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Dissociation between the neural correlates of conscious face perception and visual attention

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Abstract

Given the higher chance to recognize attended compared to unattended stimuli, the specific neural correlates of these two processes, attention and awareness, tend to be intermingled in experimental designs. In this study, we dissociated the neural correlates of conscious face perception from the effects of visual attention. To do this, we presented faces at the threshold of awareness and manipulated attention through the use of exogenous prestimulus cues. We show that the N170 component, a scalp EEG marker of face perception, was modulated independently by attention and by awareness. An earlier P1 component was not modulated by either of the two effects and a later P3 component was indicative of awareness but not of attention. These claims are supported by converging evidence from (a) modulations observed in the average evoked potentials, (b) correlations between neural and behavioral data at the single-subject level, and (c) single-trial analyses. Overall, our results show a clear dissociation between the neural substrates of attention and awareness. Based on these results, we argue that conscious face perception is triggered by a boost in face-selective cortical ensembles that can be modulated by, but are still independent from, visual attention.

KEYWORDS

conscious face perception, EEG, face processing, N170, P300, visual attention

1 | INTRODUCTION

When an image is flashed to an observer, retinal stimulation triggers a series of neural processes, a subset of which lead to conscious perception (Koch, 2004). In order to identify these brain processes, a standard approach is to compare the brain responses elicited by "seen" and "unseen" visual stimuli. For example, we previously showed that the amplitude of a face-selective occipitotemporal EEG component, peaking ∼170 ms after stimulus onset (i.e., the N170), was larger whenever subjects reported seeing a face, although the stimuli eliciting the seen and unseen conditions, at the threshold of conscious perception, was exactly the same (Navajas, Ahmadi, & Quian Quiroga, 2013). In fact, with the peak amplitude of this signal, it was possible to decode above chance the subjects' conscious reports. One limitation of this study, which also applies to most related studies (Aru et al., 2012; Fisch et al., 2009; Pitts, Martínez, & Hillyard, 2012; Pitts, Metzler, & Hillyard,

2014; Sergent, Baillet, & Dehaene, 2005; Shafto & Pitts, 2015), is that the observed modulations in the neural responses might just reflect trial-by-trial fluctuations of attention rather than the perceptual state of the observer (Navajas, Rey, & Quian Quiroga, 2014). In other words, the difference between the seen and unseen conditions may be due to a varying allocation of attentional resources.

To address this issue, we developed a paradigm where we present faces at the threshold of awareness and manipulate involuntary attention through the use of exogenous cues (Posner, 1980, 1994). We exploited the fact that approximately 1 s after the presentation of an exogenous flash attentional resources are diminished in the location where the flash was presented, an effect known as "inhibition of return" (Klein, 2000). Based on previous findings using faces as stimuli (Taylor & Therrien, 2005, 2008), we predicted that valid trials (i.e., when the location of the flash matched the one of the stimulus) should elicit larger reaction times, due
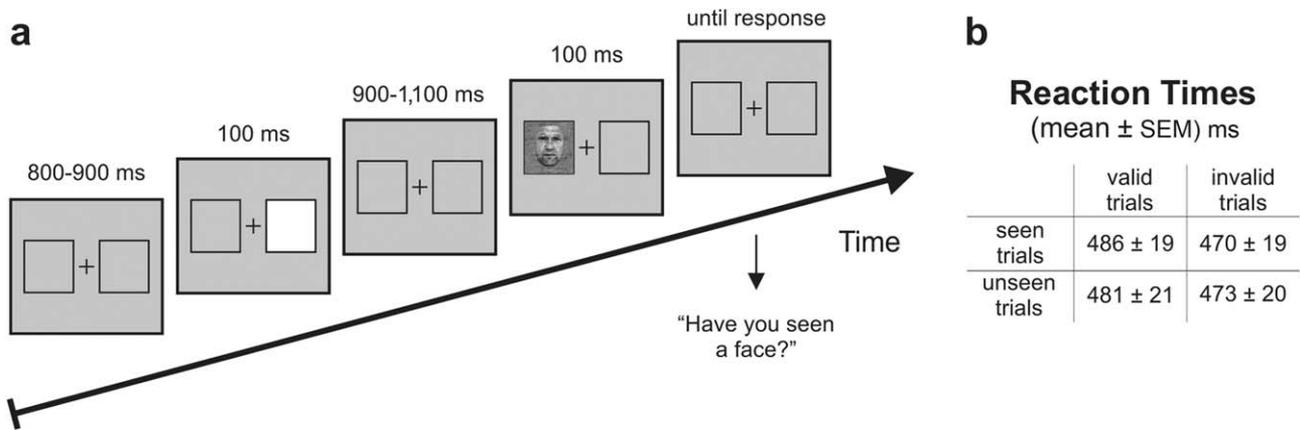
FIGURE 1 Paradigm and behavioral results. (a) Temporal structure of the experiment. Trials began with a central fixation cross and two lateral squares. After 800–900 ms, a bright flash (100 ms) was presented in one of the two sides. After another interval of 900–1,100 ms, a face or a car was presented for 100 ms on a location that matched (valid trials) or did not match (invalid trials) the one of the flash. We added zero-mean Gaussian noise to the stimuli and manipulated the variance of the noise using a double-staircase procedure that kept running throughout the experiment. Participants were instructed to report whether or not they saw a face by pressing one of two buttons in a response box. (b) Reaction times as a function of experimental condition (rows: perceptual conditions; columns: attentional conditions). Participants were faster in invalid trials compared to valid trials, irrespective of their conscious report

to a lower level of attention, than invalid trials. This experimental setting led to a 2 × 2 design that allowed a factorial analysis of the neural correlates of conscious face perception and attention. Moreover, here we rule out other possible confounds that are pervasive in the literature (Navajas, Rey, & Quian Quiroga, 2014), such as differences in the physical stimuli used to elicit the different conditions.

Altogether, we found that the prestimulus cues modulated attention, as measured by the participants' reaction times, but had no impact on the probability to perceive the faces. The neural data showed that the N170 component was modulated by attention, but still gave a reliable index of conscious perception for the same attentional conditions. An earlier positive component (the P1) was uninformative of both attention and awareness. Finally, a later EEG response with centroparietal topography (the P3), which has been previously linked to subjective awareness (Dehaene & Changeux, 2011), was indicative of conscious reports but not of the attentional state of the subjects. Overall, these results provide a dissociation of the neural mechanisms of attention and conscious face perception in scalp occipitotemporal and centroparietal EEG responses.

2 | METHOD

2.1 | Stimuli

Twenty pictures of faces in frontal view were selected from the Psychological Image Collection at Stirling (http://pics.psych.stir.ac.uk/), and 20 front views of cars were downloaded from the Internet. Twelve different levels of zero-mean Gaussian noise (equally spaced between 0 and 0.3) were added to the images using the MATLAB function *imnoise*. The brightness and spatial frequency of the entire

data set were normalized using the SHINE toolbox (Willenbockel et al., 2010). Stimuli were presented on a CRT monitor with a resolution of 1,024 × 768 pixels and a refresh rate of 100 Hz. The viewing distance was approximately 50 cm.

2.2 | Paradigm

To dissociate attention and awareness, we combined an experimental design previously used to study conscious face perception (Navajas et al., 2013) with a classic paradigm to manipulate involuntary attention through the presentation of prestimulus exogenous cues (Posner, 1980). Each trial (Figure 1a) began with a central fixation cross on a gray background and two empty squares centered 3.6 degrees off the vertical meridian (size: 2.6 degrees) that were shown for a randomly chosen time between 800 and 900 ms. After this interval, a flash appeared for 100 ms on either of the two squares and after another 900–1,100 ms, a face with added noise was presented for 100 ms on one of the two squares. Participants were instructed to report as soon and as accurately as possible whether or not they saw a face regardless of its location. Responses were given by pushing one of two buttons of a millisecond accurate Black Box Toolkit response box (Plant & Quinlan, 2013) using the right hand.

2.3 | Task and procedure

The experiment consisted of 1,680 trials of two different types: 1,568 "staircase" trials and 112 "catch" trials. The entire experiment lasted approximately 90 min. In the staircase trials, we presented faces with a variable amount of added noise using a double-staircase procedure that kept running throughout the experiment (Navajas, Rey, & Quian Quiroga, 2014).
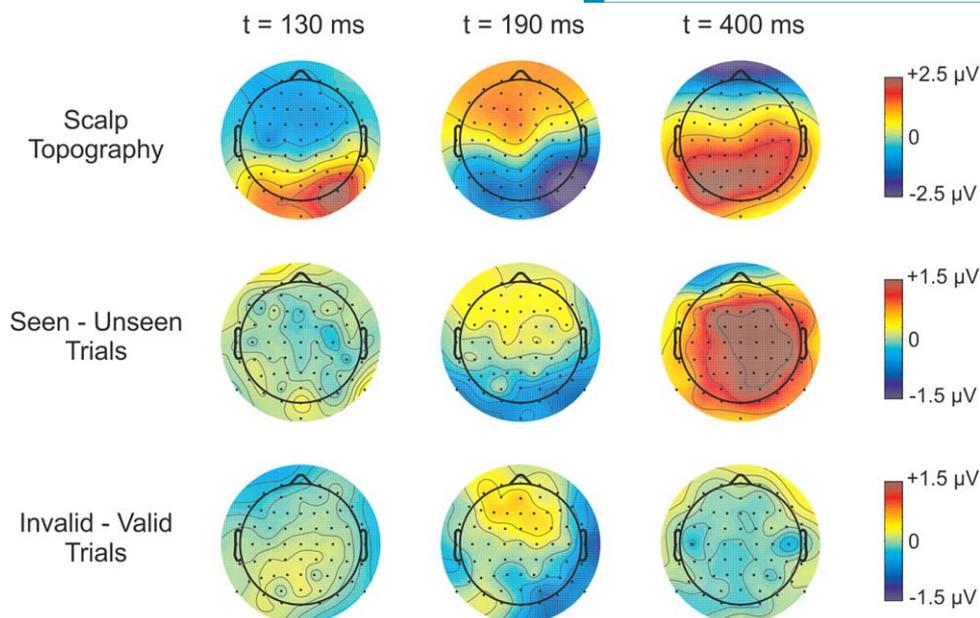
FIGURE 2 Scalp topography and differences between conditions, for stimuli presented in the left visual field, at the time of the three observed components. Columns: Left column corresponds to the P1 component, which was maximal at 130 ms; central column corresponds to the N170, which peaked at 190 ms; and right column corresponds to the P3 component, which was maximal at 400 ms. Rows: Upper row shows the scalp topography of each component, middle row displays the difference between seen and unseen trials, and lower row shows the difference between invalid and valid trials

The upper (lower) staircase always started from a noise level of 0.3 (0) with a fixed step size of 0.025. The stimulus location (left or right visual field) and the attention manipulation (valid or invalid cue) were counterbalanced across the staircase trials. Thus, cues were not predictive of the stimulus location. Catch trials were cars presented with the same level of noise as the staircase (face) trials. This type of trial was used to assess the reliability of the participants' reports by computing a false positive rate (i.e., the proportion of trials in which participants reported to have seen a face in these trials).

To ensure that the visual input was constant across conditions, we selected for each subject the level of noise that led to a face recognition rate closest to 50% (Navajas et al., 2013; Navajas, Rey, & Quian Quiroga, 2014). The number of trials in this level of noise was different for each subject (mean: 564 trials, *SD*: 114 trials). These trials were the ones used to compute ERPs across the eight conditions of our experiment (Left/Right $\times$ Valid/Invalid $\times$ Seen/Unseen). The contrast between the ERPs elicited in the unseen versus seen condition could be interpreted as the neural signals that correlate with the switch from reporting "I did not see a face" to "I saw a face" at constant retinal stimulation.

2.4 | Participants

Twenty-nine healthy adults volunteered to participate in this study. All of them were right-handed, had no history of neurological disorders, and normal or corrected-to-normal vision. All participants were recruited through advertisements at the University of Leicester, gave written informed consent, and

were paid £15 for their participation. Data from four participants were discarded due to an excessive number of false positives (more than 13%, while the range of false positive rates was 0–3.5% for the remaining participants). We discarded data from two other subjects because, after artifact rejection, they had fewer than 40 trials per condition to compute the ERPs. Hence, we report results from 23 participants (15 female, mean age: 23.6 years, range: 18–36). For these participants, we computed ERPs based on 71 ± 15 (mean $\pm$ *SD*) trials (range: 48–94 trials) per condition. We confirmed, using subsamples of our data, that this number of trials was sufficient to measure reliable ERPs (see online supporting information Figure S1).

2.5 | EEG recordings and ERP analysis

Signals were recorded with a sampling rate of 256 Hz using a BioSemi ActiveTwo 64-channel EEG system. The reference was set to the average across all electrodes. Epochs including 1 s before and 1 s after stimulus onset were extracted for further analysis and band-pass filtered with a second-order Butterworth filter between 1 and 70 Hz. This reference and filter parameters were shown to be optimal for the P1 and N170 components (Joyce & Rossion, 2005; Rousselet, Husk, Bennett, & Sekuler, 2007).

After examination of the evoked topographies (averaging all conditions together), we distinguished three clear components: P1, N170, and P3 (see top panels of Figure 2). For stimuli presented in the left visual field, the P1 (N170) component had its peak in electrode PO8 at 130 ms (190 ms). For stimuli presented in the right visual field, both the P1

and N170 had their peaks at the same time in electrode PO7. Therefore, we selected electrodes PO7/8 to further analyze these components, which is in line with previous studies (e.g., Navajas et al., 2013; Rossion & Jacques, 2008).

Given the global nature of the P3 component, an average reference is not optimal in this case, and we therefore rereferenced samples to mastoid electrodes (Joyce & Rossion, 2005). Because the P3 wave is slower than the P1/N170, we used different filter parameters to focus on this component (0.1–30 Hz). We found that the P3, averaged across all conditions, had its peak in electrode CPz at 400 ms (for stimuli presented from both sides), and thus selected this electrode for further analysis. ERP traces from other electrode sites are shown in supporting information Figure S3.

Trials containing blinks, eye movements, and other artifacts were rejected by a semiautomatic procedure applied to each subject separately. First, we epoched and filtered the data on a time window of ± 1 s around the stimulus onset. Then, we set a threshold in amplitude of ± 30 μV for a selection of channels along the midline (Fz, FCz, Cz, CPz, Pz, Oz) and preselected all trials that crossed this threshold. Finally, we visually inspected all of these trials to only reject them if they were actual artifacts. Overall, this procedure led to a rejection rate of 10.4% of the trials (range: 1.4%–21.1%) for the 23 subjects considered in our study.

For statistical analysis, we computed for each channel and subject the mean average ERP on specific time widows. For the P1 and N170, we selected time windows using the same procedure in Navajas et al. (2013); we considered 40-ms windows centered in the peak of each component (110–150 ms for the P1, 170–210 ms for the N170). For the P3, we used a 200-ms window centered in its peak (300–500 ms), as in previous studies (Pitts et al., 2012, 2014; Shafto & Pitts, 2015).

Stimuli presented at different locations (ipsilateral and contralateral visual field) were analyzed separately. Each component was submitted to a two-way repeated measures analysis of variance (rm-ANOVA) with factors attention (two levels: valid or invalid trials) and conscious report (two levels: seen and unseen). Statistical differences were assessed separately for each component. For all pairwise comparisons, we performed t tests and report for each condition the mean ± *SEM*, along with a standardized measure of effect size (i.e., 95% confidence intervals for the Hedges' g value, see Hentschke & Stüttgen, 2011).

2.6 | Assessment of correlations between behavioral and neural data

To evaluate the correlation between the observed effects in the behavioral and the neural data, we measured for each participant the mean reaction time (*mRT*) and the mean ERP amplitude (*mERP*) for the P1, N170, and P3 across all condi-

tions. Both for the behavioral and the neural data, for each subject we computed the effect of cue validity (*ECV*):

$$ECV(X) = \frac{X(v,s) + X(v,u) - (X(i,s) + X(i,u))}{\max(X)} \quad (1)$$

where X denotes either *mRT* or *mERP*, v and i denote the valid and invalid conditions, and s and u refer to the seen and unseen conditions, respectively. This allowed us to test if the behavioral effect of cue validity, as measured from the reaction times, was correlated to amplitude changes on the ERP components on a subject-by-subject basis.

We also aimed at evaluating if the effects of attention and awareness on the ERPs were correlated on a subject-by-subject basis. To this end, we computed the effect of awareness on the ERP amplitudes as:

$$EA(mERP) = $$
$$\frac{mERP(v,s) + mERP(i,s) - (mERP(v,u) + mERP(i,u))}{\max(mERP)} \quad (2)$$

## 2.7 | Single-trial analysis and decoding

We assessed the information provided by the single-trial traces using a decoding analysis. Single-trial ERPs were extracted by means of a denoising algorithm that implements a wavelet decomposition of the single-trial ERPs and denoises them by reconstructing the signals using only the wavelet coefficients related to the evoked responses, setting to zero all the others (Ahmadi & Quian Quiroga, 2013; Quian Quiroga, 2000). The set of wavelet coefficients used to extract the single-trial traces was kept constant across subjects and conditions. The single-trial N170 responses were identified as the local minimum between 140 and 220 ms, and for the P3 we used the local maximum between 250 and 550 ms.

With these peaks, we implemented a linear discriminant analysis to decode the conscious report (seen or unseen) and attentional condition (cue valid or invalid) using the MATLAB function *classify* and a leave-one-out cross validation. Chance levels were defined by repeating the procedure 1,000 times per subject using a random permutation of the labels. Statistical differences were assessed using paired t tests between the 23 observed decoding performances and the 23 mean performances obtained with random permutations. Significance levels were corrected for multiple comparisons using Bonferroni's method.

3 | RESULTS

3.1 | Behavior

The double-staircase procedure converged to a noise level of 0.078 ± 0.013 (mean ± *SEM*), with a recognition performance of 48.7 ± 7.4%. To evaluate the effectiveness of the attention
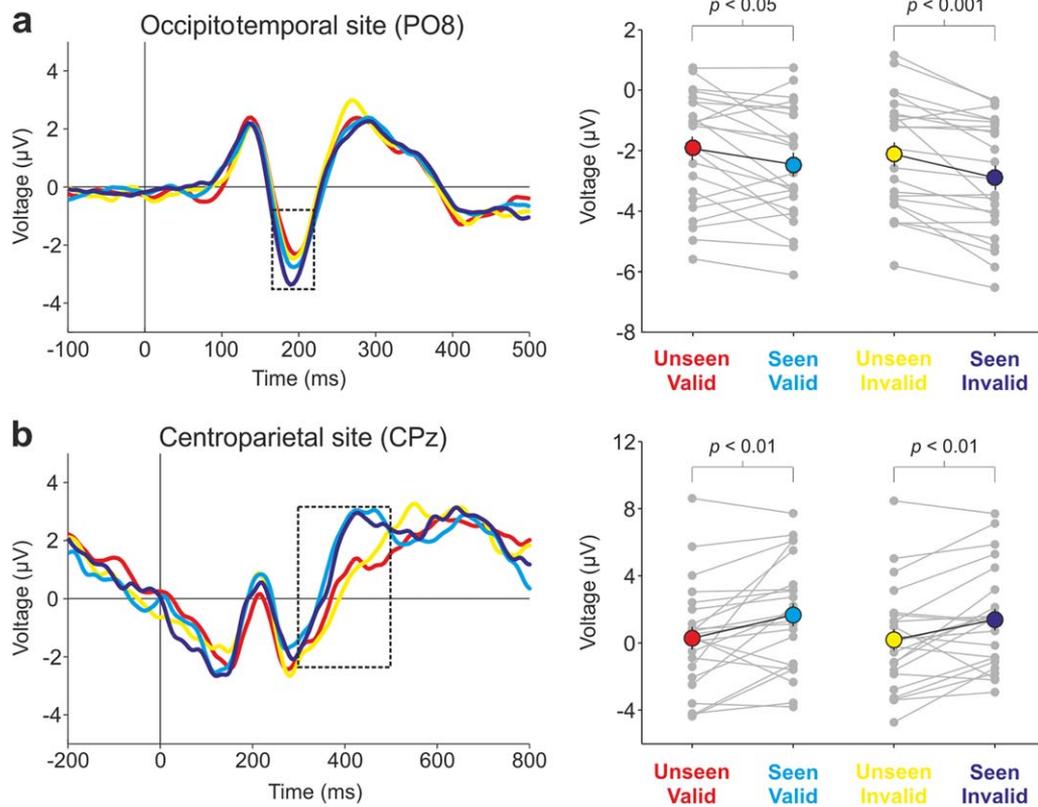
FIGURE 3 ERPs for the four conditions in this study, for stimuli presented in the left visual field. (a) Left: ERPs at electrode PO8 located at an occipito-temporal site. Dotted lines mark the time window used to measure the N170 component. Right: Colored circles and vertical lines show the mean and *SEM* of the N170 amplitudes for each condition. Gray circles connected by lines show individual data. There was a significant effect of attention and also of conscious perception. (b) Left: ERPs at electrode CPz located at a centroparietal site. Dotted lines mark the time window used to measure the P3 component. Right: same as (a) for the P3 responses. There was a significant effect of conscious perception but not of attention. Asterisks show statistically significant comparisons

manipulation, we compared the mean reaction times (Figure 1b) obtained in the different conditions using a two-way rm-ANOVA with attention and conscious report as factors. We observed a significant effect of attention, $F(1, 22) = 10.05$, $p < .01$, but not of conscious report, $F(1, 22) = 2.09$, $p = .16$, and no significant interaction, $F(1, 22) = 3.21$, $p = .11$. These results suggest that the experimental design succeeded at manipulating attention without affecting the perceptual decisions of the subjects. To further validate this observation, we measured the proportion of seen trials in valid and invalid conditions. We reasoned that, if higher levels attention correlated with a higher probability of consciously perceiving the faces, we should then observe fewer seen trials upon the valid condition, where attention is diminished through inhibition of return. However, the proportion of seen trials in the invalid condition was not significantly different from the one obtained in the valid condition (valid trials: $47.8 \pm 1.83\%$, invalid trials: $48.1 \pm 1.78\%$, paired *t* test, $t(22) = 0.15$, $p = .87$.

3.2 | Evoked responses

We identified three clear ERPs in response to faces (Figure 2). The first one was a positive component in occipital elec-

trodes peaking at ∼130 ms (the P1). The second one was a negative deflection at ∼190 ms with an occipitotemporal location (the N170). Lastly, we observed a later (∼400 ms) centroparietal wave, corresponding to the P3 component. To evaluate which of these responses were informative of the subjects' attention and conscious perception, we computed the P1 and N170 in electrodes PO7/8 and the P3 in electrode CPz (see Method). The P1 failed to show any significant main effect or interaction, both when the stimulus appeared in the left (conscious perception: $F(1, 22) = 2.53$, $p = .12$; attention: $F(1, 22) = 0.21$, $p = .65$, interaction: $F(1, 22) = 1.67$, $p = .21$) and in the right visual field (conscious perception: $F(1, 22) = 0.03$, $p = .86$; attention: $F(1, 22) = 0.13$, $p = .72$, interaction: $F(1, 22) = 0.40$, $p = .53$).

The largest N170 responses were observed in the right hemisphere (i.e., electrode PO8) upon contralateral stimulus presentation (Figure 3a). In this case, we observed both a significant effect of attention, $F(1, 22) = 6.27$, $p = .02$, and conscious perception, $F(1, 22) = 21.54$, $p < .001$, and no significant interaction, $F(1, 22) = 0.92$, $p = .35$. Post hoc tests showed that the difference between seen and unseen trials was significant both for the valid (unseen condition: -1.9 ± 0.4 µV; seen condition: -2.4 ± 0.4 µV; Hedges' *g*

CI = [0.01–0.53]; $t(22) = 2.1$, $p < .05$) and invalid (unseen condition: -2.1 ± 0.4 μV; seen condition: -2.9 ± 0.4 μV; Hedges' g CI = [0.18–0.61]; $t(22) = 4.6$, $p < .001$) conditions. No effects were observed for this electrode when the stimulus was presented in the ipsilateral field (conscious perception: $F(1, 22) = 1.85$, $p = .18$; attention: $F(1, 22) = 3.10$, $p = .10$, interaction: $F(1, 22) = 0.19$, $p = .67$). Also, no effects were observed in the left hemisphere (electrode PO7) both when the stimulus was presented in the contralateral (conscious perception: $F(1, 22) = 3.25$, $p = .09$; attention: $F(1, 22) = 0.69$, $p = .41$, interaction: $F(1, 22) = 0.08$, $p = .77$) or in the ipsilateral field (conscious perception: $F(1, 22) = 1.07$, $p = .13$; attention: $F(1, 22) = 0.63$, $p = .43$, interaction: $F(1, 22) = 1.04$, $p = .32$). These results are consistent with previous studies showing that the N170 is maximal in the right hemisphere (Rossion, Joyce, Cottrell, & Tarr, 2003) and contralateral to the stimulus location (Feng, Martinez, Pitts, Luo, & Hillyard, 2012; see Discussion).

Centroparietal P3 responses were significantly modulated by conscious perception but not by attention (Figure 3b). These effects were present both for visual stimuli presented in the left (electrode CPz, conscious perception: $F(1, 22) = 18.62$, $p < .001$; attention: $F(1, 22) = 0.76$, $p = .38$, interaction: $F(1, 22) = 0.08$, $p = .76$) and right visual field (electrode CPz, conscious perception: $F(1, 22) = 11.51$, $p < .01$; attention: $F(1, 22) = 0.16$, $p = .68$, interaction: $F(1, 22) < 0.01$, $p = .92$). Post hoc tests showed that the effect of awareness on the P3 was present for both valid (unseen condition: 0.3 ± 0.7 μV; seen condition: 1.7 ± 0.7 μV; Hedges' g CI = [0.10–0.75]; $t(22) = 2.9$, $p < .01$) and invalid (unseen condition: 0.2 ± 0.6 μV; seen condition: 1.4 ± 0.6) μV; Hedges' g CI = [0.10–0.67]; $t(22) = 3.2$, $p < .01$) trials (Figure 3b).

We also observed a negative drift in the baseline at electrode CPz, which corresponds to the contingent negative variation (CNV) component. This signal is a signature of the anticipation of an upcoming event (Macar & Vidal, 2003), a new trial in our case. Because the CNV has a slow temporal dynamics, we only observe it in Figure 3b, where signals were high-pass filtered at 0.1 Hz (as opposed to 1 Hz when in Figure 3a, see Method for details). This CNV component was present in most electrodes, including PO8 (supporting information Figure S3), but we did not observe any significant difference in the prestimulus CNV amplitude (conscious perception: $F(1, 22) = 0.94$, $p = .34$; attention: $F(1, 22) = 0.24$, $p = .63$, interaction: $F(1, 22) = 1.45$, $p = .24$).

3.3 | Correlation between behavioral and neural responses

We further examined the effect of attention on the N170 (Figure S2). First, we observed that, averaging seen and unseen trials, the N170 amplitudes were significantly larger

in the invalid compared to the valid condition (valid condition: -2.2 ± 0.4 μV, invalid condition: -2.5 ± 0.4 μV; Hedges' g CI = [0.01–0.33]; $t(22) = 2.3$, $p = .02$). This effect was independent of the assumption of normality in our data (area under receiver operating characteristic [AUROC] = 0.43, 95% CI = [0.26–0.70]; Wilcoxon sign rank test, $z = 2.3$, $p = .02$). Post hoc tests showed that the effect of attention was significant for seen trials (valid condition: -2.4 ± 0.4 μV, invalid condition: -2.9 ± 0.4 μV; Hedges' g CI = [0.01–0.29]; $t(22) = 2.12$, $p < .05$), but it was absent in the unseen condition (valid condition: -1.9 ± 0.4 μV, invalid condition: -2.1 ± 0.4 μV; Hedges' g CI = [-0.02–0.48]; $t(22) = 1.14$, $p = .26$).

To gain more confidence that attention indeed modulated the N170 component, we performed a new analysis. We evaluated if the varying modulations in the ERP components among subjects correlated with their varying degrees of attention in the task, quantified by their reaction times. To this end, we measured the effect of cue validity on the mean reaction times (i.e., an index of how effective the attentional manipulation was at the behavioral level) and correlated it with the one observed for the N170 and P3 amplitudes (see Method, Equation 1). We observed a positive correlation between the modulation of reaction times due to attention, and the changes in the N170 amplitude due to the same effect (Figure 4a, Pearson correlation coefficient $r = .47$, $p = .02$).

Consistent with the abovementioned finding that the P3 did not change with attention, we did not observe such a correlation for this component (Figure 4b, Pearson correlation coefficient $r = -.29$, $p = .16$). We then studied if the different significant effects observed at the average level (Figure 3) were correlated with each other on a subject-by-subject basis. We observed that the modulations in the N170 due to awareness were uncorrelated with the effect of attention on the same component (Figure 4c), and with the effect of awareness on the P3 component (Figure 4d). This supports the view that these two signals reflect independent neural processes.

3.4 | Discarding residual effects of attention on the N170

Valid and invalid trials led, on average, to conditions with different levels of spatial attention (Figure 1b). However, it could still be possible that other attentional processes (not captured by our manipulation) led to trial-to-trial fluctuations in attention within each condition. To test this possibility, we performed a single-trial analysis of the EEG traces. We reasoned that, if residual sources of attention modulated neural signals within each condition, then trial-to-trial changes in
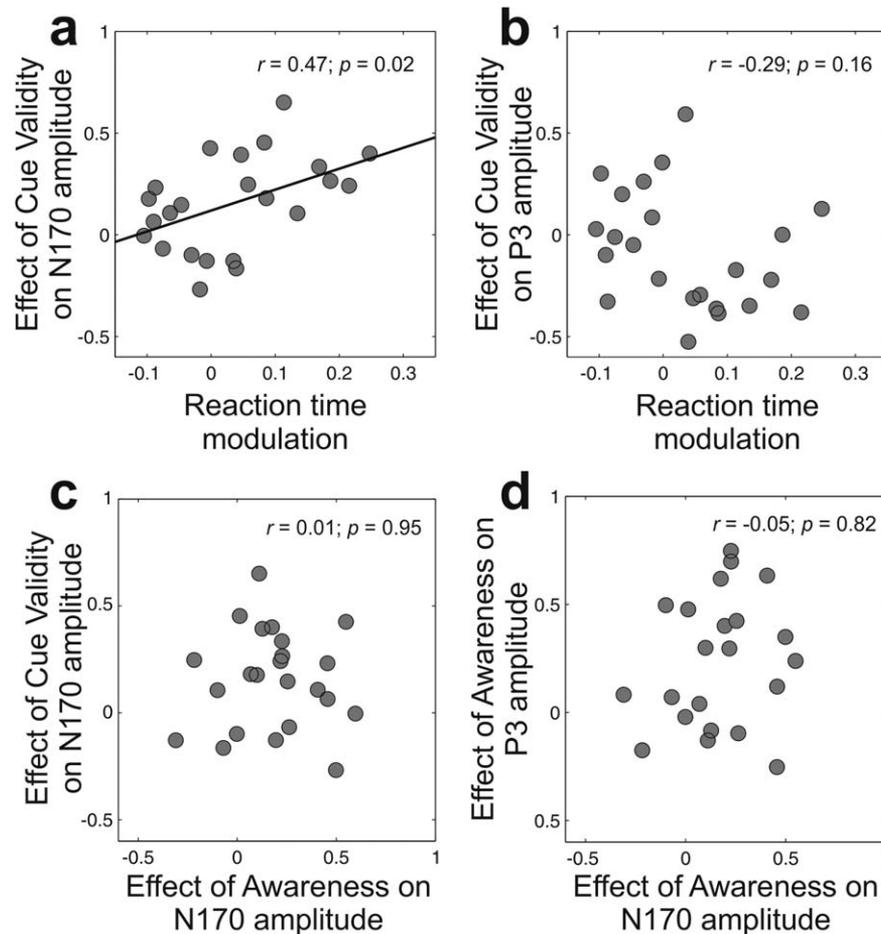
FIGURE 4 (a, b) Subject-by-subject correlation of reaction time changes (valid vs. invalid trials) and N170 (a) and P3 (b) changes (see Method and Equation 1 for details). Each dot represents results for a single subject. Pearson correlation coefficients (r) and their associated p values are shown for each plot. The line shows the linear fit in the only significant comparison. (c, d) Subject-by-subject correlation between the different significant effects observed at the average level (see Figure 3 and Equation 2 for details). (c) The effect of awareness on the N170 is uncorrelated with the effect of attention (cue validity) on the same component. (d) The effects of awareness on the N170 and P300 were not correlated with each other

reaction time (our proxy for attention) should correlate with single-trial fluctuations in the evoked responses.

We focused on the N170 peak amplitude as this was the only evoked response that showed significant modulation with attention at the average level (Figure 2–3a, 4). Single-trial peaks were extracted using a wavelet-denoising algorithm (see Method). The algorithm consists in decomposing the EEG traces using a discrete wavelet transform and reconstructing the signal using only the wavelet coefficients that are related to the average evoked responses. This procedure was previously shown to improve the estimation of single-trial peaks (Ahmadi & Quian Quiroga, 2013; Quian Quiroga, 2000), including N170 responses at the threshold of awareness (Navajas et al., 2013).
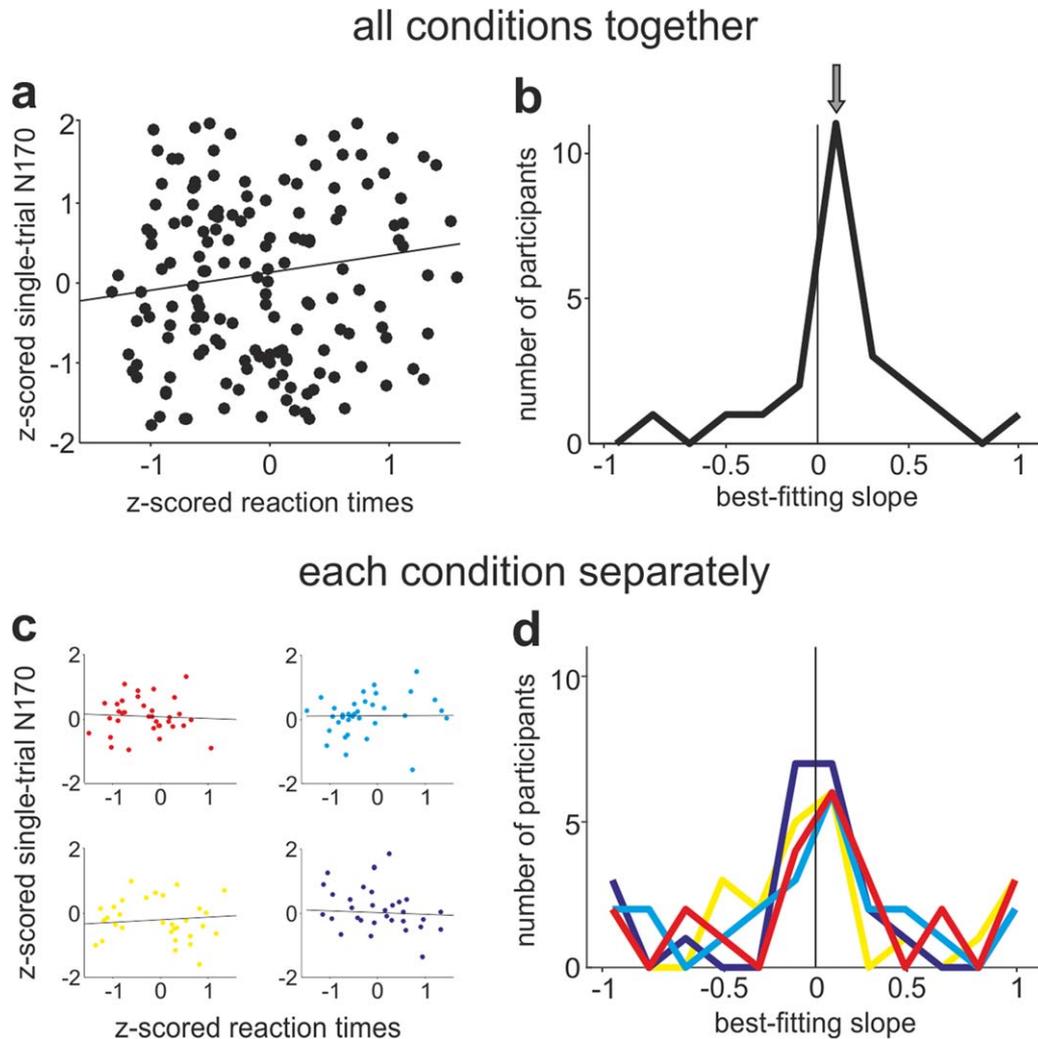
Fluctuations in single-trial N170 amplitudes were compared to trial-to-trial changes in reaction time. Lumping all conditions together, we observed that trials with higher attention (i.e., faster reaction times) had a larger N170 effect (i.e., a more negative N170). Figure 5a shows this effect for one representative participant. To quantify this observation at the

population level, we fit a linear regression to each participant and compared the distribution of slopes with zero. We found that this distribution was significantly larger than zero (Figure 5b, two-tailed sign test, $p = .01$). This finding is consistent with our previous observation that the N170 is larger for invalid trials.

We then examined each condition separately, and observed that the N170 amplitudes were uncorrelated with fluctuations in reaction time (Figure 5c,d, two-tailed sign tests of distribution of best-fitting slopes, $p > .4$ for all conditions). This indicates that, if there were any residual effect of attention within each condition, these effects did not modulate the N170. Therefore, the effects reported in this study cannot simply be explained by trial-to-trial changes in residual attentional processes.

3.5 | Decoding

Next, we asked whether the modulations in the ERP responses were strong enough to predict, at the single-trial

all conditions together

each condition separately

FIGURE 5 Testing for residual effects of attention on the N170. (a, b) Considering all conditions together, the single-trial N170 amplitude was positively correlated with reaction time. (a) *z*-scored single-trial N170 versus *z*-scored reaction times for one representative participant. (b) Distribution of best-fitting slopes among participants. The arrow points to the value of the participant selected in (a), which is the median participant. (c, d) Considering each condition separately, the single-trial N170 amplitude was uncorrelated with reaction time. (c) Based on the data of the same participant selected in (a), panels show *z*-scored single-trial N170 amplitudes versus *z*-scored reaction times for each condition. Colors are the same as in Figure 3: red for unseen valid, cyan for seen valid, yellow for unseen invalid, and blue for seen invalid. (d) Distribution of best-fitting slopes among participants for each condition

level, both the attention (attended or not) and perceptual (seen or not) conditions. From the single-trial denoised traces, we identified the N170 and P3 peaks and implemented a decoding analysis. To assess the significance of the decoding algorithm, we compared the empirically measured performances with the ones obtained using random permutations (see Method). We focused this analysis on trials in which the stimulus was presented in the left visual field, as these were the trials that yielded significant results in the evoked responses.

We did not observe any significant modulation in the single-trial latencies of the ERP components, and, consequently, we focused on the single-trial peak amplitudes. Table 1 summarizes the decoding results with the corresponding statistical significances. We first aimed at decoding the four conditions of the experiment (attended and unat-

tended; seen and unseen) based on the amplitudes of these components. Decoding performance was significantly above chance both for the N170 (measured performance: $28.1 \pm 0.5\%$, chance level: $25.0 \pm 0.2\%$, paired t test $t(22) = 5.5$, $p < 10^{-4}$, Bonferroni corrected $\alpha = .025$) and the P3 component (measured performance: $27.4 \pm 0.8\%$, chance level: $24.9 \pm 0.1\%$, paired t test $t(22) = 3.1$, $p < 10^{-4}$, Bonferroni corrected $\alpha = .025$).

Next, we asked whether we could decode conscious reports disregarding the attentional condition. In this case, decoding performance was significantly above chance both using the N170 peak (measured performance: $54.0 \pm 0.6\%$, chance level: $50.0 \pm 0.3\%$, paired t test, $t(22) = 5.9$, $p < 10^{-5}$, Bonferroni corrected $\alpha = .025$) and the P3 peak (measured performance: $54.1 \pm 1.1\%$, chance level: $50.1 \pm 0.3\%$, paired t test, $t(22) = 3.5$, $p < .001$, Bonferroni

TABLE 1 Decoding perception and awareness with different ERPs

Decoded variable	N170	P3
Conscious reports and attention	$28.1 \pm 0.5\%, p < 10^{-4}$	$27.4 \pm 0.8, p < 10^{-4}$
Conscious reports	$54.0 \pm 0.6\%, p < 10^{-5}$	$54.1 \pm 1.1\%, p < .001$
Attention	$53.1 \pm 0.4\%, p < 10^{-5}$	$50.9 \pm 1.5\%, p = .42$
Conscious reports for attended (invalid) trials	$53.8 \pm 0.9\%, p < 0.001$	$53.4 \pm 1.2\%, p < .01$
Conscious reports for unattended (valid) trials	$55.6 \pm 1.0\%, p < 10^{-4}$	$55.4 \pm 1.1\%, p < 10^{-4}$
Attention for seen trials	$54.4 \pm 0.8\%, p < 10^{-4}$	$52.3 \pm 1.4\%, p = .11$
Attention for unseen trials	$52.7 \pm 0.6\%, p < 0.01$	$48.2 \pm 2.6\%, p = .43$

Note. Decoding performance (mean $\pm$ *SEM*) for different conditions (rows) using different components (columns). Statistical comparisons were performed by comparing the measured performance with the one obtained with random permutations.

corrected $\alpha = .025$). Similarly, we studied if we could decode the attentional condition regardless of the conscious report given by the participant. Consistent with the effects observed in the evoked responses, decoding performance was significantly above chance when using the N170 (measured performance: $53.1 \pm 0.4\%$, chance level: $49.9 \pm 0.3\%$, paired t test, $t(22) = 6.1$, $p < 10^{-5}$, Bonferroni corrected $\alpha = .025$) but not when using the P3 peak (measured performance: $50.9 \pm 1.5\%$, chance level: $49.8 \pm 0.3\%$, paired t test $t(22) = 0.8$, $p = 0.4$, Bonferroni corrected $\alpha = .025$).

We then examined if conscious reports could be decoded at a constant attention level. Using the N170 peak, decoding performance was above chance both for invalid (measured performance: $53.8 \pm 0.9\%$, chance level: $49.7 \pm 0.3\%$, paired t test, $t(22) = 4.5$, $p < .001$, Bonferroni corrected $\alpha = .012$) and valid trials (measured performance: $55.6 \pm 1.0\%$, chance level: $49.7 \pm 0.4\%$, paired t test, $t(22) = 5.2$, $p < 10^{-4}$, Bonferroni corrected $\alpha = .012$). Similarly, conscious reports could also be decoded using the P3 component both with invalid (measured performance: $53.4 \pm 1.2\%$, chance level: $50.1 \pm 0.3\%$, paired t test, $t(22) = 3.0$, $p < .01$, Bonferroni corrected $\alpha = .012$) and valid trials (measured performance: $55.4 \pm 1.1\%$, chance level: $50.0 \pm 0.3\%$, paired t test, $t(22) = 5.1$, $p < 10^{-4}$, Bonferroni corrected $\alpha = .012$).

Complementing these results, we studied if the attention condition could be decoded from single-trial peaks both for the seen and unseen trials. Decoding of attention using the N170 peak was above chance for the seen (measured performance: $54.4 \pm 0.8\%$, chance level: $49.7 \pm 0.3\%$, paired t test, $t(22) = 5.6$, $p < 10^{-4}$, Bonferroni corrected $\alpha = .012$) and unseen trials (measured performance: $52.7 \pm 0.6\%$, chance level: $50.3 \pm 0.3\%$, paired t test, $t(22) = 3.4$, $p < .01$, Bonferroni corrected $\alpha = .012$). On the contrary, decoding performance was not significantly different from chance using the P3 peak both for seen (measured performance: $52.3 \pm 1.4\%$, chance level: $50.1 \pm 0.3\%$, paired t test, $t(22) = 1.6$, $p = .11$, Bonferroni corrected $\alpha = .012$) and

unseen trials (measured performance: $48.2 \pm 2.6\%$, chance level: $50.3 \pm 0.3\%$, paired t test, $t(22) = 0.8$, $p = .43$, Bonferroni corrected $\alpha = .012$). This pattern of results at the single-trial level is consistent with the analysis of the average evoked responses: the amplitude of N170 is informative of both attention and conscious perception whereas the P3 component is only predictive of conscious reports.

4 | DISCUSSION

In everyday life, attention and awareness are profoundly intertwined. We move our eyes approximately three times per second (Yarbus, 1967), only becoming aware of what we overtly attend to (Burr, Morrone, & Ross, 1994; De Pisapia, Kaunitz, & Melcher, 2010; Navajas, Sigman, & Kamienkowski, 2014). We can even fail to perceive very salient stimuli in plain sight if our attention is engaged in another task (Most et al., 2001). In order to dissociate these two cognitive processes, several studies proposed different experimental paradigms that allow a factorial analysis of attention and awareness (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Koch & Tsuchiya, 2007; Lamme, 2003). With this approach, it has been shown that BOLD signals in the primary visual cortex are modulated by attention but not by awareness (Watanabe et al., 2011), that attentional load reduces visual discrimination (Lee, Itti, Koch, & Braun, 1999) and modulates brain responses in the absence of awareness (Bahrami, Lavie, & Rees, 2007), and that the frequency band of cortical signals carrying information about awareness is different than the one related to attention (Wyart & Tallon-Baudry, 2008). Moreover, attention and awareness were shown to have opposing effects on the duration of afterimages (van Boxtel, Tsuchiya, & Koch, 2010).

However, these studies contrasted neural and behavioral responses upon conditions using different stimuli (van Boxtel et al., 2010; Watanabe et al., 2011), different cognitive load

(Bahrami et al., 2007; Lee et al., 1999), or different expectations given by predictive cues (Wyart & Tallon-Baudry, 2008). Similarly, previous studies have compared seen trials with another condition in which the stimulus is absent (e.g., Axelrod, Bar, Rees, & Yovel, 2015; Kang, Blake, & Woodman, 2011). The main caveat of these approaches is that the contrast between different conditions might conflate modulations in attention or awareness with other brain processes (Navajas, Rey, & Quian Quiroga, 2014). To overcome all these issues, we developed a paradigm that dissociates attention from awareness in a 2 × 2 factorial design where all conditions have constant retinal stimulation, cognitive load, and expectancy.

To this end, we adapted a classic paradigm that uses prestimulus exogenous cues and leads to inhibition of return (Posner, 1980, 1994), which impairs attention at the cued location approximately 1 s after the cue onset (Klein, 2000). Because cues and faces were separated by an interval of at least 900 ms, we can rule out that the evoked responses given by the faces were mixed up with those ones given by the cue. Shorter intervals (up to approximately 300 ms) would have led to enhanced attentional resources at cued locations (Klein, 2000) but only at the cost of not being able to disentangle the neural responses of the cue and the stimulus. Moreover, cues were not predictive of the stimulus location, which allowed dismissing effects of expectancy. This would have been impossible if we had used endogenous cues, as these need to be predictive of the stimulus location in order to modulate attention (Posner, 1980).

In valid trials, when the stimuli matched the location of the prestimulus cue, we observed that reaction times were slower compared to invalid trials (Taylor & Therrien, 2008). This effect was independent of the perceptual report given by the participants, which allowed the assertion that, behaviorally, attention and awareness were manipulated in an orthogonal way. This finding was further supported by the fact that the prestimulus cue did not change the probability to consciously perceive the faces in that location. In other words, this result suggests that our paradigm was able to empirically dissociate attention and awareness.

We recorded scalp EEG activity in response to faces and identified three clear components: P1, N170, and P3 (Figure 2). At the average ERP level, we observed three significant effects (Figure 3): (a) the N170 amplitude was modulated by attention for the same perceptual state, (b) the N170 was also modulated by awareness at constant attentional level, and (c) the P3 component was modulated by awareness but not by attention. These results were further supported by consistent findings at the single-subject level (Figure 4a), and by a single-trial decoding analysis (Table 1). We did not find any significant interaction (Figure 3) or correlation (Figure 4c,d) between these effects. Moreover, the P1 component was not modulated by either attention or awareness.

We observed that the N170 component was independently modulated by attention and awareness in the right occipitotemporal cortex (electrode PO8) with contralateral stimulation. Modulations with stimuli presented in the ipsilateral field and in the left occipitotemporal cortex (PO7) were not statistically significant. In line with these findings, previous studies have shown evidence supporting that the right-lateralization of face processing in the brain leads to smaller N170 responses in the left hemisphere (Rossion & Jacques, 2008, 2011; Rossion et al., 1999, 2003). Also, as with many other visually evoked EEG potentials, the N170 was larger for stimuli presented in the contralateral visual field (Feng et al., 2012). Based on these previous findings, we believe that, in trials where the stimuli were presented in the right visual field, the signal-to-noise ratio in both hemispheres was not sufficient to measure sizeable effects.

Previous studies have found that attention can sometimes amplify postperceptual signals such as the P3 component (Polich, 2007), but in our study we did not observe such modulation. This is inconsistent with theoretical accounts proposing that attention operates on a variety of cognitive systems depending on task demands, selectively processing relevant information (Hillyard, Vogel, & Luck, 1998; Lavie, 1995; Luck & Hillyard, 2000). For example, if the task consisted of memorizing letters or the identity of certain faces, we would have expected to observe modulations by attention at a timing consistent with the P3 (Luck, Woodman, & Vogel, 2000). Thus, the lack of a modulation by attention in the P3 component in our study can be attributed to the nature of our paradigm, which matched perceptual features, expectations, and cognitive loads upon all conditions.

A similar argument applies to explaining why we did not observe a modulation in the P1 component, as it has been reported in the literature (Heinze, Luck, Mangun, & Hillyard, 1990; Hillyard et al., 1998; Luck, Heinze, Mangun, & Hillyard, 1990; Mangun & Hillyard, 1991). These studies were based on paradigms where subjects were instructed to detect whether the stimulus was flashed on the left or on the right visual field. In contrast, the task in our experiment was to report whether the stimulus was a face or not. We believe that the absence of a P1 modulation in our study, and the presence of an effect of attention in the later N170 signal, is because attention was focused to high-level visual features of the stimuli—driven by the task instructions and the use of images with equal low-level visual features—which are processed by face-selective neural populations sourcing the N170 signal (Rossion & Jacques, 2011). Therefore, neural ensembles contributing to the P1 component were task irrelevant in our experiment (Rossion & Caharel, 2011). This is also in line with previous findings showing that attention rapidly activates task-related cortical modules (Schoenfeld, Hopf, Merkel, Heinze, & Hillyard, 2014). Alternatively, it might be

possible that paradigms based on inhibition of return simply do not modulate P1 responses (for a review, see Martin-Arévalo, Chica, & Lupiáñez, 2016).

In past years, there has been an extensive debate regarding the neural signals involved in conscious perception and their spatiotemporal dynamics. A vast corpus of evidence has provided support for a theoretical framework asserting that consciousness is reflected by late (>300 ms) global activity spread throughout the cortex (Dehaene & Changeux, 2011; Dehaene & Naccache, 2001; Dehaene, Kerszberg, & Changeux, 1998; Dehaene, Sergent, & Changeux, 2003; Dehaene et al., 2006). Other studies have found that localized cortical activity at a relatively earlier latency (100–200 ms after stimulus onset) is already predictive of conscious perception (Fisch et al., 2009; Koivisto & Revonsuo, 2010; Lamme, 2000; Navajas & Kaunitz, 2016; Navajas et al., 2013; Pitts et al., 2012, 2014; Sandberg et al., 2013; Shafto & Pitts, 2015). Our findings suggest that the earliest neural correlate of conscious face perception indeed occurs at ~170 ms in the occipitotemporal cortex (Navajas, Rey, & Quian Quiroga, 2014; Navajas et al., 2013). This information undergoes further processing, which leads to a modulation by awareness after 300 ms with a distributed topography (Dehaene & Changeux, 2011), potentially triggered by hippocampal activations to consciously perceived stimuli (Quian Quiroga, Kraskov, Mormann, Fried, & Koch, 2014; Quian Quiroga, Mukamel, Isham, Malach, & Fried, 2008). This second correlate of consciousness was recently linked to postperceptual processing of sensory information (Shafto & Pitts, 2015), and is believed to guide task-relevant behavior such as the production of conscious reports (Pitts et al., 2014; Tsuchiya, Wilke, Frässle, & Lamme, 2015). Similarly, a recent study has found that this second stage may even occur after a motor response, which strongly suggests that this is indeed a postperceptual process (Railo, Revonsuo, & Koivisto, 2015). Building on this evidence, we have previously argued that such late component reflects contextual awareness, following a first process of perceptual awareness (Navajas, Rey, & Quian Quiroga, 2014). In other words, the process of recognizing a specific person or item is then followed by putting it into context, for example, by recalling related experiences. In line with the distinction between an early and late conscious process, we showed that only the earlier correlate of consciousness, indexed by the N170 amplitude, was also modulated by attention. Altogether, our results provide a clear dissociation of the neural correlates of conscious face perception from the effects of visual attention.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Figure S1
Figure S2
Figure S3