



## Full Length Article

## Multiple independent components contribute to event-related potential correlates of conscious vision

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## ABSTRACT

Research has revealed two major event-related potential (ERP) markers of visual awareness: the earlier Visual Awareness Negativity (VAN, around 150–250 ms after stimulus onset), and the following Late Positivity (LP, around 300–500 ms after stimulus onset). Understanding the neural sources that give rise to VAN and LP is important in order to understand what kind of neural processes underlie conscious visual perception. Although the ERPs afford high temporal resolution, their spatial resolution is limited because multiple separate neural sources sum up at the scalp level. In the present study, we sought to characterize the locations and time-courses of independent neural sources underlying the ERP correlates of visual awareness by means of Independent Component Analysis (ICA). ICA allows identifying and localizing the temporal dynamics of different neural sources that contribute to the ERP correlates of conscious perception. The present results show that the cortical sources of VAN are localized to posterior areas including occipital and temporal cortex, while LP reflects a combination of multiple sources distributed among frontal, parietal and occipito-temporal cortex. Our findings suggest that conscious vision correlates with dynamically changing neural sources, developing in part in “accumulative fashion”: consciousness-related activity initially arises in few early sources and, subsequently, additional sources are engaged as a function of time.

The results further suggest that even early latency neural sources that correlate with conscious perception may also associate with action-related processes.

## 1. Introduction

Over the past years, great efforts have been devoted to the search for the neural correlates of consciousness (NCC). One of the main lines of study searches for the NCC that underlies the emergence of conscious visual experience. Due to their high temporal resolution, event-related potentials (ERP) measured using electroencephalography (EEG) provide excellent means to examine this issue (Luck, 2014). These studies have revealed scalp recorded electrophysiological signatures of conscious vision, but the neural processes that generate these correlates are not well understood. Here, we sought to shed light on the spatio-temporal distribution of neural sources

**Abbreviations:** EEG, electroencephalography; ERP, event-related potential; ICA, independent component analysis; LP, Late Positivity; VAN, visual awareness negativity.

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that contribute to the ERP correlates of conscious vision.

The most widely used approach to investigate the NCCs consists of presenting participants with a stimulus that they only sometimes consciously perceive. This allows contrasting the brain activity associated with subjectively “seen” and “unseen” stimuli while keeping the objective, physical stimulus constant. The comparison between the Aware (i.e., “seen”) and Unaware (i.e., “unseen”) conditions has revealed two major ERP correlates of conscious vision: a negative amplitude difference, typically occurring in the N2 time window (i.e., 200 ms after the stimulus onset) in occipito-temporal sites, called Visual Awareness Negativity (VAN), and a later enhanced positivity (i.e., Late Positivity, LP) visible at centro-parietal electrodes in the P3 time window (i.e., around 300–500 ms after the presentation of the stimulus) (Koivisto & Revonsuo, 2003, 2010; Dehaene & Changeux, 2011; Mashour et al., 2020). For the sake of clarity we want to point out that the terminology “VAN” and “LP” is specifically used for consciousness-related mechanisms, since they refer to difference waves computed subtracting Aware and Unaware conditions. N2 and P3, instead, represent common ERP components that are named after their polarity (Negative –N or Positive –P) and their ordinal position in the waveform (i.e., N2 is the second negative peak occurring in the waveform and P3 is the third positive one). These two ERP waves, that have been suggested to correlate with awareness, differ from each other in their scalp topography and cortical sources. VAN is known to be localized over occipito-temporal sites (Veser et al., 2008; Koivisto & Revonsuo, 2010; Liu et al., 2012), the topography of LP is widely distributed over multiple cerebral sources spanning occipital, parietal, temporal, and frontal cortices (Sergent et al., 2005; Del Cul et al., 2007).

These differences suggest that the two ERP correlates may reflect different cognitive processes.

A popular interpretation (Block, 1995) differentiates consciousness in *phenomenal* consciousness (i.e., the immediate subjective experience) and *access* consciousness (i.e., a higher-level form of consciousness that allows the manipulation of the contents of phenomenal consciousness). According to this differentiation, access consciousness is supposed to be enabled by higher-order areas at late stages of visual processes and emerge during the LP time-window (Dehaene & Changeux, 2011; Sergent et al., 2005). Conversely, phenomenal consciousness is thought to arise earlier (VAN) in posterior cortical areas (Förster et al., 2020; Mazzi et al., 2020; Dembski et al., 2021). In addition to debates about the best way to conceptualize consciousness, the question concerning which ERP correlate represents the proper signature of consciousness remains open (Kouider et al., 2010; Naccache, 2018). Indeed, several pieces of evidence ascribe to LP perceptual mechanisms that occur after the stimulus reaches the consciousness. In particular, it has been observed that LP seems to be engaged in task-related processing, such as reporting (i.e., accessing) the content of the conscious experience (Pitts et al., 2014a; Tsuchiya et al., 2015), rather than in processes that directly correlate with the conscious experience itself. Indeed, the relatively recent employment of no-report paradigms as method to disentangle the true NCCs from confounding neural mechanisms that conflate with awareness-related processes revealed that late activity seems to reflect decision processes that are strictly related with conscious access (Cohen et al., 2020; Sergent et al., 2021). Likewise, converging evidence suggest that the late component is also associated with task relevance, as larger LP amplitudes are elicited by task-relevant stimuli (Pitts et al., 2014b; Koivisto et al., 2016). In contrast, it has been shown that the amplitude of VAN is not modulated by report requirements nor task relevance of the stimulus, suggesting that it could reflect the electrophysiological correlate of phenomenal visual awareness.

In addition to debates concerning the timing of consciousness, also the localization of the NCC remains unclear. In particular, debate continues over how crucial frontal areas are for conscious perception: because of its involvement in cognitive functions such as attention and working memory, the prefrontal cortex is sometimes argued to play an essential role in conscious perception (Del Cul et al., 2009; Odegaard et al., 2017). Indeed, studies that seek to uncover the neural substrate underpinning NCCs by employing different techniques of neuroimaging such as fMRI, MEG and fast-optical imaging reveal that visual awareness correlates with activity in fronto-parietal areas, as well as with activity in more posterior brain regions, as early visual areas (Lee et al., 2005; Lau & Passingham, 2006; Dellert et al., 2021; Kronemer et al., 2022; Colombari et al., 2024). Researchers who assume that conscious perception is inseparably linked with the function of “accessing” perceptual information often conclude that consciousness arises in an all-or-none fashion when the relevant information is globally broadcasted to many brain regions (Mashour et al., 2020; Lau, 2022). In this account, NCCs are widespread over associative areas, thus crucially involving prefrontal cortex because of its proficiency in globally broadcasting the information.

In contrast to such “global” theories, “local” theories postulate that awareness consists of the pure subjective conscious experience (i.e., phenomenal consciousness), which can emerge in a graded manner in the lower sensory areas. In this perspective, frontal and prefrontal cortices may be neither necessary nor sufficient for consciousness (Boly et al., 2017; Raccach et al., 2021), and NCCs of conscious perception are restricted to posterior cortical regions, including occipital, parietal and temporal lobes (Koch et al., 2016; Mazzi & Savazzi, 2019). While the “global” and “local” theories represent competing accounts of the neural mechanism underlying the emergence of conscious perception, the Levels-of-Processing (LoP) hypothesis has attempted to reconcile these two views, suggesting that the extent to which conscious perception emerges in a graded vs. all-or-none fashion depends crucially on the features of stimuli the participant is required to process (Windey et al., 2014; Windey & Cleeremans, 2015). Based on the hypothesis, processing of lower level visual features (e.g., stimulus presence, or color) can yield graded changes in conscious perception, unlike higher level features (e.g., meaning of a stimulus) which tend to lead to all-or-none changes in conscious perception. While the jury is still out, empirical studies have provided support for the theory, and suggest that earlier correlates of consciousness are more likely to correlate with graded changes in conscious perception than later correlates, which are more likely to display all-or-none type processing (Jimenez et al., 2020; Filimonov et al., 2024).

Considering the heterogeneity of the concept of consciousness and the multitude of theories that try to conceptualize it, shedding further light on the neural sources that give rise to VAN and LP is of key importance in order to uncover the neural processes underlying conscious perception.

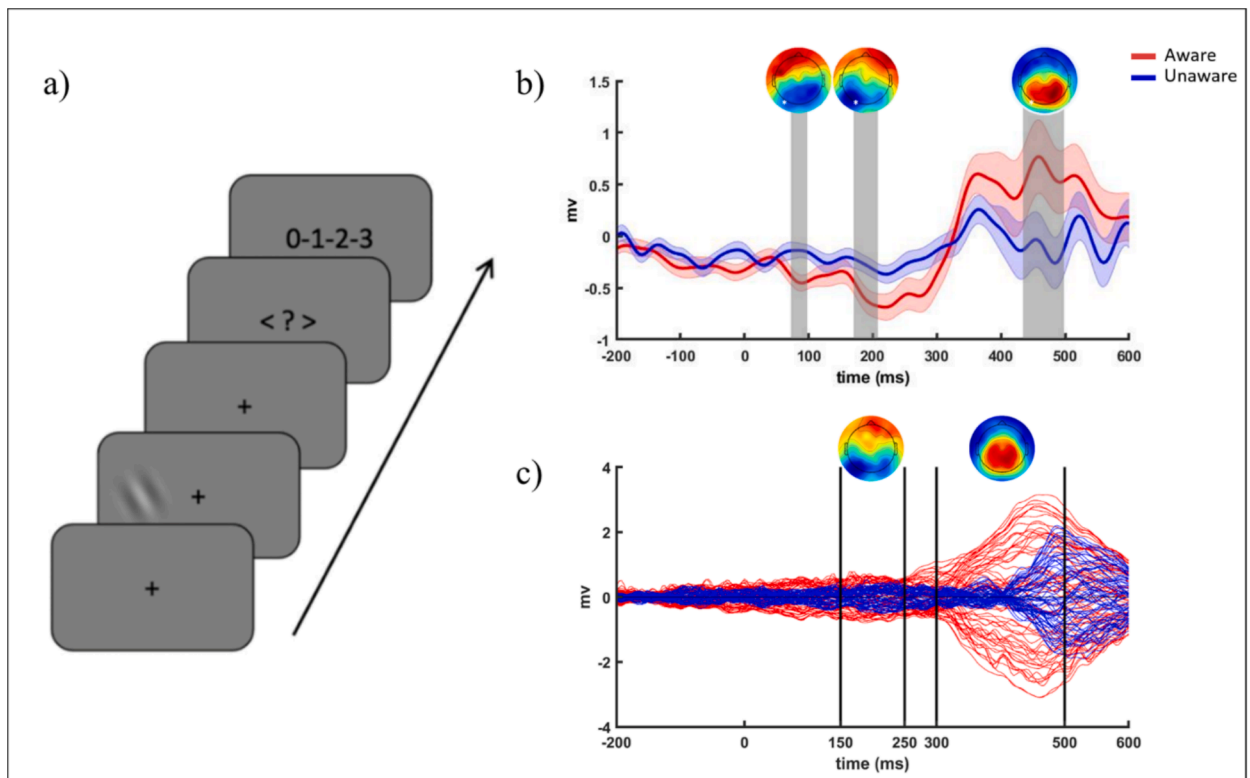
Given that ERPs are the summed activity of multiple distinct sources, correlates such as VAN and LP likely at a given time-point include a combination of consciousness-related sources. Moreover, a serious shortcoming of the ERP approach is that, because

sources with opposite polarities may cancel each other out, they may become invisible in the average ERP (Luck & Kappenman, 2012). Theories about the neural basis of consciousness typically argue that conscious perception involves recurrent activity across multiple areas, suggesting that correlates such as VAN and LP are a combination of multiple sources. According to the Global Neuronal Workspace Theory of consciousness, conscious perception involves co-organized activity across widely distributed cortical areas (Dehaene & Changeux, 2011). While early correlates are typically argued to be driven by posterior areas, it remains possible that early activity in frontal areas also correlates with consciousness if a sufficiently sensitive source separation is utilized (Thompson & Schall, 2000; Knotts et al., 2018; Kapoor et al., 2022).

During recent years, source separation approaches such as independent component analysis (ICA) have been developed to uncover sources contributing to average ERPs. In ICA, EEG is decomposed into maximally independent components (ICs) (Onton & Makeig, 2006). Each IC represents a temporally and functionally independent source of the EEG signal, with a specific scalp distribution (which is constant over time), and a specific amplitude at each time point (Onton & Makeig, 2006; Onton et al., 2006). This allows investigation of source level activity and isolating ICs that underlie the average ERP wave.

The goal of the present study was to characterize the locations and time-courses of independent neural sources that significantly contribute to the ERP correlates of visual awareness. To achieve this aim, we analyzed data previously collected by Railo and colleagues (2021) in a study whose aim was to investigate to what extent pre-stimulus activity influences subliminal perception. To do so, they presented participants with a discrimination task in which they were asked to report the side of presentation of a threshold-level stimulus and to subjectively rate its visibility. In a nutshell, low contrast Gabor patches were presented in the left or right hemifield and participants had to report the side of the target. They were instructed to give their best guess, even when they felt they could not perceive any stimulus. Afterward, they were asked to report their subjective experience using a four-step scale. The authors availed of signal detection theory to examine if subliminal perception is independent of subjective awareness, and they analyzed if subliminal perception can be predicted based of the state of the brain before stimulus appearance. They found that i) subliminal perceptual performance was predicted by conscious introspection, and that ii) pre-stimulus activity predicted behavioral performance even when the participants reported they didn't see the stimulus.

In the present study, we make use of this data with the aim of unveiling the neural sources contributing to the formation of a conscious experience, including those potentially “hidden” neural sources that the traditional ERP analysis fails to identify.



**Fig. 1.** Experimental procedure and ERP results. (A) Schematic presentation of a single experimental trial. (B) Grand-average of ERPs computed for Aware and Unaware conditions at channel O1 (marked with a white star). Amplitudes (O1 electrode) in Aware and Unaware trials were compared using t-tests (FDR-corrected) per each time sample. Time-windows with statistically significant differences are highlighted in grey. The shaded area of the waveforms represents SEM at each time point, and scalp distribution maps represent the voltage difference between conditions. (C) Butterfly plot and scalp maps at typical VAN and LP latencies.

## 2. Materials and Methods

### 2.1. Participants

The analyses presented in this study were performed on data acquired in a previous study (Railo et al., 2021), and as part of an EEG course organized at the University of Turku (same paradigm and EEG methodology as in Railo et al., 2021). In the current study, data from 36 healthy participants (mean age  $\pm$  sd = 24.14  $\pm$  3.52, range 19–36) were analyzed. All participants were students at the University of Turku and reported no neurological disorders. All of them gave their written informed consent in accordance with the Declaration of Helsinki. The study was approved by the ethics committee of the Hospital District of Southwest Finland.

### 2.2. Stimuli

The target stimuli were low contrast Gabor patches (diameter 6.5°, frequency 0.7 cycle/degree) which were presented to the left or right hemifield (about 5° from fixation on horizontal meridian) for 16.6 ms. In addition, the experiment included catch trials where no stimulus was presented (1/6th of all trials). Before starting the task, the intensity of the low contrast stimulus was individually determined using a QUEST staircase (Watson, 2017). The estimated 50 % perceptual threshold stimulus intensity was then used in the experimental task.

### 2.3. Experimental procedure

The task was a location discrimination task in which participants were asked to report the side of presentation of a low contrast Gabor patch and to subjectively rate its visibility. As shown in Fig. 1A, the trial started with a fixation period ranging from 668 to 1332 ms, during which a central black fixation cross was presented. Participants were instructed to maintain their gaze on this fixation cross throughout the task. Then, the stimulus was presented (or catch trial with no stimulus), and the fixation cross turned into an arrow pointing left and right, indicating that the participants could report the side of the target (left vs. right). After that, they were asked to rate the visibility of the stimulus by means of a four-steps scale. The scale was composed of the following four alternatives: 0) “did not see stimulus at all”, 1) “not sure but possibly saw something”, 2) “pretty sure I saw it”, 3) “saw the stimulus clearly”. A total of 400 trials was collected per participant (divided into 10 blocks of 40 trials), of which one sixth was represented by catch trials (i.e., trials with no stimulus).

### 2.4. EEG

#### 2.4.1. Recording

EEG data were recorded with a 64-channel EEG system at a sampling rate of 500 Hz. Impedance was kept near 5 k $\Omega$ . Electrode Fz served as on-line reference, and the ground electrode was placed on the forehead of the participant.

#### 2.4.2. Preprocessing

EEG data were preprocessed with MATLAB (version R2017b; the MathWorks, Inc., Natick, MA) using functions from the EEGLAB toolbox (v2020.0, Delorme & Makeig, 2004). Continuous raw data were first resampled to 250 Hz, and filtered using a high-pass filter at 1 Hz (50 % cut-off frequency 0.5 Hz, transition bandwidth: 1 Hz), in order to improve the quality of the artifact separation made by ICA (Winkler et al., 2015). Subsequently, a low pass filter at 40 Hz (50 % cut-off frequency 45 Hz, transition bandwidth: 10 Hz) was applied. *Clean\_channels* function of the *Clean\_rawdata* plugin of EEGLAB with a correlation threshold of 0.5 was used to remove channels with a bad signal (mean number of channels removed across participants = 1.61; SD = 1.84). After that, data were re-referenced to the average of all electrodes and cut into epochs ranging from –500 to 900 ms with respect to the stimulus onset. To remove epochs containing artefacts, ICA was computed using the extended Infomax runICA algorithm (Bell & Sejnowski, 1995), and trials contaminated by artefactual components were removed using the EEGLAB function *pop\_jointprob* (SD = 5 for both local threshold and global threshold). Baseline correction was then applied on the pre-stimulus period (from –500 ms to 0 ms), and ICA was computed again, identifying, for each participant, a number of components equal to the number of channels. Subsequently, the dipolar source of each component was localized using the DIPFIT plug-in (v3.3). The dipole localization was based on an average MRI, and electrode locations were co-registered based on standard channel coordinates. Because individual MRIs and subject-specific channel location information were not available, the accuracy of spatial localization in the present study is limited. Components with a residual variance of more than 15 %, and those labelled as not-brain-based with a probability of > 50 % were automatically identified by means of the *ICLabel* plugin and removed. In total, 379 ICs (average number of ICs per participant = 10.8) were selected as brain ICs. Finally, missing channels were interpolated for each participant using a spherical method using the EEGLab function *pop\_interp*.

#### 2.4.3. IC clustering

The resulting 379 brain ICs were grouped into clusters using a k-means clustering method implemented in EEGLab. Components were clustered based on dipole location, dipole orientation and ERPs. Importantly, to avoid statistical “double-dipping” (Kriegeskorte et al., 2010), the data were divided into the Aware (visibility rating = 1,2,3) and Unaware (visibility rating = 0) experimental conditions only after the clustering. On average, the number of epochs included in the analyses was 107 (SD = 35.92) for Aware and 105 (SD = 38.18) for Unaware condition. The default number of clusters suggested by EEGLab (i.e., *k* value) was 11, but it was manually

adjusted to 13 after visual inspection of the initial clustering result, in order to obtain a more homogeneous set of clusters. The results of the clustering process are reported in detail in Table 1. On average, each cluster was composed of 35.4 ICs ( $sd = 15.8$ ). Outliers ICs (35 ICs, threshold = 3 SD) that is, ICs that were not assigned into any one of the 13 clusters—were grouped in an auxiliary cluster, which was not included in the analysis. For statistical analyses, ICs of each participant within a cluster were averaged together.

#### 2.4.5. Statistical analyses

Before clustering the data, we examined average ERP correlates of conscious vision in order to ensure that the task employed in the study elicited the classical VAN-LP pattern. We thus computed the Grand-average ERP waveforms for Aware (visibility ratings > 0) and Unaware conditions (rating = 0), and then we contrasted them using paired-samples *t*-tests on each time point in channel O1. The *p*-values were corrected for multiple comparisons using Benjamini-Hochberg false-discovery rate procedure (Groppe et al., 2011) implemented in Matlab. Subsequently, for the analysis of IC correlates of conscious vision, the data were grouped into clusters and within each cluster ERPs were averaged separately for the two experimental conditions. Visual inspection of clusters suggested Aware vs. Unaware differences resembling the VAN-LP pattern, including a transient early and later more sustained difference in many clusters. To maximize statistical power (and minimize the number of statistical tests), statistical analysis (FDR corrected paired-samples *t*-tests) was focused on specific time-windows identified within each cluster by visually inspecting the data. We opted for this type of exploratory approach because a mass-univariate approach would have generated a very high number of statistical tests (e. g., time samples between 0 and 600 analyzed for each 9 clusters). Also, only analyzing traditional VAN and LP time-windows is not suitable because the IC approach is likely to yield correlates that traditional ERP analysis fails to notice. Therefore, in our analysis, all the temporal windows that suggested a difference between the Aware and Unaware condition based on visual inspection were included in the statistical analysis (counting across all clusters). Data from each time-window were averaged (separately for the two conditions Aware and Unaware). Subsequently, within each time window, a paired samples *t*-test was performed, contrasting the average activity for Aware and Unaware conditions. Since we were interested in quantifying the contribution of each cluster to the average ERP, we calculated for each cluster the percent variance accounted for (*pvarf*, which compares the variance of the whole data minus the back-projected component to the variance of the whole data) using the *std.envtopo* (v4.10) EEGLab function. *Pvarf* values indicate how much of the variance of the sensor level ERP data is explained by particular ICs. *Pvarf* values may sometimes be negative, indicating that removing these ICs from the data increases variance of the scalp recorded ERP data. This happens because ICs sometimes cancel each other out, meaning that the summed variance of all ICs is actually larger than the variance of the scalp recorded data.

### 3. Results

The behavioral results showed that participants reported perceiving the stimulus on average in 48.27 % of trials. Stimulus location discrimination accuracy was significantly greater for Aware trials ( $M = 95.02\%$ ) than Unaware trials ( $M = 64.91\%$ ;  $t(35) = 14.79$ ,  $p < 0.001$ ), indicating that in the Aware condition participants could properly discriminate the side of presentation of the stimulus. Mean RTs for Aware trials (1107.45 ms) were significantly faster than mean RTs for Unaware condition (1398.53 ms);  $t(35) = -7.54$ ,  $p < 0.001$ ). In both conditions, RTs were longer than the ERP time window of interest (from  $-200$  ms to 600 ms, with respect to the stimulus onset), suggesting that the button press response should not contaminate the observed correlates of conscious vision.

Concerning the EEG results, as expected, both the VAN and the LP were observed in the grand average ERP. Fig. 1b shows the grand average ERP for the Aware and Unaware conditions at electrode O1. Paired-sample *t*-test (FDR-corrected) between Aware and Unaware trials, performed at each time sample, revealed that at electrode O1 VAN was significant in 2 different temporal windows: between 80 and 100 ms, and between 180 and 208 ms. LP was significant between 444 and 500 ms, although visual inspection suggests that its onset was earlier (around 325 ms).

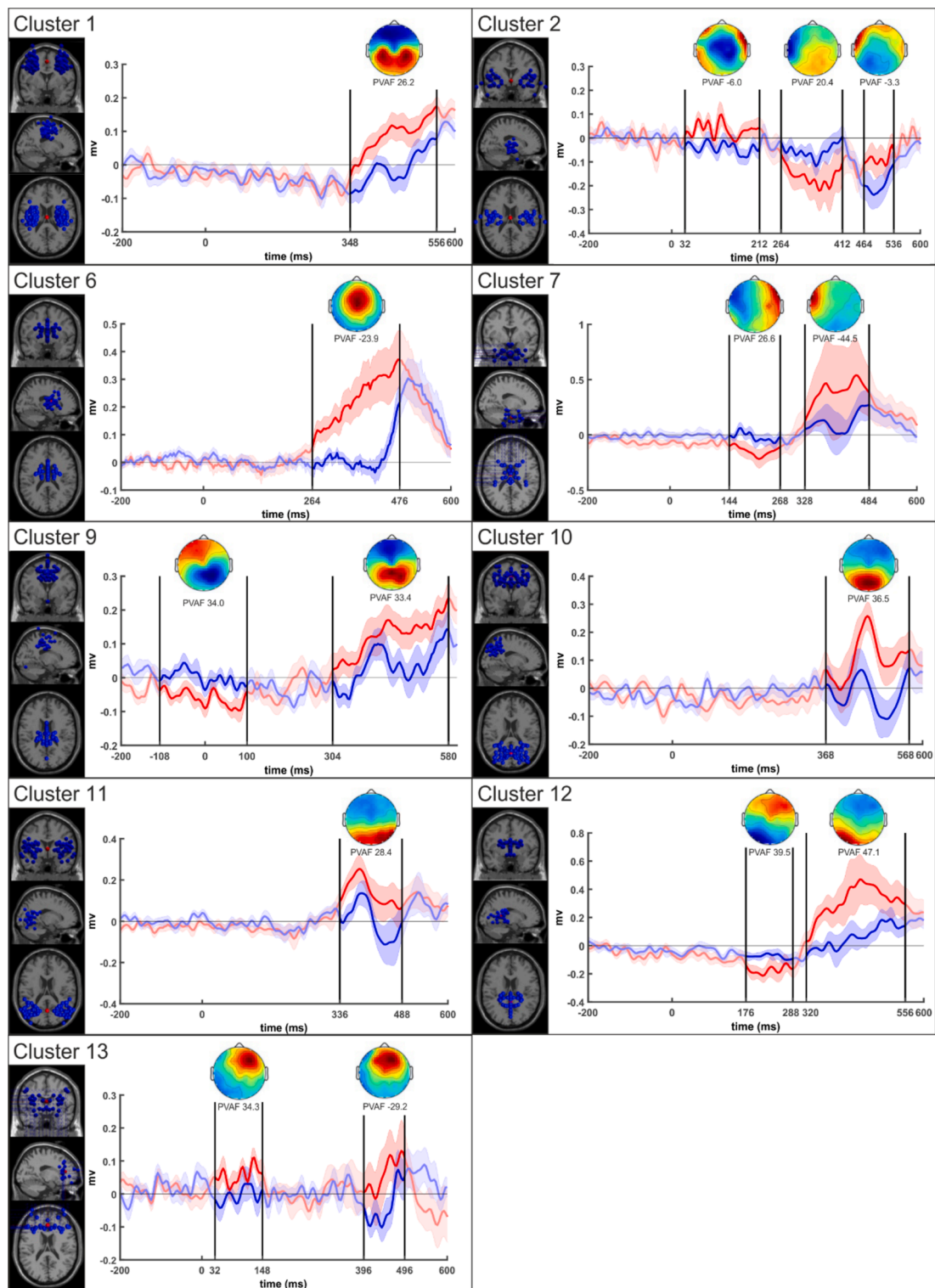
To examine the independent brain sources that contribute to the scalp recorded ERPs, and possibly correlate with conscious vision, we next analyzed the clusters of ICs. Only clusters with more than 15 components were included into the statistical analyses (cluster numbers 1, 2, 6, 7, 9, 10, 11, 12, 13). Excluded clusters contained on average 6 ICS ( $SD = 5.83$ ). Fig. 2 displays the ERP of each cluster included in the statistical analyses, as well as the locations of individual ICs within the cluster. The clusters localized to different areas of the brain. For example, Cluster 1 localized to anterior parietal/posterior frontal areas, and Cluster 2 to temporal cortex. Interestingly, Cluster 9 localized to fronto-parietal areas, involving motor and pre-motor areas. In general, visual inspection of the event-

**Table 1**

Description of clustering results. The table report how many participants and how many components are included in each cluster, as well as the average number of ICs per participants and the related standard deviation.

| Cluster | N. participants | N. ICs | Mean ICs | SD   |
|---------|-----------------|--------|----------|------|
| 1       | 26              | 62     | 2.38     | 1.20 |
| 2       | 17              | 24     | 1.41     | 0.71 |
| 6       | 23              | 56     | 2.43     | 1.37 |
| 7       | 12              | 16     | 1.33     | 0.49 |
| 9       | 19              | 34     | 1.78     | 1.08 |
| 10      | 24              | 42     | 1.75     | 1.03 |
| 11      | 25              | 36     | 1.48     | 0.58 |
| 12      | 19              | 31     | 1.63     | 1.01 |
| 13      | 12              | 18     | 1.5      | 1    |





**Fig. 2. Clusters results.** For each cluster are shown: the components' dipoles' location (on the left), the ERP waveform computed contrasting Aware (in red) and Unaware (in blue) conditions, the scalp distribution of the relative time-window and the percent variance accounted for (pvarf) each time-window. The scale of y axis changes from panel to panel because of graphical constraints. Time windows are highlighted by vertical black lines.

related responses suggested that especially in later time-windows (i.e., > 300 ms), the Aware and Unaware conditions differed. However, also earlier time-windows showed differences between the conditions, albeit smaller in amplitude (e.g., Clusters 2 and 12). Aware vs Unaware epochs were contrasted within each cluster in the selected time-windows (highlighted in Fig. 2 by vertical lines) using FDR-corrected paired-sample t-tests. The results are reported in Table 2: the first column shows the number of the cluster, while the second column shows the temporal window (expressed in milliseconds) analyzed in the corresponding cluster. The results of FDR-corrected paired-sample t-tests computed contrasting Aware and Unaware conditions are reported in the third column. Finally, the last column of the table shows the percent variance accounted for (pvaf) by each component at each temporal window. As shown in Table 2, many clusters showed statistically significant differences in the late time-windows (i.e., >300 ms after the stimulus presentation), and a few clusters also showed earlier differences. The earliest difference between Aware and Unaware conditions was observed –108–100 ms in fronto-parietal regions (Cluster 9). Also, Cluster 2 located in the temporal cortex showed a broad, early effect (32–212 ms), and also two later effects. Similar pattern is observed in Cluster 13 in the frontal cortex, although the difference between Aware and Unaware conditions was not statistically significant. Clusters 7 and 12 showed a mid-latency (roughly 150–260 ms) effect in occipito-temporal regions, in a time window corresponding to VAN in the scalp recorded grand average ERP. Finally, a later difference between Aware and Unaware conditions was observed in most of the clusters, spanning frontal, parietal, temporal and occipital regions.

The same analyses were performed also on Correct-Incorrect comparison (i.e., Correct trials are those trials in which participants reported accurately the side of presentation of the stimulus). Correct trials represented on average the 79.13 % of trials. As shown in Supplementary Fig. 1, the Correct vs Incorrect contrast yielded a grand average ERP very similar to the grand average ERP that was obtained by contrasting Aware and Unaware epochs. Also, the IC clustering, and the statistical analysis results largely replicated the result of the Aware vs Unaware comparison (see, Supplementary Fig. 2).

Because the components in Clusters 1 and 9 were located in motor and pre-motor cortex, with the aim of better understanding the possible relationship between EEG activity and response-related mechanisms, we tested if the mean difference between Aware and Unaware reaction times correlated (Pearson's  $r$ ) with the mean ERP amplitude difference between Aware and Unaware waveforms within the statistically significant temporal windows of different clusters. As depicted in Supplementary Fig. 3, Cluster 1 showed a significant correlation (Pearson's  $r = -0.65$ ,  $p < 0.001$ ) between the speed of discriminating the stimulus and awareness-related EEG activity: namely, the bigger the difference between Aware and Unaware waveforms, the faster the participants discriminated the stimulus. Similarly, also Cluster 2 and 6, whose components were located in fronto-temporal regions, showed a significant correlation (Pearson's  $r = 0.66$ ,  $p = 0.003$  and Pearson's  $r = 0.57$ ,  $p = 0.003$ , respectively) with reaction times, although notably these correlations were in the opposite direction (i.e., larger amplitude difference predicted slower RTs) when compared to Cluster 1.

#### 4. Discussion

ERP correlates of conscious vision have identified two major correlates of visual awareness (VAN and LP). While scalp recorded ERPs display excellent time resolution, the sources of VAN and LP remain open. This is an important open question as theories of consciousness make different predictions about the location and the timing of consciousness-related activity in the brain (Seth & Bayne, 2022).

The present study aimed to characterize the neural dynamics underlying conscious visual perception by decomposing ERPs into independent components. This allowed us to identify and localize the sources of neural activity that contribute to the grand-average ERP correlates of conscious perception.

Overall, in keeping with previous electrophysiological literature, the scalp recorded grand average ERPs obtained contrasting Aware and Unaware trials highlighted a significant difference in the N2 time-window (i.e., VAN), followed by a significant difference

**Table 2**

Results of FDR-corrected paired-sample t-tests computed contrasting Aware and Unaware conditions within each cluster in the reported time-windows.

| Cluster number | Temporal windows (ms) | p-value (fdr corrected) | Pvaf (%) |
|----------------|-----------------------|-------------------------|----------|
| 1              | 348–556               | 0.0030*                 | 26.02    |
| 2              | 32–212                | 0.0101*                 | –6       |
|                | 264–412               | 0.0904                  | 20.4     |
|                | 464–536               | 0.0143*                 | –3.3     |
| 6              | 264–476               | 0.0030*                 | –23.9    |
| 7              | 144–268               | 0.1168                  | 26.6     |
|                | 328–484               | 0.2237                  | –44.5    |
|                | –108–100              | 0.0023*                 | 34       |
| 10             | 304–580               | 0.0101*                 | 33.4     |
|                | 368–568               | < 0.0001*               | 36.5     |
| 11             | 336–488               | 0.0101*                 | 28.4     |
| 12             | 176–288               | 0.0395*                 | 39.5     |
|                | 320–556               | 0.0551                  | 47.1     |
|                | 32–148                | 0.1165                  | 34.3     |
| 13             | 396–496               | 0.1592                  | –29.2    |

\*= statistically significant after FDR correction

in the P3 amplitude (i.e., LP). Independent component analysis and clustering showed that activity of sources in many different cortical areas correlated with consciousness. In contrast to a serial, bottom-up driven process, the results suggest that the earliest differences between Aware and Unaware conditions were observed in parietal/frontal (cluster 9, between  $-108$  and  $100$  ms) and temporal (cluster 2, between  $32$  and  $212$  ms) regions. This activity occurred before stimulus-evoked activation. Also, early activity in prefrontal cortex correlated with conscious perception (cluster 13, between  $32$  and  $148$  ms), but this effect did not reach statistical significance. This early wave of activity was followed by correlates of conscious vision in occipito-temporal regions in a time-window corresponding to typical VAN time-window (cluster 2 until  $212$  ms, cluster 7, between  $144$  and  $268$  ms, cluster 12, between  $176$  and  $288$  ms). Finally, clusters spread over frontal, parietal, temporal and occipital areas displayed late differences in the P3 time-window. Notably, some of the sources that were active during LP time-window were active also during and before VAN (e.g., Cluster 2). Other sources were active solely during the LP (e.g., Cluster 10). This suggests that consciousness-related activity develops at least in part in “accumulative fashion” in a network of areas: consciousness-related activity in few early sources continues while additional sources are engaged as a function of time.

In general, our results are in accordance with previous source localization studies that identify the cortical generator of VAN in occipito-temporal brain regions (Vanni et al., 1996; Liu et al., 2012). Clusters 2, 7 and 12 revealed that the dipoles of components showing differences in the N2 amplitude when Aware and Unaware conditions were contrasted were localized in occipito-temporal areas. According to a popular interpretation, this activity in VAN time-window, possibly reflecting integrated, recurrent activity of multiple sources in the visual system, is the correlate of conscious visual perception (Förster et al., 2020; Mazzi et al., 2019; Dembski et al., 2021).

Conversely, dipoles of components reflecting differences in the LP amplitude were spread over frontal, parietal and occipito-temporal cortex, supporting the idea that LP has neural generators in wide-ranging cortical areas. According to a large body of literature, LP does not reflect neural processes purely related to subjective awareness of visual stimuli (Mazzi et al., 2020), but it is rather involved in later stages of processing such as processing task-relevant stimuli (Pitts et al., 2014b; Shafto & Pitts, 2015), decision making (Koivisto & Grassini, 2016; Tagliabue et al., 2019), or processes related to reporting the contents of conscious perception (Koivisto et al., 2016). Overall, although the paradigm adopted in the present study does not allow inferring the functional role of the investigated ERPs components, our results are consistent with this interpretation as some LP sources were added “on top of” earlier consciousness-related sources. While this interpretation holds that conscious perception emerges in earlier time-windows (e.g., in VAN time-window), activity in LP could be related to higher-forms of conscious processing, possibly reflecting accessing the contents of phenomenal consciousness, or (according to the LoP hypothesis) processing higher-level features of the perceived stimuli. (Jimenez et al., 2021).

Early activity observed in fronto-parietal areas in clusters 9 and 13 are so early ( $<150$  ms after stimulus onset), that they are outside the time-windows typically considered to directly enable conscious perception. These components may therefore reflect top-down mechanisms that occur before the stimulus enters the consciousness. Activity in fronto-parietal areas has been associated to visuo-spatial attention mechanisms (Corbetta et al., 2008; Parisi et al., 2020; Vossel et al., 2014), or temporal expectations related to the timing of stimulus appearance (Melloni et al., 2011; Lee, 2023; Seibold et al., 2023). In particular, it has been proposed that attentional orienting towards specific locations is enabled by a bilateral fronto-parietal network, including the intraparietal sulcus (IPS), the superior parietal lobule (SPL) and the frontal eye fields (FEF) (Corbetta et al., 2000, 2008). Since in the present study participants were asked to report on which side of the screen the stimulus was presented, it is likely that when the participants consciously detected the stimulus, they were covertly allocating their attention towards a location where the stimulus actually appeared at the correct moment in time. This allocation of attention may have helped to facilitate the entry of the visual input in visual awareness, without directly enabling conscious vision. Nevertheless, the relationship between consciousness and attention is complex, and the paradigm adopted in the present work was not designed to dissociate the two mechanisms. Moreover, distinguishing the true NCCs (i.e., the NCCs that purely reflect the conscious experience itself) from prerequisites (and consequences) of such conscious experience is even more intricate, and goes beyond the aim of the present work.

Some early components were located in motor and pre-motor areas (i.e., Clusters 1 and 9). This result is intriguing, since motor response was present in both Aware and Unaware condition, and these early correlates preceded motor responses by roughly one second. Thus, purely response-related activity is not likely to account for the difference between the two conditions. Cluster 1, whose components were located in the vicinity of motor areas, correlated with conscious perception ( $348$ – $556$  ms time-window) and this differential activity also strongly correlated with RTs across participants. Interestingly, also the differential activity in Clusters 2 ( $32$ – $212$  ms) and 6 ( $264$ – $476$  ms), although outside classical motor areas, correlated with RTs (although the direction of correlation was opposite when compared to Cluster 1). Altogether these results suggest that both early and late correlates of conscious perception could be intertwined with processes that support behaviorally “accessing” conscious contents, blurring the traditional distinction between early correlates of phenomenal consciousness and later correlates of conscious access. Given the relatively long temporal difference between stimulus presentation and RTs, and the fact that some of the correlates are outside classical motor regions, our results suggest that such associations are not simply due to “motor confounds” (i.e., directly linked to motor behavior). The association between action-related processes and correlates of conscious perception could reflect brain networks underlying the control of action through perception. For instance, locations of Clusters 2 (temporal cortex/operculum) and 9 (medial motor cortex and cingulate cortex) overlap with the action-mode network (Dosenbach et al., 2007).

Disentangling the true NCC (i.e., the minimal set of neural events sufficient and necessary for visual awareness to arise) from enabling factors and post-perceptual processes is hard and the experimental paradigm adopted in the present study didn’t allow to make this distinction. Thus, one could also argue that some early effects reported here (e.g., Clusters 2 and 9) reflect proper conscious vision, but we acknowledge that this interpretation remains to be directly tested in later research. While VAN latency is typically



around 200 ms after stimulus onset, studies also show that VAN sometimes onsets around 100 ms (Koivisto et al., 2005, 2009; Koivisto & Revonsuo, 2008). Although visual attention modulates responses in the same time-window, the awareness related effect seems to emerge independently of attention (Koivisto et al., 2005; Koivisto et al., 2006). Also, in the present study the onset of scalp-recorded VAN was before 100 ms. Therefore, it remains possible that the earliest fronto-parietal clusters also contributed to early conscious perception. This possibility is intriguing, because it could indicate that fronto-parietal areas provide key top-down modulation which enable consciously accessing simple visual features rapidly—that is, early correlates may not reflect purely “phenomenal” processes, but also associate with behaviorally accessing the contents of consciousness (Railo et al., 2015). Arguably, the large diameter visual stimuli, and simple location detection task employed in the present study were key to observing the early VAN as these visual features may be efficiently processed, enabling rapid emergence of conscious perception (Kouider & Dehaene, 2007; Jimenez et al., 2021). Previous research on the NCC has traditionally attempted to “control out” possible contributions of action-related processes (in order to isolate the “true” correlate of consciousness), but it could also be argued that the “feeling” associated with conscious experience has functional value (Cleeremans & Tallon-Baudry, 2022). If this is the case, then researchers should expect some overlap in the neural processes that support conscious perception and guidance of action, and examine the issue in futures research on conscious perception.

Although the IC-clustering method offers a promising approach to localize neural sources of the EEG signal, the method also has its limitations. First, because of the limited number of electrodes, lack of information about individual participants’ brain anatomy, and lack of information about the precise locations of electrodes in individual participants, the spatial resolution of the present source-localization is coarse. Second, ICA analysis and clustering is a statistical approach, and the results could be influenced by factors such as number of electrodes and clusters. Third, compared to the classical grand-average ERP correlates of conscious vision, the IC-correlates of conscious vision generally had smaller effect size. For these reasons, even though the sample size of the present study is larger than in most EEG studies of conscious vision, it could still be relatively limited for the proposed approach. However, to the best of our knowledge, the proposed approach represents the very first attempt to apply ICA to uncover neural sources that may be invisible in traditional ERP analyses, but contribute to the formation of a conscious experience.

## 5. Conclusion

In the search for the NCCs, the present results provide further significant information about the spatio-temporal neural dynamics involved in conscious vision, highlighting that IC-clustering represents a useful tool to investigate the neural correlates of conscious perception. The novel approach adopted in the present study enabled us to unveil how activity in multiple different brain regions, “hidden” in traditional ERP analysis, accumulates dynamically during the emergence of conscious visual perception. In addition to previously often reported correlates (VAN and LP), the results revealed earlier effects in fronto-parietal regions whose role in the emergence of visual awareness remains to be clarified.

## CRedit authorship contribution statement

**Elisabetta Colombari:** Writing – original draft, Visualization, Software, Formal analysis, Data curation. **Henry Railo:** Writing – review & editing, Supervision, Software, Resources, Project administration, Funding acquisition, Conceptualization.

## 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.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.concog.2024.103785>.

## Data availability

Data will be made available on request.

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