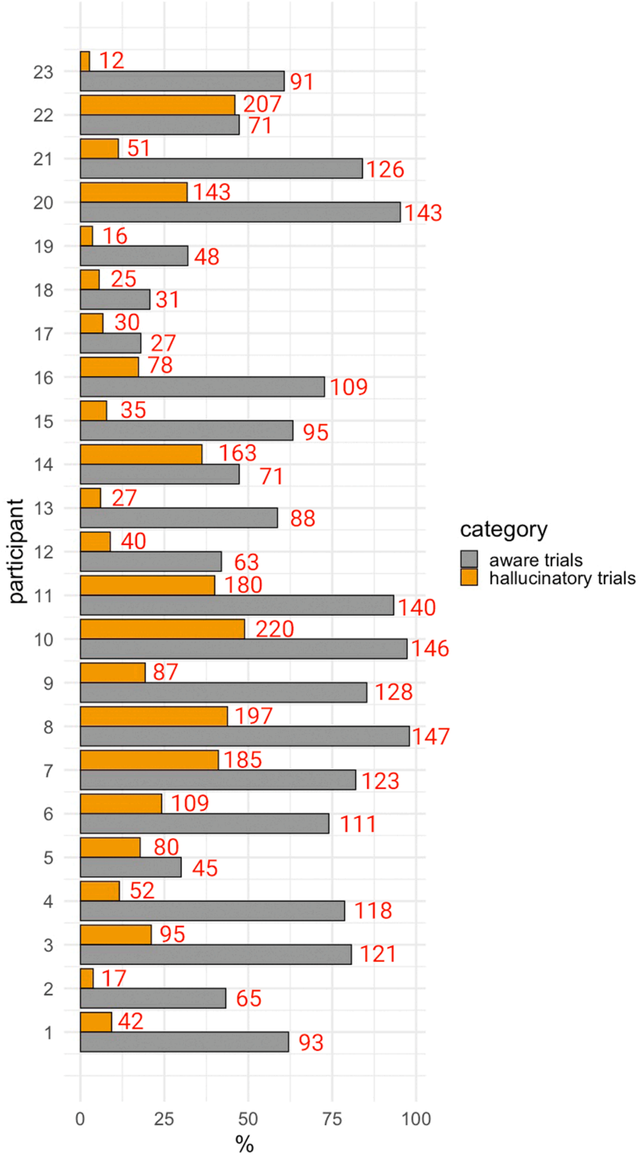

Fig. 3. The proportion of hallucinatory stimulus-absent and aware stimulus-present trials per participant. The number of trials per participant is shown in red.

Fig. 4 shows the ERP activity in response to aware and unaware stimulus-present trials and hallucinatory and unaware stimulus-absent trials at the Fz electrode. Fig. 5 shows scalp topographical plots for aware – unaware and hallucinatory – unaware differences. Fig. 6 illustrates a cluster of statistically significant activation in the hallucinatory – unaware difference and its scalp topography.

The ERP analysis revealed AAN in the expected time window from 200 to 260 ms post stimulus, mostly over central and frontal regions. The location of the AAN cluster (194 ms to 296 ms, max F value: 22.331 at 222 ms over AF7 channel, cluster-level p: 0.023, cluster mass: 6871.26) was similar to the previously reported AAN topography when a linked mastoid reference was used (Dembski et al., 2021; Eklund et al., 2019a; Filimonov et al., 2022). When aware-unaware trials with physical stimuli were compared, only the LP cluster was statistically significant (490 ms to 798 ms, max F value: 42.3771 at 794 ms over Pz channel, cluster-level p: 0.012, cluster mass: 14,660.5). AAN was not detected, most probably because four participants had only 3, 4, 7 and 10 unaware trials, which produced substantial noise, and the mass univariate analysis was not sensitive enough to detect it. Yet, Figs. 4 and 5, as well as converging evidence from other experiments (D. Filimonov et al., 2024a; D. 2024b; Eklund et al., 2019b, 2020; Eklund and Wiens, 2018), indicate its presence. A supplementary analysis with the Factorial Mass Univariate Toolbox (FMUT) (Fields and Kuperberg, 2020) confirmed the AAN cluster in stimulus-absent trials and found both AAN and LP clusters in stimulus-present trials. Additionally, the single-subject average amplitudes indicate that data from four participants with a low number of trials were outliers, which could potentially lead to a false positive decision. The difference between FMUT and LIMO results can be explained by different statistical procedures of the frameworks: while LIMO implements a hierarchical generalized linear model to account for data, FMUT is centered on factorial ANOVA methods in a mass univariate design and the methods could have somewhat opposite sensitivity to outliers. FMUT results as well as single-subject averages are available in the Supplementary Material.

4. Discussion

We have used Pavlovian conditioning to induce simple auditory hallucinations and have found AAN, while the LP was absent. Since hallucinations are contents of consciousness that emerge without physical stimuli, AAN is an NCC proper in hearing.

In our study hallucinations could, arguably, be caused by high stimulus expectation. Previous research has related conditioned hallucinations to higher prior beliefs in both normal and clinical populations (Corlett et al., 2019; Powers et al., 2017). In clinical populations, the likely cause of conditioned hallucinations may be associated with a stronger belief that the reality – i.e., the stimulus array in the experiment - is fixed, predisposing them to experience a hallucination if previous trials contained stimuli (Fletcher, 2017). In the present study, our aim was not to explore any particular mechanisms that underlie or trigger hallucinations. We focused on the conscious experience of the hallucination itself, acknowledging that various underlying mechanisms could explain how hallucinatory experiences arise. Our sample demonstrated conservative response bias (beta) and good sensitivity (d’): the hallucinatory rate was smaller compared to the relatively high perceptual awareness rate, which could be expected in a healthy population. In contrast, studies on patient populations have reported lower response

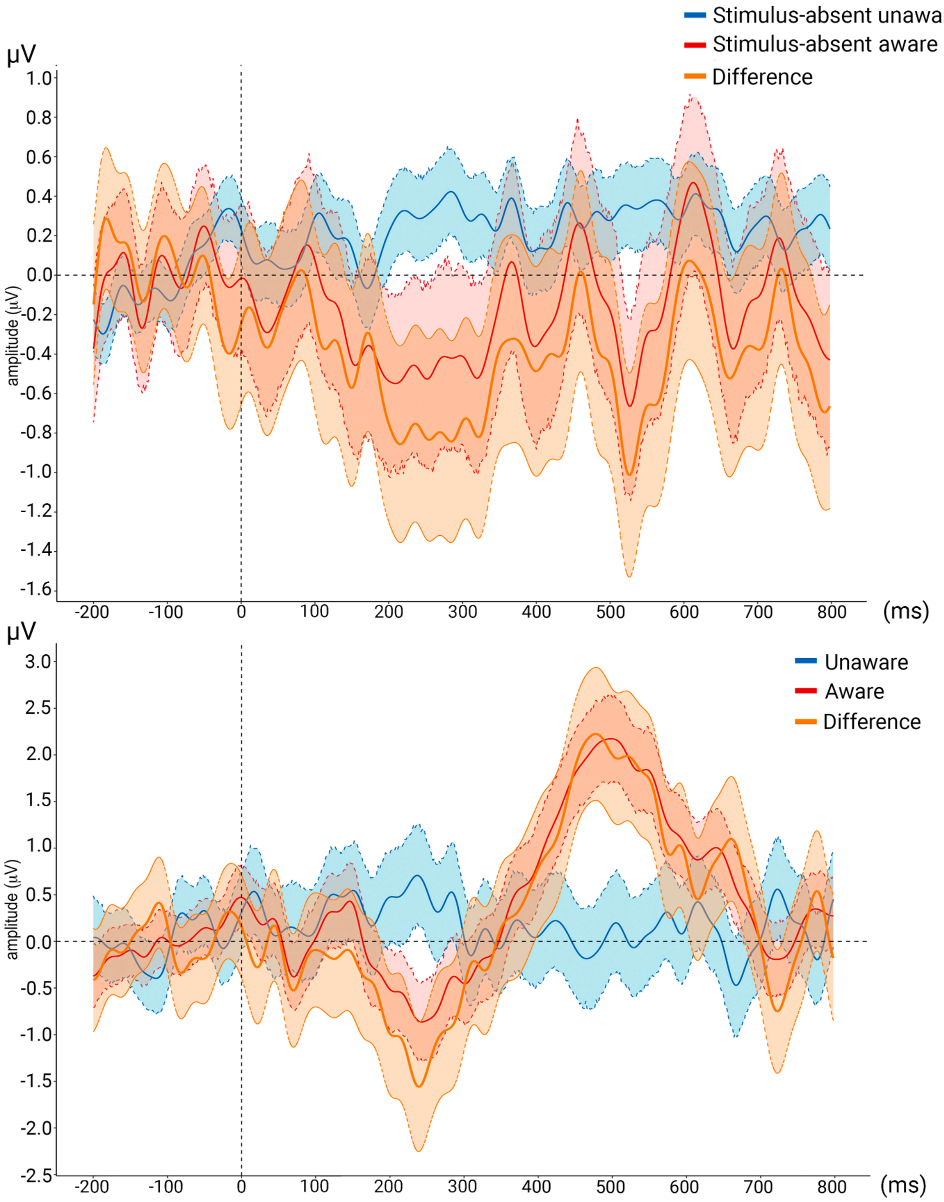

Fig. 4. ERP activity of hallucinatory and unaware stimulus-absent trials (upper panel) and of aware and unaware stimulus-present trials (lower panel) with corresponding difference waves over the Fz electrode. Within-subjects confidence intervals of the ERPs are highlighted.

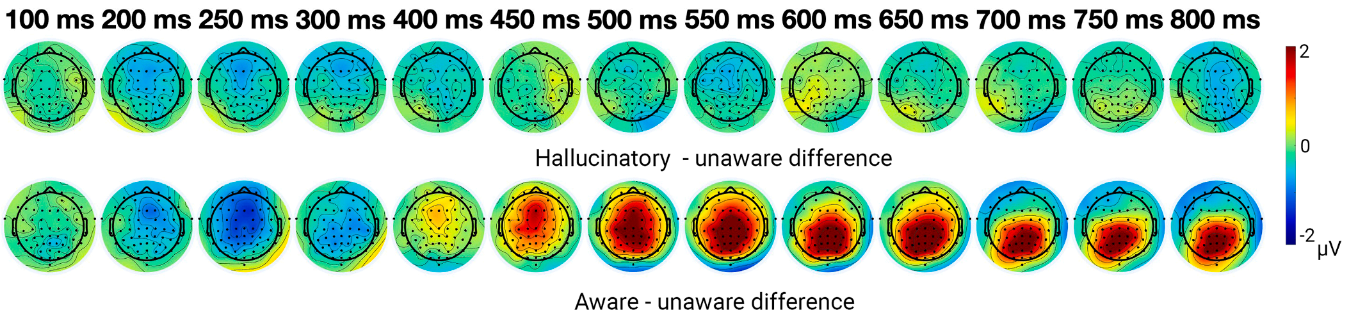

Fig. 5. scalp topographical plots of hallucinatory – unaware and aware – unaware difference waves.

bias and sensitivity values compared to healthy controls (Alganami et al., 2017; Ishigaki and Tanno, 1999).

It is also important to specify that the participants' task was not to make forced-choice responses regarding the presence or absence of stimuli but rather to rate how clearly they heard the stimulus by assessing its clarity. Perceptual awareness scale reflects consciousness arguably better than 2AFC tasks (Overgaard and Sandberg, 2021), which encourages the participants to guess when they are unsure. These

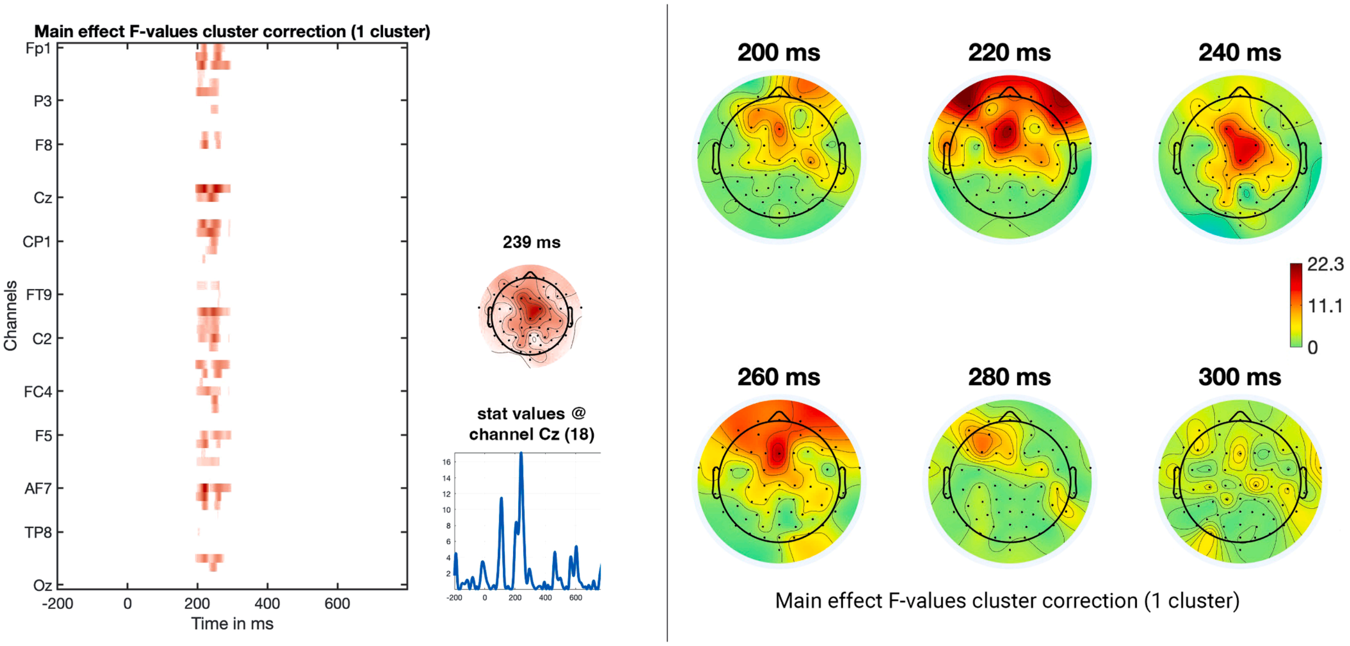

Fig. 6. Statistically significant cluster of hallucinatory – unaware difference (left) and its scalp topography in the AAN time window (right).

methodological choices imply that participants experienced hallucinations rather than merely responded without any subjective experience. Additionally, the false alarm rate in experiments on perceptual awareness in hearing is generally lower than in the present study (D. Filimonov et al., 2024a: beta = 3.251 (SD = 4.804), Eklund et al., 2018: C = 0.855 (SD = 0.313), 2019a: beta = 2.285 (SD = 0.835), 2021: beta = 2.828 (SD = 1.743)). In the previously mentioned experiments based on open access data, the criterion was more conservative (beta in our study was 1.832 (SD = 1.544)), while d' values were comparable. The differences in criterion were probably caused by a combination of no-discrimination task, conditioning, and a high number of stimulus-absent trials in the present study.

AAN was detected from 200 ms to 260 ms post stimulus at frontal and central electrodes. Studies on AAN report similar time intervals (Gutschalk et al., 2008; Eklund et al., 2019a, 2019b, 2020, 2021; Filimonov et al., 2022, 2024a, 2024b; Schlossmacher et al., 2021), with onset varying from 130 ms to 250 ms post stimulus depending on the task complexity. The scalp distribution of AAN was similar to that observed in previous studies using the linked mastoids as a reference (Filimonov et al., 2022, 2024a, 2024b), where it is typically observed over frontal, central and parietal areas. Eklund and Wiens (2019a) used a similar reference (average of P9 and P10) and investigated AAN at the Fz and Cz electrodes. With the tip-of-the-nose reference (Eklund et al., 2019a, 2019b), AAN topography shifts to central and parietal regions. I. Schlossmacher et al. (2021) reported an AAN cluster at central and frontal areas using common average reference. According to Dembski et al. (2021), AAN is mostly observed over the frontal and central areas. Studies on source reconstruction of AAN suggest that it originates from the bilateral auditory cortices (Eklund et al., 2019b, 2020; Gutschalk et al., 2008). Taken together, the AAN location in the current study is typical.

We also tend to interpret the failure to detect statistically significant AAN with multiple comparison corrections in aware-unaware stimulus-present trials as a result of low statistical power in a mass univariate analysis implemented in LIMO, caused by a low number of unaware trials and, therefore, low SNR in several participants. However, AAN was detected by FMUT with the same number of permutations, cluster correction and alpha. To ensure a reasonable experiment duration, we focused on the hallucinations rather than perceptual awareness, which has already been extensively studied in the auditory modality (Filimonov et al., 2022, 2024a, 2024b; Eklund et al., 2019a, 2019b; Eklund and Wiens, 2018, 2020). Nevertheless, this could be regarded as a limitation of the present experiment. LP amplitudes, on the other hand, were strong enough to be detected in the main and supplementary analyses.

The presence of AAN as well as the absence of LP in simple hallucinations may have several theoretical implications. First, cumulative evidence suggests that AAN is an NCC proper and that it is related to phenomenal experience (Eklund et al., 2019a, 2019b, 2021; Filimonov et al., 2022, 2024a, 2024b; Schlossmacher et al., 2020, 2021; Dellert et al., 2021, 2022). For instance, Powers et al. (2017), using a similar paradigm, reported that tone-responsive regions in the auditory cortex — which are activated in tone perception — were more active in hallucinatory trials. Therefore, current converging evidence suggests that AAN sources are similarly located in the auditory cortex and that AAN is related to the phenomenal experience. Second, our findings add evidence to the ongoing “phenomenal” vs “access” debate (Block, 1995, 2011, 2014; Revonsuo, 2009; Brown, 2012; Cohen et al., 2016), which is centered around the question of whether subjective phenomenal experience exists independently of and precedes reflective consciousness when a person can report it. To date, one empirical study (Amir et al., 2023) has reported a paradigm in which they were able to dissociate phenomenal and access consciousness. A physicalist explanation of phenomenal – access distinction also seems possible, and some information theoretical models provide it (Ji et al., 2024).

As a large and growing body of experimental evidence supports the interpretation that LP is a correlate of conscious access, and the earlier ERP responses of the PAN family (AAN in particular) are modality-specific correlates of phenomenal awareness which precedes it (M. Jimenez et al., 2021; Grassini et al., 2021; Koivisto et al., 2016a, 2016b, 2017; Eklund et al., 2020; Eklund and Wiens, 2018, 2019a; Filimonov et al., 2022, D. 2024a, D. 2024b; Pitts et al., 2014a; Shafto and Pitts, 2015; Schlossmacher et al., 2020, I. 2021; Dellert et al., 2021, 2022), we tend to agree with this view and therefore suggest that AAN observed in our study also indexes phenomenal consciousness. An obvious counterargument would be that in order to select the PAS category, participants must have a minimal form of subjective report and that stimulus detection may require minimal conscious access. Although hallucinations index pure awareness, they do not eliminate any potential post-perceptual cognitive processing. A closely related topic concerns the extent to which phenomenal consciousness, indexed by PAN, can dissociate from various forms of attention (Koivisto et al., 2009; Filimonov et al., 2024a; Bola et al., 2021; Doradzińska and Bola, 2024; Doll et al. 2024). A recent study by Doll et al. (2024) challenged the idea that AAN is independent from attention by reporting its absence in unattended stimuli. However, more investigation into the relationship between attention and AAN is needed. If hallucinations are proven to be independent from some or any form of attention (Bachmann, 2021; Aru et al., 2018), this would bring a strong argument in favor of the dissociation. In any case, irrespective of whether and to what extent phenomenal and access consciousness can be dissociated, PAN appears to be a necessary condition for subjective experience in the Nagelian "what it is like" sense (1980).

The presence of LP in aware and absence in hallucinatory trials demonstrates an interesting dissociation. LP is thought to index nonperceptual cognitive operations, usually related to consciousness (Koivisto and Revonsuo, 2010; Koivisto et al., 2017; Pitts et al., 2014a). When taking into account the depth of stimulus processing (Windey and Cleeremans, 2015; Jimenez et al., 2020), LP has been reported to be associated with the higher level of processing (Filimonov et al., 2024b; Derda et al., 2019). It has been suggested to index confidence (Ye et al., 2019, but see Salti et al., 2012), attention (Koivisto and Revonsuo, 2010; Filimonov et al., 2024a), response requirements and task-related processing in general (Filimonov et al., 2024b; Dellert et al., 2021; Pitts et al., 2012, 2014; Sergent et al., 2021), and it has been reported to be absent in the no-report condition (Cohen et al., 2020; Schlossmacher et al., 2020, 2021). Dellert et al. (2022) also showed that LP was not an NCC proper even with a trial-by-trial assessment of awareness. The list of specific cognitive operations related to LP remains inconclusive and, arguably, perceptual awareness may differ from hallucinations in a variety of covert processes. The fact that LP was absent in hallucinations while being present in perceptual awareness could support this difference. For instance, If LP reflects the attentional amplification of the physical stimulus features for selective processing, in the absence of the physical stimulus those physical features cannot be attentionally selected or amplified. Research on negative hypnotic hallucinations also reports the absence of LP (P3b) (Franz et al., 2020), and one GNWT-compatible interpretation — the Functional Neurological Disorder model (Naccache and Munoz-Musat, 2024) — suggests that conscious voluntary top-down process causes involuntary consequences and at the stage of hypnotic hallucinations LP (P3b) is absent. The authors acknowledge that alternative explanations are possible and that, in contrast with the present study, their findings were based on hypnotically induced negative hallucinations, such as induced deafness. Our investigation needs to be extended and replicated before further theoretical interpretations can be confirmed. Since LP indexes many cognitive functions, the total number of which is arguably unknown, the relationships between them are extremely complex. Its absence in hallucinations leads to the conclusion that either the functions remain similar, but their neural implementation has changed in a way that renders LP undetectable, or the neural implementation remains the same, while the set of functions differs. The absence of LP in hallucinations further corroborates the fact that LP is not an NCC proper.

Regarding the current theories, our results mainly support RPT while at the same time challenge GNWT, higher-order thought (HOT), attention schema (AST) (Graziano, 2019), and theories that propose explanations similar to GWNT and emphasize cognitive access. The GNWT explains false-alarm trials by spontaneous ignition in PFC, leading to late responses in the prefrontal cortex (van Vugt et al., 2018). Since GNWT does not support the idea of phenomenal consciousness, hallucinations would be explained as any reported false-alarm trials. AST emphasises the brain's internal modeling of attention as the basis for awareness: if attention is indexed by LP, current findings could potentially challenge the theory. According to HOT, a mental state becomes conscious only when it is the object of a higher-order representation, implying that first-order processes alone are insufficient for consciousness (Brown et al., 2019). In case PAN is a marker of a first-order state, while LP represents a higher-order access consciousness, our results can contradict the theory. Temporo-spatial theory (TTC) (Northoff et al., 2023), predictive processing theory (PPT) (Hohwy and Seth, 2020), integrated information theory (IIT) (Albantakis et al., 2023), and the Posterior Hot Zone model (Koch et al., 2016) remain neutral as long as the proposed NCC proper possesses or relates to the theory-specific features. In TTC, stimulus-related activity should align with intrinsic neural timescales, while pre-stimulus activity provides a disposition for awareness and, arguably, hallucinations: if PAN results from a non-additive pre-stimulus and post-stimulus interaction, it supports the TTC. For the IIT, PAN could be considered supportive evidence, as the theory associates "early" ERP components of the PAN family with consciousness (Boly et al., 2017; Koch et al., 2016). Possible links between these theoretical predictions, hallucinations and PAN could be further empirically investigated. (see Seth and Bayne, 2022 and Signorelli et al., 2021).

For "frontal" or "cognitive" theories, including GNWT and HOT, a possible line of argument could be to interpret PAN (and AAN in particular) in accordance with their core predictions, assigning it to access and/or attention. However, this view might be more problematic, as many studies found access and attention to elicit LP.

5. Conclusion

We investigated the electrophysiological correlates of awareness in simple auditory hallucinations with the Pavlovian conditioning paradigm and found a prolonged auditory awareness negativity in hallucinations. We further suggest that AAN is an NCC proper of phenomenal consciousness in the auditory modality or the NCC of the subjective experience in hearing.

CRediT authorship contribution statement

Dmitri Filimonov: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Saana Lenkkeri:** Investigation. **Mika Koivisto:** Writing – review & editing, Validation, Supervision. **Antti Revonsuo:** Writing – review & editing, Validation, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

EEG data and code for the data cleaning and analysis is available at doi:10.1016/j.neuroimage.2025.121168.

Acknowledgements

This research has received a grant from Signe and Ane Gyllenbergs Foundation.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2025.121168.

Data availability

EEG data and code for the data cleaning and analysis is available at https://osf.io/68na9/.

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Further readings

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