

An electrophysiological study of conscious visual perception using progressively degraded stimuli

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Previous event-related potential (ERP) studies have provided mixed results regarding the earliest manifestations of conscious visual report. One possible explanation for the results could be that conscious visual perception emerges progressively rather than appearing as a binary transition. In the present study, we used electrical neuroimaging to identify the stages of processing that lead to the successful conscious identification of a briefly presented degraded stimulus. Grayscale images of faces and butterflies were presented for 16 ms and their visibility was manipulated by means of random image structure evolution (RISE). Three levels of RISE image distortions were used for each image. First, we determined an individual detection threshold of 50% for each subject. We then added two control conditions, namely fully degraded stimuli and stimuli that yielded 80% detection. Topographic ERP analyses revealed distinct effects for identified and unidentified stimuli at the threshold of detection. Four stages were observed that distinguished successful from unsuccessful stimulus identification. This shows that the events associated with conscious perception occurs at several distinct stages in time starting as early as 220 ms after stimulus presentation, rather than translating as a single temporal event and includes marked top-down activations when identification becomes difficult.

Keywords: evoked potentials, visual consciousness, face recognition, object recognition

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Introduction

The study of conscious visual experience has received an increasing amount of attention over recent years. The prevailing idea of current models is that early visual activity

is necessary although not sufficient, for a visual stimulus to be explicitly reported (Tong, 2003). The crucial element allowing conscious report to be attained is the dynamic interplay between bottom-up processing and horizontal connections within the lower visual areas, along with top-down modulation by frontal and parietal regions on visual

areas (Baars, 1988; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Dehaene & Naccache, 2001; Lamme, 2006; Lamme & Roelfsema, 2000). Lamme (2006) suggests that widespread recurrent processing throughout an extended network—involving frontoparietal areas—is necessary for conscious access. The neural network underlying visual consciousness thus appears to be widely distributed. Moreover, it suggests that conscious report should not be associated with very early sensory processing.

Event-related potentials (ERPs) have a very high temporal resolution and thus provide a very powerful tool to investigate the time course of the constituents of consciousness. Previous ERP studies have aimed at identifying the earliest manifestations of consciousness and have produced mixed results. The suppression of early ERP components (P1, N1) was demonstrated for visual stimuli that were not consciously perceived (Pins & ffytche, 2003; Vaughan & Silverstein, 1968). Other studies suggested that a later event—the P300—might constitute a more reliable marker of conscious access (Dehaene & Naccache, 2001; Liddell, Williams, Rathjen, Shevrin, & Gordon, 2004; Sergent, Baillet, & Dehaene, 2005; Vogel, Luck, & Shapiro, 1998). Finally, more recent experimental studies have suggested the existence of an earlier component linked to visual consciousness, appearing after 200 ms, but preceding the P300. This component was observed irrespectively of whether consciousness was manipulated through the use of pattern masking (Fahrenfort, Scholte, & Lamme, 2007, 2008; Koivisto, Revonsuo, & Lehtonen, 2006; Wilenius-Emet, Revonsuo, & Ojanen, 2004), change blindness (Koivisto & Revonsuo, 2003, 2005) or contrast manipulation (Koivisto et al., 2008; Ojanen, Revonsuo, & Sams, 2003; Wilenius & Revonsuo, 2007). These apparently contradictory results suggest that access to consciousness is not an all-or-none phenomenon but rather a process consisting of multiple steps (Fahrenfort et al., 2008).

In the present study, we used electrical neuroimaging (Michel et al., 2004; Murray, Brunet, & Michel, 2008) to identify the steps leading to the emergence of a conscious percept. We investigated differences in the time course of ERP topographies/components as a function of conscious perception by identifying the topographies that best explain the data using a cluster analysis. This is a completely data-driven approach without a priori constraints on the number of components. Furthermore, we estimated the intracranial generators of the ERP topographies by means of a distributed inverse solution (LAURA; Grave de Peralta Menendez, Murray, Michel, Martuzzi, & Gonzalez Andino, 2004) in order to establish the regions playing a role in consciousness.

Here, rather than focusing on “phenomenal awareness,” i.e., the subjective experience of seeing in its simplest form, we focus on “reflective consciousness,” necessary for a complete report (Block, 2001; Koivisto, Kainulainen, & Revonsuo, 2009). Subjects saw briefly presented (16 ms) grayscale images of faces and butterflies whose visibility was manipulated by random image structure

evolution (RISE; Sadr & Sinha, 2004). Stimuli were presented at the threshold of detection (50%), at 80% detection and at full degradation. We were thus able to compare the electrical brain activity in response to stimuli that were physically identical when they were perceived or not.

Material and methods

Participants

Sixteen (5 females, aged 19–36 years, mean $\pm$ SD: 27.1 ± 5.5) participants for whom the desired thresholds of 50% and 80% detection could be established participated in the ERP experiment.

Stimuli

Stimuli were 8-bit grayscale images of 40 faces with emotionally neutral expressions (20 women, 20 men; Martinez & Benavente, 1998) and 40 butterflies that were visually degraded by applying Random Image Structure Evolution (RISE; Sadr & Sinha, 2004). This technique preserves low-level aspects of stimuli such as luminance and the frequency spectrum by applying an inverse 2D Fourier transformation of the mean amplitude spectra and randomizing varying proportions of the phase coefficients. In other words, the amplitude coefficients are retained, but their positions are altered by scrambling their phases, which gradually eliminates any semantic content from the images without altering their low-level physical properties. For each image, 20 levels of phase coherence were generated by randomly varying the percentage of the phase coefficients in linear increments of 5% (see Figure 1A for an example of stimuli). This procedure ensured that all images were equated for spatial frequency, luminance, and contrast.

Procedure

We first performed a behavioral pretest, in which subjects were presented with pictures of faces and butterflies at the 20 levels of phase coherence (see Stimuli section). Stimuli were displayed for 16 ms and subjects were instructed to indicate whether they saw a meaningful picture or not. This was done in order to determine the degree of stimulus degradation, i.e., the proportion of phase coherence of the images that was necessary for each individual to attain a 50% detection threshold. This enabled us to perform direct comparisons between reported and non-reported stimuli using physically identical images. We added two control conditions: fully

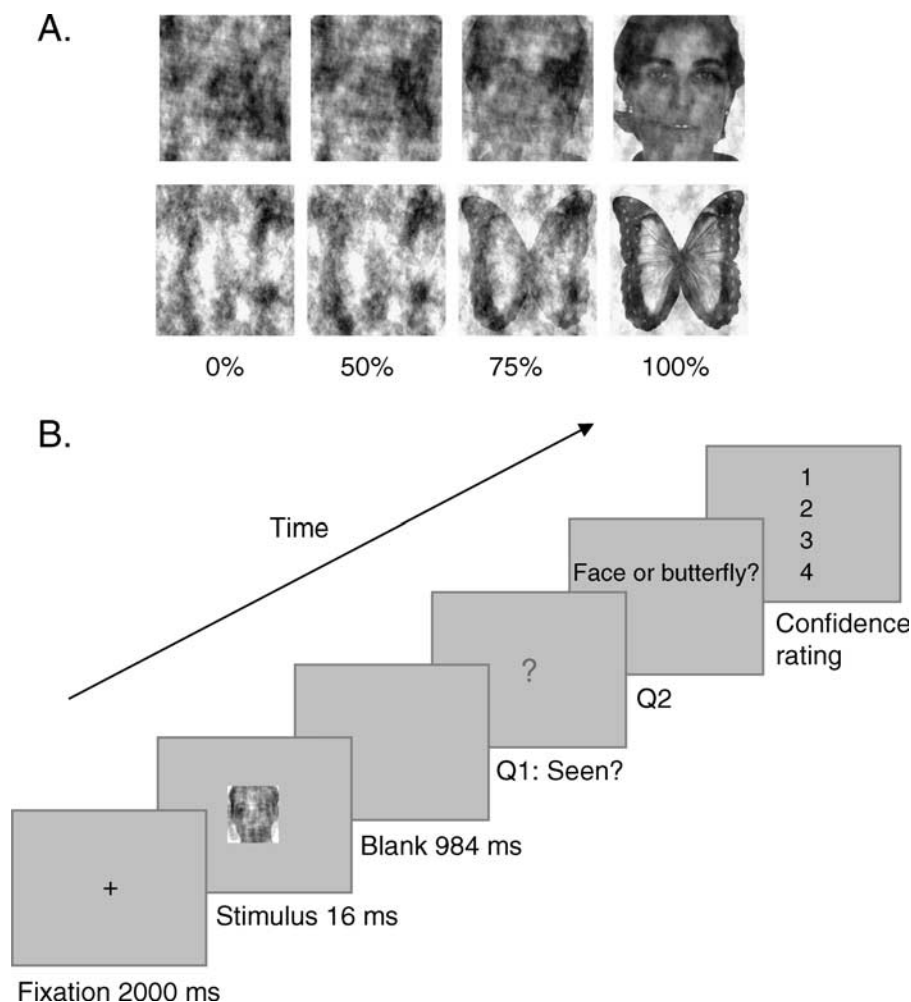


Figure 1. (A) Examples of visually degraded stimuli by applying Random Image Structure Evolution (RISE; Sadr & Sinha, 2004) at four different levels of phase coherence. (B) Experimental procedure. Stimuli were presented for 16 ms followed by a blank screen for 984 ms. Then, subjects indicated whether they saw a meaningful stimulus or not (Q1), the category of the stimulus (Q2), and how confident they were about Q1 (Q3).

degraded stimuli, which did not lead to any conscious perception and stimuli that yielded a detection rate of $>80\%$. Participants were therefore presented with stimuli that had been submitted to three levels of degradation: one that was a full degradation, containing 100% noise and thus a zero detection threshold (DT0), and two levels of noise that corresponded to detection thresholds determined individually for each stimulus category: “50% detection” (DT50) and “above 80% detection” (DT80). This allowed us to compare identical physical stimuli that yielded different responses (identified vs. unidentified stimuli at DT50’) and identical responses elicited by physically different stimuli (“identified” responses at DT50 and DT80).

The experiment consisted of 4 blocks of 160 stimuli. The stimuli were displayed at the three different levels; each stimulus was repeated twice for DT0 and DT80 (overall, 80 repetitions of each condition). In order to get a sufficient number of identified and unidentified trials, each

stimulus was repeated 4 times in the 50% detection condition (DT50). Trials were presented in a randomized order using E-prime (Psychology Software Tools).

Figure 1B depicts the experimental procedure. The stimuli were displayed at the center of a CRT screen on a dark gray background and subtended a visual angle of 3° horizontally and vertically. Each trial started with a fixation cross (2000 ms), followed by the stimulus (16 ms) and a blank (dark gray) screen (984 ms). Then, a first prompt (Q1) asked subjects whether they saw a meaningful picture or not. The response prompt remained present until the subject pressed the response key. A second prompt (Q2) then appeared asking the subjects to indicate (or guess) whether the stimulus was a face or a butterfly. A final prompt (Q3) required a confidence rating about Q1 on a scale from 1 to 4 (4 being “very confident”). Prior to the experiment, subjects were familiarized with the setting during a training session that comprised 15 trials. Subjects

performed the task in a dimly lit, electromagnetically shielded booth. They were seated about 100 cm from the screen while their EEG was recorded.

Analysis of behavioral data

We assessed the hit rates for Q1 and Q2 by means of ANOVAs with the within-subjects factors “stimulus” (face vs. butterfly) and “detection threshold” (DT0, DT50, DT80 for Q1 and DT50, DT80 for Q2, respectively). For Q3, we assessed the frequency of the four confidence levels by means with the within-subjects factors “stimulus” (face vs. butterfly) and “detection threshold” (DT0, DT50 identified, DT50 unidentified, DT80).

EEG acquisition and raw data processing

The EEG was continuously acquired from 256 AgCl carbon fiber-coated scalp electrodes using a Hydrocel Geodesic Sensor Net (HCGSN, Electrical Geodesics, USA). The EEG was digitized at 500 Hz and band-pass filtered at 0.01–100 Hz with a recording reference at the vertex; impedances were kept below 30 k Ω ; offline, the EEG was re-referenced to the average reference and digitally filtered from 1 to 30 Hz. For each trial, epochs were selected ranging from 1000-ms pre- to 1000-ms post-stimulus onset. Traces were visually inspected for eye movements or other sources of transient noise after an initial automatic rejection of sweeps containing an amplitude exceeding $\pm 100 \mu\text{V}$. Epochs with artifacts were rejected. Electrodes located on the cheeks were excluded and 204 electrodes were maintained for subsequent analysis. For each participant, channels exhibiting substantial noise were interpolated using a 3D spherical spline interpolation procedure (Perrin, Pernier, Bertrand, Giard, & Echallier, 1987). On average, 12 channels were interpolated per subject.

Analysis of event-related potentials

Event-related potentials were computed for each stimulus category (face/butterfly) at the three detection thresholds (DT0, DT50, DT80). For the DT50 condition, identified and unidentified trials were averaged separately. Importantly, in order to be certain that differences between identified and unidentified stimuli really did reflect conscious report, we selected trials where Q2 and Q3 responses were kept constant, i.e., on correct discrimination and high level of confidence (very confident and fairly confident) trials. Baseline correction was applied on the 100-ms pre-stimulus period. For group averaging, ERPs were normalized to their mean global field power (GFP; Lehmann & Skrandies, 1980). The GFP is a 1-number

measure of field strength and equivalent to the spatial standard deviation of the scalp electric field; it is calculated as the square root of the mean of the squared value recorded at each electrode. Based on previous electrophysiological evidence in consciousness (e.g., Koivisto et al., 2006; Sergent et al., 2005; Wilenius & Revonsuo, 2007), we restricted our analyses to the initial 600-ms post-stimulus period.

The data-driven analysis of evoked potentials comprised multiple steps as described previously (Britz, Landis, & Michel, 2009; Murray et al., 2008). The 1st step explored the spatiotemporal scalp configuration between the conditions across time. It was based on the examination of the spatiotemporal variations of the voltage distribution over time both within and between conditions (Brandeis & Lehmann, 1986; Lehmann & Skrandies, 1984; Michel, Seeck, & Landis, 1999; Michel et al., 2001). This approach considers the succession of electrical scalp potential maps that follow the onset of an event and determines the time periods during which these maps remain stable. Since differences in the topographies of scalp maps necessarily reflect differences in the underlying neuronal generators (Vaughan, 1982), it has been hypothesized that the periods of stable map topographies, or segments, correspond to particular steps in information processing during which a given neural network configuration is active. These periods have consequently been termed functional microstates (Lehmann, Pascual-Marqui, & Michel, 2009). Functional microstates within the ERP map series are characterized by template maps that are extracted by means of a spatial k -means cluster analysis that identifies the dominant map topographies in the Grand-Average ERPs across the experimental conditions over time (Michel et al., 2001; Pascual-Marqui, Michel, & Lehmann, 1995). The smallest set of maps that accounts for the greatest amount of variance is then selected using a cross-validation criterion (Michel et al., 2001; Murray et al., 2008; Pascual-Marqui et al., 1995; Pourtois, Delplanque, Michel, & Vuilleumier, 2008). Next, the presence of a given ERP map, previously identified in the group-averaged data, is identified in the ERPs of the individual subjects. For each subject, at each time point, a spatial correlation is computed between the momentary scalp topography and the template maps identified in the cluster analysis. Statistical analyses then compared the number of time frames (the total duration in millisecond) during which each map was present.

Finally, in order to compare our results with previous ERP studies using conventional waveform analysis techniques, we assessed amplitude differences by performing multiple t -tests for each electrode and time point in order to determine the time periods of significant amplitude differences. We restricted our analyses to the DT50 unidentified and identified conditions where stimuli were physically identical but yielded different behaviors. T -tests were performed between unidentified and identified DT50 faces, as well as unidentified and identified DT50 butterflies. The

p -value was set to 0.01, and only differences that persisted for more than 20 ms were considered.

Source localization analysis

As a final step, we used a distributed linear inverse solution (LAURA; Grave de Peralta Menendez et al. 2004) to estimate the putative sources in the brain that gave rise to the templates identified in the cluster analysis. The solution space was restricted to the gray matter of the MNI template brain. After applying a homogeneous transformation operation to the volume that rendered it to the best fitting sphere (SMAC model; Spinelli, Andino, Seeck, & Michel, 2000), a 3-shell spherical head model was used to calculate the lead field for the 204 electrodes and applied the inverse solution based on the LAURA constraint (Michel et al., 2004).

Results

Stimulus

In three subjects, the level of phase coherence of the images was relatively low. Since the distribution of the image detection tended to be binary, these subjects were removed from current analyses. The median percentage ($\pm$ SD) of phase coherence of the images was 55% ($\pm$ 2.5) for faces at DT50 and 70% ($\pm$ 1) at DT80. For butterflies, it was 55% ($\pm$ 2.5) at DT50 and 70% ($\pm$ 1) at DT80.

Behavioral performance

Figure 2 shows the behavioral results of thirteen subjects for the three measures Q1, Q2, and Q3.

Regarding Q1 (detection question), the average percentage of trials that were reported as producing a meaningful percept in the DT0 condition was 11.05% (standard error of the mean [SEM] = 4.10) for faces and 13.84% (SEM = 4.57) for butterflies. In the DT50 condition, these values were 55.38% (SEM = 6.23) for faces and 66.87% (SEM = 5.41) for butterflies. Finally, in the DT80 condition, 93.75% (SEM = 2.94) of the faces and 95.86% (SEM = 2.12) of the butterflies were reported to be perceived.

An ANOVA (2 stimuli $\times$ 3 detection thresholds) revealed a detection threshold effect as stimuli became perceptually manifest ($F_{(2,24)} = 165.43$, $p < 0.0001$) with significant differences between DT0 and DT50 ($p < 0.001$), DT0 and DT80 ($p < 0.001$), and DT50 and DT80 ($p < 0.001$). In addition, a stimulus effect was found ($F_{(2,30)} = 9.09$, $p < 0.01$). Finally, the results showed an interaction effect (stimulus $\times$ threshold; $F_{(1,12)} = 6.45$, $p = 0.05$) with

significant differences ($p < 0.05$) between faces and butterflies across all conditions except at DT0 and DT80.

With respect to Q2 (forced-choice question), the average percentage of hits in the DT50 condition was 78.26% (SEM = 5.34) for faces and 85.48% (SEM = 2.91) for butterflies. However, when considering hits in the seen trials alone (based on the Q1 response), the average percentage was 84.46% (SEM = 5.81) for faces and 97.34% (SEM = 0.63) for butterflies, performances that can be considered above chance on a binomial distribution (respectively, $Z = 6.39$, $p < 0.05$ and $Z = 9.76$, $p < 0.05$). For the unseen trials (again determined on the basis of the Q1 response), the average percentage of hits in DT50 was 70.55% (SEM = 6.05) for faces ($Z = 3.44$, $p < 0.05$) and 61.53% (SEM = 4.50) for butterflies ($Z = 1.51$, $p < 0.05$). Finally, in the DT80 condition, Q2 hits were at 96.73% (SEM = 1.53) for faces and 97.59% (SEM = 0.71) for butterflies.

A 2×2 ANOVA (2 stimuli $\times$ 2 detection thresholds) was performed on hit rates (Q2) in conditions DT50 (seen and unseen pooled) and DT80. This confirmed the improvement in performance at the higher threshold ($F_{(1,12)} = 49.83$, $p < 0.0001$).

For Q3 (confidence rating), we computed frequencies for each confidence level at each DT condition. Results showed that participants were more confident with the clear signal (DT80). Subjects were also rather confident about not having identified a stimulus (DT0 and DT50 unidentified), although to a lesser extent, and the pattern of the confidence rating was very similar for both categories of stimuli. However, the DT50-identified condition elicited a less confident behavior and frequencies were scattered among the four confidence levels; subjects tended to be more confident for butterflies than faces.

Evoked-potential results

Topographic results

The spatiotemporal segmentation procedure identified 11 template potential maps, which explained 90.76% of the total variance and which are displayed in Figure 3A. We assessed statistical differences of the duration (ms) of each map with a 2 (stimulus category) $\times$ 3 (detection thresholds) ANOVA and post-hoc linear contrasts with Tukey's test. Four of the eleven templates (maps 7, 8, 9, 10) differed significantly with respect to conscious visual perception.

Figures 3A and 3B show that differences in conscious report are not restricted to a single time window but involve changes at four different stages:

1. The first topographical difference was found after about 215 ms with Map 7, a bilateral posterior positivity. The ANOVA revealed a main effect of detection threshold ($F_{(2,72)} = 9.94$, $p < 0.001$): the duration of Map 7 decreased with the detection

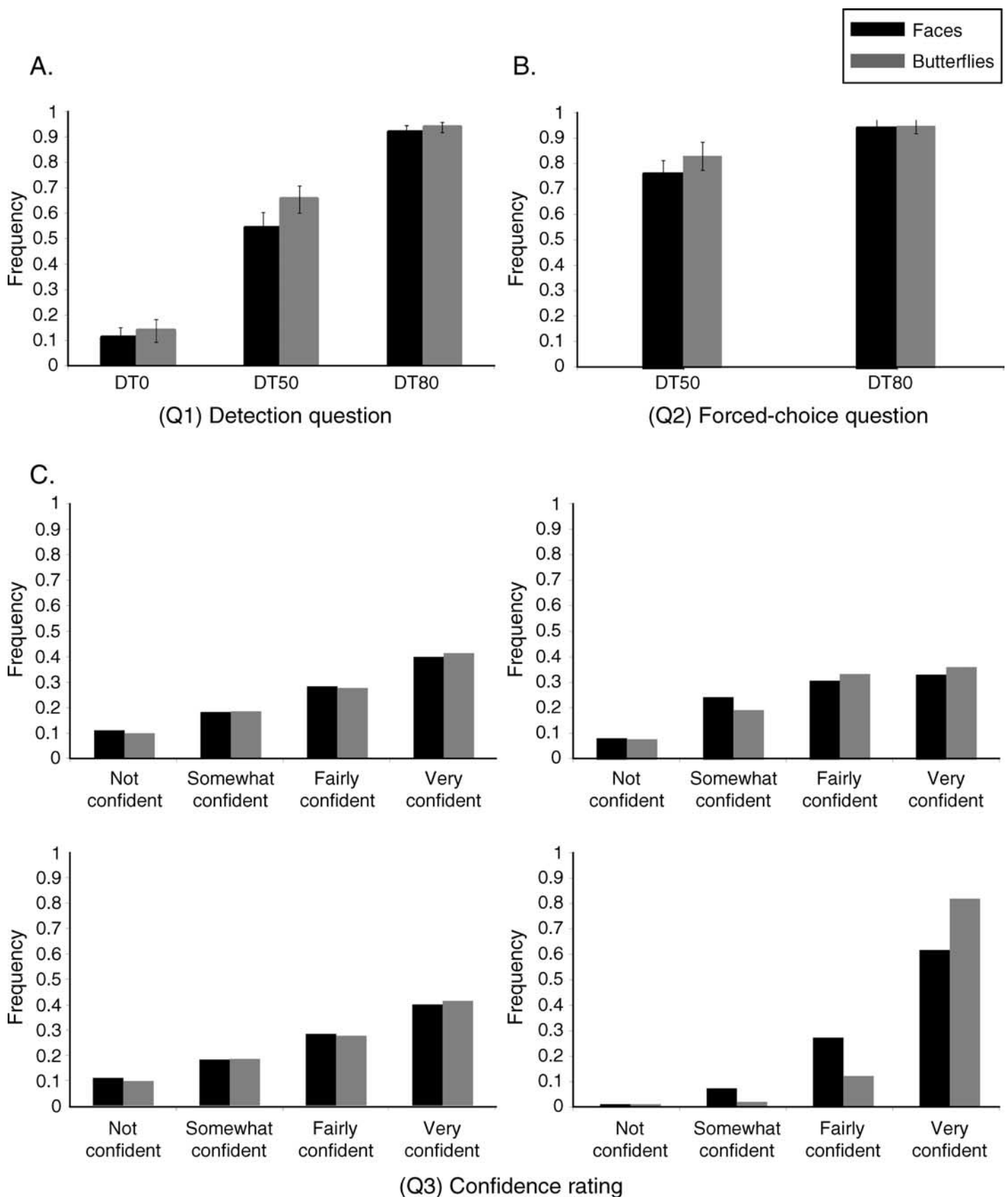


Figure 2. Behavioral results. (A) Mean frequency rates ($\pm$ SEM) for the Detection Question (Q1) for all 3 detection thresholds (DT0, DT50, DT80). Responses are depicted in black for faces and in gray for butterflies. (B) Mean frequency rates for the Forced Choice question (Q2) for DT50 and DT80. (C) Frequencies for the four confidence ratings about Q1 for each DT.

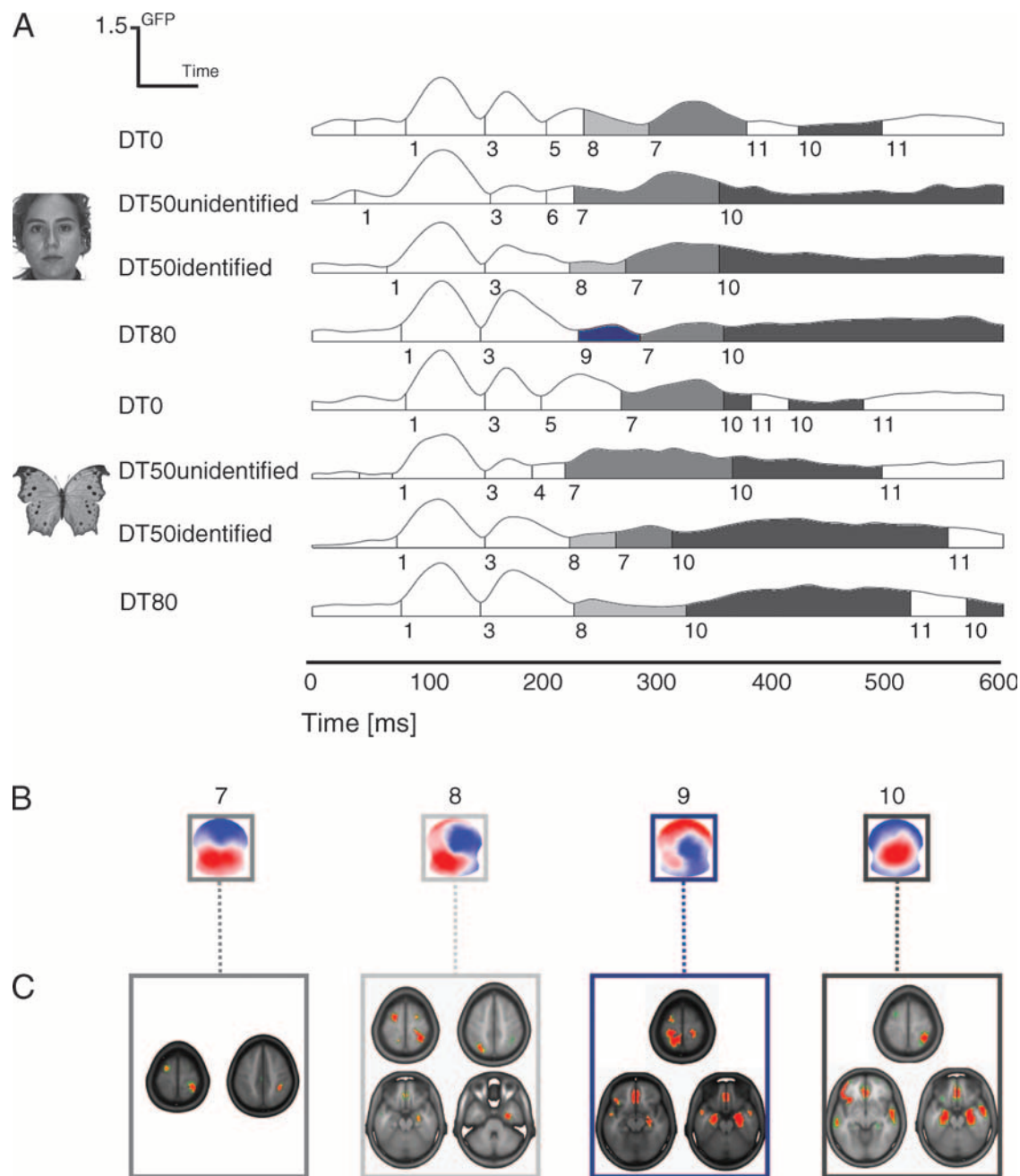


Figure 3. Results of the temporal-spatial segmentation procedure and source estimations of the scalp topographies related to conscious perception. (A) Periods of stable ERP topographies under the Global Field Power as identified by the topographic pattern analysis in the eight conditions from 0- to 600-ms post-stimulus onset. Identical color codes refer to identical map topographies. (B) Maps are displayed with left hemifield on the left and nose on top; red indicates positive and blue indicates negative potentials. (C) Electrical source imaging (LAURA) results for the maps that differed significantly between conditions (Maps 7, 8, 9, and 10). Source estimations are rendered on the MNI 152 template brain; the left hemisphere is on the left and the right hemisphere is on the right.

- threshold. This topography differentiated clearly identifiable stimuli from the two other conditions (DT80 vs. DT0, $p < 0.01$; DT80 vs. DT50, $p < 0.001$).
- The second topographic difference occurred after about 220 ms with Map 8 (a left posterior positivity). The duration changed with the detection threshold ($F_{(2,72)} = 3.80$, $p < 0.05$) and was present more frequently for clearly identifiable than for ambiguous stimuli (DT80 vs. DT50, $p < 0.05$).
 - The third topographic difference occurred after about 230 ms with Map 9, a frontal positivity similar to that reported in our previous study (Genetti, Khateb, Heinzer, Michel, & Pegna, 2009). Map 9 differentiated identified from unidentified stimuli.

There was a main effect of the detection threshold with an increase in map duration when stimuli were reported as identified ($F_{(2,72)} = 2.99$, $p = 0.05$). It lasted longer for clearly identifiable than ambiguous stimuli (DT80 vs. DT50, $p < 0.05$). There was also a main effect of stimulus: the map occurred for a longer period for faces than for butterflies ($F_{(1,72)} = 5.00$, $p < 0.05$).

4. The last topographical difference was found after about 330 ms with Map 10 (a broadly distributed central positivity). The ANOVA showed a main effect of detection threshold ($F_{(2,72)} = 11.57$, $p < 0.0001$): the map duration increased with detection threshold. There were significant differences between fully degraded and all other conditions (DT0 vs. DT50, $p < 0.01$; DT0 vs. DT80, $p < 0.001$).

In order to identify differences specifically related to conscious identification, we collapsed together faces and butterflies at DT50 and compared DT50 unidentified vs. DT50 identified stimuli. *T*-tests revealed that only Map 7 and Map 9 differed with respect to conscious identification: Map 7 lasted significantly longer for unidentified stimuli ($t = 2.67$, $p < 0.05$), whereas Map 9 lasted longer for identified stimuli ($t = -2.31$, $p < 0.05$).

Amplitude results

Figure 4A displays the grand average waveforms for correctly and confidently identified faces and Figure 5A for correctly and confidently identified butterflies. Comparison between unidentified and identified DT50 faces first showed differences over central electrodes around 100-ms post-stimulus onset, with higher amplitudes for identified faces ($p < 0.01$). Then, differences over the right occipitotemporal regions were seen between 200 and 250 ms, with lower amplitudes for identified faces ($p < 0.01$; Figures 4A and 4B). Similarly, the comparison between identified and unidentified butterflies in this analysis showed a first period of change around 100 ms over central electrodes, with higher amplitudes for identified butterflies. Then, a second period of differences occurred between 200 and 250 ms, with lower amplitudes over the right occipito-parieto-temporal leads for identified butterflies ($p < 0.01$; Figures 5A and 5B). These differences remained between 300 and 400 ms predominantly over the occipitotemporal electrodes.

Source localization

Figure 3C displays the brain regions estimated to be the active sources for the four dominant maps, which distinguished the conditions. The LAURA inverse solution revealed a large network of activations. Map 7 showed localization in the right inferior and postcentral

parietal cortex, in the right superior frontal gyrus, and in the left middle frontal gyrus. Map 8 showed localization in the region of the left middle frontal gyrus, the left parietal gyrus in the precuneus region, the right superior parietal region, and the right parahippocampal gyrus. Map 9 was produced by activity in the middle temporal gyrus bilaterally, in the parietal cortex (postcentral gyrus) bilaterally, in the left inferior and superior frontal gyrus, and in the anterior cingulate cortex bilaterally. Finally, a rather broad network of activations was found for Map 10 including bilateral—but predominantly right—activations in the frontal, temporal, and parietal lobes.

Discussion

We used spatiotemporal analysis of ERP map series to identify the sequence of events that yield subjective visual conscious experience. We identified four components that were associated with conscious identification.

The first differences between identified and unidentified stimuli emerged as of 220-ms post-stimulus onset. This initial dissimilarity between conscious and unconscious stimuli was revealed as an increase in duration of Map 8 and of Map 9 when the stimuli were reported. Map 8 and Map 9 were significantly more present for clearly identifiable stimuli (DT80). Moreover, Map 8 specifically distinguished identified (DT50 identified) and unidentified stimuli (DT50 unidentified). This time period is in line with some previous studies that show ERP amplitude differences between consciously identified and unidentified items onsetting at 150–200 ms and termed the visual-awareness negativity (VAN; Fahrenfort et al., 2007, 2008; Genetti et al., 2009; Koivisto et al., 2008; Koivisto & Revonsuo, 2003, 2005; Koivisto et al., 2006; Ojanen et al., 2003; Wilenius & Revonsuo, 2007; Wilenius-Emet et al., 2004). This awareness-related component has been reported a number of times. For instance, in a masking paradigm, Wilenius-Emet et al. (2004) presented stimuli composed of line drawings of coherent and scrambled objects at durations below (27 ms), near (40/53 ms), or above (108 ms) the subjective perceptual threshold of their group of participants. The VAN, peaking around 260–270 ms after stimulus onset, was obtained specifically for the above- and near-threshold stimuli but was missing in the below-threshold condition. Thus, the authors concluded that the VAN was a specific marker of visual consciousness. Our waveform analysis corroborates such results: ERPs were more negative for identified than unidentified items over posterior scalp channels. The topographic ERP analysis sheds more light on the nature of this difference, demonstrating that at the time of the amplitude difference, different topographies arise in the two conditions, one with a posterior positivity (Map 7) in the DT50 unidentified and another with a posterior

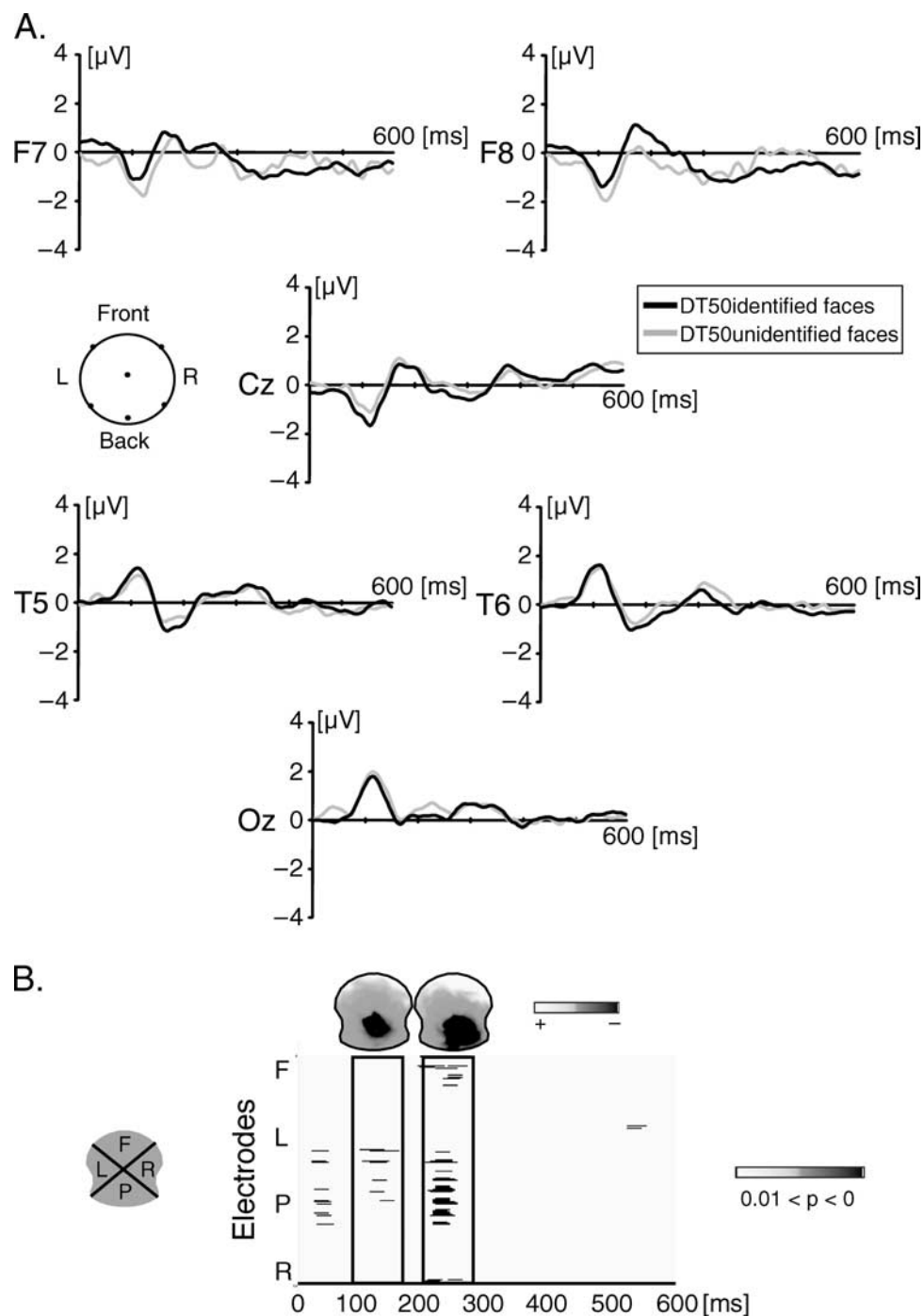


Figure 4. (A) Grand Average ERP waveforms for the correctly and confidently identified and unidentified faces from 6 exemplar electrode sites (F7, F8, Cz, T5, T6, Oz); positive polarities are plotted up. ERPs for identified faces are depicted in black, and those for unidentified faces are depicted in gray. (B) Time course of the ERP amplitude differences at the 204 electrodes assessed by point-wise paired t -tests at each electrode. Time is plotted on the x-axis, and approximate electrode locations are indicated on the y-axis. Significant differences that lasted for >20 ms ($p < 0.01$) are indicated on a grayscale. The maps show the location of the amplitude differences.

negativity in the DT50 identified (Map 9) condition with the former appearing more in the absence of consciousness.

We found additional changes for increasing levels of detection at around ~ 330 ms (Map 10). Map 10 differentiated fully degraded (DT0) stimuli from potentially identifiable stimuli (DT50, DT80). The emergence of

several electrophysiological manifestations of conscious report during the 500-ms post-stimulus period is in line with previous studies (Fahrenfort et al., 2007, 2008; Koivisto et al., 2008, 2006; Sergent et al., 2005; Wilenius & Revonsuo, 2007). In an attentional blink task, after a first difference around 250 ms, a later wave of activation,

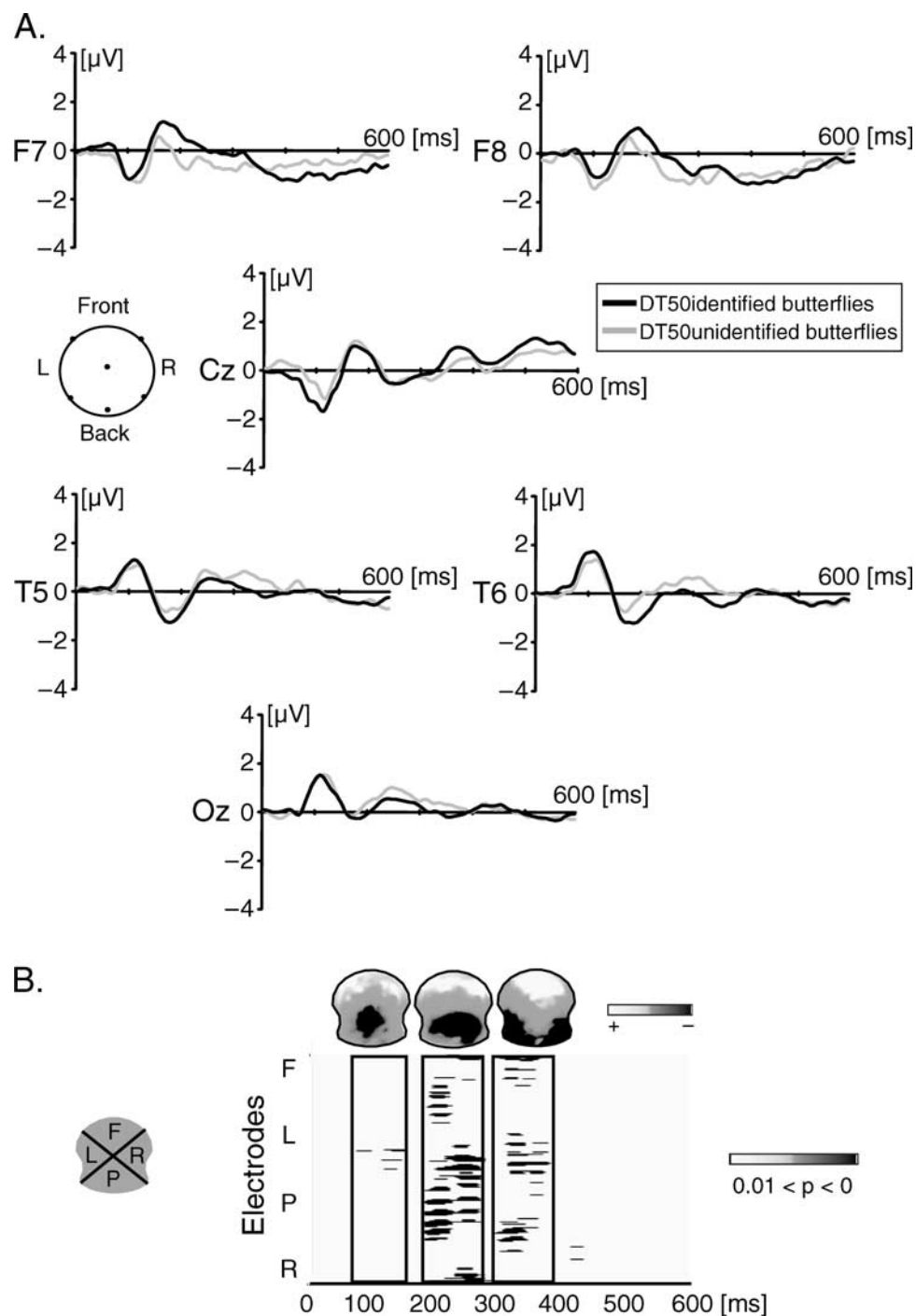


Figure 5. (A) Grand Average ERP waveforms for the correctly and confidently identified and unidentified butterflies from 6 exemplar electrode sites (F7, F8, Cz, T5, T6, Oz); positive polarities are plotted up. ERPs for identified butterflies are depicted in black, and those for unidentified butterflies are depicted in gray. (B) Time course of the ERP amplitude differences at the 204 electrodes assessed by point-wise paired t -tests at each electrode. Time is plotted on the x-axis, and approximate electrode locations are indicated on the y-axis. Significant differences ($p < 0.01$) that lasted for >20 ms are indicated on a grayscale. The maps show the location of the amplitude differences.

in the P300 range, was not detected for unseen stimuli (Sergent et al., 2005). Likewise, in a backward masking task, Fahrenfort et al. (2008) found that activity from 200 ms correlated with subjective conscious detection and

thus might represent widespread coordinated recurrent activity leading to conscious access. This was followed by strong recurrent activation found over occipitoparietal regions at 350–400 ms presumably reflecting more recurrent

processing throughout these widespread areas. Therefore, these results show that conscious access might require a several-step processing.

Both the time window and the topography of Map 10 correspond to the P3b subcomponent of the P300—a large positive wave peaking around 400–600 ms post-stimulus onset over central and parietal midline sites. It has been most commonly interpreted as the reflection of voluntary target detection (Soltani & Knight, 2000). However, the association between the P300 and consciousness has also been suggested for several decades (Dehaene et al., 2001; Pritchard, 1981; Sergent et al., 2005; Vogel et al., 1998). According to some authors, later components, such as the P300 class of potentials, reflects more than the pure subjective experience of seeing (Koivisto et al., 2008, 2006; Wilenius & Revonsuo, 2007). These later stages might represent a “secondary conscious process” (Pins & fytche, 2003) or “reflective consciousness” (Block, 2001; Koivisto et al., 2008), which would be required for a complete report (e.g., identification, naming, categorization of the stimulus). For instance, the P300 period has been correlated with the confidence of conscious decision (Eimer & Mazza, 2005; Koivisto et al., 2006) and associated with internal decision-making processes (Nieuwenhuis, Aston-Jones, & Cohen, 2005). Eimer and Mazza (2005) observed a modulation of the P300 amplitude, which depended on the participants’ confidence level regarding their perceptual judgment. Therefore, early and later stages might contribute to subjective conscious experience in a different manner, with the former corresponding to the initial experience of seeing and the latter reflecting higher order processes that rely on the first stage.

According to the feedforward–feedback model, multiple reentrant loops—or recurrent interactions throughout the brain—enable a more flexible mechanism, which is necessary for an elaborate and detailed evaluation of the visual stimulus with respect to current needs and goals (Lamme, 2003). This mechanism can provide a more deliberate behavioral response than feedforward processing alone. This is consistent with the idea that a wide propagation of activation beyond the visual cortex is necessary for conscious access (Dehaene et al., 2006; Lamme, 2006). Accordingly, we found a rather broad network of bilateral activations for Map 8, Map 9, and Map 10, which are interspersed with other topographies that show more focal sources including frontal, temporal, and parietal lobes, which might be involved in this spread of activation.

In addition to the scalp topographies that increased with conscious experience, we also observed topographies that decreased in occurrence with greater conscious report. The increasing map durations described above co-occurred with a decrease in duration of Map 7. Map 7 was localized in the right inferior and postcentral parietal cortex, in the right superior frontal gyrus, and in the left middle frontal gyrus, very similar to the “visual attentional network” involved in the maintenance of top-down bias signal and target detection (for example, Kanwisher &

Wojciulik, 2000). One possible interpretation of this result is that the topography reflects recruitment of top-down resources aimed at finding meaning in ambiguous or degraded stimuli. As suggested in recent years, the brain is not a passive machine, which merely process inputs from the outside environment (Bar, 2003, 2007; Summerfield et al., 2006). Rather, its goal is to obtain an accurate interpretation of its environment through top-down modulations, using a complex system predicting outcome and errors (Bar, 2009). In a study that combined fMRI and magnetoencephalography, conscious recognition of objects evoked activity in the left orbitofrontal cortex 50 ms earlier than temporal regions (related to object recognition; Bar et al., 2006). Moreover, these data showed that the presence of low spatial frequencies modulated the activity in the orbitofrontal cortex. According to Bar’s (2007) model, while a visual input is being processed in detail along the classic visual stream, rough information (low spatial frequencies) can be rapidly extracted from it and then projected to the orbitofrontal cortex. This brain area would facilitate associations between the rough bottom-up analysis and the stored representations and then enable the generation of predictions about the initial visual input. In line with this model, our data suggest the presence of EEG microstates dedicated to active top-down activity that is required to make sense of perceptually weak stimuli, thus compensating for the insufficient amount of perceptual information.

Faces belong to a category of biologically relevant stimuli. In this study, we used two categories of stimuli: faces and butterflies that are both biological and symmetrical stimuli. Nevertheless, these stimuli vary along several dimensions including their global shape and the internal features that distinguish them. A careful post-hoc observation of the identification rate of each stimulus on an individual basis (as opposed to the group as a whole) revealed that not all of them were situated at the 50% threshold. Rather, certain stimuli (roughly a fifth) were either systematically detected or never identified. Since ERPs are the result of an averaging procedure across all stimuli, the contribution of these suboptimal images to the final results was most probably minimal. Nevertheless, these observations suggest a certain degree of caution when interpreting our findings since it is possible that other physical features, unaffected by the degradation procedure, may have played a part in the final outcome. Along these lines, subjects in our study identified butterflies more easily and more confidently than faces. After the experiment, most of them reported verbally that butterflies could be identified more easily than faces from their global outline. Confidence ratings showed that the participants’ certainty when rejecting a stimulus (i.e., labeling it as unidentified) was independent of the actual visual input (DT0, DT50 unidentified conditions). Yet, confidence in accepting a stimulus (i.e., labeled as identified) depended on the category: subjects were more confident in detecting butterflies than faces. This again

points to the possibility that certain physical features may have contributed to stimulus detection, particularly for butterflies. However, the specific map topographies that co-occurred with conscious report were similar for both categories (apart from Map 9) and no interaction was found between stimulus and detection thresholds. This suggests that the underlying neural networks were at the very least not category-specific and most probably reflect some aspect of the conscious visual experience of a stimulus.

Our study shows that subjective conscious report cannot be linked to a single electrophysiological component. Instead, the emergence of a clear conscious percept affect several different time periods beginning as early as 220 ms and lasting until after about 400 ms. Moreover, our source localization data show that higher tier areas become active quite early suggesting that top-down processes become active for stimuli to be detected, even though this does not necessarily lead to successful detection.

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