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The earliest electrophysiological correlate of visual awareness? ☆

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Abstract

To examine the neural correlates and timing of human visual awareness, we recorded event-related potentials (ERPs) in two experiments while the observers were detecting a grey dot that was presented near subjective threshold. ERPs were averaged for conscious detections of the stimulus (hits) and nondetections (misses) separately. Our results revealed that hits, as compared to misses, showed a negativity around 180–350 ms at occipital and posterior temporal sites. It was followed by a positive wave after 400–500 ms, peaking at parietal sites. These correlates were not affected by a manipulation of attention. The early negativity, called 'visual awareness negativity' (VAN), may be a general, primary electrophysiological correlate of visual awareness. The present data show that it can be observed in response to appearance of a stimulus in visual awareness and that it generalizes across different manipulations of stimulus visibility.

Keywords: Attention; Awareness; Consciousness; Detection; EEG; ERP; Perception

1. Introduction

Visual awareness or phenomenal visual consciousness refers to the subjective experience of seeing, as contrasted to unconscious visual processes or later conscious processes performed on the experienced contents (Block, 2001; Revonsuo, 2006). Recently, visual awareness has become a popular research area in Cognitive Neuroscience (Kanwisher, 2001; Rees & Lavie, 2001; Rees, Kreiman, & Koch, 2002). To reveal the neural correlates of awareness, researchers aim to measure brain activation that is specific to changes in the content of visual awareness while the physical stimulus remains unchanged, for example, during binocular rivalry (Lumer & Rees, 1999), binocular fusion (Moutoussis & Zeki, 2002), change blindness (Beck, Rees, Frith, & Lavie, 2001), masking (Bar et al., 2001), or low-contrast stimuli (Pins & ffytche, 2003). Functional brain imaging studies suggest that the activation of the ventral visual stream, a set of pathways from V1 to inferotemporal cortex, known to participate in object recognition, is involved in generating conscious visual perceptions (Bar et al., 2001; Beck et al., 2001; Moutoussis & Zeki, 2002; Overgaard, Nielsen, & Fuglsang-Frederiksen, 2004; Pins & ffytche, 2003; Vanni, Revonsuo, Saarinen, & Hari, 1996). In addition, the activation of parietal and prefrontal areas, involved in control of attention, has been associated with conscious visual perception (Beck et al., 2001; Lumer & Rees, 1999).

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Pins and ffytche (2003) attempted to reveal the timing of the networks correlating with visual awareness by studying conscious perception of stimuli at the subjective threshold by combining fMRI and event-related potential (ERP) measurements. In their study, the earliest ERP component correlating with awareness was an early positive wave (P1) which showed more positive amplitudes to conscious stimuli as compared to nonconscious ones in occipital electrodes. They concluded that early activity in the occipital lobe 100 ms after the stimulus onset is likely to represent a primary correlate of conscious perception, while activity from 260 ms onwards in parietal, frontal, motor and auditory regions represents secondary processes, influenced by earlier perceptual activity but not contributing directly to perception. These conclusions rest on the assumption that neural activity around 100 ms really correlates with awareness. Earlier electrophysiological studies on awareness, not discussed by Pins and ffytche (2003), do not support such an interpretation. A number of studies have failed to find any correlates of awareness in the P1 window but show instead that the earliest correlate of visual awareness of stimuli, as compared to stimuli which do not enter awareness, is an increase of negativity at posterior sites around 200 ms after the stimulus. This correlate has been observed during binocular rivalry (Kaernbach, Schröger, Jacobsen, & Roeber, 1999), in conscious change detection (Koivisto & Revonsuo, 2003), with contrast manipulation (Ojanen, Revonsuo, & Sams, 2003) or in masking experiments (Koivisto, Revonsuo, & Lehtonen, 2006; Koivisto, Revonsuo, & Salminen, 2005; Wilenius-Emet, Revonsuo, & Ojanen, 2004). This enhancement in negativity has been named *visual awareness negativity* (VAN) (Koivisto & Revonsuo, 2003; Ojanen et al., 2003; Wilenius-Emet et al., 2004).

Electrophysiological correlates of visual awareness have been studied also by using experiments which make use of such phenomena as attentional blink and change blindness. Attentional blink is demonstrated in rapid serial presentation as a failure to detect the second target stimulus when attention is engaged with the first target stimulus presented about half a second earlier (Shapiro, Arnell, & Raymond, 1997). The most reliable electrophysiological effect during attentional blink is that the P3 potential is suppressed in relation to control condition (Kranczioch, Debener, & Engel, 2003; McArthur, Budd, & Michie, 1999; Vogel, Luck, Bischof, & Shapiro, 1998). Change blindness is manifested as a considerable difficulty of detecting changes in unattended stimuli, when two versions of the same scene are separated by a brief interruption (Simons & Levin, 1997). Similarly to attentional blink, during change blindness the most common finding has been a reduced P3 amplitude in relation to change detection (Fernandez-Duque, Grossi, Thornton, & Neville, 2003; Niedeggen, Wichmann, & Stoerig, 2001; Turatto, Angrilli, Mazza, Umiltá, & Driver, 2002), but also reduced negativities around 200 ms, followed by a reduced P3, have been reported (Eimer & Mazza, 2005; Koivisto & Revonsuo, 2003). Common to attentional blink and change blindness is that both phenomena are strongly dependent on attention and the experimental tasks measuring them involve a working memory component (Shapiro et al., 1997; Simons & Levin, 1997). Thus, it may be a failure of memory or some other postperceptual deficit that causes the participants not to report the stimuli in these paradigms, not necessarily a failure of visual awareness itself. This interpretation fits well with the finding that P3, a component associated to postperceptual processes and working memory (Donchin & Coles, 1988), is reduced during attentional blink and change blindness. In line with this interpretation, Eimer and Mazza (2005) showed that the P3 effect during change blindness reflects the response confidence of observers.

The review of studies above suggests that VAN may be the earliest, primary electrophysiological correlate of visual awareness. The P1 correlate has been observed only in one study (Pins & ffytche, 2003), while the P3 effect seems to have too late latency and it typically appears after VAN (Koivisto et al., 2005). However, the experimental tasks in earlier studies showing VAN have called for higher-level processing of the stimuli, for example, categorization of the stimuli as objects or nonobjects (Ojanen et al., 2003; Wilenius-Emet et al., 2004), categorization of letters as targets or nontargets (Koivisto et al., 2005), or line orientation judgments (Koivisto et al., 2006). Thus, it is possible that VAN correlates with awareness of higher-level task-relevant information, but not with the appearance of the stimulus in visual awareness *per se* which might correlate with P1.

Here we studied ERPs elicited by the conscious detection of the appearance of a stimulus, as compared to trials in which the same stimulus is not detected. Our aim was to study, by using as simple perceptual detection tasks as possible, which one of the previously suggested effects (P1, VAN, or P3) is the primary electrophysiological correlate of visual awareness and is elicited in response to mere detection of the appearance of a stimulus, with only minimal requirements on working memory and without any need for higher-level categorization of the stimulus. In Experiment 1, the stimulus was presented between a forward mask and a backward mask, in Experiment 2 a low-contrast stimulus was kept near the subjective threshold by manipulating its' duration from trial to trial based on participants performance. In both experiments the observers indicated after each trial whether they had consciously detected a stimulus or not. The differences in ERPs between hits (correctly detected stimuli) and misses (undetected stimuli) were defined as the electrophysiological correlates of visual awareness.

2. Experiment 1

2.1. Method

2.1.1. Participants

The data from five observers were rejected because of either too high or too low level of performance for

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permitting EEG analyses separately for each variable. The remaining 13 participants (three males, mean age = 23.8 years, range = 20–31) were healthy, right-handed (Oldfield, 1971) and had normal or corrected-to-normal vision. All the participants gave their informed consent before the experimental session begun.

2.1.2. Stimuli and procedure

The stimuli were presented on a white background (16 cd/m^2). Each trial began with a black-white pattern mask (0.80° × 0.80°; 0.27 cd/cm^2) in the center of the computer screen for 1200 ms. This forward mask served also as the fixation point and a warning signal. It was replaced with the stimulus that was a grey dot (0.76° in diameter; 12 cd/cm^2) for 83 ms. The stimulus was followed by a blank screen for 83 or 116 ms[1] until a mirror-imaged version of the mask appeared (backward mask) for 1200 ms. The inter-trial interval from the offset of the backward mask to the onset of the forward mask of the next trial was 1600 ms. The observers were asked to press the "yes" button if they consciously perceived the stimulus and to press the "no" button if they did not have a conscious experience of the stimulus. They were encouraged not to guess but to respond on the basis of their conscious visual experience. The response hand (right vs. left) was balanced across the observers. The observers were asked to keep fixation at the center of the screen and to avoid blinks and eye movements during the trials.

The experiment was run in three blocks, each including 80 stimulus-present trials and 80 stimulus-absent (catch) trials. The experimental trials were preceded by a show-up and practice block, in which the stimulus-backward mask interval was gradually decreased to the level used in the experimental blocks.

EEG was recorded using tin electrodes attached to Electro-Cap electrode system (Electro-Cap International, Inc., USA) with international 10/20 system sites FP1, FP2, F3, F4, F7, F8, Fz, P3, P4, Pz, C3, C4, Cz, T3, T4, T5, T6, O1 and O2. In addition, an electrode placed below the left eye was used for monitoring vertical eye movements and blinks and an electrode 1.5 cm to the right of the right eye was used for monitoring horizontal eye movements. Nose was used as reference and an electrode between Fz and Cz as ground. EEG was amplified (SynAmps) using a band pass of 0.05–100 Hz, with the sampling rate of 500 Hz. A 50 Hz notch filter was used to reduce 50 Hz interference. The impedance of the electrodes was kept below 5 kΩ. Baseline was corrected to the activity in the –100 to 0 ms preceding the stimulus. Trials with artifacts (>70 μV) in any of the electrodes were rejected off-line. Average rejection rate was about 17% of trials. ERPs were averaged separately for hits ("yes" responses to the presence of the stimulus), misses ("no" responses to the presence of the stimulus), and correct rejections ("no" responses in catch trials).

[1] Two stimulus-backward mask intervals were included in the experiment to ensure that a sufficient number of hits and misses for averaging ERPs would be available for each participant either within the shorter or longer interval condition. However, preliminary analyses showed that, although the difference was significant ($p < .01$), the performance rates in stimulus-present trials differed only with 6% in favour of the longer interval, while there was no difference in stimulus-absent trials. Therefore the ERPs from the two stimulus-backward mask interval conditions could be collapsed together.

2.2. Results

The participants responded by pressing yes to 37% ($SD = 22$) of trials involving the stimulus (hits) and "no" to 61% ($SD = 22$) of the trials involving the stimulus (misses). They correctly responded "no" to 96% ($SD = 5$) of the catch trials (correct rejections). A signal detection analysis, taking into consideration both the hit and false alarm rates, was used to compute d' and β values. The d' value is an index of sensitivity, with values higher than 0 indicating sensitivity to signal. The d' value (mean = 1.5, $SD = 0.6$) was significantly higher than zero ($t(12) = 8.7$, $p < .001$), showing that detection performance was above chance level. The β value is measure of response bias, with values less than 1 indicating a bias toward the "yes" response and greater than 1 indicating a conservative bias toward the "no" response. The β value (mean = 6.9, $SD = 4.3$) was significantly higher than 1 ($t(12) = 5.0$, $p < .001$), suggesting that the participants used a conservative criterion and pressed the "yes" button on the basis of their conscious experience and did not make guesses.

The time windows for statistical analyses of ERPs were determined on the basis of the grand average waves. Greenhouse–Geisser corrections were applied to the p values when the degrees of freedom were greater than 1. The peak amplitudes and latencies for ERPs (Fig. 1) were analysed in time windows of 100–160 ms (P1), 130–230 ms (N1), 210–370 ms (P2), 300–420 ms (N2) and 450–750 (P3). P1, N1, P2 and N2 were analysed in posterior temporal (T5, T6) and occipital electrodes (O1, O2), in which they were most clearly identified. P3 showed the strongest peaks in parietal sites and it was analysed at Pz.

The ANOVAs with Stimulus type (3: hits, misses and correct rejections), Lobe (temporal and occipital) and Hemisphere for peak amplitudes and latencies in the P1 time window did not reveal any differences between the stimulus types ($F(2,24) = 1.40$). The P1 amplitudes were larger in the occipital than in the temporal electrodes ($F(1,12) = 12.09$, $p < .01$) and the peak latencies were shorter in temporal than occipital electrodes ($F(1,12) = 12.03$, $p < .01$).

The analyses of N1 revealed larger negativity over the temporal than the occipital electrodes ($F(1,12) = 9.05$, $p < .02$), particularly over the left temporal lobes ($F(1,12) = 15.71$, $p < .01$). Peak latencies were shorter in occipital than temporal electrodes ($F(1,12) = 7.42$, $p < .02$).

P2 amplitudes were more positive in the occipital than in the temporal electrodes ($F(1,12) = 13.99$, $p < .01$). Importantly, the main effect for Stimulus type was significant

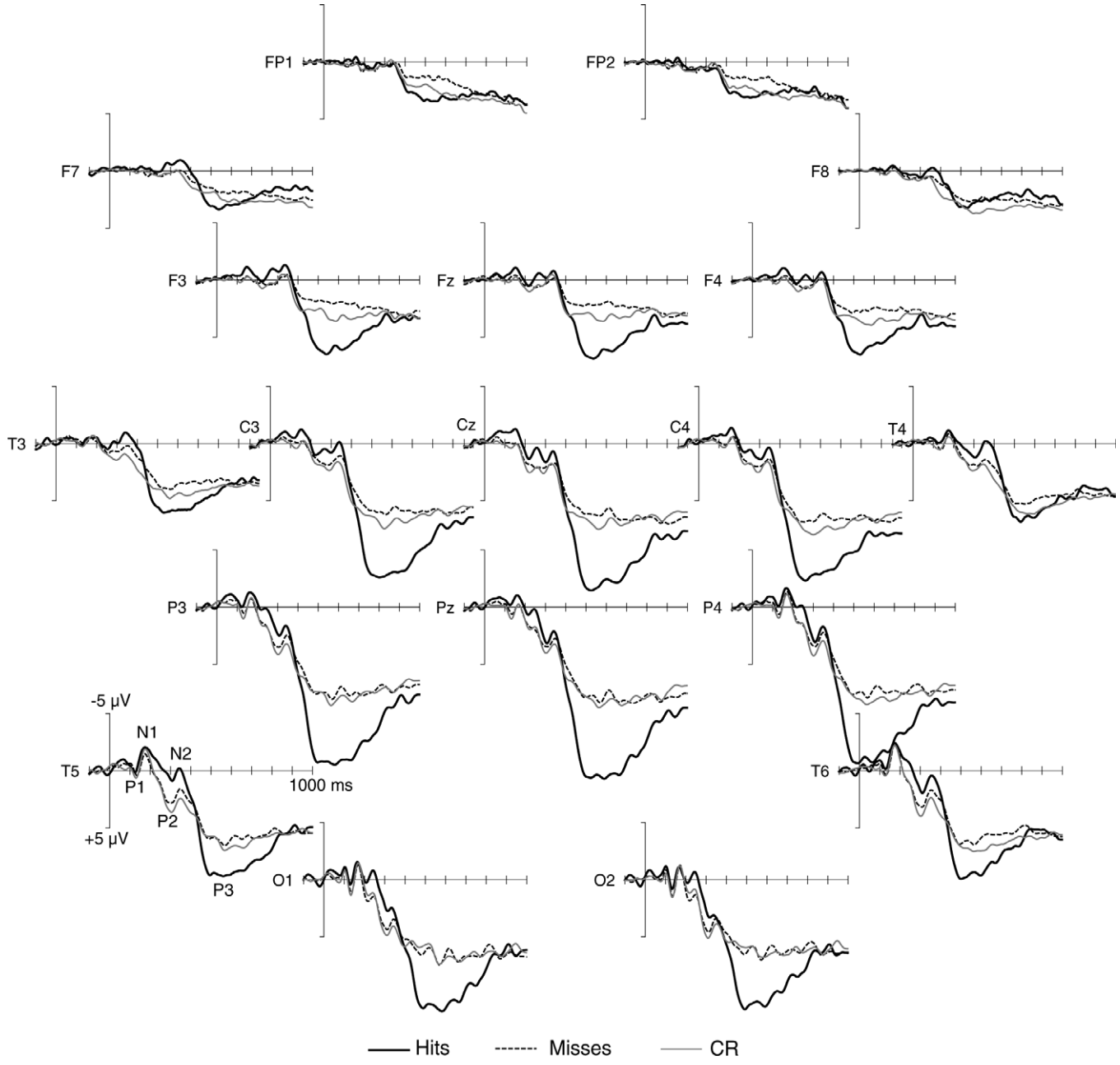

Fig. 1. Experiment 1: event-related potentials to hits, misses and correct rejections.

($F(2,24) = 8.26$, $p < .01$), showing that the ERPs to hits were less positive than those to misses ($p = .025$) or to correct rejections ($p < .01$). Stimulus type interacted with Hemisphere ($F(2,24) = 5.14$, $p < .02$), showing that the amplitude difference between hits and misses was larger over the left than the right hemisphere. In other words, consciously detected stimuli elicited more negative responses (VAN) than nondetected stimuli, particularly over the left hemisphere.

The N2 was stronger in temporal than in occipital electrodes ($F(1,12) = 15.82$, $p < .01$). The main effect for stimulus type was significant ($F(2,24) = 5.13$, $p < .05$), showing more negative responses to hits than to correct rejections.

A one-way ANOVA on the P3 peak amplitudes in Pz revealed a significant main effect for stimulus type, $F(2,24) = 23{,}26$, $p < .001$. Responses to hits were more positive than to the misses ($p < .001$) and correct rejections ($p < .001$).

To illustrate the differences between consciously detected stimuli and nondetected stimuli more clearly, we computed a difference wave by subtracting the ERPs to misses from those to hits. As Fig. 2 shows, the earliest marker of conscious detection is a negative amplitude shift, corresponding to the effects observed in P2 and N2 range above. The scalp distribution of the negativity (see also Fig. 4) was analysed by entering the peak

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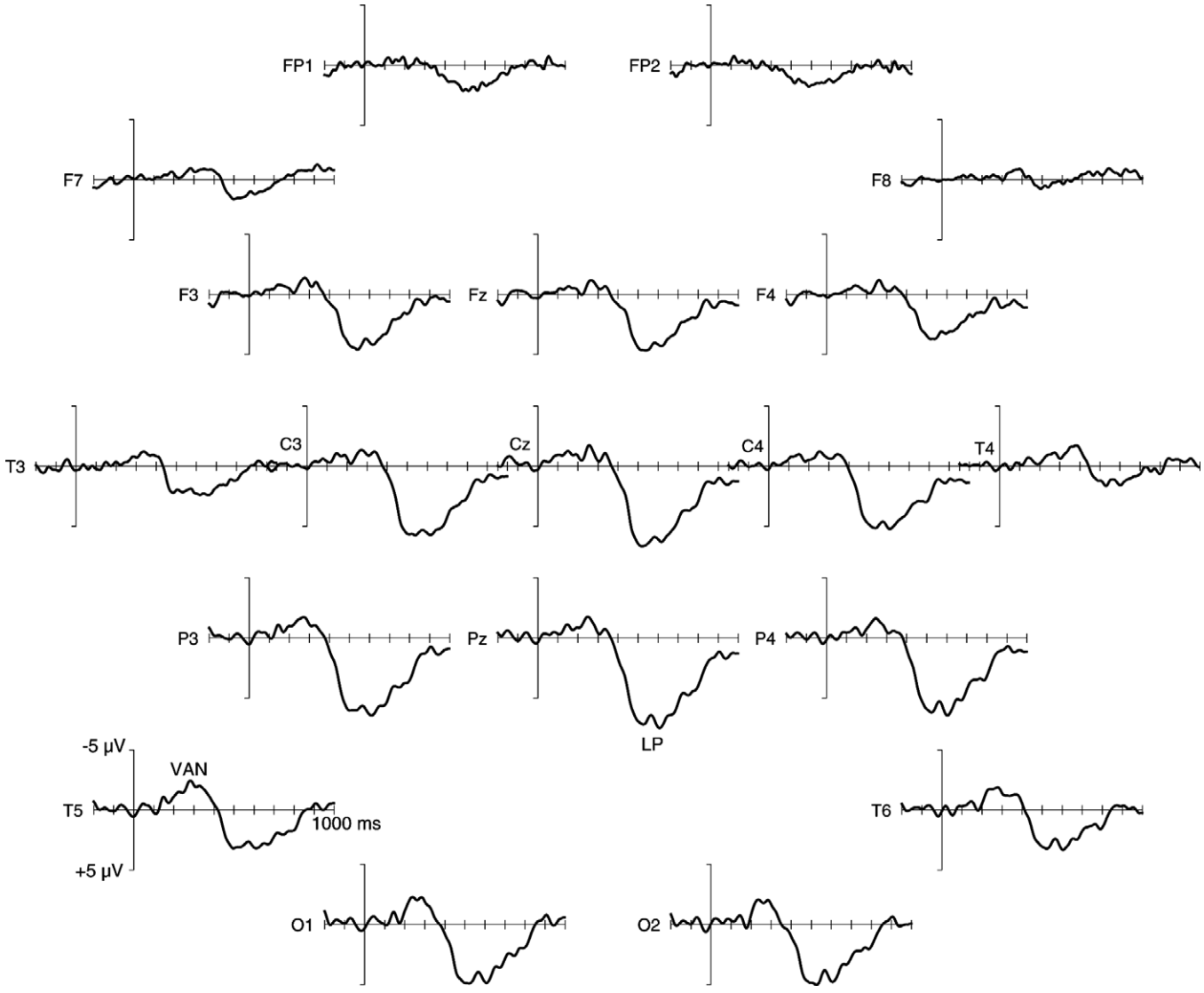

Fig. 2. Experiment 1: the difference wave (hits–misses) shows that visual awareness negativity (VAN) is the earliest wave correlating with visual awareness. It is followed by the late positive difference (LP).

amplitudes (determined from the difference waves, the most negative peak 180–400 ms from stimulus onset) into a Hemisphere (2) × Site (6: occipital [O1, O2], posterior temporal [T5, T6], anterior temporal [T3, T4], parietal [P3, P4] and frontal [F3, F4]) ANOVA. It revealed a main effect for Site ($F(4,48) = 5.13$, $p < .01$), indicating that the negativity was larger in occipital and posterior temporal sites than in than in anterior temporal and frontal sites (all $p < .02$). An identical ANOVA on peak latencies showed a main effect for Site ($F(4,48) = 3.75$, $p < .05$), indicating that the latency of the negative peak was shorter in occipital sites (277 ms) than in posterior (330 ms) and anterior (296 ms) temporal sites (all $p < .02$). The latency in anterior temporal sites was longer than in all the other sites (all $p < .05$). The negativity peaking in occipital and posterior temporal sites corresponds to VAN (Koivisto et al., 2005, 2006; Ojanen et al., 2003; Wilenius-Emet et al., 2004).

2.3. Discussion

Two electrophysiological correlates of visual awareness emerged. First, a negative wave (VAN) was elicited by hits as compared to misses, peaking at posterior temporal and occipital sites around 200–350 ms after the stimulus. VAN was followed by a positive wave after 400 ms, peaking at parietal sites. This pattern replicates the electrophysiological pattern associated with visual awareness in our previous studies (Koivisto & Revonsuo, 2003; Koivisto et al., 2005, 2006; Wilenius-Emet et al., 2004) with a task requiring simple detection of the presence or absence of the stimulus. The previous studies had used experimental tasks requiring higher-level categorization of the stimuli.

We did not find any evidence for the claim (Pins & ffytche, 2003) that occipital activity around 100 ms after the stimulus would correlate with visual awareness. This should have been observed as an enhancement of P1

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amplitude to detected stimuli at occipital sites. It is possible that the enhanced P1 observed by Pins and ffytche (2003) was related to attention rather than awareness, because they used a procedure in which the onset of the stimulus was not predictable. We used a constant ISI between the fixation mark and the onset of the stimulus which helped the observers to allocate their attentional resources on the stimulus in the proper moment. If the onset of the stimulus is not constant, the effects of attention are more poorly controlled for. In random stimulus onset, it is possible that the stimulus is more likely to be detected when attentional allocation accidentally occurs at the temporally correct moment. When attention fails to target the stimulus at the correct moment, then the stimulus is less likely to be detected. On the other hand, when two stimuli (e.g., the fixation stimulus and the target) are presented in predictable intervals, a negative deflection called contingent negative variation (CNV) is elicited after the first stimulus (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). In Experiment 1, the onset of the stimulus could be anticipated, but there was only a nonsignificant difference in CNV to hits as compared to misses at early latencies after the stimulus. This effect occurred in Cz but not in the occipital and posterior electrodes where VAN was the strongest. Nine of the 13 participants showed evidence of a stronger CNV to hits than misses, but the mean amplitudes (75–175 ms from stimulus onset) between hits and misses in Cz did not differ statistically significantly ($t(12) = 1.77$). Thus, it is unlikely that the ERP differences between detected and undetected stimuli in posterior electrodes might reflect CNV rather than VAN. However, because there must be some difference in the cognitive processes (in addition to awareness of stimulus) between detected and undetected stimulus trials, the rudimentary CNV suggests that the observers were better prepared for the detection task in detected than undetected stimulus trials.

3. Experiment 2

A difference between Experiment 1 and that of Pins and ffytche (2003), which showed an enhancement of P1 amplitude to detected stimuli, is that we presented the stimulus between forward and backward masks, whereas Pins and ffytche used a low-contrast stimulus which was kept near the subjective threshold by manipulating its' duration from trial to trial based on participants performance. Although the onsets and offsets of the masks contribute to the overall pattern of ERPs in Experiment 1, they should not have any effects on the correlates of visual awareness *per se*, because their effects should stay constant across trials in which the stimulus is detected (hits) or is not detected (misses). However, the electrophysiological effects generated by masks may make it more difficult to measure the signal (here, the ERP response related to visual awareness) from noise.

Here we did not use masks and followed the procedure of Pins and ffytche (2003) and varied the duration of the stimulus from trial to trial based on participants' response. After conscious detection of the stimulus, the stimulus duration was decreased (by one screen refresh rate) in the next trial, and after missed stimulus, it was increased (by one screen refresh rate) to keep the stimuli near the subjective threshold. In addition, we manipulated the onset of the stimulus to test whether the electrophysiological correlates of visual awareness would be influenced by this factor (e.g., via producing different levels of CNV or attentional preparation between hit and miss trials). In the constant onset condition, the stimulus appeared always after a constant ISI after the fixation mark like in Experiment 1, making it possible for the participants to focus their attention in the moment when the stimulus appeared. In the random onset condition, the ISI between the fixation cross and the appearance of the stimulus varied randomly from trial to trial. In this condition, attention or preparation cannot be expected to be as well controlled across hit and miss trials as in the constant onset condition (although the nonsignificant CNV in Experiment 1 suggests that preparation may vary also within the constant onset condition). One could assume that the possible enhancement of P1 in random onset condition occurs because in those trials in which the stimulus is detected the participants manage to focus attention temporally more successfully than in the trials in which they do not detect the stimulus—thus the ERP difference between detected and undetected trials would reflect the effects of attention rather than awareness.

3.1. Method

3.1.1. Participants

The data from two of the participants were rejected because of artifacts and from three participants because of too low level of performance for permitting EEG analyses separately for each variable. The remaining 14 participants (seven males, mean age = 24 years, range = 21–29) were healthy, right-handed (Oldfield, 1971), had normal or corrected-to-normal vision, and none had participated in Experiment 1. All the participants gave their informed consent before the experimental session begun.

3.1.2. Stimuli and procedure

The stimulus was a grey dot (0.76° in diameter; 16.7 cd/cm^2), presented on a grey background (17.3 cd/m^2). Each participant accomplished two stimulus onset conditions in separate experimental blocks: the constant and the random conditions. In the constant condition the timing of the stimulus was always fixed and predictable, while in the random condition the timing of the stimulus was unpredictable and nonfixed. The order of these conditions was counterbalanced across the participants.

In the constant condition, each stimulus-present trial began with a black fixation cross in the center of the computer screen for 500 ms. After the fixation cross, the screen was blank for 500 ms until the stimulus was presented in fixation position in the stimulus-present trials. The stimulus was followed by a blank screen for

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1000 ms until a black question mark "?" appeared, indicating that the response should be given. In the catch trials, in which no stimulus was presented, a blank screen was displayed instead of the stimulus. The inter-trial interval from the response to the onset of the next trial was 2000 ms. If the participant detected the stimulus in the stimulus-present trial, the duration of the stimulus was decreased with one screen refresh (16.7 ms) in the next stimulus-present trial. If the participant did not detect the stimulus, the stimulus duration was increased with one screen refresh in the next stimulus-present trial. The duration of the blank screen in catch trials varied according to the responses in stimulus-present trials, but the responses to catch trials did not affect the stimulus durations in stimulus-present trials.

In the random stimulus onset condition, the procedure was otherwise identical to the constant one, but the duration of the blank screen presented between the fixation cross and the stimulus onset varied randomly between 500 and 1500 ms, and the blank screen between the stimulus offset and the question mark varied randomly between 1000 and 2000 ms. Therefore the observer could not predict the exact moment when the stimulus appeared.

In both conditions, the observers were asked to press the "yes" button if they consciously perceived the stimulus and to press the "no" button if they did not have a conscious perception of the stimulus. They were encouraged not to guess but to respond on the basis of their conscious visual experience. The response hand (right vs. left) was balanced across the observers. The observers were asked to keep fixation at the center of the screen and to avoid blinks and eye movements during the trials.

Both the constant and random conditions included 160 stimulus-present trials and 40 catch trials. In the beginning of both conditions, the duration of the first stimulus was 200 ms. The first five trials were eliminated from the analyses to allow the stimulus duration to reach the threshold.

EEG was recorded using 20 electrodes (Ag/AgCl) with international 10/20 system sites FP1, FP2, F3, F4, F7, F8, Fz, P3, P4, Pz, C3, C4, Cz, T3, T4, T5, T6, O1, O2 and OZ. In addition, an electrode placed below the left eye was used for monitoring vertical eye movements and blinks and an electrode 1.5 cm to the right of the right eye was used for monitoring horizontal eye movements. Nose was used as reference and an electrode between FP1 and FP2 as ground. EEG was amplified (SynAmps) using a band pass of 0.1–30 Hz, with the sampling rate of 500 Hz. A 50 Hz notch filter was used to reduce 50 Hz interference. The impedance of the electrodes was kept below 5 kΩ. Baseline was corrected to the activity in the –100 to 0 ms preceding the stimulus. Trials with artifacts (>70 μV) in any of the electrodes were rejected off-line. Average rejection rate was about 10% of trials. ERPs were averaged separately for hits ("yes" responses to the presence of the stimulus), misses ("no" responses to the presence of the stimulus) and correct rejections ("no" responses in catch trials).

3.2. Results

3.2.1. Behaviour

The hit rate was 51% ($SD = 3$) and the false alarm rate was 12% ($SD = 11$) in the constant stimulus onset condition. The corresponding rates were 49% ($SD = 3$) and 12% ($SD = 7$) in the random condition, respectively. Possible performance accuracy differences between the conditions were analysed with d' which takes into consideration both the hit and false alarm rates. This measure did not show any differences between constant (mean = 1.4, $SD = 0.6$) and random (mean = 1.3, $SD = 0.4$) ($t(13) = 0.71$) stimulus onset conditions. The d' values were higher than zero in both conditions (all $t(13) > 8.5$, $p < .001$). Possible response bias differences were analysed by comparing β between the conditions. The constant (mean = 4.5, $SD = 4.8$) and random (mean = 3.0, $SD = 2.1$) conditions did not differ in this index ($t(13) = 1.14$). However, the β values are rather high in both conditions (and significantly above 1, all $t(13) > 2.7$, $p < .02$), suggesting that the participants used a conservative criterion and pressed the "yes" button only when they really subjectively saw the stimulus. In other words, they performed according to the instructions stressing the subjective (conscious) detection and did not respond by guessing. Additional analyses of β with gender as a variable did not reveal any differences between male and female participants (Fs < 1).

The influence of the stimulus onset manipulation was manifested in the stimulus durations needed for conscious detection. In the constant onset condition, the average stimulus duration was 150 ms ($SD = 19$) for hits and 133 ms ($SD = 20$) for misses. In the random onset condition the corresponding values were 219 ms ($SD = 32$) and 200 ms ($SD = 31$). A Condition (2) × Stimulus Type (2) ANOVA on stimulus durations shows a main effect for condition ($F(1,13) = 14.12$, $p < .01$), indicating that the durations were 68 ms longer in the random onset condition. In addition, the main effect for Stimulus Type ($F(1,13) = 219.09$, $p < .001$) shows that the duration of hits was on average 19 ms longer than that of the misses. We shall argue later that this rather small difference, as compared to that between the stimulus onset conditions, did not have any effects on the electrophysiological correlates of visual awareness.

3.2.2. ERPs

The time windows for statistical analyses of ERPs were determined on the basis of the grand average waves. Because the ERP waves did not reveal any clear peak structure for misses and correct rejections due to the low contrast of the stimuli, we decided to use mean amplitudes as dependent measures in this experiment. The mean amplitudes for ERPs (Fig. 3) were analysed in time windows of 80–130 ms (P1), 180–400 ms (early negativity, EN) and 400–700 ms (P3). P1 and EN were analysed in posterior temporal (T5, T6) and occipital electrodes (O1,

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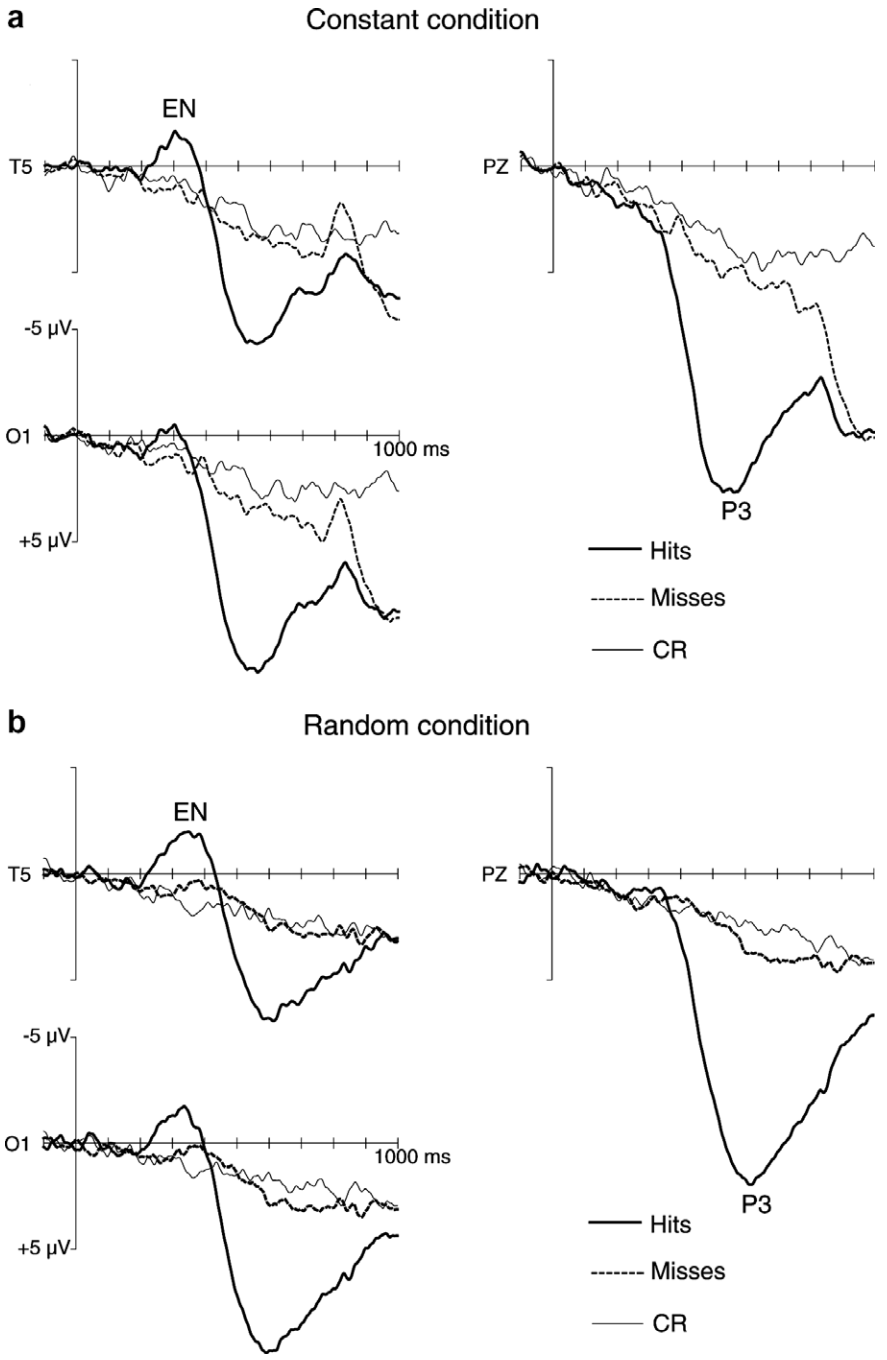

Fig. 3. Experiment 2: event-related potentials to hits, misses, and correct rejections in (a) constant stimulus onset condition and (b) random stimulus onset condition. In both conditions, the early negativity (EN) is larger in response to hits than to misses. This difference is visual awareness negativity (VAN), which is followed by the late positive difference in P3 time window.

O2), in which they were expected to occur and were also most clearly identified. P3 showed the strongest peaks in parietal sites and it was analysed in Pz. We analysed also the latest part in the epoch (800–1000 ms; Pz) where the stimulus onset conditions seem to produce a clearly different pattern of ERPs. CNV was not analysed because visual inspection did not reveal any evidence for it in either of the onset conditions. Greenhouse–Geisser corrections were applied to the p values when the degrees of freedom were greater than 1.

A 2 (Condition: constant vs. random) $\times$ 3 (Type: hit, miss and correct rejection) $\times$ 2 (Lobe) $\times$ 2 (Hemisphere) analysis of variance (ANOVA) on P1 amplitudes did not reveal any statistically significant effects.

The corresponding ANOVA on EN revealed a main effect for Type ($F(2, 26) = 4.48$, $p < .05$), showing that the ERPs to hits were more negative than those to correct rejections ($p < .01$) and showing a trend for the ERPs to hits to be more negative than those to misses ($p = .08$), while ERPs to misses and correct rejections did not differ

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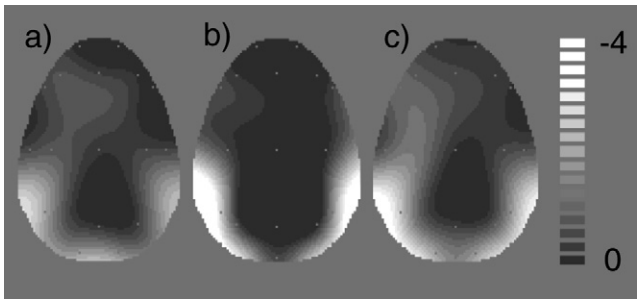

Fig. 4. The scalp distribution of VAN in Experiment 1 (a) and in the constant (b) and random (c) stimulus onset conditions of Experiment 2, calculated from the difference waves (detected vs. undetected) at the time point of 300 ms after the onset of the stimulus. The negative difference between detected and undetected stimuli (VAN) is shown by the white areas.

from each other. This effect was modified by Type × Lobe ($F(2,26) = 8.08$, $p < .01$), Type × Hemisphere ($F(2,26) = 6.09$, $p < .01$) and Type × Lobe × Hemisphere ($F(2,26) = 10.11$, $p < .01$) interactions. These effects show that particularly in left posterior temporal electrodes ($F(2,26) = 15.71$, $p < .001$), hits were associated with larger negativity than misses ($p < .01$) and correct rejections ($p < .001$). This negative difference is VAN.

A 2 (Condition) × 3 (Type) ANOVA on P3 amplitudes in parietal electrode site (PZ) revealed a main effect for Condition ($F(1,13) = 8.24$, $p < .02$): amplitudes in the constant condition were more positive than those in the random condition. The main effect for Type ($F(2,26) = 67.97$, $p < .001$) indicates that ERPs in response to hits were more positive than those to misses ($p < .001$) or correct rejections ($p < .001$), whereas the ERPs to misses and correct rejections did not differ from each other.

In the late 800–1000 ms time window, the ERPs in the constant onset condition showed larger positivity than those in the random onset condition ($F(1,13) = 20.71$, $p < .01$). The significant main effect for Type ($F(2,26) = 28{,}62$, $p < .001$) shows that all the three stimulus types differed from each others. However, this effect was modified by a significant Condition × Type interaction ($F(2,26) = 11.46$, $p < .01$) which shows that in the constant condition particularly the ERPs to hits and misses showed larger positivity than those to correct rejections. In the random condition, the P3 elicited by hits has not yet returned to the baseline level, and therefore hits were associated with larger positivity than the other stimulus types.

3.2.3. Scalp distribution of VAN

Fig. 4 shows the scalp distributions of the VAN effect in Experiment 1 and in the two stimulus onset conditions of Experiment 2. They were generated from the difference waves (hits–misses). The scalp distributions of VAN in Experiment 2 were analysed statistically in an identical manner to Experiment 1 by using the peak amplitudes and latencies between 180 and 400 ms from the difference waves (hits–misses), but now also the stimulus onset condition was included as a factor.

In the 2 × 2 × 5 ANOVA with Condition (constant vs. random stimulus onset), Hemisphere and Site (occipital, posterior temporal, anterior temporal, parietal and frontal) as factors the only statistically significant effects were the main effects for Hemisphere ($F(1,13) = 7.27$, $p < .02$) and Site ($F(4,52) = 8.34$, $p < .01$). VAN was larger over the left than the right hemisphere and larger over occipital and posterior temporal sites than over parietal and frontal sites (all $p < .02$). In the analysis of peak latencies, the main effect for Site was significant ($F(4,52) = 15.61$, $p < .001$). Similarly to the results of Experiment 1, the latencies were longer in anterior temporal sites (331 ms) than in all the other sites (all $p < .05$). In occipital sites, VAN peaked faster (300 ms) than in posterior temporal sits (316 ms) ($p = .01$). The latencies in parietal and frontal sites were shorter than in posterior temporal and occipital sites, but these effects are due to the fact that VAN was hardly observable in parietal and frontal sites. The stimulus onset condition did not have any statistically significant effects in the analyses of peak amplitudes and latencies (all $p > .05$).

Finally, we combined the peak amplitude and latency data from the two stimulus onset conditions of Experiment 2 and compared the scalp distributions of VAN between Experiment 1 and Experiment 2. A 2 × 2 × 5 ANOVA on peak amplitudes with Experiment, Hemisphere and Site (occipital, posterior temporal, anterior temporal, parietal and frontal) as factors did not show any effects for Experiment (all $p > .21$). The main effect for lobe was significant ($F(4,100) = 11.95$, $p < .001$). While there was no significant difference between occipital and posterior temporal sites ($p > .33$), VAN was larger in these two sites than in the other sites (all $p < .01$). In frontal sites, VAN was smaller than in the other sites (all $p < .05$). The analysis of peak latencies showed only a main effect for lobe ($F(4,100) = 10.86$, $p < .001$), indicating shorter latencies in occipital sites than in posterior temporal sites ($p < .001$). In addition, the latencies over anterior temporal areas were longer than over any of the other areas (all $p < .01$), and they were longer over posterior temporal areas than over parietal and frontal areas (all $p < .05$).

3.3. Discussion

Experiment 2 replicates the basic pattern of ERPs found in Experiment 1. The electrophysiological responses associated with visual awareness (the differences in ERPs between hits and misses) were characterised by an early negativity (VAN) that was followed by a later positive difference in P3 time window. On the basis of the signal detection analyses, a more conservative response style was used in Experiment 1 ($\beta = 6.9$) as compared with that in Experiment 2 ($\beta = 3.0$ and 4.5). However, both experiments revealed a similar pattern of electrophysiological correlates of visual awareness (VAN, followed by later

positivity), suggesting that the conservative style of responding does not explain the results. In both experiments, VAN emerged most clearly in posterior temporal and occipital sites, with shorter latency in occipital than in temporal sites. Importantly, all these effects occur similarly independent of whether the stimulus was presented between a forward and a backward mask (Experiment 1) or not (Experiment 2), suggesting that possible additional noise to ERPs from the masking procedure did not hinder the accurate identification of the electrophysiological correlates of awareness. In addition, the manipulation of the stimulus onset (constant vs. random) had no statistically significant effect on either of these electrophysiological responses.

The analyses of the P3 and the latest time window (800–1000 ms) show that the manipulation of the stimulus onset was effective. Although the late positive difference in P3 time window between hits and misses did not differ between the onset conditions, in the constant onset condition the ERPs show a general increase in positivity in P3 amplitudes, followed by another increase in positivity for hits and misses in the latest time window. The general increase of positivity may be related to greater arousal due to stimulus predictability in constant onset condition, as P3 has been shown to correlate with measures of arousal (Friedman, Hakerem, Sutton, & Fleiss, 1973). The later effect was not present in the random onset condition. One should note that the participants were allowed to make their responses only after the question mark appeared 1000 ms after the stimulus offset in the constant condition and 1000–2000 ms after the offset in the random condition. Thus, when the onset and offset of the stimulus was predictable, the participants knew when to expect the question mark to appear, and the ERP difference in the latest time window between the onset conditions is likely to be associated to this aspect of the experiment. Because the latest increase in positivity in the constant condition was observed also for misses, we must assume that this effect reflects the workings of an implicit mechanisms that was triggered by the appearance of the stimulus irrespective of whether the observer was conscious of the stimulus or not.

Although the detection performance did not differ as a function of the predictability of the stimulus onset, this does not mean that the stimulus onset manipulation did not have any effect on detection. In fact, the equal accuracy in detection was expected because we kept the stimulus exposure duration near the subjective threshold by changing it after each trial according to participant's response. That the onset conditions differed in cognitive demand was reflected in different stimulus durations needed for conscious detection of the stimulus. In the random condition the participants were unable to temporally focus their attention in the correct moment, which was reflected in longer stimulus durations in this condition.

The stimulus durations were systematically about one screen refresh longer for hits than for misses. This physical difference was very unlikely to produce the ERP differences between hits and misses (i.e., the electrophysiologial correlates of visual awareness). First, the difference in stimulus duration (19 ms) was less than 30% compared to the overall difference in durations between the stimulus onset conditions (68 ms). In spite of the large difference between conditions, the overall shape of the ERPs (and VAN) did not differ as a function of the stimulus onset condition in the early time windows (before 400 ms) where the physical properties of the stimuli are most likely to have their effects. Second, ERPs are time-locked to the onset of stimuli or changes in the stimulus field, and therefore the slightly longer physical presence of the stimuli in hit trials is not likely to contribute to the ERPs elicited by the onset of the relatively long-lasting stimuli.

The results failed to replicate the enhancement of P1 to consciously detected stimuli reported by Pins and ffytche (2003), although we used a random onset of the stimulus and a similar method as they did to vary the duration of the stimulus based on participants' response. It should be noted that Pins and ffytche tested ERPs with only five participants and their data (see Pins & ffytche, 2003, Fig. 6) seems rather noisy. Similarly to our Experiment 2, there was no P1 for undetected stimuli (misses) in Pins and ffytche's study. However, detected stimuli (hits) elicited a small positive peak around 100 ms in O2, but this peak can be hardly discriminated from the random noise present in the waveforms. The amplitude difference between hits and misses was statistically significant in O2 when tested with a paired *t*-test and treating the results from two blocks of trials as two independent estimates for each five participants so that there were 10 paired samples. It would be interesting to know whether this effect would have been detected by using conventional statistical methods and, for example, with a general ANOVA including a larger sample of electrodes.

Our Experiment 2 included 14 participants, with on average 146 accepted hit trials and 153 accepted miss trials after artifact rejections. Therefore Experiment 2 should have had enough statistical power to detect the P1 effect if it is a real one. Note also that according to the results of Pins and ffytche, the P1 effect should be elicited in response to hits and not to misses, so that it should be related to awareness but not directly to the physical properties of the stimulus. Although our stimulus was a low-contrast stimulus and it did not elicit a P1 wave in miss trials (replicating the result of Pins & ffytche, 2003), the behavioural results clearly indicate that in hit trials the participants were conscious of the stimulus, but no P1 was associated with conscious perception. Thus, the P1 effect in Pins and ffytche (2003) does not seem entirely convincing to begin with, and the present study failed to replicate the finding in a similar setting. Furthermore, it has never been reported in any other ERP study on visual awareness. Taken together, we suggest that visual awareness does not have any realiable effects on ERPs in the P1 time window.

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4. General discussion

In both experiments, the participants were asked to respond according their conscious perception and not to make guesses. The relatively high exclusion rate of participants, particularly in Experiment 1, may have biased the results by excluding observers with very good or poor perceptual abilities or observers using either extremely conservative or liberal response strategies. The signal detection analyses revealed that the included participants followed a conservative strategy, suggesting that they reported being conscious of the stimulus only when they really were conscious of it, without making guesses. In principle, it remains possible that also in missed trials the participants were to some extent conscious of the stimulus but they did not report awareness of it because of the conservative strategy. If the participants would have been conscious of missed stimuli, then ERPs to misses could be expected to differ from those to catch trials in the same direction as ERPs to detected stimuli (hits) did. The ERP data does not support this interpretation, because in the critical time windows the ERPs to missed stimuli did not differ from those to catch trials. Thus, these waveform patterns suggest that missed stimuli were regarded as absent by the brain.

The results showed two electrophysiological correlates of visual awareness in both experiments. First, a negative wave (VAN) was elicited by hits as compared to misses, peaking at posterior temporal and occipital sites around 200–300 ms after the stimulus. VAN was followed by a positive wave after 400–500 ms, peaking at parietal sites. This pattern of early negativity, followed by later positivity corresponds to that found in previous studies on electrophysiological correlates of visual awareness (Koivisto & Revonsuo, 2003; Koivisto et al., 2005; Koivisto et al., 2006; Wilenius-Emet et al., 2004). While these previous studies have measured VAN by using rather complex categorization tasks, the present study extends the previous ones by showing that VAN is elicited as a response to mere conscious detection of a simple stimulus. Thus, in order for VAN to emerge, the task need not call for any higher-level feature discrimination processes that are required in object decision tasks (Ojanen et al., 2003; Wilenius-Emet et al., 2004) or other task requiring discrimination between different types of stimuli (Koivisto et al., 2005; Koivisto et al., 2006).

There was no support for the finding (Pins & ffytche, 2003) that occipital activity around 100 ms after the stimulus (as indicated by P1) would correlate with awareness but not with the nonconscious activity elicited by the physical presence of stimuli. Our participants were clearly aware of the low-contrast stimulus (in hit trials), as indicated by the signal detection analyses, but awareness did not correlate with P1 wave. Thus, the P1 activity is not an electrophysiological correlate for visual awareness. The present study found in both experiments that VAN is the earliest electrophysiological correlate of visual awareness.

VAN seems to be a general marker of visual awareness as it occurs across different tasks and is independent of the method by which the presence of visual awareness is manipulated: binocular rivalry (Kaernbach et al., 1999), change blindness (Koivisto & Revonsuo, 2003), masking (Koivisto et al., 2005; Koivisto et al., 2006; Wilenius-Emet et al., 2004), or contrast manipulation (Ojanen et al., 2003). Also stimuli that are consciously recognised in rapid serial visual presentation elicit a waveform similar to VAN, if the ERPs elicited by unrecognised stimuli (attentional blink) are used as a baseline (Sergent, Baillet, & Dehaene, 2005). VAN may correlate with the subjective experience of seeing the stimulus, that is, with ''visual phenomenal consciousness'', as opposed to later conscious processes performed on the contents phenomenal consciousness (Block, 2001; Revonsuo, 2006). The later positive difference, corresponding to P3 class of potentials, is likely to correlate with later stages of conscious processing (''reflective consciousness'') that involve higher cognitive operations in working memory over attentionally selected contents of phenomenal consciousness, that is, with ''secondary conscious processes'' (Pins & ffytche, 2003) or ''reflective consciousness'' (Block, 2001; Revonsuo, 2006). Thus this latter effect is not directly related to visual (phenomenal) awareness but may require it as a prerequisite (Koivisto et al., 2005; Koivisto et al., 2006) or it may reflect the confidence of the conscious decision (Eimer & Mazza, 2005).

In line with the distinction between phenomenal consciousness and reflective consciousness, our recent studies have revealed that VAN emerges relatively independent of different attentional manipulations. When observers attended to target stimuli and ignored nontargets, both targets and nontargets elicited VAN (Koivisto & Revonsuo, 2007; Koivisto et al., 2005). The early part of VAN (130–200 ms) was identical for targets and nontargets, and only the later part of VAN in left posterior temporal site (200–260 ms) was modulated by the manipulation of selective attention which produced a *selection negativity* (SN) in this time window. SN is reflected as a negative amplitude shift in response to targets at posterior electrode sites around 200 ms after the stimulus onset, providing a high-resolution measure of the time at which a particular feature is selectively processed in the brain (Hillyard & Anllo-Vento, 1998; Proverbio & Zani, 2003). SN was observed also in response to undetected targets, suggesting that this effect can be dissociated from visual awareness and VAN (Koivisto & Revonsuo, 2007; Koivisto et al., 2005). However, the late positive difference in P3 time window was strongly dependent on selective attention. Similarly, a strong VAN was observed independent of whether attention was focused on the global aspects (overall shape) of a stimulus or on the local parts of the stimulus, but the late positive difference in P3 time range was absent or greatly attenuated in the local attention condition (Koivisto et al., 2006). The absence of the late positive difference for consciously recognised stimuli in the local attention condition suggests that

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this deflection cannot be a direct correlate of visual (phenomenal) awareness. Thus, the electrophysiological correlate of visual awareness appearing consistently across different tasks and attentional conditions is VAN.

Although the studies manipulating visual awareness and attention at the same time (Koivisto & Revonsuo, 2007; Koivisto et al., 2005; Koivisto et al., 2006) seem to suggest that the early neurophysiological processes leading to visual awareness are relatively independent of selective attention, this conclusion may be generalised only to clearly visible, full-contrast stimuli which were used in the earlier studies. According to a more typical view, attention is necessary for visual awareness (Dehaene & Naccache, 2001; Mack & Rock, 1998). In addition, a large literature on attention, typically using suprathreshold stimuli, has shown increased firing rate of neurons in visual cortical areas when attention is directed to particular locations or stimulus features (for reviews, see Hillyard & Anllo-Vento, 1998; Proverbio & Zani, 2003). The competition among groups of cells coding for neighbouring objects is biased in favour of the attended one (Crick & Koch, 2003). Therefore, top-down attentional modulations may increase the level of cortical activation at the same ventral areas that are associated with visual awareness, making near-threshold stimuli that would otherwise remain unconscious more easily accessible to visual awareness. This is consistent with the finding in Experiment 2 that a low-contrast stimulus near the threshold for visual awareness could be consciously detected with a shorter stimulus duration in the condition where the stimulus onset could be predicted and hence accurate temporal allocation of attention was possible, as compared with unpredictable condition. Thus, although the question whether some type of attention is always a prerequisite for visual awareness or not remains to be solved (Lamme, 2004), at least attention can facilitate access to visual awareness under difficult viewing conditions.

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