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Short Communication

The P3 component of the ERP reflects conscious perception, not confidence

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ABSTRACT

Consistent with numerous electrophysiological studies, we recently reported that conscious perception is associated with a widely distributed modulation of the P3 component (Lamy, Salti, & Bar-Haim, 2009). We also showed that correct objective performance in the absence of subjective awareness is associated with a spatially more restricted modulation of the P3. The relatively late occurrence of the P3 along with lack of control for post-perceptual processes suggests that this component might reflect processes related to stimulus evaluation or confidence rather than to visual awareness or objective performance. The main aim of the current study was to test this hypothesis. While EEG was recorded, participants performed a forced-choice localization task and reported their subjective perception of the target on a 3-level scale that also indexed their confidence. The results showed that our previous findings are replicated when confidence is controlled for.

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1. Introduction

Event-Related Potential (ERP) recordings have been extensively employed to study the temporal dynamics of the neural correlates of conscious perception.[1] In a typical experiment, the neuronal signatures of seen and unseen stimuli are compared in order to identify the moment in time in which a stimulus accesses subjective awareness. An important challenge in such studies is to equate all conditions in the seen and unseen trials, such that the only difference between these trials is whether or not they are consciously perceived by the observer (Baars, 1988). Thus, researchers have often resorted to paradigms in which perception is liminal: visual input is invariant but subjective experience fluctuates between aware and unaware states, such that any difference in neural activity between these two states cannot be attributed to differences in sensory stimulation (e.g., Babiloni, Vecchio, Miriello, Romani, & Rossini, 2006; Pins & Ffytche, 2003 but see also Koivisto, Revonsuo, & Lehtonen, 2006; Wilenius-Emet, Revonsuo, & Ojanen, 2004).

1.1. Dissociating subjective awareness from objective performance

In a recent study, we suggested that even when concerns related to potential differences in physical stimulation are addressed, differences in neural activity that are attributed to subjective awareness may in fact reflect, at least in part, differences associated with the extent of processing of seen relative to unseen stimuli (Lamy, Salti, & Bar-Haim, 2009). Most previous studies have relied on subjective measures of awareness: participants are asked whether or not they have seen the

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[1] In this paper the terms "conscious perception", "consciousness", "conscious awareness" and "awareness" will be used interchangeably.

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target (e.g., Pins & Ffytche, 2003) or to rate the target's visibility (e.g., Eimer & Mazza, 2005). When participants are also required to make a forced-choice response concerning some attribute of the target, they often perform above chance, despite denying any conscious perception of the target (for a review, see Merikle, Smilek, & Eastwood, 2001). Importantly, however, performance on this objective measure of perception is typically lower for unseen targets than for seen targets. That is, not all unseen stimuli share the same fate: some undergo enough processing to elicit correct performance while others do not. It follows that differences in neural activity between seen vs. unseen targets may include differences between processed and barely processed targets which do not uniquely characterize awareness-related differences.

To avoid this confound, we dissociated performance from conscious perception by measuring both subjective perception and objective performance on a forced-choice localization task (Lamy et al., 2009). We compared the neural signature of subjectively seen and unseen targets that elicited the same performance level, that is, which participants localized correctly ("Aware-Correct" and "Unaware-Correct"). The earliest difference between Aware-Correct and Unaware-Correct trials occurred in the P3 component.

1.2. Dissociating subjective awareness from post-perceptual processes

The P3 (or P300) component, a positive voltage in the latency range of 300–650 ms, is one of the most extensively researched components of the ERP. The dominant view is that P3 amplitude indexes post-perceptual evaluative processes, namely, updating of working memory in response to task-relevant, subjectively unexpected events (e.g., Donchin, 1981). This view mainly relies on findings from the "oddball" task, in which subjects are presented with random sequences of a rare and a frequent stimulus. The subject's task is to monitor the occurrence of the rare stimulus, the target. The smaller the relative probability of the target occurrence is, the larger amplitude of P3.

However, other factors have been found to affect P3 amplitude in the absence of variations in target probability. For instance, in "single-stimulus" paradigms in which only the target stimulus occurs randomly, the time between events was found to strongly modulate P3 amplitude (e.g., Gonsalvez & Polich, 2002). Likewise, in our previous study, the same target was present on most trials and was subjectively perceived ("aware" trials) on slightly less than 40% of trials, yet the P3 amplitude was larger on aware than on unaware trials.

Other accounts have been suggested, that are more closely related to the interpretation of the P300 as a correlate of conscious perception. In particular, the P300 has been hypothesized to reflect the closure of perceptual events (e.g., Verleger, 1988) or stimulus categorization processes controlled by the joint operation of attention and working memory (e.g., Kok, 2001). The latter view fits nicely within the framework suggested by Lamme (2003), according to which conscious perception arises from the recurrent interactions between visual and memory-related areas and shares neural mechanisms with working memory.

Our finding that conscious perception is associated with modulation of the P3 component (Lamy et al., 2009) is in line with the outcomes of numerous previous studies (e.g., Babiloni et al., 2006; Koivisto & Revonsuo, 2003; Pins & Ffytche, 2003; Sergent, Baillet, & Dehaene, 2005; Vogel, Luck, & Shapiro, 1998; Wilenius-Emet et al., 2004). However, relying on the dominant conceptualization of this component as reflecting post-perceptual evaluation processes (e.g., Nieuwenhuis, Aston-Jones, & Cohen, 2005) the concern has been raised that it might in fact reflect processes that follow conscious perception rather conscious perception per se. In particular, it has been suggested that the P3 may index processes related to how confident participants may feel that they have seen the critical stimulus. As mentioned above, stimuli are often presented near threshold in order to ensure that awareness and absence thereof occur under the same stimulus conditions. Thus, the percept is ambiguous and participants are often unsure/unconfident of whether or not they have seen the critical stimulus. If a participant adopts a conservative response criterion, the difference in neural activity between the aware and unaware condition might reflect differences related to confidence rather than to consciousness. In other words, equating the physical attributes of the stimuli to avoid confounds related to processes that precede visual awareness may introduce confounds related to processes that follow it, such as post-perceptual evaluation. In fact, confidence level ratings are sometimes used as a measure of consciousness, based on the assumption that a subject is more confident of having seen the target when he consciously perceives the target than when he does not (e.g., Wilenius & Revonsuo, 2007).

Eimer and Mazza (2005) were the first to point at confidence as a possible confound. Using a change detection task they compared the neuronal activity associated with detected-change, undetected-change and no-change conditions. Besides reporting whether they had seen a change, participants were required to rate their confidence level on every trial on a three-point scale (fully confident, partially confident, not confident). The amplitude of the P3 component was higher when participants reported seeing the change than when they reported not seeing it. However, this difference was modulated by the participants' level of confidence: it was significant when confidence was high, but not when confidence was low. Eimer and Mazza concluded that confidence level rather than awareness modulates the P3. We (Lamy et al., 2009) recently challenged this interpretation by noting that it overlooks the significant effects of subjective awareness on P3 amplitude when confidence was high. We pointed out that if conscious awareness modulates the amplitude of the P3 for a constant confidence level, then confidence cannot account for this modulation. The first objective of the present study was to directly examine whether the association between the P3 and awareness can be replicated when confidence is controlled for.

1.3. Reexamining the neural correlates of objective performance

In our previous study (Lamy et al., 2009), P3 amplitude was modulated by awareness (it was higher for "Aware-Correct" than for "Unaware-Correct" trials) but also by performance (higher P3 amplitude was also found for "Unaware-Correct" than for "Unaware-Incorrect" trials). However, while the awareness-related modulation was recorded across all scalp regions, the modulation related to performance was confined to parietal regions. We interpreted this difference in topography as a qualitative difference between conscious perception and perception that leads to correct performance without awareness. A possible alternative interpretation, however, is that the performance effect on P3 resulted from a subset of "Aware" trials that had been erroneously tagged as "Unaware". The second objective of the study was to examine this possibility in order to clarify whether the P3 component is uniquely associated with subjective awareness or whether it also indexes correct performance.

1.4. Overview of the task

In order to achieve these objectives we used a modified version of the task described in Lamy et al. (2009). In the target display only one tilted line was presented in one of the four corners of an imaginary square. The masking display consisted of four Xs that appeared at all the potential target locations. The participants were required to provide two separate responses. They first made a speeded forced-choice localization response to the target, and immediately afterward reported their subjective perception of the target. In order to create conditions in which the participants are highly confident both in the "Seen" and in the "Unseen" trials, we used a three-level rather than a two-level scale: Subjects were instructed to report whether they were absolutely sure they saw the target, absolutely sure they did not see the target or not sure whether or not they saw it. We emphasized that a target appeared on each trial and that the participants should therefore report their subjective experience rather than what they believed happened on the screen based on their knowledge about the task.

We derived ERP waveforms from high-confidence trials, that is, from trials in which the participants were either sure that they had seen the target or sure that they had not. Thus, we compared three conditions (Aware-Correct, Unaware-Correct and Unaware-Incorrect) with the participants' confidence in their report being high in all conditions.

We expected to replicate the main finding of our previous study (Lamy et al., 2009) when awareness is not confounded with confidence level. Namely, we expected to find higher P3 magnitude across brain regions when the participants correctly localize the target and report being confident of seeing it than when they correctly localize it but are sure not to have seen it. We expected the comparison between Unaware-correct and Unaware-Incorrect trials to reveal whether correct performance in the absence of subjective awareness is also associated with modulation of P3 amplitude when confidence reports allow one to clearly distinguish unaware trials from aware trials.

2. Methods

2.1. Participants

Twenty-one right-handed students (6 men, 22–31 years of age) participated in partial fulfillment of a course requirement. All reported normal or corrected-to-normal visual acuity as well as no history of neurological or psychiatric condition.

2.2. Stimuli

The target was a line segment subtending 0.5° of visual angle tilted by 25° to the right. On target-present trials, the target was randomly presented at one of four possible locations (upper-left, upper-right, lower-left, or lower-right) and centered at an eccentricity of 4° of visual angle from the fixation point. On catch trials, no target was displayed. The masking display consisted of the presentation of two line segments in two orientations (25°, as the target, and 15°) in the four possible locations. The fixation display was a superimposition of the target and the mask lines centered at fixation. All stimuli were gray on a black background.

2.3. Behavioral procedure

On each trial, the fixation display appeared for 500 ms. The target display was then presented for a variable duration, as described below. The masking display immediately followed and remained on the screen for 500 ms. The experiment included a calibration phase followed by an experimental phase.

In the calibration phase subjects were required to produce two responses. First, they made a speeded forced-choice response to the location of the target by pressing one of four designated keys with one hand (localization response). A question mark appeared immediately after the first response, prompting the participants to indicate whether they had seen the target or merely guessed its location (awareness response) by pressing one of two other designated keys with their other hand. A new trial began 1100–1300 ms after the second response (determined randomly with 100 ms intervals).

The calibration phase was designed to determine the target-display exposure duration that would yield an approximately equal number of trials in which the target stimulus would be seen vs. not seen (a 50% detection threshold). We used a modified version of the staircase procedure described by Levitt (1971). Initial exposure duration was set at 16 refresh cycles (~200 ms), and then exposure duration changed every six trials by steps of one refresh cycle (~12.5 ms) based on the participant's awareness responses. Exposure duration was shortened when the participant reported seeing the target on more than three out of six trials and was lengthened when the participant reported not seeing the target on more than three out of six trials. Exposure duration remained unchanged when the participant reported seeing the target on exactly three out of six trials. The calibration phase included 130 trials. A participant's detection threshold was defined as the lowest target exposure duration that was maintained over two consecutive blocks of six trials.

The experimental phase was similar to the calibration session except for the following changes. Subjects were asked to report if they were certain they had seen the target, certain they had not seen the target or not sure whether they had seen it, by pressing one of three designated keys. This allowed us to remove the ambiguous (low-confidence) trials from the analyses. The experiment included 520 trials divided into four blocks, with a rest period allowed between blocks. There were four types of trials randomly mixed within the blocks: catch trials (7% of all trials); above-threshold trials, in which the target display was presented for a duration of six refresh cycles (~75 ms) above the detection threshold individually determined for each participant during calibration (7% of the trials); and threshold exposure trials, in which exposure duration was set at the detection threshold (86% of all trials). Above-threshold trials were included in order to verify that the participants indeed complied with the instructions: They were expected to report being aware of the target on a high proportion of such trials. (See illustration of the experimental phase in Fig. 1).

2.4. EEG recordings and analysis

Continuous EEG was recorded from 64 active channels while participants performed the behavioral task. EEG data were recorded using an Electrical Geodesics (EGI) system and dense array geodesic sensor nets. All EEG channels were collected referenced to the vertex. All electrode impedances were kept below 40 kΩ. For both EEG and EOG, sampling rate was 500 Hz with filter settings of 0.1 Hz high pass and 100 Hz low pass. Further processing and analysis of the EEG signal were carried out off-line using Net-Station 4.2.1 (EGI Company). Artifactual EEG (±100 μV) was automatically removed from further analysis. Artifactual EEG (Max–Min > 200 μV) were automatically removed from further analysis. Eye blinks that appeared in the EOG signal were removed based on a criterion of Max–Min > 140 μV in windows of 640 ms. Trials containing horizontal eye movements were removed from further analysis. Overall, 5% of the trials were removed due to artifacts in the EEG signal, with similar percentages of trials removed from each condition (Aware-Correct, Unaware-Correct, Unaware-Incorrect). Before derivation of the ERPs, the EEG signal was subjected to a 30-Hz low-pass digital filtering and digitally transformed to an average reference. Separate ERP waveforms were derived for each participant by averaging trials in each of the high confidence experimental conditions (Aware-Correct, Unaware-Correct, Unaware-Incorrect). ERP waveforms were measured relative to a baseline epoch of 100 ms preceding the target matrix onset. Based on inspection of the grand-averaged ERPs, mean amplitudes (μV) for all experimental conditions were computed within the following time windows: N2 (264–350 ms), and P3 (400–622).

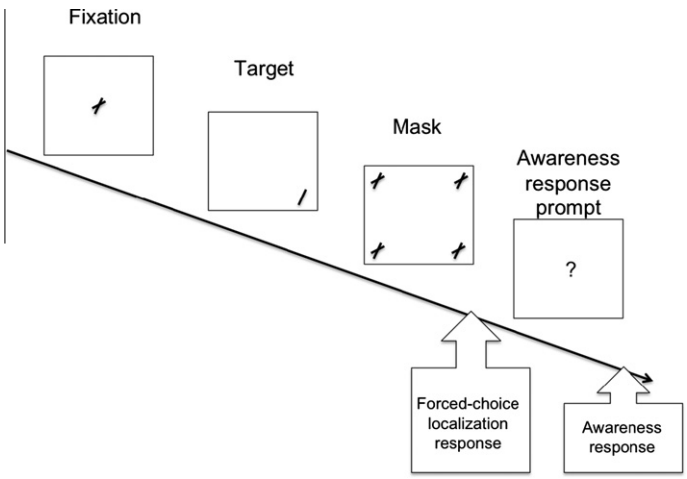

Fig. 1. Sequence of events on a target-present trial. In this example, the target appears in the lower left corner. Luminance polarity was inverted in the actual experiment (gray lines on a black background).

3. Results

3.1. Behavioral responses

The data from six participants were excluded. For one subject, the calibrated exposure duration was too long (14 refresh cycles, which amounts to four standard deviations above the average exposure duration). Three participants had a high proportion of false alarms on catch trials (more than 23%, which amounts to two standard deviations above average) and two showed high miss rates (more than 40%) on above-threshold trials. Such high exclusion rate is customary in this type of experiments (Eimer & Mazza, 2005; Wilenius & Revonsuo, 2007; Woodman, 2010; Woodman & Luck, 2003). Thus, the data from 15 participants were analyzed.

The mean percentage of false alarms ("certain I saw" responses on catch trials) was 7% (SE = 2.06), confirming the reliability of the participants' self-reports. The mean percentage of misses ("certain I did not see" responses on target-present trials) in the above-threshold condition was 14.3% (SE = 3.09). The individual threshold exposure times ranged from 2 to 6 screen refresh cycles (~25–75 ms, respectively). Mean percentage of "certain I saw" responses on target-present trials was 35.8% (SE = 4.64). For these, 92.3% (SE = 3.87) of the localization responses were correct. Mean percentage of "certain I did not see" trials was 30.7%, for which percentage of correct responses was 40.2% (SE = 4.13). Localization performance was therefore clearly above chance (25%) when the participants reported being certain they did not see the target. "Not sure" trials represented 31.9% of the trials, with a percentage of correct responses of 69.0% (SE = 5.78).

An ANOVA was conducted on localization reaction times data with Awareness (certain I saw, unsure, and certain I did not see) and performance (Correct, Incorrect) as factors. The main effect of awareness was significant [$F(2,26) = 11.58$, $p < .001$]. Follow-up comparisons showed that "certain I saw" responses were faster than "certain I did not see" responses [$F(1,13) = 11.53$, $p = .005$] and than "unsure" responses [$F(1,13) = 20.77$, $p = .001$]. Response latencies were not significantly different in the "certain I did not see" and "unsure" conditions [$F < 1$]. There was a main effect of performance [$F(1,13) = 13.67$, $p = .003$], with faster responses for correct vs. incorrect localization trials. These factors interacted [$F(2,26) = 7.41$, $p = .003$]. Correct trials were faster than incorrect trials in the "certain I saw" condition [$t(13) = 3.52$, $p = .004$] and in the "unsure" condition [$t(13) = 4.57$, $p < .001$] but not in the "certain I did not see" condition [$t < 1$] (see Table 1 for RTs. Note that one subject did not have any Aware-Incorrect responses).

3.2. Event-related potentials

Fig. 3 shows grand averaged stimulus-locked ERPs for the Aware-Correct, Unaware-Correct, and Unaware-Incorrect conditions for each of the scalp regions. Stimulus-locked ERPs analyses were carried out on mean ERP amplitudes over five scalp regions: frontal, temporal, central, parietal and occipital. Regions were determined based on the 10–20 system (see Fig. 2 for details).

We compared the ERP waveforms associated with trials that were identical in terms of physical stimulus, exposure time, participants' responses to the target (correct responses only), participants' confidence (high confidence only) and differed only in the participants' subjective experience, that is, in whether they reported being sure they had seen the target or sure that they had not seen it. An ANOVA with awareness condition (Aware-Correct vs. Unaware-Correct) and scalp region (frontal, temporal, central, parietal, occipital) as within-subject factors was conducted on the mean amplitudes of the N2 and P3 components of the ERP (as they were the only components in which differences were apparent on visual inspection).

There were no significant effects or remarkable trends involving conditions of awareness (Aware-Correct vs. Unaware-Correct) in the N2 time window [$Fs < 1$]. The mean amplitude of the P3 component was significantly larger in the Aware-Correct condition ($M = 0.197$, SE = 0.082) than in the unaware-correct condition ($M = -0.35$, SE = 0.105) [$F(1,14) = 5.78$, $p = .031$]. This effect interacted with scalp region [$F(4,56) = 3.537$, $p = .012$]. Follow-up comparisons showed that the awareness effect reached significance over the parietal [$t(14) = 2.23$, $p = .043$], and frontal regions [$t(14) = -2.339$, $p = .035$]. However, the effect over the frontal region was inverted, such that the amplitude of the P3 component in the Aware-Correct condition was more negative than in the Unaware-Correct condition.

We then compared the ERP waveforms associated with trials that were identical in terms of physical stimulus, exposure time, participants' confidence (high confidence only) and the participants' subjective experience (target unseen) and differed only in participants' performance, that is, in whether they responded correctly or not. An ANOVA with performance accuracy condition (Unaware-Correct vs. Unaware-Incorrect) and scalp region (frontal, temporal, central, parietal, occipital) as within-subject factors was conducted on the mean amplitudes of the N2, and P3 components. There were no significant effects or remarkable trends involving performance accuracy condition (Unaware-Correct vs. Unaware-Incorrect) in the N2 time

Table 1
Mean reaction times (RTs) and standard errors (SEs) in milliseconds (ms) for all conditions.

Condition	Aware-Correct	Aware-Incorrect	Unsure-Correct	Unsure-Incorrect	Unaware-Correct	Unaware-Incorrect
Mean RTs	725	885	887	1066	975	994
SE	32.53	46.47	42.86	46.99	46.99	60.67

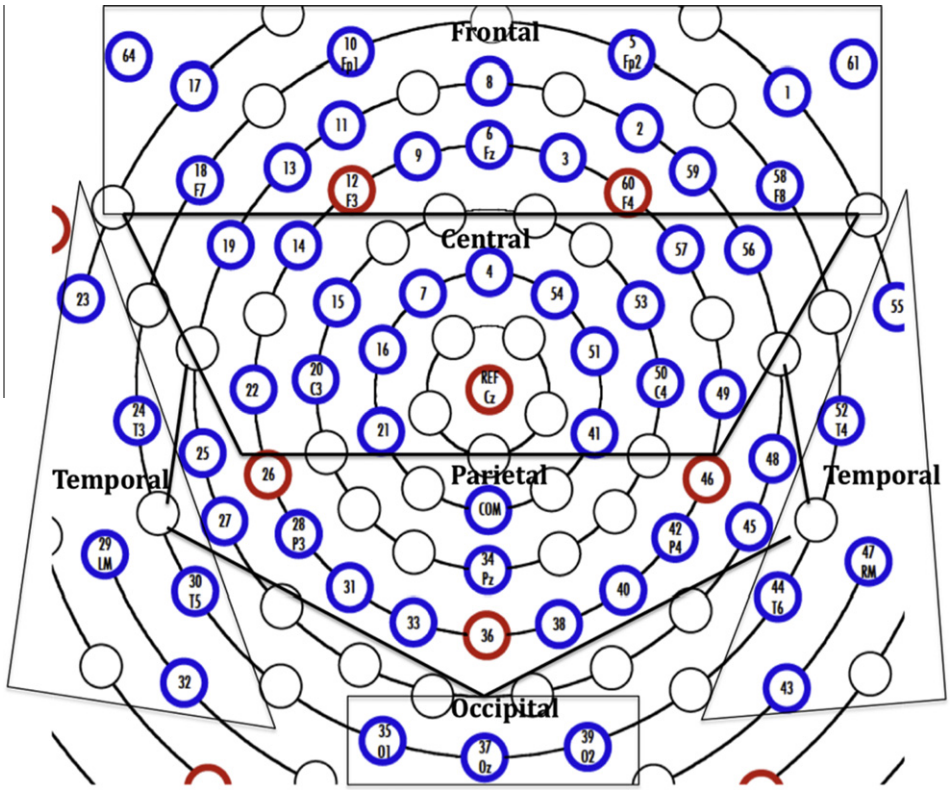

Fig. 2. Electrodes distribution on the scalp and their allocation to the different regions.

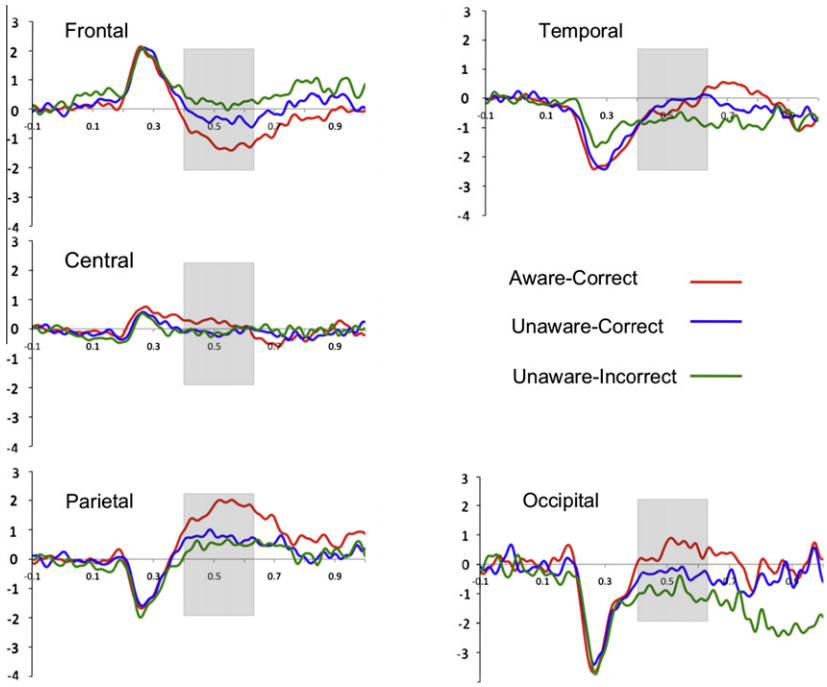

Fig. 3. Grand mean event-related potentials (ERPs) of the Aware-Correct (red), Unaware-Correct (blue), and Unaware-Incorrect (green) conditions. The ERPs are time locked to target display onset and are calculated relative to a 100-ms baseline. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

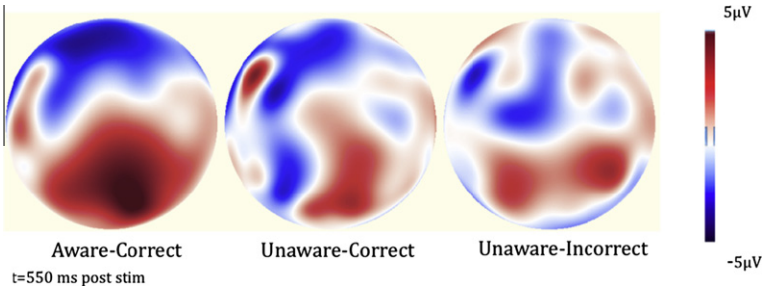

Fig. 4. Scalp maps of the Aware-Correct, Unaware-Correct and Unaware-Incorrect 550 ms post stimuli.

window [$F < 1$]. Visual inspection suggested that there might be a difference in the temporal region ($M = -1.83$ SE = 0.61 vs. $M = -1.07$, SE = 0.35 in the Unaware-Correct and Unaware-Incorrect conditions, respectively), but this was not confirmed by statistical analysis, [$t(14) = -1.085$, $p = .296$]. The effect of condition in the P3 time window approached significance, exhibiting a less negative deflection in the Unaware-Correct condition ($M = -0.35$, SE = 0.105) than in the Unaware-Incorrect condition ($M = -0.179$, SE = 0.13) [$F(1,14) = 3.646$, $p = .077$]. The interaction with scalp region also approached significance [$F(4,56) = 2.15$, $p = .087$]. Follow-up comparisons showed that the effect of performance reached significance only over the frontal region [$t(14) = -2.264$, $p = .04$].

4. Discussion

The main objective of this study was to examine the possibility that the P3 component that has been repeatedly associated with conscious perception (Babiloni et al., 2006; Del Cul, Baillet, & Dehaene, 2007; Fernandez-Duque, Grossi, Thornton, & Neville, 2003; Kranczioch, Debener, & Engel, 2003; Niedeggen, Wichmann, & Stoerig, 2001; Sergent et al., 2005; Turatto, Angrilli, Mazza, Umilta, & Driver, 2002) might actually reflect post-perceptual evaluation processes such as confidence. When we compared only trials in which participants were highly confident in their report, we found larger P3 amplitude for seen than for unseen targets. This finding supports our interpretation of Eimer and Mazza's (2005) results and suggests that the P3 component reflects conscious perception rather than confidence.

One might object that the less visible a stimulus is, the less confident the observer becomes, with minimal confidence when the observer does not see anything at all. According to this argument, high confidence can only be associated with seeing something and the participants construed the response category "fully confident that I did not see" as "not confident at all that I saw the target". However, it is important to realize that, beyond the fact that this argument does not accord with introspection, it is also problematic because it entails that confidence is always necessarily confounded with conscious awareness, from which it follows that the notion that P3 reflects confidence rather than conscious awareness cannot be falsified, by definition.

Differences in objective performance were also associated with modulation of neural activity in the P3 time window, which was more restricted than the P3 modulation associated with subjective awareness (see Fig. 4), thus conceptually replicating our previous results (Lamy et al., 2009). However, in the current study, performance-related P3 modulation was confined to the frontal region,[2] whereas in the previous study, it was restricted to the parietal region. This discrepancy could stem from the fact that we used different references in the two experiments. While in the previous study, electrodes were referenced to the chin, in this study electrodes were referenced to the vertex during acquisition and re-referenced to an average reference offline. Change of reference has been shown to affect the scalp distribution of differences between conditions (Murray, Brunet, & Michel, 2008).

As in our previous study, the P3 was the earliest component associated with conscious awareness of the target stimulus. This finding stands in contrast with the claim put forward by Koivisto and his colleagues that negative components occurring around 200 ms after stimulus onset and referred to as N2 or the visual awareness negativity (VAN) constitute the earliest marker of visual awareness in the ERP. These authors also suggested that "...the appearance of a stimulus in masking experiments typically produces a transient signal accompanied with a sensation of change or movement which may be sufficient for correct localization of the stimulus, although the participant may not really consciously see the stimulus...". Accordingly, our failure to observe the VAN may be due to the fact that subjects did not actually see the target but gathered enough information to elicit a correct response which could then be monitored in order to produce a subjective report. This interpretation cannot account for our results, however, because such sensation of change without visual awareness would have been most likely to enter the "not sure that I saw" category: indeed, our participants were expressly requested to report seeing the target only when they were absolutely sure that they had.

[2] It is noteworthy that for both critical comparisons (Aware-Correct vs. Unaware-Correct and Unaware-Correct vs. Unaware Incorrect), the polarity of the P3 component over in frontal electrodes was negative rather than positive. Such inversion was reported in other studies (e.g., Del Cul et al., 2007; Sergent et al., 2005) and seems to be related to the choice of the reference electrode.

In fact, we suggest that the opposite may be true: while P3 is a neural correlate of visual awareness, earlier components and more specifically the VAN may reflect other cognitive processes that are the precursors of awareness yet are not awareness per se. In line with this possibility, Sergent et al. (2005) and Del Cul et al. (2007) found the N2 component to be linearly correlated with visibility and concluded that this component may reflect a stage of cortical processing at which the representation of a brief visual target progressively gains strength before it actually enters consciousness. Accordingly, the N2 difference should be larger when the seen and unseen stimuli differ substantially in the extent to which they are processed (e.g., Ojanen, Revonsuo, & Sams, 2003) than in paradigms in which there processing differences are brought to a minimum (as in our studies), because of range restriction.

A recent study by Del Cul et al. (2007) provided additional support for this interpretation of the N2 component. The authors varied target-to-mask SOA (16–100 ms) and compared the neural responses when the target was seen vs. unseen. On average, the comparison of seen and unseen targets yielded differences on both the N2 and the P3 component. However, not surprisingly, the proportion of unseen targets was larger with short SOAs than with long SOAs. When seen and unseen trials were compared at an intermediate SOA that was associated with roughly the same amount of seen and unseen targets, differences were still observed on the P3 component but no longer on the N2 component.

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