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Cycle XXXI

# Isolating the proper neural correlates of visual awareness from its neural consequences

S.S.D. M-PSI/01

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## ABSTRACT

One of the major challenges in the neuroscience of consciousness is to disclose the timing and neural mechanisms underlying visual awareness, the subjective experience of seeing. Electroencephalography (EEG) studies investigating the time course of consciousness-related neural processes have found two potential correlates of visual awareness: the N2 and the P3 ERP components. However, recent works have suggested that only N2 correlates to visual awareness, whereas later neural activity expressed by the P3 component reflects post-perceptual processes related to subjects' report or to accumulation of sensory evidence leading to decision-making.

Building upon this observation, the objective of this study was to provide further evidence that the P3 component reflects a post-perceptual process. To this end, we designed two EEG experiments in which we directly manipulated decision making processes and visual awareness while keeping constant the physical property of visual stimuli. This experimental manipulation allowed us to identify the possible influences of post-perceptual processing over the time course of neural responses and determine the temporal window at which such influence occurs.

In Experiment 1, we manipulated participant's decision criterion by inducing, respectively, a liberal and a conservative decision bias in two different experimental sessions. The aim of this first Experiment was to determine whether our manipulation of the decision processes would produce a modulation of P3 ERP component. Experiment 2 was identical to Experiment 1 except that participants were not requested to adjust their decision criterion (own criterion session). The aim of this experiment was to examine whether in a condition in which there was no manipulation of post-perceptual processes, N2 and P3 ERP component would distribute differently. Electrophysiological and Behavioral results of Experiment 2 were then compared with those of Experiment 1.

If the amplitude of the P3 reflects post-perceptual processes related to decision making processes, one would expect to find some differences in the topography or in the time-course of the P3 between the condition in which a decision criterion was imposed (Experiment 1) and the condition in which there was not a decision bias induced (Experiment 2).

ERP results of Experiment 1 revealed that the amplitude of the N2 and the P3 components were enhanced for those trials were subjects reported to have seen the

stimulus as compared to unaware trials. Importantly, the amplitude of the P3 was modulated by the decision criterion: it was enhanced when participants adopted the liberal criterion compared to the conservative criterion, suggesting that P3 reflects brain processes related to decision making that occurs after that awareness has emerged.

ERP data of Experiment 2 confirmed that aware responses were associated with enhanced N2 and P3 amplitude than unaware responses. Interestingly, the decision criterion manipulation had an effect on P3 component revealing that the own and the liberal criteria were associated with an increased positivity over central areas if compared to the conservative criterion. In addition, we found that the amplitude of the N2 was enhanced for the own session if compared to conservative and liberal sessions.

Overall these results suggest that when sensory information was relevant for the task (own session) a bigger N2 was observed. On the contrary, P3 amplitude was sensitive to the manipulation of the decision criterion, suggesting a critical role of neural activity expressed by the P3 component in decision making processes. These findings support the hypothesis that P3 might reflect post-perceptual processes that occur after that awareness has emerged while the N2 component reflects a proper correlate of visual awareness.

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# 1. Introduction

## 1.1 The Neural Correlates of Consciousness

Amongst the many unsolved questions in Neuroscience, one that has challenged and excited researchers during the last decades is the search for the neural basis of conscious perception, which involves the attempt to find out a causal link between neural states and conscious states. The goal is to determine whether a particular conscious experience correlates with a specific neural activation and flow of information processing that distinguish it from other mental states (Dehaene and Naccache, 2001).

Thus, one of the major aims of current research on neurobiological basis of consciousness is to find the Neural Correlates of Consciousness defined as "*the minimal neuronal mechanisms jointly sufficient for any specific conscious percept*" (Koch, 2004). The word minimal is emphasized in this definition because the question of interest is to find which are those neural substrates whose activity is actually needed for a particular conscious experience (Tononi and Koch, 2008). For example, the neural correlates of perceiving a face correspond to that pattern of neural activity, whose activation, enable us to consciously experience that face.

Koch's definition has two implications on consciousness research. First of all, the neural correlates supporting a specific content of experience, (i.e., a face) are different from the neural correlates supporting another experience (i.e., a cat). So, different contents of consciousness lead to different neural correlates (Koch et al., 2016; De Graaf and Sack, 2015). Moreover, Koch's emphasis on sufficiency indicates that not all neural processes that correlate to consciousness should be considered a NCC (Koch et al., 2016; Tononi et al., 2016a), but it may be that some of them have facilitative effects on consciousness, i.e. attention, while others represent a consequence of conscious perception, i.e. working memory updating (Aru et al., 2012; De Graaf and Sack, 2014; Tsuchiya et al., 2015).

## 1.2 How can we study NCC?

Most of the knowledge that we have accumulated during the last decades on NCC comes from studies in visual perception. In fact, the possibility of selectively manipulating visual percepts has made vision a particular advantageous modality for investigating the correlation between neural events and conscious perception. NCC of visual awareness, which is defined as the subjective of seeing (Searle, 1992; Block, 1995), are also the main subject of this investigation, and accordingly we will mainly focus our attention on consciousness research concerning visual system.

There are different paradigms that can be used to study visual awareness, but in a typical experimental setting, visual awareness is manipulated to produce condition that differ with respect to conscious perception (the so-called contrastive method; Baars,1988). The content of awareness reported by the participant is assessed using objective or subjective measures.

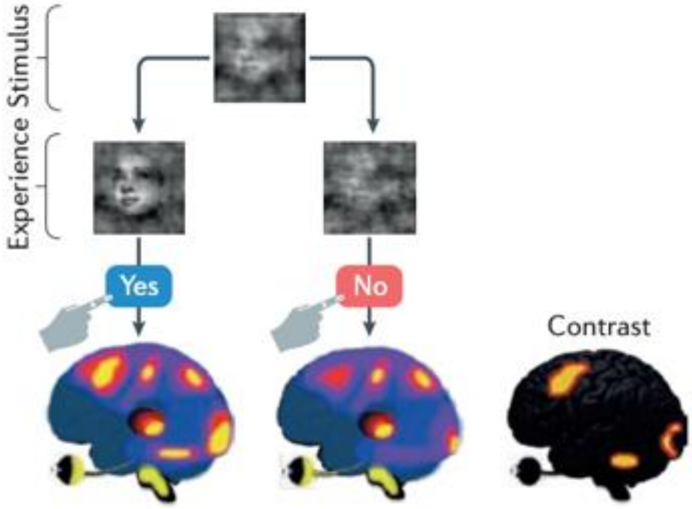

**Figure 1.** Contrastive method: Example of a contrastive method paradigm based on subject's report. The physical properties of the stimulus are kept constant, but awareness fluctuates across trials due to experimental manipulation (i.e. masking paradigm). Participants press a button when they perceive a stimulus (in this case seeing a face) and another button when they do not see the stimuli. Then, brain activity elicited by detected stimuli (seeing a face) is contrasted to brain activity related to undetected stimuli (not seeing a face). Thus, the brain activity isolated with this contrast is thought to reflect neural basis of visual awareness (figure from Koch et al., 2016).

Basically, in the contrastive method paradigms (Figure 1), the physical properties of the stimulus are kept constant while awareness is experimentally manipulated, so that, approximately in half of the trials observers are able to detect the stimuli (aware condition) while in the other half of trials they are not (unaware condition). The basic principle of this method is that if the stimuli does not change whereas observer's awareness fluctuates between conscious and unconscious states, as a consequence, the difference in neural activity between these two states should not be attributed to the property of the stimulus but to changes in visual awareness (Aru et al., 2012; De Graaf et al., 2012).

There are several paradigms that can be used to find the minimum intensity of stimulus that can be detected 50% of the time, the so called absolute threshold. One of these is the method of constant stimuli (Urban, 1910). In this procedure, the experiment chooses a fixed range of stimuli intensities, some of which are above observers' threshold while others below his/her threshold. On each trial one of these stimuli is randomly presented to the participant, who has to report whether detected the target or not. The absolute threshold corresponds to that stimulus' intensity value that elicits aware responses on 50% of the trials.

Behavioural measures of consciousness are used to quantify how much an experimental subject is conscious of a visual stimulus (Irvine, 2013), and are divided into objective and subjective measures (Cheesman and Merikle, 1984; Seth et al.; 2008). Subjective measures are based on participants' report of their mental state (Seth et al.; 2008), for example a subject has to report verbally or by button press if a stimulus was present or not. However, the fundamental problem of this method is that it relies on the assumption that all mental states are accessible to conscious report (Timmermans and Cleeremans, 2015) and thus, it does not take into account that, a subject may report to have not seen a stimulus not because he/she does not have knowledge about it but, because he/she is too conservative in responding or he/she has a very low confidence (Timmermans and Cleeremans, 2015).

Objective measures are based on the ability of the observer to choose between different alternatives (Seth et al., 2008). The conscious experience of the subject is then estimated from participants' performance in the task. An example is the two forced choice paradigm, in which, on each trial the subject is forced to choose between two alternatives which one is the correct and, even if he is not sure about the answer he is forced to guess. According to this view, a success in discriminating between alternative stimuli is an index of awareness whereas a failure indicates unawareness. So, the main difference between these two methods is that subjective measures of awareness are based directly on participants' report, while objective measures use statistical analysis to assess participants performance in the task (Irvine, 2013).

Signal detection theory (SDT; Green and Swets, 1996) is a statistical framework used on perception studies in order to provide an objective, response bias free, measure of consciousness (Irvine, 2012). It is widely applied to investigate decision-making processes under condition of uncertainties and bias.

The starting point of SDT is that decision processes are not exclusively based on perceptual information but are taken by filtering such information with an internal criterion (Abdi, 2007). So, decision depends on the ability of an observer to discriminate a signal from noise as well as from the participants' criterion (Wickens, 2002).

The goal of SDT is to estimate two components of the decision process, sensitivity (d') and criterion (C). Sensitivity is a measure that describes the detectability of a signal. Or better, how easily an observer can differentiate a signal from a background noise. A d' > 0 indicates that the observer can easily discriminate the signal. C reflects the subjects' inclination to categorize stimuli as a signal or noise. For example, if the amount of evidence for the signal exceeds the decision criterion, the subject says that the signal was present, and vice versa. A participant who tend to say "signal absent" is taken as an evidence of a conservative bias, whereas a more liberal participant tends to say "signal present" more often. Thus, the power of SDT in consciousness studies is that it allows to measure the impact of criterion bias on perceptual decision making.

During the last decades, neuroimaging studies contrasting brain activity associated to conscious states with brain activity associated to unconscious states have provided important evidence about the anatomical and physiological bases of consciousness.

Anatomical bases of NCC have been predominantly located in the posterior cortex including occipital, parietal and lateral temporal area (Boly, et al., 2017, Tononi et al., 2016b). The role of the prefrontal cortex in consciousness still remains a question of debate. While several authors suggested that prefrontal cortex has a causal role in access consciousness (Dehaene, 2014; De Cul, et al., 2009), more recent studies suggest that activity in frontal regions may be related to subject's report or to the cognitive processing of the stimulus rather than to conscious perception (Mazzi et al., 2018; Kock et al., 2016; Aru et al., 2012).

Regarding the temporal course of NCC, important advances have been achieved thanks to Event-related potentials (ERPs) method. ERPs are voltage fluctuations generated by neural structures in response to a sensory or cognitive event (Luck, 2014). They mainly reflect post synaptic field potentials produced by the activity of large populations of neocortical pyramidal cells which fire synchronously (Buzsàki et al., 2012, Nunez and Srinivasan, 2006). ERPs can be elicited by sensory, cognitive or motor events (for example the presentation of a visual stimulus) and represent a powerful non-invasive approach for investigating the temporal dynamics of neural processing with a millisecond resolution (Luck and Kappenmann, 2015; Donchin, 1981). ERPs are characterized by a sequence of positive and negative deflections known as "components", "peaks" or "waves". It is commonly accepted that the time-course of ERP waves following a stimulus reflect the time-course of neural processes activated by the same stimulus. The first components observed after stimulus presentation (within 100 ms), are called sensorial or exogenous, and are thought to depend on the physical properties of the stimulus (Luck, 2012; Coles et al; 1995;). On the contrary, later components, which are named cognitive or endogenous, have been related to decision and response processes (Luck and Kappenman, 2011; Polich, 2007). Thus, analyses on mean peak amplitude, latency and scalp distribution of ERP waves can provide useful information about the time course of neural processing (Cohen, 2014).

### 1.3 ERP correlates of consciousness

There are numerous ERP paradigms available to study neural correlates of visual awareness, however, the most common approach is based on contrastive method. As mentioned above, in a typical experiment the physical stimulation of the retina is kept constant throughout the experiment, while conscious experience fluctuates as a result of experimental manipulation (for a review of the different ways in which visual awareness can be manipulated see Koivisto and Revonuso, 2010). Then, the NCC would correspond to the difference between the "aware" and the "unaware" states. Another useful strategy to isolate the effect of awareness on ERP components consists on computing difference waves (Figure 2B). That is, subtracting the ERP wave for the aware condition from the ERP wave for the unaware condition. In this way, the neural activity that is common between the two conditions is canceled out while the resulting

ERP is thought to reflect the difference in neural processing between detected and undetected stimuli.

The results obtained in several studies using different paradigms for manipulating awareness have found two main ERP correlates of visual awareness: an increased negativity occurring in the N1-N2 time windows followed by an enhancement of positivity observed in the P3 time range (Figure 2A; for reviews see Koivisto and Revonuso, 2010; Railo et al., 2011).

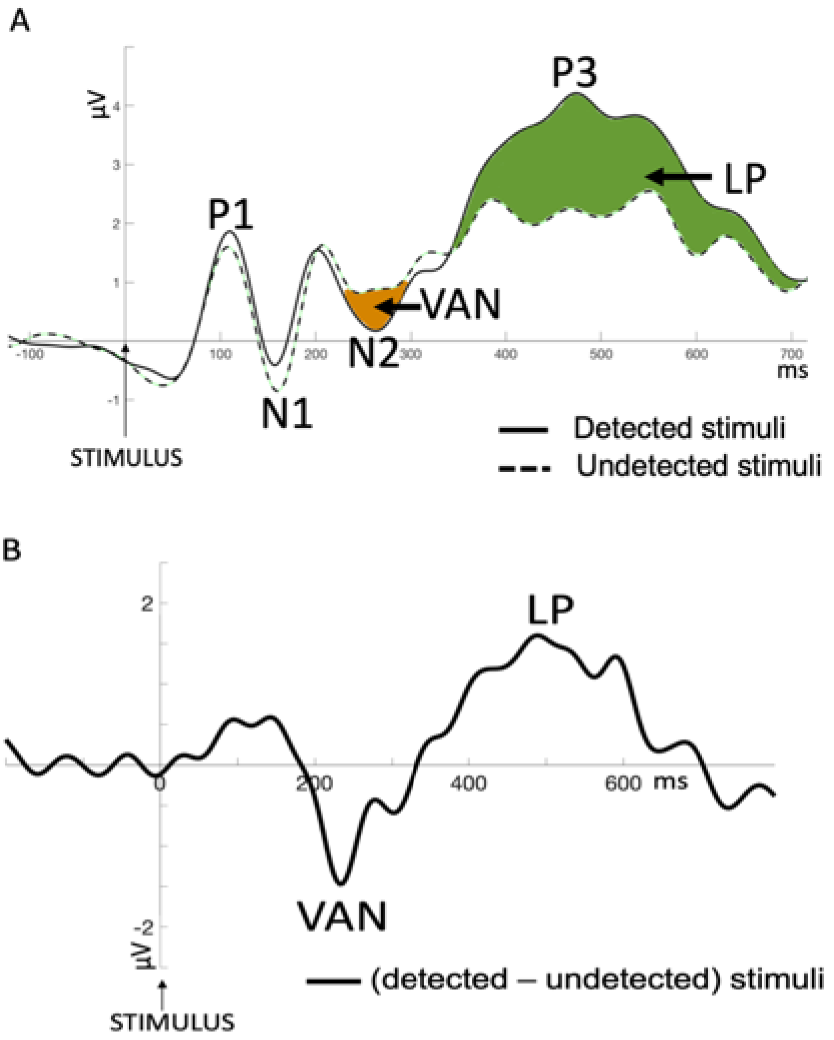

**Figure 2.** ERP correlate of visual consciousness: **(A)** Example of a classical ERP waveform. The continuous line represents the ERPs in response to detected stimuli while the dashes line the ERPs in response to undetected stimuli. Colored area indicates the condition differences for the N2 (orange area) and for the P3 (green area). **(B)** Use of difference waves to isolate the VAN and the LP. The two components were isolated by means of difference waves in which the ERP elicited by the detected stimuli was subtracted from the ERP elicited by the undetected stimuli. Usually the VAN overlaps in time with the N1-N2 component, whereas the LP overalps with the P3 wave.

Also the amplitude of the P1 has been proposed as a correlate of visual awareness (Pins & ffytche, 2003). However, many studies did not find any correlations between the P1 and awareness (Koivisto et al., 2008; Lamy et al., 2009; Melloni et al, 2011). It has been proposed that neural processes underlying P1 may reflect attentional processes (NCC-pr) related to the stimulus before it enters into consciousness rather than consciousness itself.

The presence of two components that correlate to awareness is confirmed by difference waves (Figure 2B). Awareness correlates with a negative deflection occurring around 200 ms after stimulus presentation, labeled Visual Awareness Negativity (VAN) and typically observed at posterior electrodes (occipital, temporal and posterior parietal areas; Koivisto and Revonuso, 2003; Tagliabue et al., 2016). The VAN is followed by a large positive wave called Late Positivity (LP), occurring after 300 ms stimulus presentation, that is predominantly observed at occipital and central electrodes (Del Cul et al., 2007; Turatto et al., 2002).

However, during the last years, much of the ongoing debate on neural correlates of consciousness is about whether consciousness arises from early activation of posterior cortex (within 200 ms) or whether it depends on later brain activity (after 300 ms) involving also the prefrontal lobes. The assumption that consciousness arises from the functional connectivity between cortical regions of fronto-parietal network is at the basis of the global neuronal workspace theory (Dehaene and Changeux, 2011). On the other hand, more recent studies support the notion that only earlier brain activity in the posterior cortex (Boly et al., 2017; Aru et al., 2012) expressed by the VAN represents the true correlates of consciousness, whereas the LP reflects higher order cognitive processes related to the task or to the stimulus evaluation.

Consistent support for the hypothesis that P3 does not reflect awareness but post-perceptual processes came from many ERP studies. For instances, Pitts and colleagues (Pitts et al., 2014a) used a modified inattentional blindness paradigm combined with EEG recording, in which they systematically varied the task relevance of a critical stimulus across different experimental sessions. In a first phase of the experiment a unexpected stimulus was presented to the participants who did not noticed it because it was task-irrelevant (unaware condition). In a second phase of the experiment the participants were aware of the critical stimulus, but it still was irrelevant for the task.

In practice, participants did not need accessing perceptual information of the critical stimulus for report. Finally, in a third phase, the same stimulus became relevant for the task, so that participants need accessing and maintaining perceptual information in working memory for report.

In this way, the authors created a condition in which participants were aware vs unaware of identical stimuli without requiring a trial by trial report. Interestingly, results showed that only the VAN was consistently observed in all the aware sessions. On the contrary, the amplitude of the P3 component was prominent only when the critical stimulus was relevant for the task and not when participants were aware of the stimulus, but it was task irrelevant. The authors concluded that only the VAN correlates to consciousness, whereas the P3 is likely to reflect post-perceptual or attention-based process necessary for completing the task. A similar pattern of results was replicated in an additional series of experiments carried out by Pitts and colleagues (Pitts et al., 2014b). The authors, using a similar inattentional blindness paradigm, in which visual awareness and task relevance were independently manipulated, investigated whether induced gamma band activity and the P3 wave reflected awareness or its consequences (NCC-co). Again, they found that gamma activity and the P3 were evident only when the stimuli were relevant to the task, confirming their hypothesis that the P3 reflect post-perceptual processes and not consciousness.

Another study from Koivisto and colleagues (Koivisto et al., 2016a) aimed at dissociating NCC from post-perceptual processing using a GO-NOGO paradigm. In different sessions participants were asked to respond when they were aware of the stimulus and not to respond when they were unaware (aware-GO) or, vice versa, to withheld responding when they were aware of the stimulus and responding when they were unaware (aware-NOGO). ERP results showed that the VAN was observed in both conditions predominantly over occipital and posterior temporal cortex, and was not influenced by the request to respond or withhold responding when subjects were aware of the stimulus. In contrast, a large LP wave was observed when subjects were aware of the stimulus and were requested to respond, suggesting that the amplitude of the P3 was related to response requirements. The authors concluded that neural activity at occipital areas around 200 ms should be considered the best predictor of visual awareness, while the P3 reflects post-perceptual processes.

In another study, Koivisto and colleagues (Koivisto et al., 2018), investigated the relationship between working memory (a post-perceptual processing) and visual consciousness in a dual-task paradigm. Basically, participants had to perform a visual detection task while concurrently either temporally maintaining information in their memory (maintenance condition) about another stimulus or performing an executive task (subjects had to manipulate the content of their working memory by subtracting numbers in steps of 3; load condition). Experimenters were interested in investigating whether LP amplitude was sensitive to their manipulation of working memory processes. Interestingly, results showed that the amplitude of the LP was reduced in the load condition compared to the maintaining condition, whereas the VAN presented the same amplitude in both conditions. The result that working memory processes share common neural resources (LP time-window) required for conscious perception were interpreted by the author as an indication that P3 reflects post-perceptual processes and not consciousness.

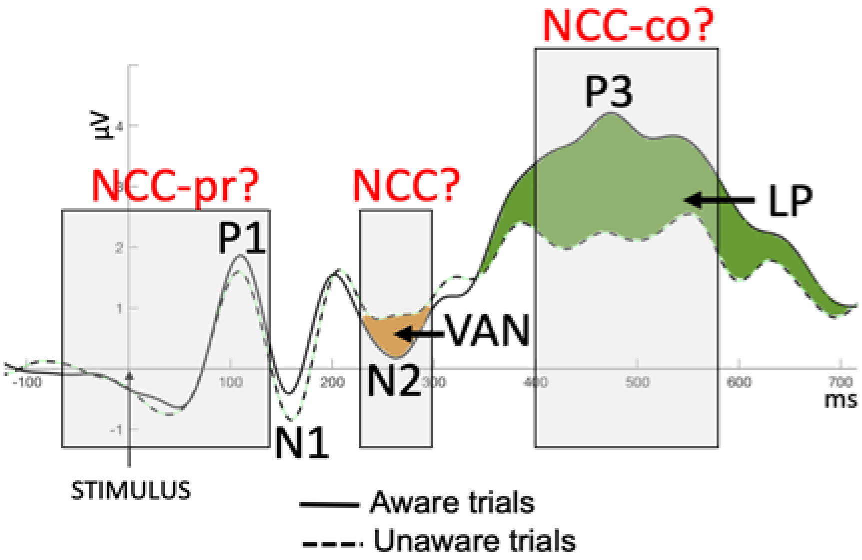

**Figure 3.** Proposed interpretation of ERP findings in visual awareness studies: Colored area indicates the condition differences for the N2 (orange area) and for the P3 components (green area). The neural processes underlying P1 probably do not reflect visual awareness, but pre-conscious processes (NCC-pr) related to attention. The N2 (peak ~200 ms) represents the earliest correlates of visual awareness (NCC or true NCC). The P3 might reflect post-perceptual processes or consequences of consciousness (NCC-co), such us working memory updating or cognitive manipulation of perceptual information.

Taken together, these recent studies support the view that visual awareness emerges earlier (around 200 ms), and that the VAN is the best predictor of visual consciousness (NCC; Figure3). Moreover, anatomical bases of visual consciousness seem to be restricted to a posterior cortical hot zone not including the prefrontal areas (Koch et al., 2016; Boly et al., 2017; Havlík et al., 2017). Later brain activity (after 300 ms) expressed by the P3 component is likely to reflect post-perceptual processes that follow conscious perception (NCC-co; Figure3) and to be related to task-monitoring or response report (Koivisto et al., 2018)

## 1.4 Rationale

The aim of the present study was to provide further evidence that the P3 component reflects a post-perceptual process. To this end, we designed two EEG experiments in which we directly manipulated post-perceptual processing and visual awareness while keeping constant the physical property of the stimuli.

Participants performed a visual task consisting in discriminating the orientation of horizontal or vertical gabor patches presented at perceptual subjective threshold, so that sometimes they could be consciously perceived and sometimes not. We experimentally manipulated subjects' decision criterion for reporting target-present stimuli by inducing a conservative and a liberal bias in different sessions (Experiment 1). In Experiment 2 the same participants as in Experiment 1 performed the same task but this time they were not instructed to adjust their decision criterion.

The advantage of this approach was that we created a paradigm in which the subjective report of consciousness differs across sessions while the physical property of the stimuli was kept constant. This allowed us to test whether post-perceptual processes related to decision making differently modulate behavioral and ERPs responses to the same stimuli.

If our manipulation of post-perceptual processes would produce a modulation on the P3 component, one could speculate that the P3 does not reflect the phenomenal experience per se, but could be related to other cognitive processes which are relevant to the task execution but not to consciousness.

The aim of Experiment 1 was to determine whether our manipulation of the decision criterion would produce a modulation of N2 and P3 ERP components.

Experiment 2 was conducted to provide further evidence that the P3 component reflects differences in post-perceptual processing rather than an index of conscious perception. The same participants as in Experiment 1 performed the same task, but this time we did not manipulate participants' decision criteria. Here, we assessed whether the N2 and P3 components would be modulated differently from Experiment 1. This allowed us to compare neural correlates of conscious perception (Experiment 2) with those underlying decision processes (Experiment 1).

If the P3 component reflects different post-perceptual processing related to the act of criterion setting, we would expect to find a different modulation of P3 amplitude between Experiment 1 and Experiment 2. On the contrary, if the P3 component correlates with awareness the amplitude of the P3 component should not vary significantly across sessions.

## 2. Experiment 1

### 2.1 Material and Methods

### 2.2 Subjects

Seventy-three healthy participants were recruited for the experiment. An initial threshold assessment (see below) was conducted to determine the stimuli to be used in the EEG session of Experiment 1 and Experiment 2 (see below). The sample obtained at the end of Experiment 1 was recalled after a period of at least two weeks to perform Experiment 2. Importantly, as the within-subjects comparisons between the sessions of the two experiments was crucial for our analysis, participants excluded after EEG session of Experiment 2 were also excluded from the analyses of Experiment 1.

After the threshold assessment, data from 29 subjects were excluded from threshold analysis and did not take part to the experiments due to failure to find a clear modulation of the criterion used in the two sessions (see below), i.e. it was not found a frequency value corresponding to 50% of aware responses. Data from 22 participants were excluded after the EEG session of Experiment 1 due to excessive artefacts (4 subjects excluded), or because after the pre-processing the number of trials for each condition was less than 10% of total trials (18 subjects excluded). At the end of the Experiment 1 the sample was composed of 22 participants.

At the end of Experiment 2, data from 5 participants were excluded due to excessive EEG artefacts (4subjects) or because the number of trials per condition was less than 10% (1 subject). Thus, the final sample was then composed of seventeen right handed participants (13 females, mean age 22.5 ± 2.11).

All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. The study was approved by the local ethic committee and all the participants gave their written informed consent according to the 2013 Declaration of Helsinki prior to participate to the study. All participants were paid for their participation.

### 2.3 Stimuli

The visual stimuli consisted of gabor patches of 2-degree visual angle in diameter (Michelson contrast = 0.50), oriented horizontally (0°) or vertically (90°). The frequency of the stimuli was determined individually for each participant before the EEG experiment by means of a threshold assessment procedure consisting of two different sessions. Within each session seven different pre-selected horizontal frequency values (4.5, 5.0, 6.0, 6.5, 7.0, 7.5, 8.5 cycles/degree) and seven different pre-selected vertical frequency values (4.5, 5.0, 6.0, 6.5, 7.0, 7.5, 8.5 cycles/degree) were randomly presented to the participants on a grey background. All Gabor stimuli were generated using MATLAB (The Mathworks, Inc., Natick, MA, USA), while stimulus presentation and behavioural data collection in the threshold assessment and EEG experiment were performed using E-prime 2.0 software (E-Prime Psychology Software Tools Inc., Pittsburgh, USA).

At the end of the threshold procedure one horizontal frequency value and one vertical frequency value corresponding to the value at which the participant reported to have seen the stimulus on 50% of presentations were obtained for each participant. These values were then used in the subsequent EEG experiment.

## 2.4 Threshold assessment

Participants were welcomed and seated in a light-dimmed room in front of a 17 in. CRT monitor (with a resolution 1024 x 768 and a refresh rate of 85 Hz) at a viewing distance of 57 cm, with their head supported by a chin-rest in order to secure head position and stabilize fixation.

The absolute thresholds were estimated for each participant by adopting a three alternative forced choice task in combination with the method of constant stimuli.

Subjects completed two separate sessions of threshold assessment, which were identical in terms of the stimuli employed but different in terms of decision criterion requirement. In one session (liberal session), participants were asked to report the orientation of the gabor whenever they had a minimal impression, while in the other session (conservative session), subjects were instructed to respond only if they were sure of having detected the orientation of the stimulus.

Other than decision criterion the procedure was identical in both sessions (Figure4): on each trial, a central fixation cross followed by a brief warning tone (1000 Hz) was presented to the subject. Then, after a random interval (ranging from 300to 500 ms) one of the preselected stimuli appeared for 36 ms on a grey background (3.9 cd/m$^2$)

at the top center of the screen. Subjects had to report by pressing one of three different keys whether they perceived a vertical gabor, a horizontal gabor or whether they did not know which the orientation of the stimulus was. No feedback was provided.

Each session was divided into six blocks for a total of 462 trials. Each block consisted of 77 trials, including 70 target trials (each Gabor's frequency was tested five times), and 7 catch trials (in which both horizontal and vertical spatial frequencies were superimposed). The order of the two sessions was counterbalanced among participants.

At the end of the procedure, a horizontal frequency value and a vertical frequency value yielding 50% aware responses (i.e. all responses excluding the "I don't Know" response, which is considered the unaware response) were calculated for each of the two sessions (liberal and conservative). Then, the mean between the two horizontal values and the mean between the two vertical values were calculated separately and used as spatial frequency of the target stimuli employed during the second part of the experiment.

### 2.5 EEG Experiment

All participants took part in two experimental sessions with a short break of 15 minutes between them. Both sessions were identical in protocol, except that subjects were asked to adopt a different decision criterion on each session. In one session participants were asked to adopt a conservative criterion while in the other session they were instructed to adopt a more liberal criterion. The stimuli were those determined by previous individual threshold assessment.

The trial sequence started with a fixation cross, followed by a 1000 Hz warning tone, and a variable random interval (300-500 ms). Then, randomly, a near threshold vertical or horizontal gabor patch was presented on the top center of the screen for 36 ms. After each stimulus, participants had to report (Figure 4), as fast and as accurate they could, by pressing one of three buttons, whether the stimulus was horizontal, vertical, or whether they did not know which was the orientation of the stimulus. The order of the two sessions was counterbalanced across participants. Each experimental session consisted of 6 blocks. Each block consisted of 77 trials (35 horizontal Gabor's, 35 vertical Gabor's and 7 catch trials), yielding a total of 462 trials across each session.

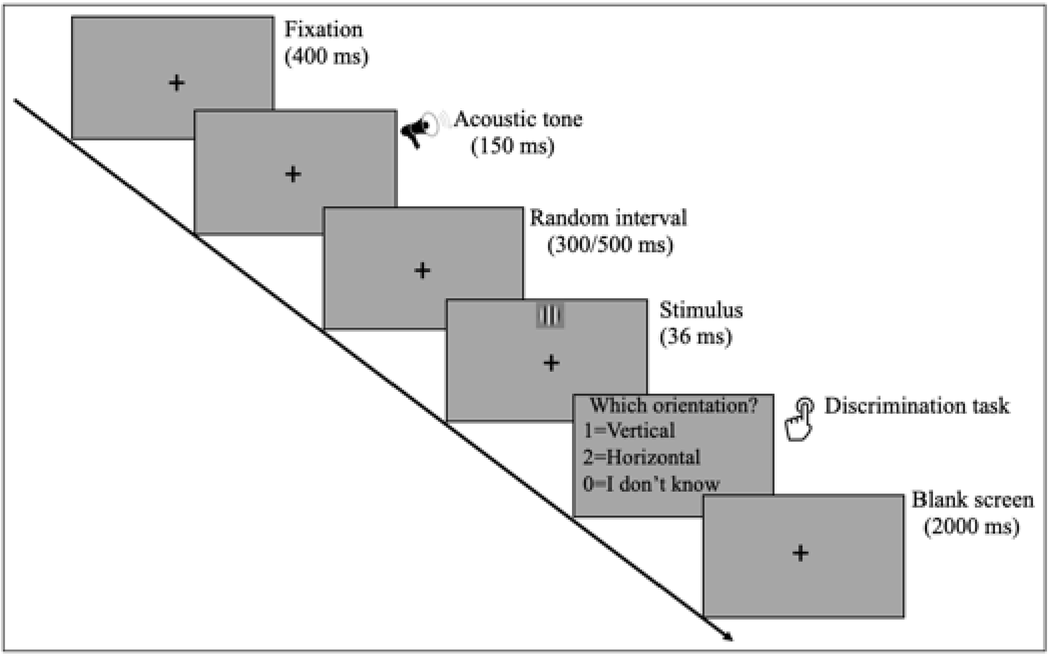

**Figure 4.** Experimental procedure: First, a fixation cross was presented for 400 ms followed by an acoustic tone lasting 150 ms. Then after a random interval of 300 or 500ms the stimulus was presented on the top center of the screen for 36 ms. At this point participants had to discriminate the orientation of the stimulus by pressing a button on a keyboard.

### 2.6 EEG Acquisition and event-related potential (ERP) analysis

Raw EEG signal was continuously recorded with a BrainAmp system (Brain Products GmbH, Munich, Germany – Brain Vision Recorder) using an EasyCap consisting of 64 Ag/AgCl electrodes arranged according to the 10-10 International System (EasyCap, GmbH, Herrshing, Germany). All electrode sites were referenced on-line to the right mastoid and re-referenced off-line to the mastoid average, while electrode Afz served as ground. Additionally, four electro-oculogram (EOG) electrodes were placed immediately adjacent to the left and right canthi and above and below the right eye to monitor for horizontal and vertical eye movements respectively. All electrodes' impedance was kept below or equal to 5KΩ. The data were acquired with a sampling rate of 1000 Hz (with a time constant of 10 s as a low cut-off and a high cut-off of 250 Hz.

Raw EEG data were initially processed off-line using BrainVision Analyzer 2 (Brain Products, Gilching, Germany). Data were down-sampled to 500 Hz, high-pass filtered with a cut-off at 1.0 Hz (12 dB/octave) and a 50 Hz notch filter was applied to remove power line-noise.

The data were then exported to EEGLAB (Delorme and Makeig, 2004), segmented into epochs (-1000 to 1000 ms) and visually inspected to detect segments and channels with large artifacts. Independent component analysis (ICA) for data decomposition was then performed separately for each subject using the InfoMax algorithm (Bell and Sejnowski, 1995) to separate neural activity from artifacts. Data were then low pass filtered at 40 Hz (12 dB/octave), segmented into epochs starting 200 ms before stimulus onset and continuing until 800 ms after stimulus presentation. The 200 ms activity before stimulus onset was used as the baseline. Before averaging, each trail was visually inspected to check for residual artifacts and then down-sampled to 250 Hz. Finally, stimulus-locked grand average ERPs for aware (those trials in which the participant reported to have detected the stimulus) and unaware trials were calculated separately for each criterion (conservative and liberal).

### 2.7 Analysis

The behavioral analyses were conducted using the R programming language (http://www.r-project.org, version 3.5.1). Mean percentage of aware responses for each criterion were analyzed with a t-test for paired samples. A Paired t-test was also performed on the mean percentage of correct responses to determine whether accuracy levels for each session were significantly higher than chance (50%).

The N2 component was measured from electrode Cp5, while the P3 from electrode Cpz. The electrodes used for statistical analyses were selected according to previous studies (Koivitsto and Revonuso, 2010; Tagliabue et al., 2017) and on the basis, that when looking at the difference waves they showed the highest peak amplitude for the N2 and P3 components.

Grand average ERPs were submitted to a 2-way repeated-measure ANOVA with factors Awareness (Aware, Unaware) and Criterion (Conservative, Liberal). Main effects were detected with the Study procedure implemented in EEGLAB (Delorme and Makeig, 2004). To explain the interaction between the two factors, follow-up analyses on the N2 and P3 mean peak amplitude were then conducted with the Mass Univariate ERP Toolbox (Groppe et al., 2011) implemented in Matlab.

## 3. Results

### 3.1 Threshold assessment

Figure 5 shows the psychometric function representing the percentage of aware answers as a function of the spatial frequency of the stimuli, for the conservative and the liberal sessions (vertical and horizontal stimuli collapsed together). As expected, the proportion of aware responses increased as a function of frequency intensities in both the conservative and the liberal session. The mean spatial frequency value related to 50% of aware responses was 6.0 for the liberal session and 6.8 for the conservative session.

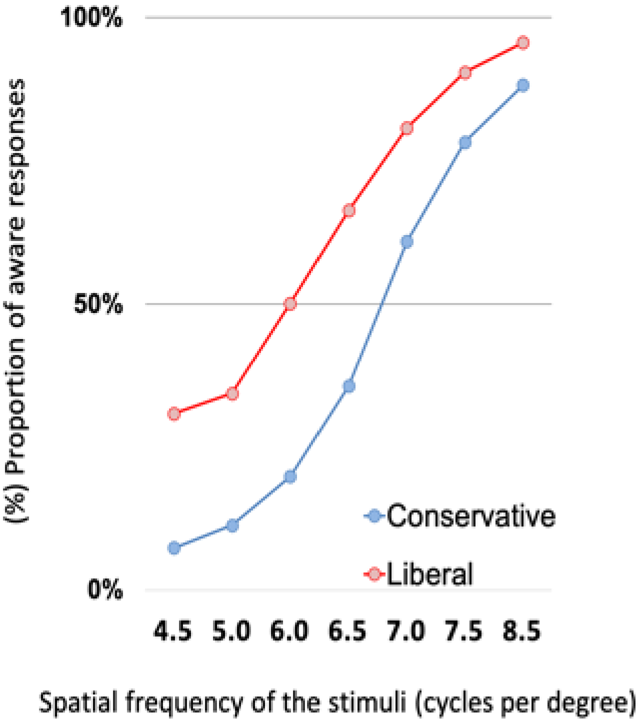

**Figure 5.** Psychometric function: Psychometric function for the decision criteria representing the average number of aware responses as a function of the spatial frequency (cycles per degree) of the stimuli (horizontal and vertical Gabor's collapsed together). The blue line indicates the threshold function obtained for the conservative criterion, while the red line depicts the threshold function obtained for the liberal criterion. Each dot indicates the mean performance at each frequency value for the two decision criteria.

The aim of threshold assessment was to find a horizontal frequency value and a vertical frequency value that participants should, on average, detect on 50% all trials. To do that, we firstly estimated a threshold for vertical and horizontal stimuli on each session (conservative and liberal). Then, the mean between the two horizontal values and the mean between the two vertical values were calculated separately and used as spatial frequency of the target stimuli employed during the EGG sessions of Experiment 1 and Experiment 2. Following this procedure, the mean spatial frequency values obtained were 6,71 cycles/degree for the horizontal Gabor's and 6,04 cycles/degree for the vertical Gabor's.

### 3.2 EEG Experiment behavioral results

As shown in Figure 6A participants reported to be aware of the stimuli more frequently in the liberal session 68.76% than in the conservative session 48.61%, (t = -5.6281, df = 16, p-value = 0.0000377). In other words, participants were able to set their decision criterion differently in the two sessions, thus confirming that our manipulation of post-perceptual processes was successful.

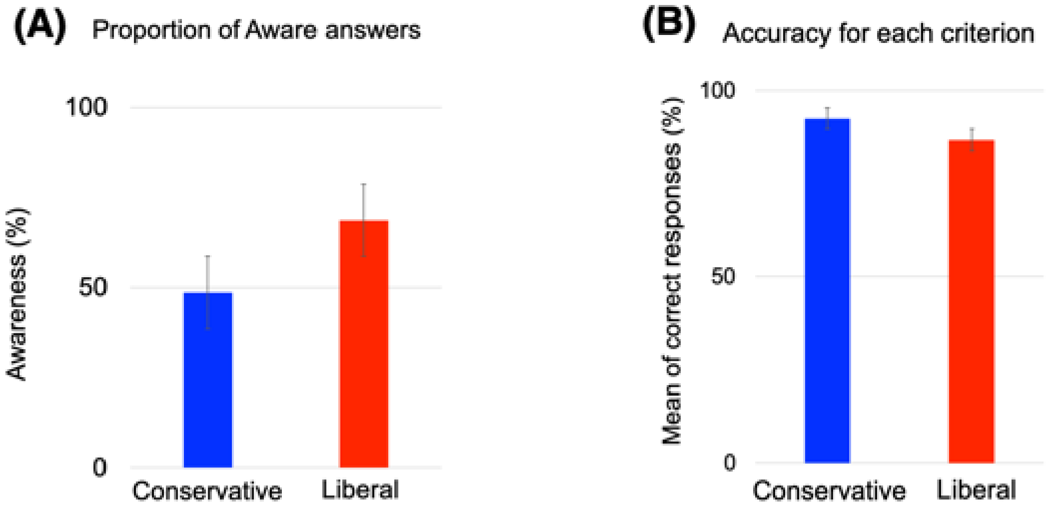

**Figure 6.** Behavioral results: **(A)** Mean percentage of aware responses for the Conservative and Liberal sessions. Error bars represent standard errors. **(B)** Mean percentage of correct responses for each session. Error bars represent standard errors.

One sample t-tests were run to check whether the mean percentage of correct responses (Figure 6B) on each session were significantly greater than chance level. Results showed that accuracy was higher than 50% on both sessions Conservative and Liberal (all ps < 0.001). Moreover, as shown in Figure 5B observers were more accurate in the conservative session (92.42%) compared to the liberal session (86.76%), (t = 4.6376, df = 16, p-value = 0.0002738).

Participants detected the catch trials with a 94.55% accuracy in the conservative session, and a 95.52% accuracy in the liberal session, thus indicating the reliability of their performance.

Altogether these results indicate that the performance of the participants across the two sessions differed significantly in terms of subjective report and accuracy.

### 3.3 ERPs results

Figure 7A and Figure 7D show Aware and Unaware grand average ERPs for the N2 and P3 components measured from electrode Cp5 and Cpz, respectively. The N2 component emerged as an enhanced negativity peaking at about 280-380 ms post-stimulus at lateral-parietal electrodes of the left hemisphere (Figure 7C). The P3 component was visible as a more positive voltage distributed over almost all electrodes (Figure 7F) in the time-window between ~400-600 ms. Figure 7B and Figure 7E show topographic scalp maps for the VAN and the LP components. These maps were calculated by subtracting the ERP to unaware responses from ERP to aware responses in the time window of 306-326 ms for the VAN, and the time window of 442-542 ms for the LP. Figure 8A and Figure 8B show grand-averaged ERP from electrode Cp5 and Cpz for each decision criterion. Figure 9A and Figure 9B show the VAN and the LP components measured from the aware minus unaware difference waves at the electrode Cp5 and Cpz. The VAN can be observed as an enhanced negativity in the time-window of 240-340 ms. The LP is associated with an increased positivity in the time window of 400-600 ms.

### 3.3.1 N2

The ANOVA measuring the effect of conscious detection on N2 amplitude revealed a significant main effect for awareness ($p < 0.05$), indicating that aware responses were associated with a more negative peak amplitude than unaware responses, especially over temporal and parietal lateral electrodes. Difference waves calculated on this time-window revealed a negative peak that corresponded to the VAN component. In contrast, there was no main effects of the decision criterion on N2 amplitude ($p > 0.05$) nor an interaction effect, thus suggesting that post-perceptual processes had no effect on the modulation of N2 component.

### 3.3.2 P3

The P3 component showed a significant main effect for Awareness ($p < 0.05$), indicating that aware responses were associated with a larger P3 if compared to unaware responses. Thus, difference waves confirmed the presence of the LP component peaking over almost all electrode sites. In addition, P3 showed a main effect of the decision criterion ($p < 0.05$), revealing that P3 amplitude was significantly larger for the Liberal vs the Conservative condition, particularly over central areas. Planned post-hoc analysis did not show any significant interaction (ps > 0.05).

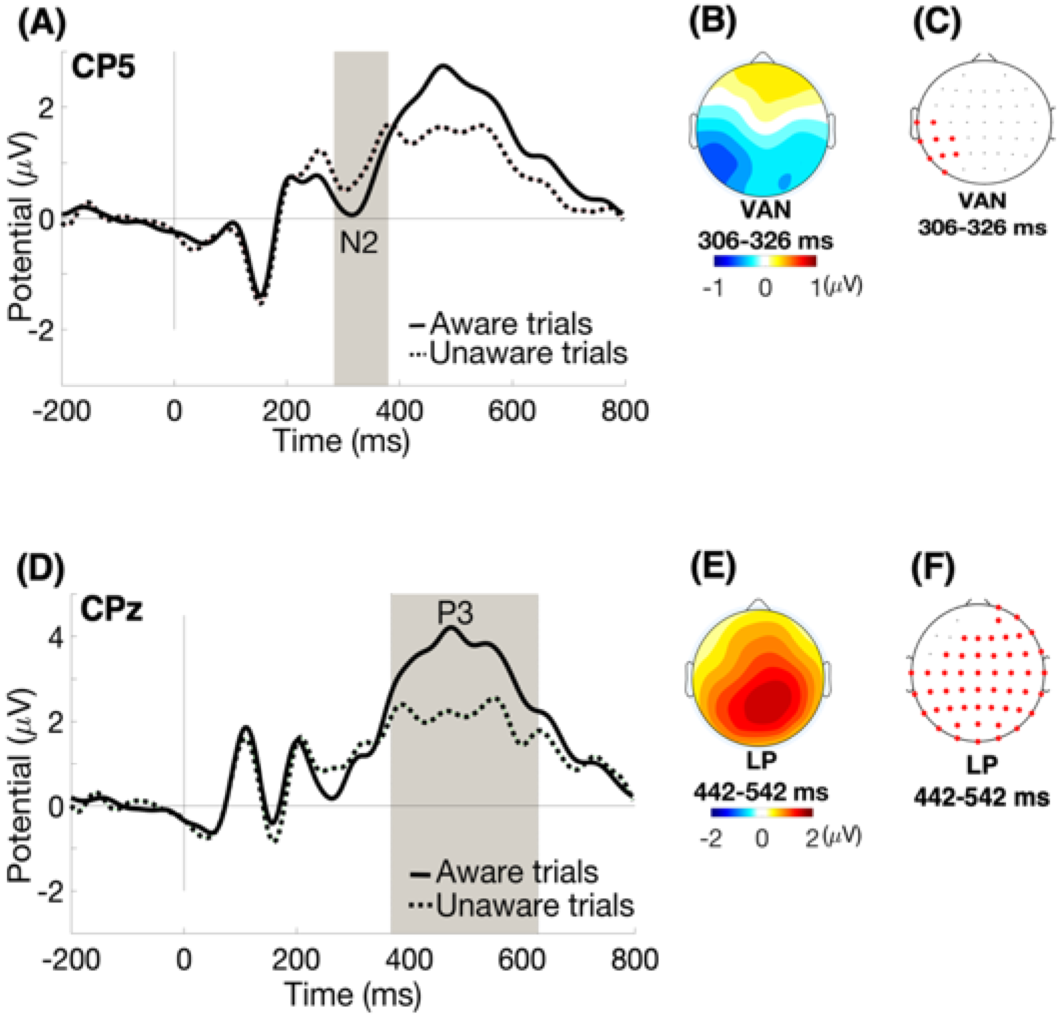

**Figure 7.** ERPs: **(A)** Grand average ERP for aware and unaware responses for electrode Cp5. Gray area indicates the time-window for the N2 component. **(B)** Scalp topography map showing the ERP difference between Aware and Unaware responses in the VAN time-window (306-326 ms). **(C)** Scalp map of p values showing significant electrodes when comparing aware and unaware responses in the VAN time-window ($p < 0.05$). **(D)** Grand average waveforms in response to aware and unaware stimuli for electrode Cpz. Gray box marks the component of interest (P3). **(E)** Scalp topographic maps of aware minus unaware difference waves for the LP component in the time window of 442-542ms. **(F)** Scalp map of p values showing significant electrodes when comparing aware and unaware responses in the LP time-window ($p < 0.05$).

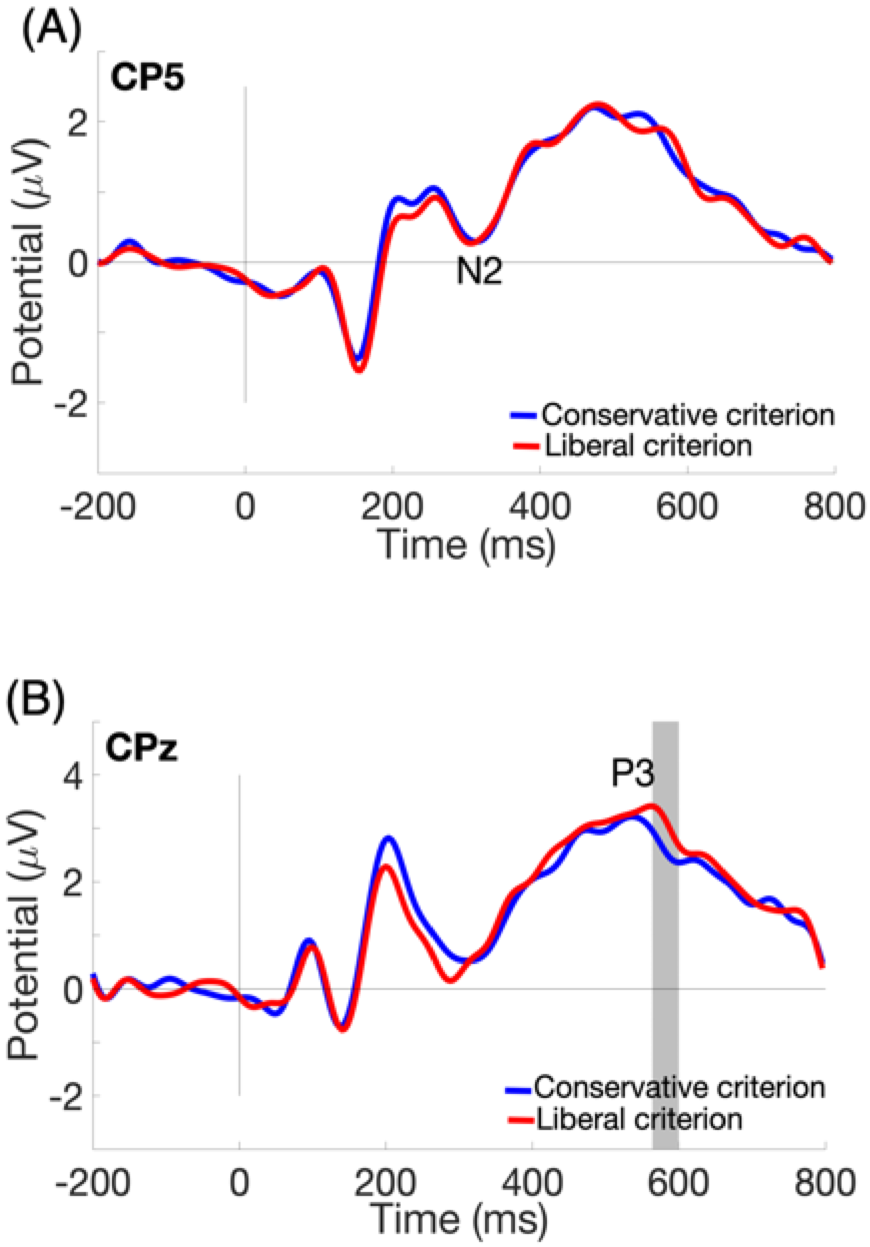

**Figure 8.** Grand average ERPs for each criterion: **(A)** Grand average waveforms in response to each criterion for electrode Cp5 (N2 component). **(B)** Grand average waves in response to each criterion for electrode Cpz. Grey box marks the component of interest (P3 component).

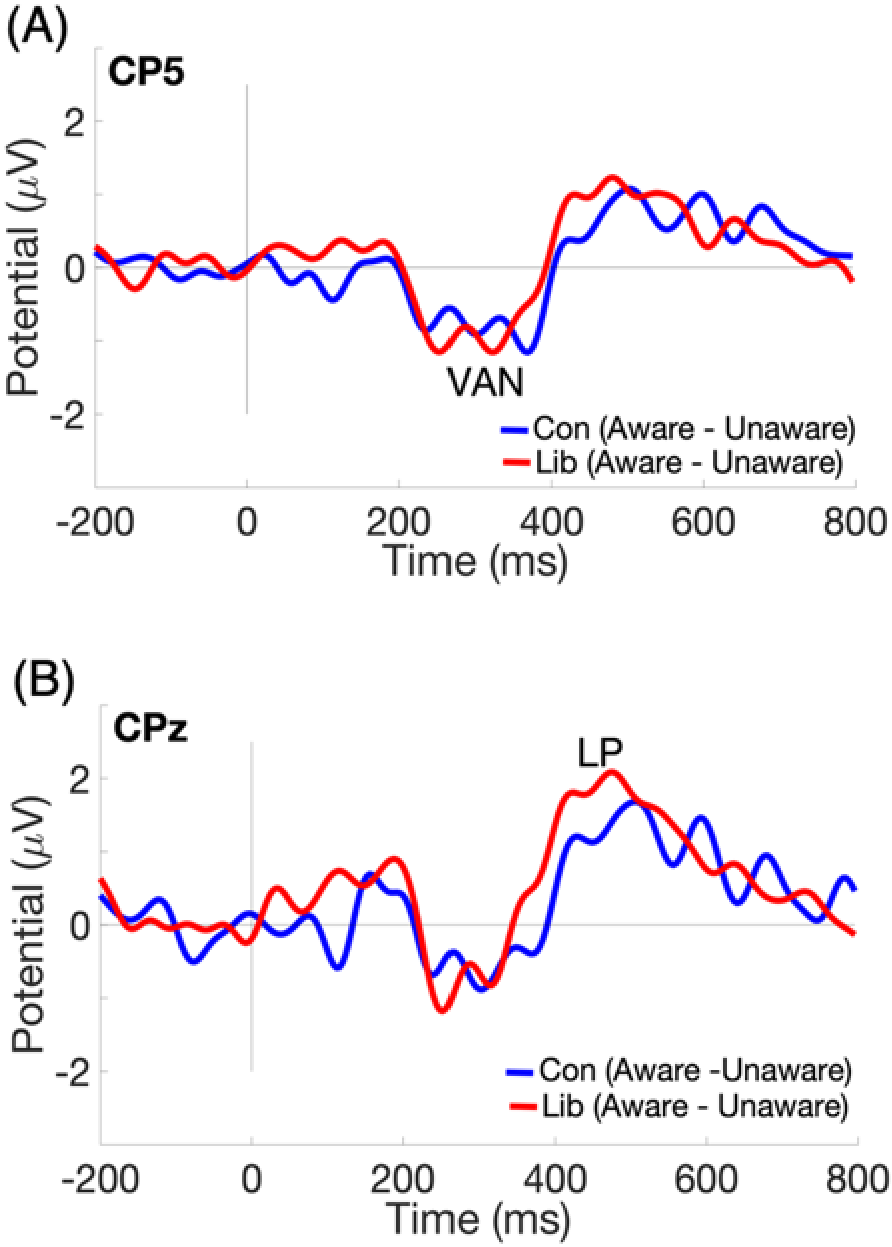

**Figure 9.** ERP difference waves: **(A)** Difference waves (aware minus unaware trials) related to Conservative and Liberal criteria for electrode Cp5. **(B)** Grand average difference waves related to each criterion for electrode Cpz.

## 4. Discussion

In this experiment we investigated whether our manipulation of the decision criterion would produce a corresponding modulation on P3 amplitude. This would implicate that P3 does not reflect only visual awareness but that it shares common neural resources with decision-making processes.

Behavioural results showed that our manipulation of the decision criterion induced a perceptual decision bias in the participants, resulting in an increased observers' propensity for aware responses in the liberal session than in the conservative session.

As in previous studies (Koivisto et al., 2008; Tagliabue et al., 2016), after contrasting ERPs to detected and undetected stimuli it was possible to isolate the VAN, which was largest over temporo-parietal areas. VAN was followed by an enhanced positivity, the LP, which was prominent over almost all electrode sites.

Importantly, the ERP analyses revealed that the P3 component was sensitive to the manipulation of the decision criterion, with a larger P3 amplitude for the liberal compared to the conservative condition, whereas the N2 was not affected by the decision criterion. These results suggest that neural activity expressed by P3 wave may reflect post-perceptual processes related to response criterion setting rather than a mere neural correlate of consciousness.

To further corroborate our hypothesis that P3 reflects post-perceptual processes we run a second experiment to examine whether in a no bias condition (Own session), in which the participants are not forced to adopt a specific decision criterion, ERP would distribute differently on the N2 and P3 time-window. If effectively in the first experiment the P3 was sensitive to the bias effect induced by the manipulation of the decision criterion, one would expect to find some differences in the topography or in the time-course of the P3 between the bias condition (Experiment 1) and the no bias condition (Experiment 2).

## 5. Experiment 2

### 5.1 Material and Methods

### 5.2 Subjects and Stimuli

The sample obtained at the end of Experiment 1 was asked to participate in Experiment 2. Moreover, the same stimuli obtained during threshold assessment and used in Experiment 1 were employed in this experiment.

### 5.3 EEG Experiment

EEG setting was identical to Experiment 1. Participants completed one experimental session identical in structure to each session of Experiment 1. Participants performed the same task as in Experiment 1, but this time there was no a decision criterion bias imposed and participants were free to respond whenever they detected a stimulus (Own-criterion session).

### 5.4 EEG acquisition and Event Related Potential (ERP) analysis

EEG recording setting and data pre-processing were the same as in Experiment 1. At the end of the pre-processing procedure stimulus-locked grand-average ERPs for aware and unaware trials were computed separately for each condition.

### 5.5 Analysis

Behavioral and ERPs data from Experiment 2 were compared with those of Experiment 1. The proportion of aware responses for the own-criterion session were compared to those of each session of the Experiment 1 (Conservative session and Liberal session) by means of paired two-tailed t-tests. Paired t-tests were also used to test whether accuracy score obtained in the own-criterion session was significantly different the conservative and liberal sessions.

As in Experiment 1, grand average ERP waveforms were submitted to a two-way repeated-measure ANOVA with Criterion (Conservative, Liberal, Own) and Awareness (Aware; Unaware) as within-subject factors. Main effects were detected with the Study procedure implemented in EEGLAB (Delorme and Makeig, 2004) while post-hoc analyses were conducted with the Mass Univariate ERP Toolbox (Groppe et al., 2011) implemented in Matlab. The time-window and electrodes used for analysis of the N2 and P3 components were chosen based on inspection of grand averaged ERP across all conditions and using the results of Experiment 1 as a guide.

# 6. Results

## 6.1 Behavioral results

In the own criterion session, participants reported to have detect the stimuli during 78.64% of all trials (Figure 10A) with an 88.76% accuracy (Figure 10B). One sample t-tests performed to check whether accuracy was greater than 50% confirmed that participants' performance was significantly above chance level (p < 0.001) in the own-criterion session. Catch trials were detected with a 97,48% accuracy, thus revealing the reliability of the participants performance.

Behavioral data from Experiment 2 were then compared with corresponding data obtained in Experiment 1. For the accuracy measures, results indicated that participants were more accurate in the own-criterion session than in the conservative session (p = 0.005958). Whereas, no significant difference on accuracy scores was observed among the own-criterion session and the liberal session (p = 0.1695).

There was a significant difference in the proportion of aware responses between the own-criterion session and the conservative session ( p = 0.000062). Whereas, between the own-decision criterion session and the liberal session there was not a significant difference in the mean proportion of aware responses ( p = 0.08199).

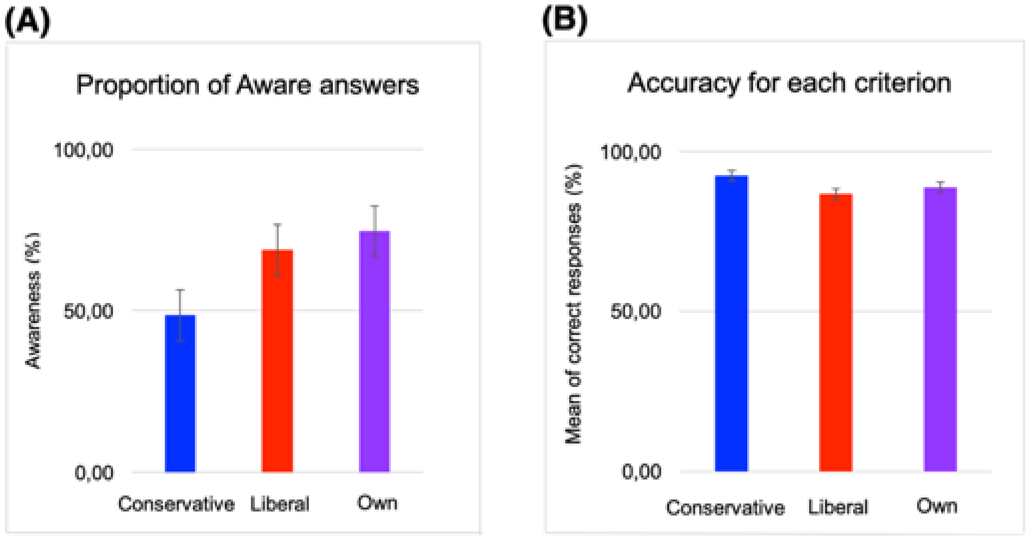

**Figure 10.** Behavioral results: **(A)** Mean percentage of aware responses for the Conservative, Liberal and Own sessions. Error bars represent standard errors. **(B)** Mean percentage of correct responses for each session. Error bars represent standard errors.

### 6.2 ERPs results

Figure 11A and Figure 11D show ERP waves from Cp5 and Cpz electrodes for Aware and Unaware responses. Visual inspection of the grand average ERP revealed the presence of the N2 and the P3 component peaking respectively at 308 ms (N2) and 458 ms (P3) after stimulus presentation. The effect of awareness on N2 and P3 components was quite similar to that observed in Experiment 1. In fact, Aware responses elicited a more negative N2 and a more positive P3 than Unaware responses. Figure 11C and Figure 11F illustrate electrodes with statistically significant differences ($p < 0.05$) between aware and unaware responses for the VAN and LP components, respectively. Figure 11B and Figure 11E show the scalp distribution of differences (μV) between Aware and Unaware stimuli for the VAN and LP time-window. Figure 12A and Figure 12B show grand-averaged ERP from electrode Cp5 and Cpz for each decision criterion. Figure 13A and Figure 13B show the VAN and the LP component measured from the aware minus unaware difference waves at the electrode Cp5 and Cpz for each condition.

#### 6.2.1 N2

For the N2 components, the results of the within-subject ANOVA with factor awareness showed that aware responses were associated with an increased N2 amplitude than unaware responses ($p < 0.05$) over a cluster of temporo-parietal electrodes located on the left hemisphere. The repeated measures ANOVA with criterion as within-subject factor showed that N2 amplitude was sensitive to the effect of the criterion ($p < 0.05$). Pairwise comparisons showed that the component was larger (more negative) in the Own session if compared to the Liberal ($p < 0.05$) and to the Conservative sessions ($p < 0.05$).

#### 6.2.2 P3

Corresponding analysis on the P3 time-window showed a main effect of awareness indicating that aware responses elicited an increased positivity compared to unaware responses ($p < 0.05$). The largest effect was measured in the time-window of 400-600 ms and was present over almost all electrodes sites. There was also a significant main effect of the criterion ($p < 0.05$) on P3 amplitude. Follow-up analyses indicated that the P3 elicited by the Own criterion was significantly more positive than the P3 elicited by the Conservative criterion, and that the P3 of the Liberal criterion was significantly larger than the P3 of the Conservative criterion. No other effects or interactions were significant.

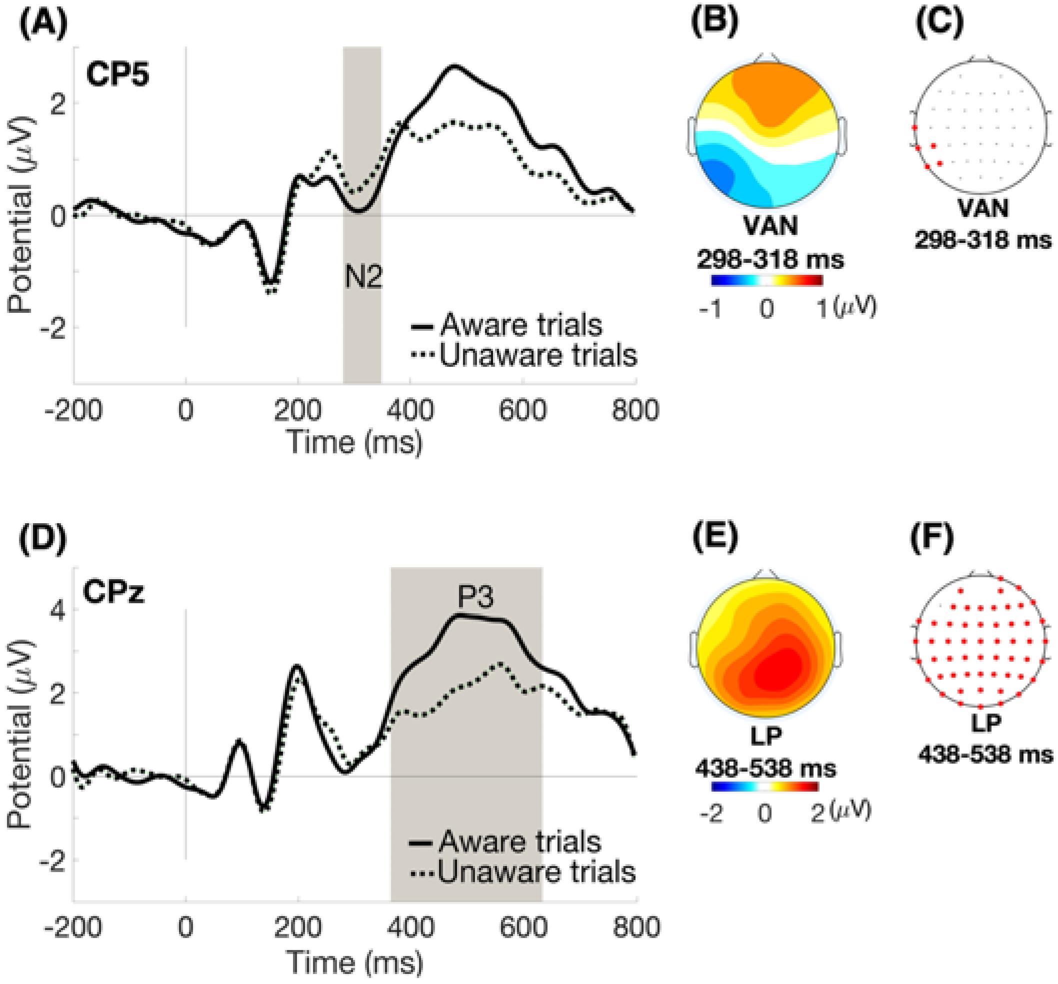

**Figure 11.** ERPs: **(A)** Grand average ERP for aware and unaware stimuli for electrode Cp5. Gray area indicates the time-window for the N2 component. **(B)** Scalp topography map showing the electrophysiological difference between aware and unaware responses in the VAN time-window (298-318 ms). **(C)** Scalp map of p values showing significant electrodes when comparing aware and unaware responses in the VAN time-window ($p < 0.05$). **(D)** Grand average waveforms in response to aware and unaware stimuli for electrode Cpz. Gray box marks the component of interest (P3). **(E)** Scalp topographic maps of aware minus unaware difference waves for the LP component in the time window of 438-538ms. **(F)** Scalp map of p values showing significant electrodes when comparing aware and unaware responses in the LP time-window ($p < 0.05$).

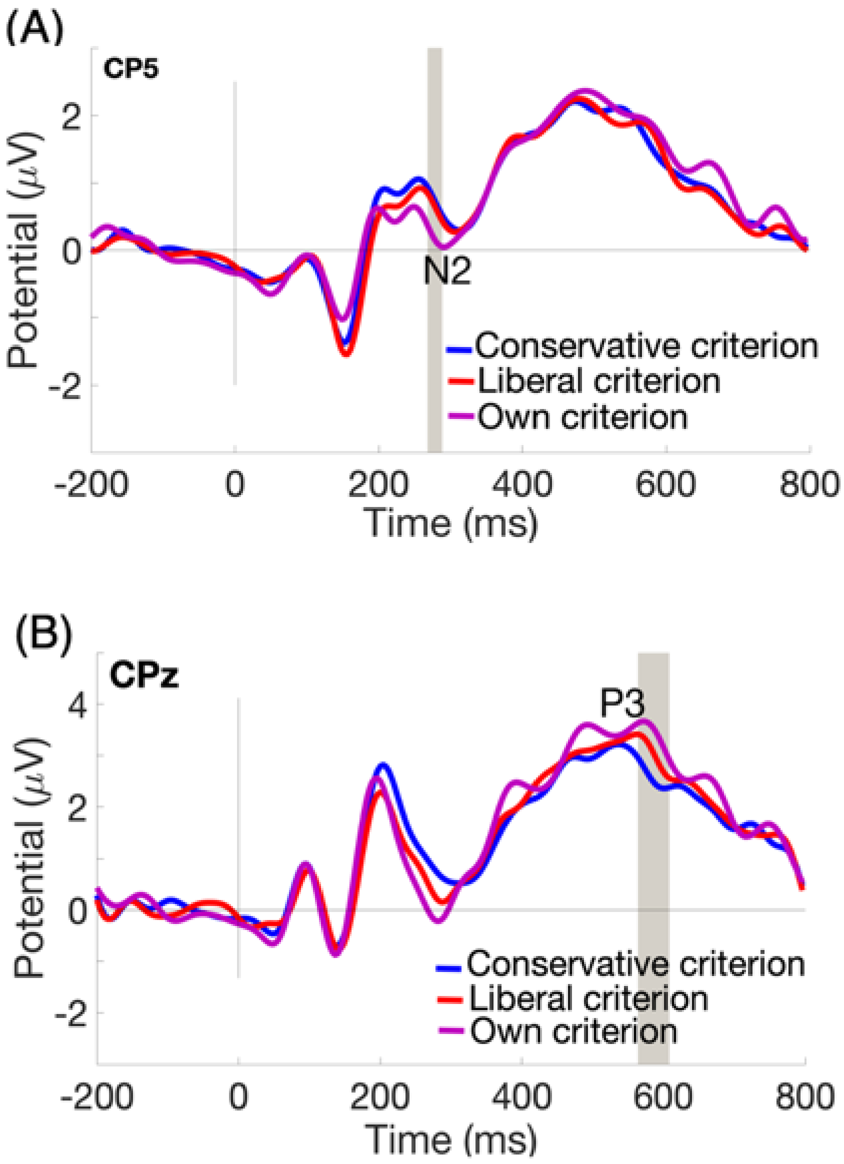

**Figure 12.** Grand average ERPs for each criterion: **(A)** Grand average waveforms in response to each criterion for electrode Cp5. Gray box indicates the component of interest (N2) **(B)** Grand average waves in response to each criterion for electrode Cpz. Grey box marks the component of interest (P3 component).

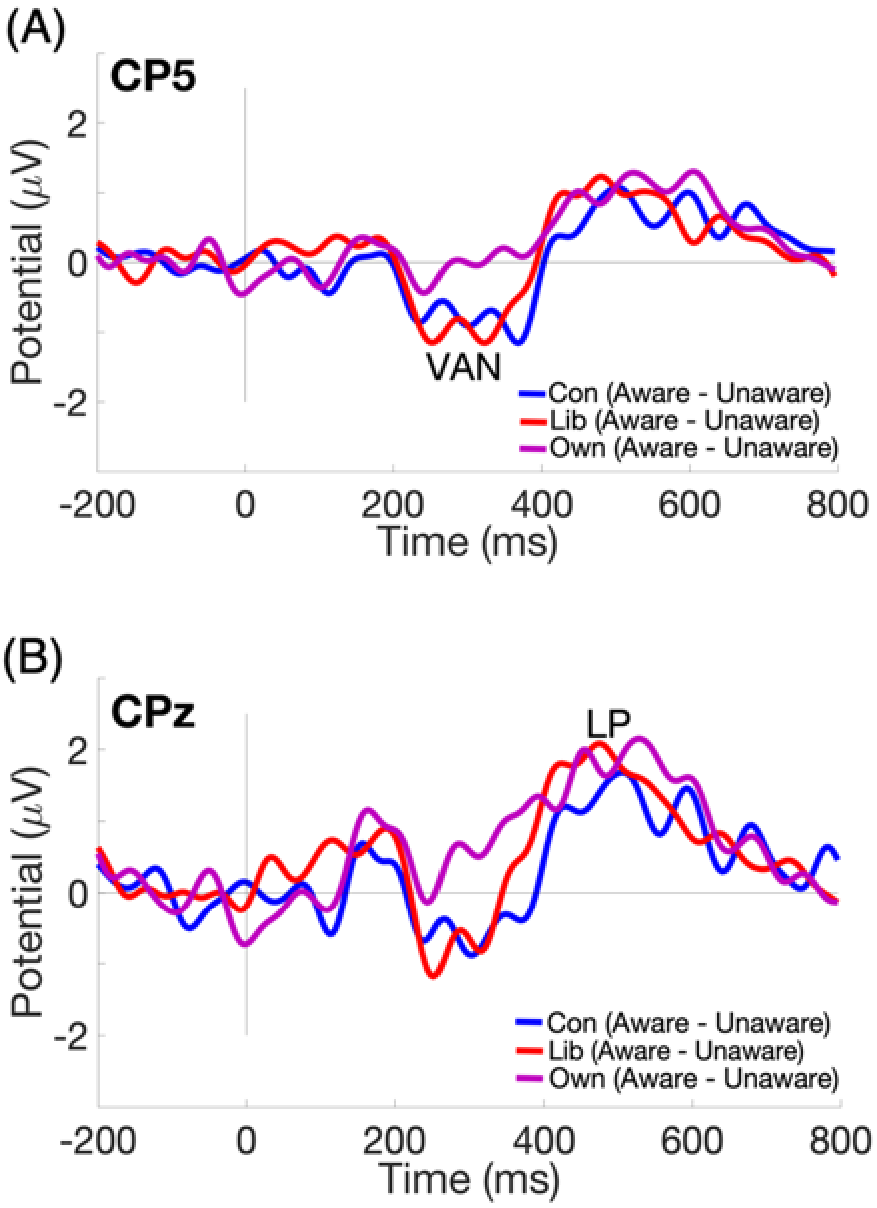

**Figure 13.** ERP difference waves: **(A)** Difference waves (aware minus unaware trials) related to each criterion for electrode Cp5. **(B)** Grand average difference waves related to each criterion for electrode Cpz.

## 7. Discussion

Behavioral and ERP results obtained in this experiment were analyzed together with those obtained in Experiment 1. The aim of this experiment was to examine whether in a condition in which decision processes were not manipulated, the N2 and P3 components would distribute differently from Experiment 1.

As in Experiment 1, the contrast to ERPs to detected and undetected stimuli revealed the presence of the VAN, which was followed by an enhanced positivity, corresponding to the LP wave.

Importantly, behavioral results suggested that participants shifted their decision criterion depending on the experimental session. In the conservative session, the decreased proportion of aware responses and an increased accuracy suggests that participants effectively adopted a more conservative strategy compared to the liberal and own-criterion sessions. While, on the contrary, their own criterion was not different from the liberal criterion. These results were also reflected on the electrophysiology of P3 component revealing an enhanced positivity over central areas associated with the liberal and own criteria if compared to the conservative criterion. In addition, a stronger N2 was elicited by the own criterion if compared to the liberal and conservative criteria.

Taken together, these findings suggest that experimentally induced manipulation of decision criterion is associated with a reduced N2 amplitude. On the contrary, when sensory information was relevant for the task (own session) a stronger N2 component was observed. These results suggest that N2 represents the best predictor of visual awareness whereas P3 modulation might reflect post-perceptual processes related to decision making.

## 8. General discussion

Two patterns of brain activity expressed by the N2 and the P3 ERP components have been reported in the literature as the main neural correlates of consciousness (Koivisto and Revonuso, 2010; Railo et al., 2015). However, one of the major problems of the classical paradigms used in visual awareness studies arises from the fact that observers' report is essential for establishing the quality of a perceptual experience, for example whether the participant saw or not a visual stimulus. This means that neural correlates that support awareness may be confounded with neural processes involved in accessing and reporting perceptual information (Aru et al., 2012; De Graaf et al., 2012). The aim of this study was to investigate whether the P3 component may actually index post-perceptual processes (NCC-co) related to decision bias. Our major finding was that, the amplitude of P3 was modulated by the decision criterion, suggesting that P3 might indeed reflect brain activity occurring after that awareness has emerged.

In this series of experiments, we experimentally induced a decision bias to create an experimental condition in which the physical stimulation of the retina was held constant while post-perceptual processes required to carry out the task varied across sessions. Thus, the experimental conditions differed between each other in decision making requirements, that is a post-perceptual process. This manipulation allowed us to examine the possible influences of post-perceptual processes over the time course of neural responses.

Behavioral results showed that the manipulation of decision criterion had an effect on reported "aware" trials, as the proportion of aware responses was greater in the own and liberal sessions as compared to the conservative session. The behavioral results are in line with the view that criterion shifts are obtained by strategically biasing sensory evidence depending on task demand (Klosterman et al., 2018). Thus, the decision to give more or less aware responses was based on comparing available sensory evidence with an internal criterion and occurred after the subject was already conscious of the stimulus (i.e. post-perceptually).

Consistent with previous ERP studies (Railo et al., 2011; Koivisto et al., 2016b), we found that aware responses elicited more robusts N2 and P3 waves compared to unaware responses.

Importantly we found that the amplitude of P3 component was modulated by the manipulation of decision criterion. It was reduced in the conservative session as compared to the own and liberal sessions. In other word, the same modulatory effect induced by the manipulation of decision criterion at behavioral level was reflected on the electrophysiology of P3 component. Nevertheless, we cannot exclude that the order of experiments (Experiment 2 was performed always at least two weeks after Experiment 1) may have acted as a confounding variable an influenced the results.

However, these results suggest that neural mechanisms underlying criterion setting occurred during the P3 time-window. Indeed, since perceptual decision are taken after comparing sensory evidence with an internal criterion, the modulation observed in the P3 time-window must be attributed to decision-making processes. This is consistent with the view that P3 reflects access consciousness (Block, 2005), that is the availability of perceptual information to cognitive system for reporting purpose and action planning (Pitts et al., 2014a; Boly et al., 2017).

In addition, ERP results showed that the amplitude of the N2 was greater in the own session compared to the conservative and liberal sessions. Thus, in the own session, in which participants were requested to base their responses solely on sensory input, a bigger N2 was observed. This result suggest that the N2 component might reflect participants' awareness to the presence of the stimuli.

Our findings are in line with the results obtained by recent studies investigating the role of the P3 in perceptual decision. Kelly and colleagues (Kelly and O' Connell, 2013) identified an ERP component called Centro parietal positive potential (CPP), an equivalent to P3 wave (Twomey et al., 2015), which has been related to the accumulation of sensory evidence. It has been suggested that the amplitude of the CPP component influences decision making performance and the timing of decision report. A general implication of this finding is that P3 or CPP does not correlate solely with stimulus identification, but it reflects all the identification processes leading to a decision.

Additional findings come from signal detection experiments. In a study on NCC (Koivsto and Grassini, 2016) the authors investigated whether sensitivity index (d') and response bias (c), computed on the basis of participants awareness rating, correlated with the VAN and LP components. Interestingly, the authors found that the better the subjects were in discriminating between the presence or the absence of the stimuli, the larger was the VAN. On the contrary, the LP did not correlate to awareness sensitivity but to response bias, where a conservative response bias was associated with a more reduced LP amplitude. These results were interpreted by the authors as an indication that the VAN correlates with visual awareness, whereas brain activity expressed in the P3 time-window was related to decision mechanisms concerning processing of task-relevant features in working memory.

In conclusion, the results of the present study suggest that the increased negativity occurring around 200 ms reflected by the VAN component represents the best predictor of visual awareness. The later activity, instead, expressed by the P3 may reflect brain processes related to further processing of stimulus-related features.

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