The early but not the late neural correlate of auditory awareness reflects lateralized experiences

Rasmus Eklund * , Billy Gerdfeldter, Stefan Wiens

Gösta Ekman’s Laboratory, Stockholm University, Sweden

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ABSTRACT

Theories disagree as to whether it is the early or the late neural correlate of awareness that plays a critical role in phenomenal awareness. According to recurrent processing theory, early activity in primary sensory areas corresponds closely to phenomenal awareness. In support, research with electroencephalography found that in the visual and somatosensory modality, an early neural correlate of awareness is contralateral to the perceived side of stimulation. Thus, early activity is sensitive to the perceived side of visual and somatosensory stimulation. Critically, it is unresolved whether this is true also for hearing. In the present study (N = 26 students), Bayesian analyses showed that the early neural correlate of awareness (auditory awareness negativity, AAN) was stronger for contralateral than ipsilateral electrodes whereas the late correlate of auditory awareness (late positivity, LP) was not lateralized. These findings demonstrate that the early but not the late neural correlate of auditory awareness reflects lateralized experiences. Thus, these findings imply that AAN is a more suitable NCC than LP because it correlates more closely with lateralized experiences.

1. Introduction

Theories disagree on how neural activity generates awareness. Two theories in particular have attracted the most attention because they are on opposite ends of whether low or high levels of processing is critical for awareness ( Pitts et al., 2018 ). The recurrent processing theory ( Lamme, 2006 ) suggests that: (1) early feedforward activity from sensory stimulation is an unconscious process, (2) early local feedback loops between the primary sensory cortices and hierarchically higher areas generate the subjective sensation of what an experience is like (phenomenal awareness), and (3) later, global feedback loops enable introspection and reporting of the experience (access consciousness). Although the global neuronal workspace theory ( Dehaene et al., 2006 ) agrees that early feedforward activity is unconscious, it suggests that early recurrent processing is preconscious and that only late, global activity mediates consciousness.

Neural activity that is associated with awareness is commonly referred to as the neural correlate of consciousness (NCC; Crick and Koch, 1990). One common method of identifying the NCC is through a contrastive analysis: The same stimulus is presented over multiple trials, and the NCC is the difference in neural activity between trials rated as aware and trials rated as unaware ( Aru et al., 2012 ).

Research on NCC has focused mainly on vision ( Koivisto and Revonsuo, 2010 ), whereas research on hearing and touch has been sparser ( Dykstra et al., 2017 ; Meyer, 2011 ; Snyder et al., 2015 ). The NCC has been extensively studied with electroencephalography (EEG) and magnetoencephalography (MEG) because of their excellent temporal resolution.

Two common NCC have been identified. In EEG, these appear as an early (at about 200 ms) negativity and a late (after 300 ms) centro-parietal positivity (late positivity, LP). The early NCC is referred to as visual awareness negativity (VAN) in vision ( Koivisto and Revonsuo, 2010 ) and as auditory awareness negativity (AAN) in hearing ( Eklund and Wiens, 2019 ).

Because the early NCC is localized to sensory areas ( Andersen et al., 2016 ; Eklund et al., 2020 ; Eklund and Wiens, 2019 ; Forschack et al., 2020 ; Koivisto and Revonsuo, 2010 ) and involves recurrent processing ( Auksztulewicz and Blankenburg, 2013 ; Boehler et al., 2008 ), these findings support recurrent processing theory. Furthermore, whereas global neuronal workspace theory emphasizes the role of late activity (LP) in awareness, recurrent processing theory postulates that LP reflects only post-perceptual processing. In support, LP is strongly affected by response manipulations (e.g., Förster et al., 2020 ; Pitts et al., 2018 ; Tsuchiya et al., 2015 ; Dembski et al., 2021 ).

* Corresponding author.
E-mail address: rasmus.eklund@psychology.su.se ( R. Eklund).

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In further support of the idea that the early NCC matches phenomenal experience, the location of early processing in sensory areas corresponds to the perceived side of stimulation. Specifically, the visual awareness negativity is contralateral to visual stimulation (Boehler et al., 2008; Eklund and Wiens, 2018; Koivisto and Grassini, 2016), and the early NCC of touch is contralateral to tactile stimulation (Auksztulewicz and Blankenburg, 2013; Forschack et al., 2020). Notably, this research suggests that the late NCC in vision and touch are not lateralized (as suggested by their scalp topographies).

In hearing, previous research does not clarify whether early and late NCC are lateralized. Whereas the visual and somatosensory pathways are clearly lateralized contralaterally, the auditory pathway afferently bifurcates and decussates at several junctions (Pickles, 2015). As a result, the NCC in hearing may not be as clearly lateralized as the NCC in vision and touch.

Although many studies have investigated neural responses to lateralized auditory stimulation in various contexts, this research did not explicitly examine awareness (e.g., Butcher et al., 2011; Gutschalk and Steinmann, 2015; Virtanen et al., 1998; Woldorf et al., 1999). Furthermore, research that has investigated activity more closely related to awareness does not lend itself to resolving this question, for one or more of the following reasons (Alain et al., 2001; Hautus and Johnson, 2005; Königs and Gutschalk, 2012; Sanders et al., 2008): First, because a contrastive analysis was not used, the NCC could not be isolated. Second, it is unclear whether lateralized perception was captured. Third, because trials rated as aware and unaware differed physically, the NCC may have been confounded by physical stimulus differences. Fourth, because stimuli were presented only on one side, a contralateral response that was stronger than the simultaneous ipsilateral activity could simply reflect that one hemisphere responds more strongly.

Here, we examined whether the early NCC (AAN) and the late NCC (LP) in hearing are lateralized by playing soft clicks heard to the left or right side. The main hypotheses of the study were that AAN is lateralized and that LP is not. Bayesian hypothesis testing is preferable to null hypothesis significance testing because it quantifies the strength of evidence for (or against) a predicted effect (Wagenmakers et al., 2016).

2. Method

We preregistered the primary hypotheses, methods, and analyses (https://doi.org/10.17605/OSF.IO/PSRJF) to avoid bias (Luck and Gaspelin, 2017; Nosek et al., 2018). Supplementary material is available at a university repository (Wiens et al., 2021). This material includes all raw data, scripts, and results of all analyses.

2.1. Participants

The rationale for sample size and recruitment was similar as in our previous study (Eklund et al., 2020). Because departmental regulations restricted subject recruitment because of COVID-19, data collection was extended until October 2020. The sample consisted of 28 student volunteers (12 male; 25 right-handed; age: M = 27.5, SD = 3.1). Ethical review and approval were not required for the study on human participants in accordance with local law and institutional requirements. The experiment adhered to the declaration of Helsinki. Participants provided their written informed consent to participate in this study and that their raw data will be shared anonymized.

We deviated from the preregistration by excluding two subjects who lacked trials (less than 5) in one of the conditions. These subjects clearly did not follow the task instruction of distributing their responses evenly (left and right) when they did not hear the click (as described below). The final sample for the preregistered analyses consisted of 26 subjects (12 male; 23 right-handed; age: M = 27.9, SD = 3.0).

2.2. Apparatus and stimuli

Stimuli were auditory clicks (4 ms) lateralized to the left or right ear (stimulus EE1 from Thaler et al., 2017). Lateralization was manipulated with an interaural time difference (±0.25 ms) and an interaural level difference (±8 dB). Clicks were presented through in-ear tubephones (ER2; Etymotic Research Inc., IL; www.etymotic.com). Instructions were displayed on a BenQ XL2430T, 24-inch gaming monitor (at 144 Hz, 1920 × 1080 resolution). PsychoPy v 3.0 (Peirce, 2007) was used to run the experiment and to collect behavioral data.

Awareness was measured with the perceptual awareness scale (Sandberg et al., 2010). The almost clear rating was not included as a response option, as in our previous research (Eklund and Wiens, 2018, 2005; K...
2.3. Procedure

The procedure resembled that of our previous study (Eklund et al., 2020). Subjects performed a detection and discrimination task that comprised 800 trials (720 critical and 80 catch). Critical trials contained a click that was lateralized to either left or right and was presented at the individual auditory awareness threshold (see below). Catch trials did not contain a click. The trials were divided into eight blocks. Each block comprised 100 trials (90 critical and 10 catch). Within each set of 20 trials (9 left, 9 right, and 2 catch trials), trial order was randomized. There was a short break between blocks.

Fig. 1 shows the time course of a trial. On each trial, a fixation cross was shown for 1000 ms. On critical trials, a left or right click was played 500 ms after trial onset. After each trial, subjects first indicated with their right hand whether they heard a left or right click by using one of two buttons (“left arrow” and “right arrow,” corresponding to left click and right click, respectively). Afterward, they rated with their left hand their subjective awareness of the click by using one of three buttons (“1”, “2”, and “3,” corresponding to “I did not hear a click,” “I heard the click weakly,” and “I heard the click clearly,” respectively). Subjects were instructed to evenly distribute their responses (left and right) when they did not hear the click to discourage using a strategy in the discrimination task (e.g., always guessing left click when not hearing the click). Subjects were also instructed to focus on rating their awareness accurately rather than responding quickly.

Before the experiment, subjects familiarized themselves with the experimental procedure through a short practice session; this session was identical to the experiment but with clearly audible clicks. Then, psychophysical staircases were used to calibrate the left and right click separately to an intensity level at which an individual subject reported hearing the click (i.e., rated it as weakly or clearly audible) on approximately 50% of the trials; this level was designated the individual auditory awareness threshold for each click side. The staircase procedure and the calibration procedure were similar to that in our previous study (Eklund et al., 2020) except that each procedure contained 45 critical trials per click side.

2.4. EEG recording

The EEG recording was identical to that of our previous study (Eklund et al., 2020). EEG data were recorded from 64 electrodes at standard 10–20 position with an Active Two BioSemi system (BioSemi, Amsterdam, Netherlands). An EEG cap (Electro-Cap International, Eaton, OH) was used to position these electrodes together with system-specific electrodes (https://www.biosemi.com/faq/cms&drl.htm). Two additional positions (tip of the nose and right cheek) were recorded. Data were sampled at 1024 Hz and filtered with a hardware low-pass filter at 208 Hz.

2.5. EEG preprocessing

As in our previous study (Eklund et al., 2020), the data from the 64 standard electrode positions, together with the tip of the nose and the right cheek, were processed and analyzed offline with MNE-Python (Gramfort et al., 2013, 2014, 2014; Appelhoff et al., 2019; Pernet et al., 2019). The behavioral analyses included all trials, whereas in the EEG data analyses, some trials were excluded (see below). The continuous EEG data were processed offline. Although it was not mentioned in the preregistration, we downsampled the data to 256 Hz to speed up preprocessing. For each subject, data were average referenced, a 1-Hz high-pass filter was applied to remove slow drift, and the electrodes were visually inspected to detect noisy electrodes. Only a few electrodes had to be interpolated (spherical spline interpolation) from neighboring electrodes ($M = 0.77, SD = 1.09$). Eye blinks were automatically detected from the eye blink channel (i.e., Fpz vs. cheek). Independent component analysis (fastica) was conducted. On the basis of their topography and their correlation with the eye blink channel, eye blink components were manually inspected and then excluded ($M = 1.15, SD = 0.36$). Afterward, the data were re-referenced to the tip of the nose.

Epochs were extracted from 100 ms before tone onset to 600 ms after tone onset. Each epoch was baseline corrected to the mean of the 100-ms interval before tone onset (~100 to 0 ms). For each subject, maximum amplitude ranges were extracted for individual epochs (after a 30-Hz low-pass filter), and the distribution of these amplitude ranges was inspected for outliers. The number of outliers removed per subject was $M = 21.12 (SD = 19.60)$, corresponding to $M = 2.64\% (SD = 2.45)$. The exclusion thresholds were set for each individual because subjects showed substantial variability in these amplitude ranges. Critically, inspection of trials was blinded to trial type (critical, catch), click side, identification response, and awareness ratings to avoid bias (Keil et al., 2014).

2.6. EEG analysis

As preregistered, aware trials were clicks rated as “I heard the click clearly” or “I heard the click weakly,” whereas unaware trials were clicks rated as “I did not hear a click.” The AAN-relevant interval was the period between 160 and 260 ms after stimulus onset, and the LP-relevant interval was the period between 350 and 550 ms. The electrodes designated as left were F7, F5, F3, F1, FT7, FC5, FC1, T7, C5, C3, C1, TP7, CP5, CP3, and CP1. The electrodes designated as right were F8, F6, F4, F2, FT8, FC6, FC4, FC2, T8, O6, C4, C2, TP8, CP6, CP4, and CP2. These intervals and this set of electrodes were most sensitive to AAN and LP in our previous studies (Eklund et al., 2019, 2020).

For each click side, difference waves were calculated from correctly lateralized trials rated as aware (aware correct) minus correctly and incorrectly lateralized trials rated as unaware. Thus, these difference waves represented the NCC. On some trials, subjects reported awareness of the click on the wrong side. On these aware incorrect trials, subjects may have pressed the wrong button (lapse trial), or the response may have actually reflected their experience (Eklund et al., 2020). Although aware trials could be grouped according to the experienced laterality, this would introduce a physical confound in the contrastive analysis for each click side. Specifically, trials rated as aware would include clicks from both sides, whereas trials rated as unaware would include clicks from only one side. Therefore, aware incorrect trials were excluded.

Then, four difference waves were computed as defined by the combination of click side (left or right) and electrode laterality (contralateral or ipsilateral). For example, left contralateral reflected the NCC to a left click across right-sided electrodes, whereas left ipsilateral reflected the NCC to a left click across left-sided electrodes.

As a manipulation check for an overall AAN and overall LP, mean amplitudes were computed across the four difference waves. For AAN (recorded between 160 and 260 ms), we predicted a negative mean amplitude across electrodes. For LP (recorded between 350 and 550 ms), we predicted a positive mean amplitude across electrodes.

To examine whether AAN and LP were lateralized, a new difference wave was calculated from the mean of the two contralateral difference waves (i.e., left contralateral and right contralateral) and the mean of the two ipsilateral difference waves (i.e., left ipsilateral and right ipsilateral). If AAN is lateralized, this difference should be negative between 160 and 260 ms after stimulus onset. If LP is lateralized, this difference should be positive between 350 and 550 ms.

As preregistered and similar to our previous study, the Bayes Factor (BF) was computed from Bayesian one-sample t tests of difference scores (Dienes and McLatchie, 2018). A BF$_{10}$ > 1 implies that there is more evidence for the alternative hypothesis than the null hypothesis, whereas BF$_{10}$ > 1 implies that there is more evidence for the null hypothesis than the alternative hypothesis. We used an interpretation scheme of the continuous BF to facilitate verbal communication.
The alternative hypothesis was modeled as a uniform distribution \( (1\mu V \to 1\mu V) \), and the likelihood was modeled as a \( T \) distribution. We also report the 95% confidence intervals for mean amplitudes.

### 3. Results

#### 3.1. Behavior

Table 1 shows the descriptive statistics for the behavioral data \((N = 26)\). Clicks were presented close to the individual awareness threshold (50%); that is, close to 50% of the critical left and right clicks were rated as aware. Of the clicks rated as aware, most were rated as weakly heard \((M = 97.8\%, \ SD = 9.3)\). The mean false alarm rate was 12.1\% \((SD = 11.5)\).

![Fig. 2. Grand mean waves for aware (correct) trials, unaware (correct and incorrect) trials, and their difference (aware minus unaware), separated by click side and electrode laterality. Click side is organized by column, and electrode laterality is organized by row (contralateral on top and ipsilateral on bottom). Auditory awareness negativity (AAN) was measured between 160 and 260 ms after click onset, and late positivity (LP) was measured between 350 and 550 ms after click onset. These intervals are marked in gray. The data were referenced to the tip of the nose. In the plots, the data were low-pass filtered at 30 Hz.]()

#### 3.2. Electrophysiology

##### 3.2.1. Nose reference

Fig. 2 shows the grand mean waves for individual combinations of click side and electrode laterality for aware trials, unaware trials, and their difference (with nose reference). Across subjects, the minimum number of trials in any condition was 51. The mean numbers of trials were 161.6 \((SD = 48.9)\) for aware trials to left clicks, 167.5 \((SD = 51.7)\) for unaware trials to left clicks, 165.1 \((SD = 55.5)\) for aware trials to right clicks, and 168.3 \((SD = 53.6)\) for unaware trials to right clicks.

As predicted, results showed that the overall AAN (across all conditions) was negative \((M = -1.2 \mu V, BF_{10} > 100)\). Critically, AAN was lateralized in that the contralateral electrodes were more negative than the ipsilateral ones \((M = -0.3 \mu V, BF_{10} = 50.5)\). There was weak evidence that this difference (contra minus ipsi) was similar for left and right clicks \((interaction M = 0.2 \mu V, 95\% CI [-0.1, 0.6], BF_{01} = 1.6)\).

The overall LP (across conditions) was positive \((M = 1.5 \mu V, BF_{10} > 100)\); however, LP did not differ between contralateral and ipsilateral electrodes \((M = -0.1 \mu V, BF_{01} = 7.6)\). There was moderate evidence that the difference (contra minus ipsi) was similar for left and right clicks \((interaction M = 0 \mu V, 95\% CI [-0.2, 0.2], BF_{01} = 7.3)\).

Although these results suggest that only AAN was lateralized, further analyses revealed a problem with the nose reference, as discussed below. Therefore, complete results for the preregistered analyses are reported as supplementary material \((Wiens et al., 2021)\).

##### 3.2.2. Average reference

Although the nose-referenced analyses supported the conclusion that
AAN is lateralized whereas LP is not, close inspection of Fig. 2 suggested that there appeared to be a general drift during baseline and that AAN to left clicks began immediately after tone onset.

Further analyses showed that the nose electrode deviated substantially from the other electrodes in most subjects (see supplementary material; Wiens et al., 2021). Because the nose electrode served as the reference in the preregistered analyses, it may have distorted the results.

To reduce any distorting effects of the nose electrode, we pre-processed the data again exactly as preregistered except that the nose electrode served as the arithmetic average across all electrodes. Importantly, there is no a priori reason to believe that the choice of reference should bias the results.

With an average reference, the mean number of interpolated channels was 0.77 (SD = 1.09); the mean number of removed eyeblink components was 1.15 (SD = 0.36); and the mean number of trials removed as outliers were $M = 21.12$ (SD = 19.60), corresponding to $M = 2.64\%$ (SD = 2.45). Across subjects, the minimum number of trials in any condition was 50. The mean numbers of trials were 158.1 (SD = 48.0) for aware trials to left clicks, 163.6 (SD = 50.4) for unaware trials to left clicks, 161.6 (SD = 54.8) for aware trials to right clicks, and 164.3 (SD = 51.7) for unaware trials to right clicks.

The top panel of Fig. 3 shows the butterfly plot of the aware minus unaware difference across left and right clicks, and the bottom panel shows topographies for AAN and LP across left and right clicks. Although AAN and LP were both apparent, their topography and latency differed slightly from the results of the preregistered analyses (as would be expected by changing the reference electrodes). Therefore, electrodes and intervals were adjusted slightly. For AAN, the interval was between 130 and 230 ms; left electrodes were CP3, CP5, TP7, C3, C5, T7, FC3, FC5, and FT7; and right electrodes were CP4, CP6, TP8, C4, C6, T8, FC4, FC6, and FT8. For LP, the interval was between 350 and 450 ms; left electrodes were C1, C3, PO3, P1, P3, CP1, CP3, and CP5; and right electrodes were C2, C4, PO4, P2, P4, P6, CP2, CP4, and CP6. Supplementary figures show the raw mean ERP waves for aware trials, unaware trials, and their difference, separated by click side and electrode laterality.

Results for AAN are shown in Fig. 4, and results for LP are shown in Fig. 5. In each figure, the upper panels show the grand mean difference waves (aware minus unaware) for left and right clicks for contralateral (solid) and ipsilateral (dotted) electrodes. The lower panels show topographies for left and right clicks. Importantly, Figs. 4 and 5 suggest that excluding the nose and using an average reference reduced problems with drift and with an early negativity immediately after stimulus onset. Table 2 shows the descriptive and inferential statistics for the main analyses.

Critically, Fig. 4 shows a clear negativity peaking at around 180 ms after click onset (i.e., AAN), but this negativity was stronger for contralateral than ipsilateral electrodes. In support, the overall AAN (across all conditions) was negative ($M = -0.1 \mu V, BF_{10} = 3.0$); however, AAN was lateralized toward the contralateral electrodes ($M = -0.4 \mu V, BF_{10} = 268.3$). There was anecdotal evidence that this difference (contra minus ipsi) was similar for left and right clicks (interaction $M = 0.3 \mu V$, 95% CI $[-0.1, 0.7]$, $BF_{10} = 1.2$).

Fig. 5 shows a clear positivity peaking at around 400 ms after click onset (i.e., LP), but this positivity was similar for contralateral and ipsilateral electrodes. In support, the overall LP was positive ($M = 0.6 \mu V, BF_{10} > 100$), and LP did not differ between contralateral and ipsilateral electrodes ($M = 0.1 \mu V, BF_{10} = 0.3 \approx BF_{10} = 3.6$). There was moderate evidence that this difference (contra minus ipsi) was similar for left and right clicks (interaction $M = -0.1 \mu V$, 95% CI $[-0.3, 0.2]$, $BF_{01} = 5.1$).

4. Discussion

We hypothesized that in hearing, the early NCC (AAN) is lateralized whereas the late NCC (LP) is not. Lateralized binaural clicks were presented at the individual threshold of hearing, and a contrastive analysis was based on each individual’s perception of the clicks (aware vs. unaware). Nose-referenced analyses showed clear evidence for AAN and LP, but only AAN was lateralized in relation to auditory stimulation, that is, it was stronger for contralateral than ipsilateral electrodes. This was
supported by very strong evidence ($\text{BF}_{10} = 51$) for a lateralization of AAN and moderate evidence ($\text{BF}_{01} = 8$) for no lateralization of LP. However, closer inspection of the data revealed that the nose electrode deviated in most subjects. Because the nose served as the reference electrode in the preregistered analyses, it may have biased the results. Therefore, the data were reanalyzed in the same manner as preregistered after excluding the nose and referencing the data to an average reference. Results matched those for the preregistered analyses: Only the AAN was lateralized ($\text{BF}_{10} > 100$), whereas the LP was not ($\text{BF}_{01} = 4$). Therefore, our findings demonstrate that only the early NCC (but not the late NCC) matches the side of the perceived stimulus in hearing.

The present findings are important because previous research in auditory lateralization could not resolve whether early and late NCC are lateralized (e.g., Butcher et al., 2011; Gutschalk and Steinmann, 2015; Virtanen et al., 1998; Woldorff et al., 1999; Alain et al., 2001; Hautus and Johnson, 2005; Königs and Gutschalk, 2012; Sanders et al., 2008). Most of these studies did not measure awareness, and those that did lacked a contrastive analysis in which trials rated as aware are contrasted with trials rated as unaware to identify the NCC. In experiments that code trials only on the basis of objective performance, awareness is not isolated (Eklund et al., 2020). Instead, subjective reports are necessary as markers of awareness (Ramsay and Overgaard, 2004). Accordingly, previous research that did not use a contrastive analysis on the basis of awareness ratings may have identified contralateral auditory processing without demonstrating awareness-related auditory lateralization. To avoid this problem, we used a contrastive analysis and stimuli that subjects perceived as lateralized clicks. As the contrastive analysis was conducted for trials that were physically identical, physical stimulus confounds were avoided. Thus, AAN and LP were computed to physically identical clicks. Furthermore, in contrast to previous research, AAN and LP were measured to both the left and right side.

We showed that lateralized clicks were associated with a lateralized AAN. Because the topography of the AAN changed in relation to the perceived location of the sound (left or right), this finding supports the idea that AAN is an index of the conscious perception of lateralized sounds. Importantly, similar results have been reported for vision and touch. In vision, lateralized (left or right) visual field stimulation results in a stronger contralateral than ipsilateral visual awareness negativity (Eklund and Wiens, 2018; Koivisto and Grassini, 2016). Similarly, in touch, lateralized (left arm) sensory stimulation results in awareness-related activity in the right somatosensory cortex (N140; Auksztulewicz and Blankenburg, 2013; Forschack et al., 2020). Because the neural sources of the early NCC have been found to be localized to sensory areas (Eklund and Wiens, 2019; Koivisto and Revonsuo, 2010), these findings in combination strongly suggest that these different versions of the early NCC capture processes that are similar in function even though they may originate from different sensory areas (Dembski et al., 2021).

Although AAN is a correlate of awareness, the present results do not resolve whether AAN is an index of awareness or either a prerequisite or consequence of awareness (Aru et al., 2012; de Graaf et al., 2012). The issue of whether low or high levels of processing are critical for awareness is central for many theories of awareness, however, global neuronal workspace theory and recurrent processing theory are mainly discussed because they represent opposite ends of the debate (Pitts et al., 2018). The global neuronal workspace theory suggests that early
sensory activity is preconscious and that only late global activity mediates consciousness (Dehaene et al., 2006). From this perspective, AAN (as the early NCC) indexes preconscious processing (i.e., it is a prerequisite) rather than consciousness per se. Accordingly, it is irrelevant for the global neuronal workspace theory that AAN is lateralized whereas LP (the late NCC) is not. Nonetheless, because our findings show that AAN is lateralized whereas LP is not, they imply that AAN is a more suitable NCC than LP because it correlates more closely with lateralized experiences. Furthermore, because LP varies with other phenomena such as response manipulations, it does not appear to be a pure index of awareness but is also affected by the consequences of consciousness (Tsuchiya et al., 2015; Förster et al., 2020; Dembski et al., 2021).

Strictly speaking, our findings cannot support recurrent processing theory over the global neuronal workspace theory. Nonetheless, we suggest that AAN is an indirect index of recurrent processing, as suggested by research in other sensory modalities (Aukstulewicz and Blankenburg, 2013; Boehler et al., 2008). In the visual domain, Boehler et al. (2008) showed that contralateral visual recurrent processing correlates with visual awareness. The authors compared visual targets rated as aware with targets rated as unaware as neural activity was recorded with magnetoencephalography. Feedforward and feedback activity were spatiotemporally tracked along the visual hierarchy. Only feedback activity from higher visual areas to the contralateral primary visual area between 110 and 170 ms after target onset correlated with reported awareness of the visual targets. In the somatosensory domain, Aukstulewicz and Blankenburg (2013) showed that contralateral recurrent processing correlates with awareness. The authors stimulated the left median nerve at the subject’s detection threshold while recording EEG. Dynamic causal modeling suggested that recurrent processing in the right somatosensory cortex 140 ms after stimulus onset correlated with reported awareness of the somatosensory stimulation. Taken together, these findings are consistent with recurrent processing theory (Lamme, 2006): Feedback from hierarchically higher sensory areas to primary sensory areas enables awareness of sensory content. In our study, the timing of AAN (after about 100 ms) corresponds well to the findings in vision (Boehler et al., 2008) and in the somatosensory modality (Aukstulewicz and Blankenburg, 2013), as it matches the expected interval of recurrent processing. However, because we did not track the feedforward and feedback activity directly, future research needs to examine whether AAN reflects recurrent processing.
In conclusion, Bayesian analyses provided very strong evidence that the early correlate of auditory awareness (AAN) is stronger for contra-lateral than ipsilateral electrodes and moderate evidence that the late correlate of auditory awareness (LP) is not lateralized. These findings demonstrate that the early but not the late neural correlate of auditory awareness reflects lateralized experiences. Thus, these findings imply that AAN is a more suitable NCC than LP because it correlates more closely with lateralized experiences.

Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2021.107910.

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Credit author statement

Rasmus Eklund: Designed the study, programmed the experiment, collected the data, wrote the scripts to analyze the behavioral and EEG data, and wrote the manuscript. Billy Gerdfelder: Designed the study, collected the data, and wrote the manuscript. Stefan Wiens: Designed the study and wrote the manuscript.

Ethical approval and consent to participate and publish

The experiment adhered to the declaration of Helsinki. Participants provided their written informed consent to participate in this study and that their raw data will be shared anonymized.

Open practices statement

The data and materials for all experiments and analyses are available at a university repository (Wiens et al., 2021). This study was preregistered at OSF (https://doi.org/10.17605/OSF.IO/PSRJF).

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