Neural Correlates of Subjective Awareness and Unconscious Processing: An ERP Study

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Abstract

■ The aim of the present study was to dissociate the ERP correlates of subjective awareness from those of unconscious perception. In a backward masking paradigm, participants first produced a forced-choice response to the location of a liminal target presented for an individually calibrated duration, and then reported on their subjective awareness of the target's presence. We recorded (Event-Related Potentials) ERPs and compared the ERP waves when observers reported being aware vs. unaware of the target but localized it correctly, thereby isolating the neural correlates of subjective awareness while controlling for differences in objective performance. In addition, we compared the ERPs when participants were subjectively unaware of the target's presence and localized it correctly versus incorrectly, thereby isolating the neural correlates of unconscious perception. All conditions involved stimuli that were physically identical and were presented for the same duration. Both behavioral measures were associated with modulation of the amplitude of the P3 component of the ERP. Importantly, this modulation was widely spread across all scalp locations for subjective awareness, but was restricted to the parietal electrodes for unconscious perception. These results indicate that liminal stimuli that do not affect performance undergo considerable processing and that subjective awareness is associated with a late wave of activation with widely distributed topography. ■

INTRODUCTION

The search for the neural correlates of consciousness (NCC) has become one of the most challenging issues in neuroscience research in the last two decades. This search relies on the premise that only some neural activity correlates with conscious experience (Crick & Koch, 1998). To isolate this neural activity, a condition in which the observer reports being aware of a critical stimulus is compared to a condition in which the observer reports being unaware of it.

In real-life situations, consciously perceived stimuli typically differ from stimuli that remain outside awareness in their physical characteristics (e.g., high-acuity vs. degraded stimuli), the time allowed to process them, or the amount of attentional resources allocated to them. However, to isolate the neural correlates of perceptual awareness, one must experimentally produce a difference in subjective experience that cannot be attributed to objective differences in stimulation, exposure time, or attention. Researchers have endeavored to meet this goal by designing paradigms in which visual input remains the same, whereas conscious perception varies between aware and unaware states. Such variations in awareness might take the form of alternations between two different interpretations of the same stimulus as in phenomena of perceptual bistability such as binocular rivalry (e.g., Logothetis, 1998; Tong, Nakayama, Vaughan, & Kanwisher, 1998), between change blindness and change detection (e.g., Fernandez-Duque, Grossi, Thornton, & Neville, 2003; Koivisto & Revonsuo, 2003), or between missed and seen targets in the attentional blink (e.g., Kranczioch, Debener, & Engel, 2003; Vogel, Luck, & Shapiro, 1998) and in threshold detection tasks (e.g., Pins & ffytche, 2003).

In the present study, we used event-related potentials (ERPs) recorded during a threshold detection task to investigate the chronometry of neural responses elicited by stimuli that participants report seeing (henceforth, "seen" or "aware" stimuli) and stimuli that participants report not seeing (henceforth, "unseen" or "unaware" stimuli). Previous ERP studies of the neural correlates of perceptual awareness have consistently found the amplitude of the P3 component, a large positive deflection in the ERP occurring 300 to 600 msec after stimulus onset, to be markedly reduced on unaware trials relative to aware trials (e.g., Babiloni, Vecchio, Miriello, Romani, & Rossini, 2006; Sergent, Baillet, & Dehaene, 2005; Wilenius-Emet, Revonsuo, & Ojanen, 2004; Koivisto & Revonsuo, 2003; Pins & ffytche, 2003; Vogel et al., 1998).

Differences in earlier ERP waveforms between seen and unseen targets have also been reported, albeit with less consistency across studies and with large variability as to the earliest component found to be modulated by conscious awareness. Some studies reported awareness-related amplitude modulation as early as on the P1

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component (Pins & ffytche, 2003), the N1 component (e.g., Koivisto, Revonsuo, & Lehtonen, 2006; Hunter, Turner, & Fulham, 2001; Kaernbach, Schroger, Jacobsen, & Roeber, 1999), the P2 component (Vogel et al., 1998), or the N2 component (e.g., Sergent et al., 2005; Wilenius-Emet et al., 2004; Koivisto & Revonsuo, 2003; Ojanea, Revonsuo, & Sams, 2003). Other studies, however, found no awareness-related modulation in ERP amplitudes prior to the P3 component (e.g., Babiloni et al., 2006; Fernandez-Duque et al., 2003; Kranczioch et al., 2003; Turatto, Angrilli, Mazza, Umilta, & Driver, 2002; Niedeggen, Wichmann, & Stoerig, 2001). Although these amplitude differences in ERP waveforms could sometimes be attributed to physical differences between the stimuli presented in the aware and unaware conditions (e.g., Wilenius-Emet et al., 2004; Koivisto & Revonsuo, 2003), most studies used identical stimuli in the two conditions.

Conscious and Unconscious Perception

In experiments designed to investigate unconscious perception (e.g., Sidis, 1898; see also Merikle, Smilek, & Eastwood, 2001), when participants report not seeing a stimulus (unaware trials), a distinction is made between trials in which no perception occurs and trials in which the stimulus is unconsciously perceived, that is, influences behavior outside of subjective awareness. In a typical experiment, the critical stimulus is presented under conditions that prevent conscious perception. Two types of measures are contrasted: one is an explicit report of whether or not a stimulus has been subjectively seen; the other is an indirect measure that bypasses the participant's introspection and reveals whether the stimulus is capable of influencing the participant's behavior. For instance, despite denying any perception of a masked word, the observer may provide the correct response more often than would be expected by chance when forced to choose among alternative words. Such above-chance performance for an unseen stimulus, however, is typically poorer than when the stimulus is seen. Therefore, all unseen targets do not share the same fate: Some undergo enough processing to elicit a correct response, whereas others do not.

Previous ERP studies of the neural correlates of perceptual awareness typically did not dissociate between awareness and task performance. Indeed, they used only one behavioral measure designed to index the participants' subjective awareness of the critical stimuli, and did not provide a separate measure of the extent of processing on unaware trials. In consequence, trials that were classified as "unaware," in fact included two different categories of trials, namely, "unconscious perception" trials and "no perception" trials. One important implication of the failure to distinguish between these categories is that differences in neural activity that were attributed in previous studies to differences in processing of seen versus unseen targets may have also included differences between processed and barely processed targets. Such differences do not specifically reflect the neural correlates of consciousness, as they can also occur between unseen targets on different trials, namely, between "unconscious perception" and "no perception" trials. To illustrate, a participant will report not seeing a stimulus when blindfolded, yet obviously, the conclusion that retinal stimulation is correlated with visual awareness is of little informative value because retinal stimulation is also correlated with any type of visual processing, whether conscious or unconscious.

Subjective and Objective Measures of Awareness

Within the framework of the debate surrounding the existence of unconscious perception, the use of subjective measures of awareness to distinguish between conscious perception and absence thereof has been sharply criticized (e.g., Draine & Greenwald, 1998; Holender, 1986). Objective measures of awareness were suggested as a more accurate method for assessing whether stimuli are perceived with or without awareness. With objective measures, it is assumed that any ability to discriminate between alternative stimulus states at a better-than-chance level of performance indicates that the critical stimulus was perceived with awareness. An inability to do so reflects absence of awareness. Accordingly, the neural correlates of consciousness derived from comparing the neural activity associated with a subjectively seen versus unseen stimulus may amount to comparing different levels of awareness and fail to capture potential qualitative differences between conscious and nonconscious processing.

In the present study, we contrasted the neural activity evoked by "aware" and "unaware" stimuli while addressing the potential confounds associated with the distinction between perception with versus without subjective awareness on the one hand, and between subjective versus objective measures of awareness on the other hand, within the same experiment. On each trial, a target was presented in one of four possible locations for a near-threshold exposure time determined individually for each participant in a calibration phase, such that under constant stimulus conditions, the target was subjectively seen on roughly half of the trials. Participants were required to provide two separate responses. They first made a speeded forced-choice localization response to the target, and immediately afterward indicated whether their decision was based on their conscious perception of the target or on guessing. We derived ERP waveforms associated with three distinct categories of trials: (1) trials in which participants were subjectively aware of the stimulus and correctly localized it (*aware-correct* condition); (2) trials in which participants were subjectively unaware of the stimulus, yet correctly localized it (*unaware-correct* condition); and (3) trials in which participants were subjectively unaware of the stimulus and incorrectly localized it (*unaware-incorrect* condition). Importantly, all three categories of trials involved identical stimuli. We expected only a very small number of trials in which participants were subjectively aware of the stimulus, yet incorrectly localized it (*aware-incorrect* condition). Therefore, this condition was not included in the planned analyses.

On the one hand, we contrasted the neural activity evoked by seen and unseen targets that underwent enough perceptual processing to elicit a correct response. This comparison between the aware-correct and unaware-correct conditions allowed us to narrow the potential differences in perceptual processing between subjectively seen versus unseen targets because localization performance was equated between the two conditions, and thereby to better circumscribe the differences in neural activity that are specifically associated with subjective perceptual awareness.

On the other hand, based on previous studies of perception without subjective awareness, we expected localization performance for unseen targets to be better than chance, that is, we expected unconscious perception to occur. Thus, because above-chance localization performance indicates that participants are able to discriminate between different states of the target stimulus (i.e., its location), according to the objective-measure approach, participants should be considered objectively aware of the target in the unaware-correct condition (at least on those trials in which the correct answer is not arrived at by chance). By contrast, one can be confident that participants are objectively unaware of the target when they are unable to localize it (unaware-incorrect condition). Thus, the neural correlates of awareness defined according to the objective-measure approach may be studied by comparing unaware-correct trials and unaware-incorrect trials. It is important to emphasize that this rationale is contingent on above-chance localization performance for unseen targets. To illustrate, it would be absurd to claim that in a task in which participants perform at chance, correct trials are trials in which they are objectively aware of the target and incorrect trials are trials in which they are objectively unaware of it.

In this study, in order to avoid confusion, we will adopt the terminology associated with the subjective-measure approach of awareness and label above-chance forced-choice performance in the absence of subjective awareness "unconscious perception" rather than "objective awareness."

METHODS

Participants

Twenty three right-handed students (6 men, 22–28 years of age) participated for pay ($10). All reported normal or corrected-to-normal visual acuity.

Stimuli

The fixation display was a cross subtending 0.5° of visual angle. The target display was a 15 × 15 matrix made up of line segments tilted to the right, each of which subtended 0.5° of visual angle. On target-present trials, a square region of 3 × 3 line segments was randomly chosen at one of four possible locations: the upper-left, upper-right, lower-left, or lower-right corner of the matrix, and centered at an eccentricity of 4° of visual angle from the fixation point (Figure 1). Line segments within this square region were tilted by 25°, whereas line segments in the remainder of the matrix were tilted by 15°. The resulting percept was a square figure against a background. On catch trials, all line segments in the target display had the same orientation, thus no square figure was visible. The masking display consisted of the matrix with two line segments in the two possible orientations (that of the background and that of the square) superimposed in each cell. All stimuli were gray on a black background.

Behavioral Procedure

On each trial, the fixation display appeared for 500 msec. 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 msec. Participants 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 by pressing one of two other designated keys with their other hand whether they had seen the target or merely guessed its location (awareness response). A new trial began 500 msec after the second response. Response-to-hand mapping was counterbalanced between participants.

The experiment consisted of a calibration phase followed by an experimental phase. The calibration phase

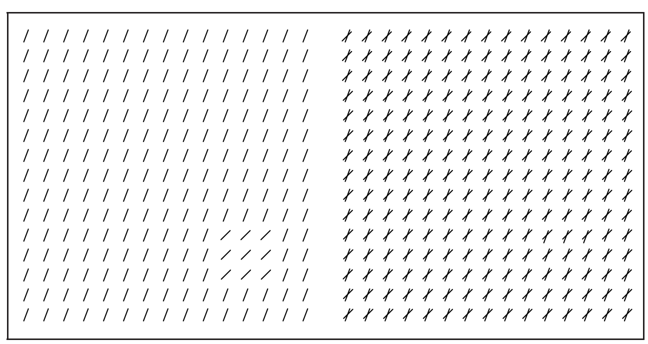

Figure 1. Example of the target (left) and mask (right) stimuli. In this example, the target appears in the lower right corner. Luminance polarity was inverted in the actual experiment (gray lines on a black background).

was designed to determine the target-display exposure duration that would yield an approximately equal number of trials in which the target square would be seen or not seen (a 50% detection threshold). We used a modified version of the threshold estimation procedure described by Levitt (1971). Initial exposure duration was set to 16 refresh rates (~200 msec), and then exposure duration changed every six trials by steps of one refresh rate (~12.5 msec) 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. It included 520 trials divided into four blocks, with a rest period allowed between blocks. It included 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 6 refresh rates (~75 msec) above the detection threshold individually determined for each participant during calibration (7% of the trials); short-exposure trials, in which exposure duration was set at one refresh rate below the detection threshold (43% of all trials); and long-exposure trials, in which exposure duration was set at the detection threshold (43% 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. Short-exposure trials were included because pilot data indicated that due to practice effects, some of the participants tended to achieve higher percentages of awareness with the same exposure times in the experimental phase relative to the calibration phase.

EEG Recordings and Analysis

Continuous EEG was recorded from 20 scalp sites (Fp1, Fp2, F7, F3, Fz, F4, F8, T3, T4, T5, T6, C3, Cz, C4, P3, Pz, P4, O1, Oz, and O2, plus the left and right mastoids) while participants performed the behavioral task. EEG data were recorded using a stretch Lycra cap (Electro-Cap, Eaton, OH) with pure-tin electrodes located according to the International 10–20 System. All EEG channels were collected referenced to the chin. Vertical and horizontal EOG were recorded from above and below the left eye and at the right and left outer canthi, respectively. All electrode impedances were kept below 5 kΩ. EEG and EOG signals were amplified with Ceegraph IV bioamplifier (Biologic Systems), and were digitized onto a PC using a 16-bit A/D converter and Ceegraph IV data acquisition software. For both EEG and EOG, sampling rate was 256 Hz with bioamplifier 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 BPM software package (Orgil Company). Artifactual EEG (±100 μV) was automatically removed from further analysis. Eye blinks that appeared in the EOG signal were regressed out of the EEG using a procedure based on the methods described in the literature (e.g., Miller & Tomarken, 2001; Lins, Picton, Berg, & Scherg, 1993). 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.

Separate ERP waveforms were derived for each participant by averaging trials in each of the experimental conditions (aware correct, unaware correct, unaware incorrect) and for each exposure duration (short and long). ERP waveforms were measured relative to a baseline epoch of 200 msec 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: P1 (109–150 msec), N1 (148–187 msec), P2 (178–261 msec), N2 (230–304 msec), and P3 (375–550 msec).

RESULTS

Behavioral Responses

The data from three participants were excluded because the ERP recordings for these were lost due to technical failure. Thus, the data from 20 participants were analyzed.

The mean percentage of false alarms (''aware'' responses on catch trials) was 6.5% (SD = .05) on short-exposure trials and 6.2% (SD = 0.07) on long-exposure trials. The mean percentage of misses (''unaware'' responses on target-present trials) in the above-threshold condition was 11.2% (SD = 0.12), confirming the reliability of the participants' self-reports. Because the false alarm rate was low and because catch trials made up only 7% of all trials, there were not enough data in the relevant cells to perform a reliable signal-detection estimation of sensitivity and criterion (Green & Swets, 1966).

The individual threshold exposure times ranged from 2 to 8 screen refresh rates for the short exposure (~25 to 100 msec, respectively) and from 3 to 9 screen refresh rates for the long exposure (~37 msec to 112 msec). Mean percentage of ''aware'' responses on target-present trials was 25.8% (SD = 0.13) for the short exposure and 50.5% (SD = 0.17) for the long exposure, confirming that the percentage of aware trials established in the calibration phase was generally maintained in the experimental phase. Of these, 89.0% (SD = 0.15) were responded to correctly for the short exposure and 96.1% ($SD = 0.06$) for the long exposure. On unaware trials, that is, on the remaining 74.2% of the trials for the short exposure, and 49.5% of the trials for the long exposure, the percentage of correct responses was 51.6% ($SD = 0.16$) and 59.3% ($SD = 0.15$) for the short and long exposures, respectively. Localization performance was therefore clearly above chance (25%) when the participants reported being unaware of target presence. The distribution of trials per condition is summarized in Table 1.

An analysis of variance (ANOVA) was conducted on localization reaction times data with condition (aware correct, unaware correct, and unaware incorrect) and threshold exposure (short vs. long) as factors. None of the effects approached significance. There was no main effect of threshold exposure [$F < 1$ ($M = 526$ msec, $SD = 73$ vs. $M = 522$ msec, $SD = 78$ for the short vs. long exposure conditions, respectively)] and no main effect of condition [$F(1, 19) = 1.21$, $p > .3$ ($M = 508$ msec, $SD = 68$ for the aware-correct condition; $M = 538$ msec, $SD = 56$ for the unaware-correct condition; and $M = 536$ msec, $SD = 70$ in the unaware-incorrect condition)]. Specifically, despite a numerical trend, there was no significant difference in reaction times between the two correct-performance conditions [$F(1, 19) = 1.55$, $p > .2$], and the interaction between condition and threshold exposure was nonsignificant [$F(1, 19) = 1.39$, $p > .2$].

Event-related Potentials

Figure 2 shows grand-averaged ERPs for the aware-correct, unaware-correct, and unaware-incorrect conditions for each of the recorded electrode sites for the short exposure (top) and for the long exposure (bottom). Preliminary ANOVAs were conducted to examine potential lateralization effects on the mean amplitudes of each of the preselected ERP components. In one set of analyses, electrode site (20), condition of awareness (aware correct vs. unaware correct in one analysis and unaware correct vs. unaware incorrect in another analysis) and side of target appearance (right vs. left) served as factors. In another set of analyses, scalp region (frontal, temporal, central, parietal, and occipital), condition of awareness, and side of target appearance served as factors. These analyses yielded no significant interactions involving condition of awareness and side of target appearance. Therefore, subsequent analyses were carried out on mean ERP amplitudes over five scalp regions: frontal (mean amplitude of Fp1, Fp2, F7, F3, Fz, F4, F8), temporal (mean amplitude of T3, T4, T5, T6), central (mean amplitude of C3, Cz, C4), parietal (mean amplitude of P3, Pz, P4), and occipital (mean amplitude of O1, Oz, O2), and collapsed across sides of target appearance.

Table 1. Mean Percentage of All Trials by Conditions of Awareness (Aware or Unaware, Subjective Measure) and Localization Performance (Correct or Incorrect, Objective Measure) for the Short and for the Long Exposure Durations

	Aware Correct	*Aware Incorrect*	*Unaware Correct*	*Unaware Incorrect*
Short exposure	23.0%	2.8%	38.3%	35.9%
Long exposure	48.5%	2.0%	29.4%	20.1%

Subjective Measure of Awareness (Subjective Report)

We compared the ERP waveforms associated with trials that were identical in terms of physical stimulus, exposure time, and participants' responses to the target (correct responses only), and differed only in the participants' subjective experience, that is, in whether they reported being aware or unaware of the target. An ANOVA with condition (aware correct vs. unaware correct), scalp region (frontal, temporal, central, parietal, occipital), and exposure (short vs. long) as within-subject factors was conducted on the mean amplitudes of the P1, N1, P2, N2, and P3 components of the ERP. Statistical data are presented in Table 2.

The mean amplitude of the P3 component was significantly higher in the aware-correct condition ($M = 4.36$, $SE = 0.61$) than in the unaware-correct condition ($M = 1.99$, $SE = 0.80$) [$F(1, 18) = 18.04$, $p < .0001$]. This effect interacted with scalp region [$F(4, 76) = 5.34$, $p < .001$]. Follow-up comparisons showed that although significant effects of condition were obtained for all scalp regions, these were more pronounced over the central and parietal regions (see Table 3 for statistics).

Visual inspection of the ERPs for the P2 component suggested that for the short exposure (Figure 2, top), there was a trend toward larger amplitude in the aware-correct relative to the unaware-correct conditions over the central and frontal scalp regions. This observation was confirmed by t tests [$t(18) = 1.97$, $p < .07$ and $t(18) = 1.91$, $p < .08$ for the frontal and central regions, respectively[1]]. There were no significant effects or remarkable trends involving condition (aware correct vs. unaware correct) for any of the other ERP components.

In the present study, there were only four alternative localization responses, such that a nonnegligible portion of the unaware-correct trials were trials in which participants responded to correctly by chance. Thus, the observed unaware-correct ERP waveform, in fact, represented a mixture of the neural response to unaware trials that were responded to correctly due to sufficient perceptual processing and of the neural response to unaware trials that were responded to correctly by chance. By contrast, the portion of aware-correct trials that were responded to correctly by chance was inconsequential because accuracy on those trials was very high. Brain activity associated with chance performance can be indexed by the ERP waveform on unaware-incorrect trials, for which the amplitude of the P3 component was substantially

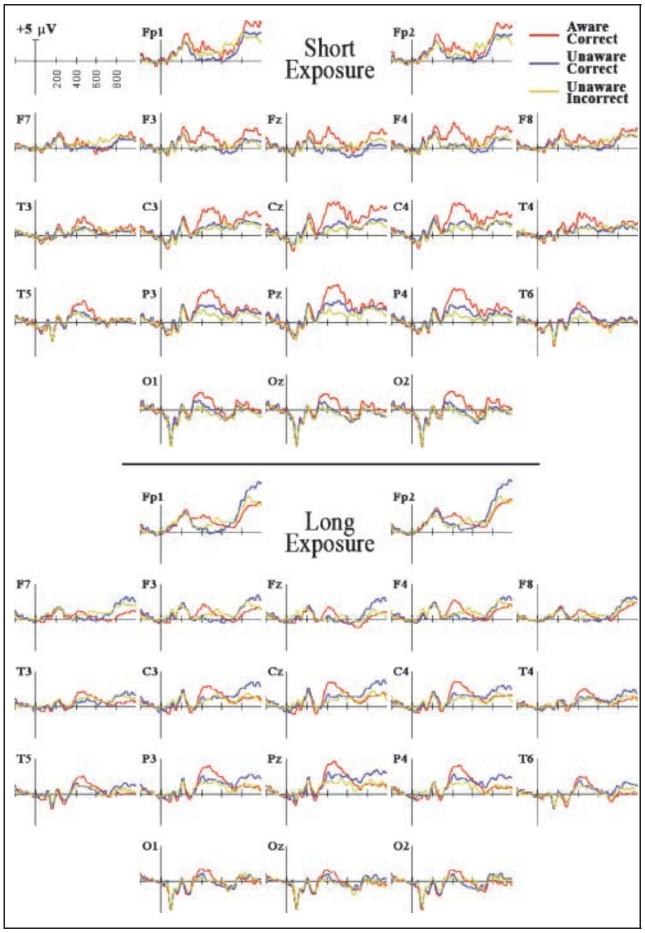

Figure 2. Grand mean event-related potentials (ERPs) of the aware-correct (red), unaware-correct (blue), and unaware-incorrect (yellow) conditions for the short-exposure condition (top) and for the long-exposure condition (bottom). The ERPs are time-locked to matrix display onset and are calculated relative to a 200-msec baseline.

smaller than its amplitude on correct-performance trials (see Figure 2). It follows that the observed lower mean amplitude in the unaware-correct waveform relative to the aware-correct waveform on the P3 component may result from the higher proportion of chance responding in the latter relative to the former condition. One might therefore argue that there is, in fact, no difference between aware-correct and unaware-correct trials on the P3 component, when chance responding is taken into account.

We conducted additional analyses to examine this possibility. Specifically, we sought to mathematically estimate whether the amplitude of the P3 component of the ERP waveform corresponding to unaware-correct trials that were not responded to correctly by chance (henceforth, chance-free unaware-correct trials) would remain lower in amplitude than the P3 amplitude of the aware-correct waveform. Note that although the finding that localization accuracy on unaware trials was well above chance tells us that such chance-free unaware-correct trials indeed occurred, one cannot determine whether an individual trial was a chance trial or a chance-free trial. Thus, we could only estimate the amplitudes of the waveform corresponding to chance-free unaware-correct trials. The calculations used to derive a hypothetical approximation of the unknown chance-free unaware-correct waveform from the known waveforms corresponding to chance trials (unaware-incorrect waveform) and to unaware-correct trials are described in the footnote.[2] We conducted an ANOVA on ERP mean amplitudes in the P3 time window with condition (aware correct vs. chance-free unaware correct), scalp region (frontal, temporal, central, parietal, occipital), and exposure (short vs. long) as factors and found that the amplitude of the P3 component remained significantly larger in the aware correct than in the chance-free unaware-correct condition in all scalp regions (see Tables 2 and 3 for statistics). Note that although the estimated chance-free unaware-correct waveform does not reflect the neural processes that actually took place in the participants' brains, it should provide a reasonable approximation for the purpose of rejecting the argument that chance responding alone accounts for the P3 difference attributed to subjective awareness.

Unconscious Perception (Objective Performance)

To examine the neural correlates of unconscious processing, we compared the ERP waveforms associated with trials that were identical in terms of physical stimulus,

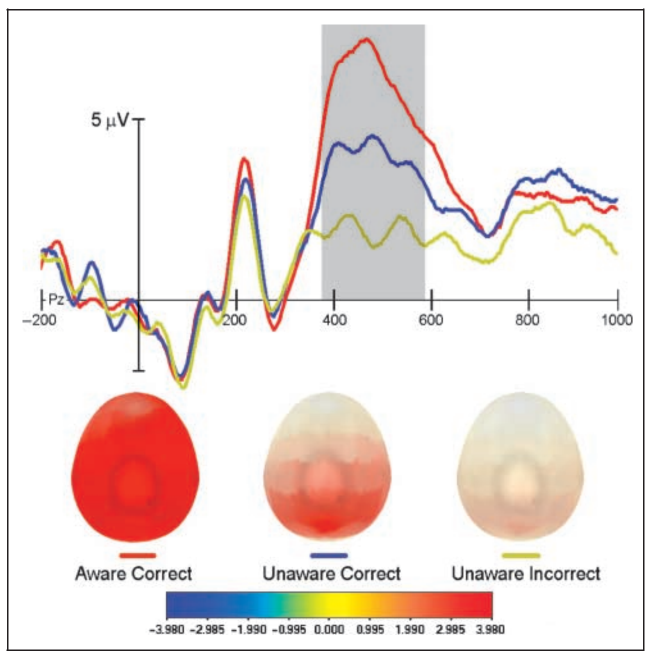

Figure 3. Mean of long and short exposures ERP waveforms at Pz for the aware-correct, unaware-correct, and unaware-incorrect conditions. The time window for the P3 component used for analyses is depicted in light gray. Below are scalp current density maps for the three experimental conditions during the P3 time window. The aware-correct condition elicited a widespread positivity across the entire scalp, the unaware-correct condition elicited a positivity restricted to the parietal scalp region, and the unaware-incorrect elicited little activation across the scalp.

Table 2. Significance Values of the Effects of Subjective Awareness (Condition: Aware Correct vs. Unaware Correct) and Objective Performance (Condition: Unaware Correct vs. Unaware Incorrect) and Relevant Interactions on the Mean Amplitude of Each Component of the ERP

	Condition		*Condition × Region*		*Condition × Exposure*		*Condition × Region × Exposure*	
	df(1, 19)		*df(4, 76)*		*df(1, 19)*		*df(4, 76)*	
ERP Component	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Aware Correct vs. Unaware Correct								
P1	<1	*ns*	<1	*ns*	<1	*ns*	<1	*ns*
N1	<1	*ns*	1.10	*ns*	<1	*ns*	<1	*ns*
P2	<1	*ns*	1.32	*ns*	<1	*ns*	<1	*ns*
N2	1.26	*ns*	1.21	*ns*	1.93	*ns*	<1	*ns*
P3	18.04	<.0001	5.34	<.001	<1	*ns*	<1	*ns*
P3[a]	12.04	<.003	2.61	<.08	<1	*ns*	<1	*ns*
Unaware Correct vs. Unaware Incorrect								
P1	<1	*ns*	<1	*ns*	<1	*ns*	<1	*ns*
N1	<1	*ns*	<1	*ns*	<1	*ns*	1.46	*ns*
P2	<1	*ns*	1.56	*ns*	<1	*ns*	<1	*ns*
N2	<1	*ns*	<1	*ns*	<1	*ns*	<1	*ns*
P3	<1	*ns*	9.7	<.0001	<1	*ns*	<1	*ns*
P3[a]	1.37	*ns*	3.75	<.003	<1	*ns*	<1	*ns*

[a]Chance-free unaware-correct condition.

stimulus exposure duration, and subjective awareness (unaware trials), and differed only in the accuracy of the participant's localization response (correct vs. incorrect). It is important to note that our operational definition of unconscious perception or correct objective performance departs in important ways from the one commonly used. Typically, the objective performance threshold is defined as the stimulation conditions (e.g., level of stimulus degradation or stimulus-to-mask SOA) at which the observer performs at chance in discriminating different states of that stimulus. Thus, stimulation conditions necessarily differ between a stimulus that an observer does not perceive (incorrect objective performance) and a stimulus that the observer perceives unconsciously (correct objective

Table 3. Significance Values of the Effects of Subjective Awareness (Aware Correct vs. Unaware Correct) and Objective Performance (Unaware Correct vs. Unaware Incorrect) on the Mean Amplitude of the P3 Component in Each Scalp Region

	Frontal		*Temporal*		*Central*		*Parietal*		*Occipital*	
	df(1, 19)		*df(1, 19)*		*df(1, 19)*		*df(1, 19)*		*df(1, 19)*	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Aware Correct vs. Unaware Correct										
	8.67	<.007	8.43	<.009	19.24	<.0001	24.19	<.0001	22.91	<.0001
Chance-free[a]	6.02	<.03	5.08	<.04	8.55	<.009	9.64	<.006	7.04	<.02
Unaware Correct vs. Unaware Incorrect										
	1.27	>.3	<1	*ns*	1.92	*ns*	6.76	<.02	2.99	<.1
Chance-free[a]	1.61	<.3	<1	*ns*	2.00	*ns*	7.04	<.02	3.26	<.09

[a]Chance-free unaware-correct condition.

performance). Here, it was critical to keep the stimulus constant across all conditions so as to ensure that differences in neural responses held to reflect differences in objective performance were not confounded with differences in physical stimulation. Because localization performance was clearly above chance, stimulus conditions were such that observers unconsciously perceived the target *on average*. Yet, on those individual trials in which the observers produced an incorrect response, it is reasonable to claim that they did not perceive the target. Such trials were therefore defined as ''no-perception'' trials.

We conducted an ANOVA on ERP mean amplitudes with condition (unaware correct vs. unaware incorrect), scalp region (frontal, temporal, central, parietal, occipital), and exposure (short, long) as factors (see Table 2 for statistics). The mean amplitude of the P3 component was higher in the unaware-correct than in the unaware-incorrect condition only over the parietal region. There was no main effect of condition (unaware correct vs. unaware incorrect) or remarkable trends in earlier ERP components (P1, N1, P2, and N2) and no significant interactions involving this factor. Note that the difference between the unaware-correct versus unaware-incorrect waveforms was underestimated because the unaware-correct condition included a nonnegligible portion of chance correct trials. However, the same analyses using the hypothetical chance-free unaware-correct waveform instead of the raw unaware-correct waveform yielded no additional significant effects (see Tables 2 and 3 for detailed statistics).

The comparison between the ERP correlates of subjective awareness and unconscious perception is illustrated in Figure 3.

DISCUSSION

Our procedure allowed us to isolate the ERP correlates of subjective awareness by comparing the aware and unaware conditions when these did not differ in the observers' objective performance on a forced-choice localization task, and the stimulus parameters were identical in the two conditions. We could also distinguish between the ERP correlates of subjective awareness and those of unconscious perception, which was reflected behaviorally in above-chance localization of the target when the observers reported being unaware of its presence. Contrasting subjective and objective measures of perception is a widely used method to study perception without subjective awareness in healthy observers (Merikle et al., 2001; Draine & Greenwald, 1998; Merikle & Reingold, 1998; Marcel, 1983) and in patients with neuropsychological conditions associated with impaired awareness such as neglect (e. g., Driver & Vuilleumier, 2001) or blindsight (Lamme, 2001; Cowey & Stoerig, 1995). Yet, to our knowledge, the present study is the first ERP experiment to apply this method to investigate the neural correlates of visual consciousness.

We found that the amplitude of the P3 component was larger in the aware relative to the unaware condition. This awareness-related difference was widely distributed over the scalp, as is clear from the highly significant differences in P3 amplitudes across all scalp regions. It specifically reflected only subjective awareness of the target because seen and unseen target displays were physically identical, appeared for the same duration, and elicited the same correct localization response. The amplitude of the P3 component was also larger when a target that was not seen was correctly localized vs. incorrectly localized. However, unlike the wide scalp distribution of the activity related to subjective awareness, the difference in P3 amplitude associated with correct objective performance was strictly limited to parietal electrodes.

The amplitude of early ERP components (P1, N1, P2[3], and N2) was not affected by whether the observers were subjectively aware of the target or missed it, or by whether or not they localized it accurately. Preservation of early perceptual components in the absence of subjective awareness suggests that although a stimulus is more likely to be consciously seen if it undergoes enhanced perceptual processing, perceptual processing is not sufficient for reportable awareness (e.g., Super, Spekreijse, & Lamme, 2001; Marcel, 1983).

Visual Awareness or Confidence Level?

It could be argued that the P3 differences observed here might reflect variations in the participants' confidence level rather than variations in awareness. Such a proposal was recently put forward by Eimer and Mazza (2005). They suggested that the P3 amplitude modulations observed in ERP studies of visual awareness (and specifically of change detection) primarily reflect variations in observers' confidence with respect to the presence versus absence of the critical stimulus. To test this claim, they used a change detection task in which participants first indicated whether they detected a change, and then rated how confident they were of their decision. Thus, for instance, a high confidence level, together with an ''I did not see'' response, indicated that the participant was highly confident of not seeing the change, whereas a high confidence level with an ''I saw'' response indicated that the participant was highly confident of seeing the target. 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' confidence: It was significant when confidence was high, but not when confidence was low. Eimer and Mazza concluded that P3 modulations were determined by participants' confidence levels rather than by variations in their awareness of the change.

However, this interpretation overlooks the fact that significant effects of subjective awareness (detection vs.

no detection) on P3 amplitude were found when confidence was high, that is, for a constant confidence level. Obviously then, variations in confidence cannot account for this difference. In addition, P3 amplitude did not differ between detection and no-detection trials when confidence was low, which further supports the notion that P3 is associated with variations in subjective awareness. When confidence is low, participants are likely to choose their response (''I saw'' or ''I did not see'') at chance, and awareness level should be similar on the two types of trials, hence, the null effect on low-confidence trials. It follows that, although an alternative account of our findings in terms of confidence level cannot be rejected on the sole basis of the present data, the results reported by Eimer and Mazza (2005) do not favor an alternative account for P3 modulations by awareness in terms of varying confidence levels.

Relation to Previous Findings

Our results are consistent with the conclusions from previous reports involving a wide array of stimuli and paradigms, according to which the amplitude of the P3 component is the primary ERP correlate of visual awareness (Del Cul, Baillet, & Dehaene, 2007; Babiloni et al., 2006; Sergent et al., 2005; Fernandez-Duque et al., 2003; Kranczioch et al., 2003; Turatto et al., 2002; Niedeggen et al., 2001). However, the present study goes beyond previous ERP findings because it allows dissociating between subjective awareness and objective performance.

Previous studies compared the neural fate of seen and unseen targets without considering potential differences in objective performance relative to unseen targets. Two ERP studies to date (see also Lau & Passingham's, 2006 fMRI study for a similar rationale) have concomitantly collected behavioral measures of subjective awareness and objective performance but the specific procedures they used did not allow them to dissociate between the neural correlates of the two behavioral measures. In a recent study by Babiloni et al. (2006), participants were required first to localize a target preceded by a barely visible cue that was spatially either congruent or incongruent with the position of a subsequent target and then to indicate whether or not they had seen the cue. Subjective report of seeing the cue was the measure of conscious processing and the effect of congruency on response latencies to the target for unseen cues was the measure of unconscious processing. Average reaction times on incongruent-cue trials were faster than on congruent-cue trials, which indicated that unconscious processing occurred in that study. However, it was not possible to distinguish between the individual trials in which unconscious processing occurred and those trials in which it did not occur because the congruency effect could only be measured across the experiment as a whole. In other words, one could not infer from the reaction time obtained on a particular trial in which the cue had not been seen whether this trial belonged to the unconscious perception or to the no-perception category. Accordingly, in Babiloni et al.'s study, the neural correlate of subjective awareness was defined as the difference between seen and unseen cues, and subjective awareness and objective performance were therefore confounded.

Del Cul et al. (2007) varied target-to-mask SOA and collected two responses with regard to a masked target, namely, a forced-choice discrimination as to whether the target digit was smaller or larger than the digit 5 (objective measure of perception) and a rating of how visible the target was (subjective measure of perception). To investigate the neural correlate of subjective awareness, they compared ERPs at the liminal exposure of 50 msec between seen and unseen trials, irrespective of objective performance. In addition, to assess the neural correlates of unconscious processing (or correct objective performance), these authors compared ERPs on target-present correct-performance trials with ERPs on no-target trials, acknowledging that there were not enough trials in their experiment to analyze the more revealing conditions of correct and incorrect performance target-present trials with the same SOA. Thus, unlike in the present experiment, the ERP correlate of subjective awareness in Del Cul et al.'s study could also reflect differences in objective performance, and the ERP correlate of objective performance could also reflect physical stimulus differences (target plus mask vs. mask only).

Relation to Existing Models of Visual Awareness

Our results argue against the view that the differences between conscious and unconscious processing arise at early stages of perceptual processing (e.g., Pins & ffytche, 2003). In our study, the ERP correlate of subjective visual awareness was reflected in an upsurge of neural activation about 375 msec after stimulus onset (P3 component). This awareness-related activation was characterized by enhanced P3 amplitude with a widely distributed topography (evident over all recorded electrode sites). These topographical and temporal characteristics are in line with recent findings supporting the global workspace model (Block, 2001; Dehaene & Naccache, 2001). For instance, Sergent et al. (2005) compared the ERP waveforms associated with seen versus unseen targets in an attentional blink task and concluded that the transition toward access to consciousness is associated with a late P3 wave of activation that spreads through a widely distributed network of cortical association areas. In the same vein, using a backward masking procedure, Del Cul et al. (2007) found that a considerable amount of processing of unseen targets occurs early on, whereas access to subjective awareness relates to a late and highly distributed fronto-parieto-temporal activation corresponding to the P3 component of the ERP.

The finding that subjective awareness is associated with the late activation of a widely distributed cortical network appears to stand in contrast with other views of visual awareness, which associate it with brain activity limited to specific regions of the prefrontal cortex (e.g., Lau & Passingham, 2006; Sahraie et al., 1997) or with recurrent processing in posterior areas of the brain (e.g., Lamme, 2001). However, it is important to note that the findings supporting these alternative views were obtained using different methodologies and might therefore capture other aspects of the difference between the aware and unaware conditions.

Specifically, the studies favoring the prefrontal cortex as the seat of visual awareness used fMRI, the temporal resolution of which may have been insufficient to reveal the relatively short-lived widespread activations reported in the present and previous ERP studies. The studies favoring the recurrent-processing hypothesis typically used TMS in humans (e.g., Pascual-Leone & Walsh, 2001), V1 lesions in monkeys (e.g., Cowey & Stoerig, 1995) or blindsight patients (e.g., Lamme, 2001). A common characteristic of the latter studies is that they showed that recurrent processing in posterior cortical areas is necessary for visual awareness. However, because they focused on early visual areas, they typically did not investigate what other regions are activated while or after reentrant processing occurs in the posterior cortex. Thus, the findings from these studies are not necessarily incompatible with the notion of a widespread network of brain areas being activated in the transition to visual awareness.

Is the Difference between Conscious and Unconscious Processing Quantitative or Qualitative?

The question of whether the difference between subjective awareness and unconscious processing (reflected by above-chance objective performance) is quantitative or qualitative has been hotly debated using behavioral methods, yet remains unresolved (e.g., Debner & Jacoby, 1994 vs. Snodgrass, 2002). In previous ERP studies, this question could not be addressed because conscious processing was compared with nonconscious processing, which included both unconscious processing (accurate objective performance in the absence of subjective awareness) and processing associated with failed perception (incorrect objective performance). In the present study, the ERP modulations associated with subjective awareness and unconscious processing were observed on the same component, P3. Indeed, without subjective awareness, P3 amplitude was larger when participants localized the target correctly than when they did not, and P3 amplitude was even larger when correct localization was accompanied by subjective awareness. This pattern appears to be consistent with a quantitative modulation of neural activity by different levels of awareness.

However, the scalp topography of the neural activity associated with each awareness condition points to a qualitative difference. Although the P3 difference related to subjective awareness was observed in recordings over the entire scalp, modulation by objective performance was restricted to recordings over the parietal region only. Because the P3 difference was maximal over the parietal electrodes for both measures and the effect was more pronounced for subjective awareness than for unconscious perception, it could still be argued that the apparent difference in topographic distribution between the two effects may be quantitative: that is, the weaker effects of unconscious processing simply did not reach significance over regions other than the parietal. Yet, closer examination of the ERP waveforms indicates that this is not the case. In particular, the amplitude of the P3 component tended to be higher in the unaware-incorrect relative to the unaware-correct condition over the frontal electrodes, that is, showing a trend in the direction opposite to the effect of subjective awareness. It will be important to further refine this claim in future research by exploring the neural underpinnings of conscious and unconscious perception using source estimation techniques allowing for multiple source modeling and converging fMRI evidence.

Conclusion

In the ever-expanding investigation of the neural correlates of awareness, various ways of limiting subjective awareness are used in a wide array of experimental paradigms. However, the extent to which such procedures affect objectively measured performance may vary in ways that have not yet been fully described. Thus, the dark side of awareness may conceal different shades of gray. As electrophysiological and neural imaging procedures rely on subtractive methods, the definition of the "unaware" baseline condition can dramatically affect which neural processes or brain regions are labeled "neural correlates of consciousness." In this perspective, the present study illustrates the potential benefits of integrating fine-grained definitional distinctions developed by cognitive behavioral research into the study of the neural correlates of awareness.

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Notes

1. The analyses were conducted excluding one outlier.
2. We first calculated the actual proportion of unaware-correct trials that were correctly responded to by chance (henceforth, $\%UC_{Chance}$), separately for each participant. In our task, because there are four possible responses, when an observer performs at chance, that is, produces a response that

is not based on successful perceptual processing, 75% of her or his responses are expected to be incorrect and 25% of his or her responses are expected to be correct. All unaware-incorrect trials were chance trials and made up 75% of all chance trials in the unaware condition, with the remaining 25% being UC_{Chance} trials. Thus, for each participant:

$$\%\text{Unaware Trials}_{\text{Chance}} = (\%\text{Unaware Incorrect trials})/0.75$$

$$\begin{aligned}\%\text{UC}_{\text{Chance}} &= \%\text{Unaware Trials}_{\text{Chance}} \times 0.25 \\ &= ((\%\text{Unaware Incorrect trials})/0.75) \times 0.25\end{aligned}$$

Then, we mathematically derived the estimated waveform corresponding to chance-free unaware-correct trials. This estimation rested on the premise that the observed waveform corresponding to unaware-correct trials included a proportion of trials, $\%UC_{Chance}$, on which the correct response was produced by chance and a proportion of trials, $\%UC_{Chance\ free} = 1 - \%UC_{Chance}$, on which the correct response was based on perceptual processing. Thus, for each time point the amplitude of the hypothetical waveform corresponding to chance-free unaware-correct trials—henceforth, $A(UC_{Chance\ free})$—was estimated as follows:

$$\begin{aligned}A(\text{UC}_{\text{observed}}) = {} & \%\text{UC}_{\text{Chance}} \times A(\text{UC}_{\text{Chance}}) \\ & + (1 - \%\text{UC}_{\text{Chance}}) \times A(\text{UC}_{\text{Chance free}})\end{aligned}$$

Thus, as neural activity on chance trials is reflected by the unaware-incorrect (UI) waveform:

$$\begin{aligned}A(\text{UC}_{\text{Chance free}}) = {} & [A(\text{UC}_{\text{observed}}) - \%\text{UC}_{\text{Chance}} \\ & \times A(\text{UI}_{\text{observed}})]/(1 - \%\text{UC}_{\text{Chance}})\end{aligned}$$

3. A trend for earlier modulation of neural activity by subjective awareness emerged roughly 200 msec poststimulus onset over the frontal electrodes (P2 component) for the short-exposure condition (see Figure 2). A similar suppression of the P2 component when participants were unaware of the target was reported in an attentional blink task by Vogel et al. (1998; see also Vogel & Luck, 2002). However, further research is needed before firm conclusions can be drawn with regard to P2 modulation by subjective awareness because, in our study, the observed trends did not reach significance and occurred only with one exposure duration.

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