

Independence of Visual Awareness from the Scope of Attention: an Electrophysiological Study

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Recent brain imaging studies have revealed that increased neural activity along the ventral visual stream and parietal and frontal areas is associated with visual awareness. In order to study the time-course and temporal aspects of awareness, we examined electrophysiological correlates of conscious vision in two masking experiments. The differences in event-related potentials (ERPs) between unmasked (consciously recognized) and masked (unrecognized) stimuli were considered to be electrophysiological correlates of awareness. Two attentional conditions (global, local) were included to examine the relationship between the scope of attention and awareness. Two ERP-deflections were found to correlate with awareness. First, awareness was associated with a posterior negative amplitude shift 130–320 ms after the stimulus. This effect was present in both attention conditions, suggesting that it emerges independent of the scope of attention. Second, ERPs to unmasked stimuli became more positive as compared with masked stimuli around 400 ms, peaking at parietal sites. This effect was attenuated in the local attention condition, although the participants were aware of the stimuli, suggesting that the late positivity does not directly correlate with visual awareness. The results imply that the earlier negativity is the earliest and most direct correlate of visual awareness.

Keywords: attention, consciousness, EEG, ERP

Introduction

Recently, a growing number of brain imaging studies have begun to reveal the neural correlates of visual awareness: the brain areas which are involved in generating subjective visual experience (for reviews, see Kanwisher, 2001; Rees and Lavie, 2001; Rees, Kreiman, and Koch, 2002). These studies have indicated several different brain areas whose activation correlates with awareness of visual stimuli. There is a consensus among the researchers that the activation of the ventral visual stream, a set of pathways from V1 to the inferotemporal cortex, plays an important role in generating conscious visual experience (Bar *et al.*, 2001; Beck *et al.*, 2001; Moutoussis and Zeki, 2002). It has been suggested that the ventral activation correlates with the content of visual awareness (Kanwisher, 2001). However, the ventral stream can also be activated by unperceived stimuli which escape awareness (Driver *et al.*, 2001; Moutoussis and Zeki, 2002), suggesting that ventral activation is not sufficient for awareness to arise. In addition to the activation of the ventral stream, activations of parietal and prefrontal attention areas are commonly associated with conscious visual perception (Lumer and Rees, 1999; Beck *et al.*, 2001).

Electrophysiological methods and event-related brain potentials (ERPs) have an inferior spatial resolution as compared with

those of positron emission tomography or functional magnetic resonance imaging, but their fine temporal resolution might illuminate the time-course of the neural events that lead to aware visual perception. A magnetoencephalography (MEG) study used a masking procedure and found that the right lateral occipital cortex showed signals correlating with aware object detection between 258 and 297 ms after the stimulus onset (Vanni *et al.*, 1996). The same stimuli and procedure were used in an ERP study (Wilenius-Emet *et al.*, 2004), reporting a 'visual awareness negativity' (VAN) that correlated with the crossing of the subjective perceptual threshold and peaked in the same time window as in the MEG study. However, the negative deflection (VAN) as well as response times may be delayed if low intensity (contrast) stimuli are used (Ojanen *et al.*, 2003). Studies on binocular rivalry (Kaernbach *et al.*, 1999) and change blindness (Koivisto and Revonsuo, 2003, 2005) have measured ERPs to a change in the content of visual awareness while the physical stimulation remains constant. In these studies the change in visual awareness was associated with enhanced posterior negativity peaking soon after 200 ms. In harmony with the above findings from normal subjects, neglect patients who fail to see a stimulus in the contralesional side of space when presented together with an ipsilesional stimulus show reduced negativity in the N1 time window when they are not aware of the neglected stimulus (Marzi *et al.*, 2000; Driver *et al.*, 2001).

Usually the early negative enhancement in the N1–N2 time window (VAN) is followed by a later enhancement of positivity for aware stimuli, peaking at parietal sites around 400 ms in the P3 time window (Kaernbach *et al.*, 1999; Koivisto and Revonsuo, 2003, 2005; Wilenius-Emet *et al.*, 2004). Similar positivities during the P3 time window, but without the preceding negativity, have also been associated with aware perception in other recent change blindness studies (Niedeggen *et al.*, 2001; Turrato *et al.*, 2002; Fernandez-Duque *et al.*, 2003) and in attentional blink (Vogel *et al.*, 1998; McArthur *et al.*, 1999; Kranczioch *et al.*, 2003).

The neural correlates of visual awareness have usually been operationally defined as the difference between brain responses to consciously perceived and unperceived stimuli. Assuming that consciously perceived stimuli receive more attention than unperceived stimuli, the neural correlates of awareness may be affected by attention as well as awareness. The relationship between attention and awareness is a timely topic in cognitive science and cognitive neuroscience (Lamme, 2004; Block, 2005), but adequate empirical experiments capable of timing their independent neural effects and of determining their interactions are lacking. In the present ERP study, visual

awareness and attention were manipulated at the same time in order to test, first, which one of the two potential electrophysiological correlates of visual awareness (VAN or late positivity) is a more direct correlate of awareness, and second, whether either of them emerges independent of the attentional manipulation. We manipulated attention to the global (whole) versus local (part) level of hierarchical stimuli, because this type of manipulation has been shown to have effects on both early and late ERP components (Han *et al.*, 2000).

According to the global precedence hypothesis, perceptual processing of complex objects proceeds from the global structure to the analysis of the local elements (Navon, 1977, 1981). The basic finding is that response times are faster for global shapes than for local shapes (e.g. Navon, 1977, 1981; Luna *et al.*, 1990; Paquet, 1999), although under some conditions a local precedence can be observed (Pomerantz, 1983). In addition, a global dominance is observed when the global and local structures are inconsistent (e.g. a global E made of local Hs): the global shapes interfere with the identification of local shapes more strongly than the local shapes interfere with identification of global shapes (Navon, 1977, 1981). ERP studies using supraliminal stimuli have revealed differences between electrophysiological responses to global and local targets in early sensory as well as late endogenous components. For example, Han *et al.* (1997, 1999, 2000, 2001) have consistently reported enhanced posterior P1 and N2 amplitudes in response to local, as compared with global, targets, and sometimes enhanced posterior N1 amplitudes for local targets (Han *et al.*, 2000) and enhanced frontal P2 amplitudes for global targets (Han *et al.*, 2000, 2001). However, other studies have not reported differences in P1 (Proverbio *et al.*, 1998) or have found enhanced P1 amplitudes for global targets (Heinze *et al.*, 1998). Proverbio *et al.* (1998) report enhanced N1 for global targets. The most consistent result in this literature seems to be that attention has an effect on the P3 potential: the P3 amplitude is larger and/or the P3 latency is shorter in ERPs to global targets as compared with ERPs to the local level (Han *et al.*, 1997, 1999, 2000, 2001; Proverbio *et al.*, 1998).

Because attention to the global or local level may modulate nonconscious processes as well as conscious ones (Koivisto and Revonsuo, 2004), and electrophysiological effects of attention may be observed in different processing stages from early sensory to later endogenous processing stages, we manipulated both consciousness and attention at the same time to track the time point when these two factors start to interact. In Experiment 1, the participants tried to recognize the orientation of the global or the local corners of Navon-like hierarchical stimuli (Navon, 1977). The stimuli were followed by a mask to make them consciously visible or invisible (see Fig. 1). On the basis of the earlier ERP studies using supraliminal stimuli (Han *et al.*, 1997, 2001; Proverbio *et al.*, 1998), we predicted that at least the late potentials (P3) to consciously perceived stimuli should be attenuated in local attention condition as compared with global condition. Therefore, observing a VAN in both attention conditions but no later positive enhancement (in the P3 range) in local condition would suggest that of these two effects, only VAN is a direct correlate of visual awareness. On the other hand, if the late positivity is observed in both attention conditions but the VAN is present in only one or none of the conditions, then only the late positivity is a direct correlate of visual awareness.

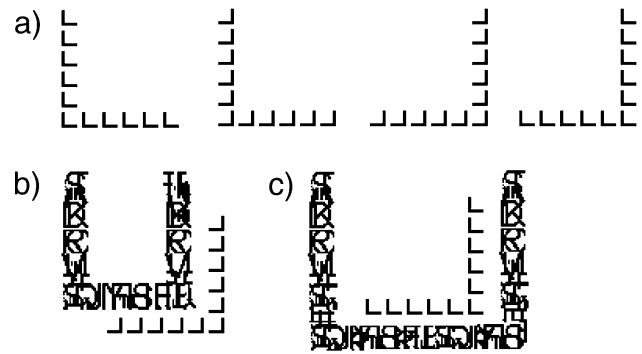


Figure 1. Examples of the target stimuli (a). In order to keep the stimuli constant while the level of attention was manipulated, hierarchically structured stimuli were used: global corners made up of local corners. In two different conditions, attention was directed either to the global or to the local shape. The two examples on the second line show the smaller (b) and the larger (c) mask, and illustrate the spatial relationship between the targets and masks in the 'unmasked' condition. Note that the targets are masked when one keeps the positions of the stimuli constant but changes the masks from the smaller one to the larger one and vice versa.

Experiment 1

Materials and Methods

Participants

The 12 participants were right-handed (Oldfield, 1971), healthy students (six males), 21–25 years old, with normal or corrected to normal vision from the University of Turku. They sat in a comfortable chair in a dimly lit room and completed two conditions (global and local attention) presented in a counterbalanced order. The experiment was undertaken with the understanding and written consent of each participant.

Stimuli

The target stimuli were left and right global corners ($1.7 \times 1.7^\circ$) which were composed of left or right local corners ($0.2 \times 0.2^\circ$) (Fig. 1a). The corners at the two different levels of hierarchy were either consistent (e.g. global left corner made up of local left corner) or inconsistent (e.g. global left corner made up of local right corner) with each other. Two versions of a backward mask, one smaller and one larger, were used. They were angular U-shapes ($5.0 \times 5.0^\circ$ and $7.0 \times 8.3^\circ$) made up of random local letters (line width: 0.06°). The masks always appeared in the centre of the screen. The target was positioned in the centre of the screen or 1.6° below, to the left or to the right of it. When the target was positioned below the centre and to the left (left global corners) or right (right global corners), it was masked by the left/right corner of the larger mask but was visible outside of the smaller mask (Fig. 1b). When the target was in the centre, followed by the smaller mask, it was masked. When it was followed by the larger mask, it was visible inside the U-shape of the mask (Fig. 1c). Thus, the duration of the targets and masks and their stimulus-onset asynchrony could be kept identical in the unmasked and masked conditions, so that the ERP differences between the conditions would not be confounded by the different timing of the masks.

Procedure

The stimuli were presented in black (0.2 cd/m^2) on a white background (17.5 cd/m^2) on a 21" computer screen. The target (or blank screen) was presented for 27 ms, followed immediately by a mask for 40 ms. The interstimulus interval between the participant's response and the next trial was 1 s.

Two attentional conditions (global and local) were conducted, each involving 320 trials presented in two blocks. In the global condition, the participants were asked to recognize the global shape of the target, whereas in the local condition they were asked to recognize the local shape. The order of the conditions was counterbalanced across the participants. Each condition contained 128 masked trials, 128 unmasked

trials in which the mask did not mask the target and 64 catch trials involving only the mask with a blank screen in the place of the target. Half of the hierarchical targets were consistent and the other half were inconsistent. The participants held a response box on their lap with their left hand and used the right hand for responding by pressing one of three buttons. The computer recorded the responses and the response times from the stimulus onset. The participants were asked to respond to left corners with the index finger, to right corners with the middle finger, and to press a 'pass' button with the ring-finger when they could not recognize or see the corner. They were told that in some of the trials only the mask would be presented without any preceding stimulus. The participants were told that accuracy and response times were measured. They were asked to maintain their fixation on the centre of the screen and not to move their eyes during the trials.

EEG Recording

EEG was continuously recorded using the following nine scalp electrodes (Ag/AgCl) arranged according to the international 10/20 system: F3, F4, CZ, P3, P4, T5, T6, O1 and O2. An electrode below the left eye was used for monitoring blinks and vertical eye movements, and an electrode placed 1.5 cm to the right of the right eye was used for monitoring lateral eye movements. The nose was used as a reference and the forehead as ground. Electrode impedances were kept below 5 k Ω . EEG was amplified (SynAmps Model 5083) by using a band-pass of 0.15–30 Hz. The sampling rate was 250 Hz. The ERP components were analysed with the NeuroScan equipment. Baseline correction was performed to the activity in the –100 to 0 ms preceding the onset of the target. All epochs involving voltage peaks >70 μ V in the EEG or the EOG electrodes were rejected offline. ERPs were averaged separately for correctly recognized unmasked trials and unrecognized masked trials (pass response) in the two attention conditions as a function of consistency.

Results

Performance

The accuracy rates in different conditions are presented in Table 1. On average, the performance level was high in unmasked trials (92% correct) and low in masked trials (1% correct; 99% were 'pass' responses). In catch (mask-only) trials, responses indicating perception of 'left corner' or 'right corner' were extremely rare: three responses in the global condition and one response in the local condition, each made by different subjects. A 2 (attention: global, local) \times 2 (consistency: consistent, inconsistent) analysis of variance (ANOVA) was conducted on accuracy scores in the unmasked conditions. This analysis revealed a significant main effect for attention [$F(1,11) = 8.99, P < 0.02$], showing that the accuracy level was higher in the global (96%) than the local (86%) condition. Other effects were not statistically significant.

Mean response times (RTs) were measured from the stimulus onset. The RTs for correct responses in unmasked trials were 521 ± 41 ms for consistent global targets and 550 ± 54 ms for inconsistent global targets. The corresponding values for consistent and inconsistent local targets were 788 ± 183 and 797 ± 159 ms, respectively. The attention \times consistency ANOVA on RTs showed a main effect for attention [$F(1,11) = 27.58, P < 0.001$], indicating faster responses to global targets (536 ms) than to local targets (793 ms). The main effect for consistency was nearly significant [$F(1,11) = 4.65, P = 0.054$]. The attention \times consistency interaction was not statistically significant ($F < 1$).

Table 1

The percentage of correct recognition and the percentage of pass-responses in unmasked and masked trials as a function of attention (global versus local) and consistency in Experiment 1 (standard deviations in parentheses)

Attention	Consistency	Unmasked		Masked	
		Correct	Pass	Correct	Pass
Global	Consistent	96 (2)	2 (3)	1 (1)	99 (2)
	Inconsistent	96 (3)	2 (5)	1 (2)	98 (2)
Local	Consistent	85 (12)	8 (7)	0 (1)	100 (1)
	Inconsistent	88 (13)	6 (8)	0 (1)	100 (1)

ERPs

Figures 2 and 3 display the ERPs in different conditions. Visual inspection of the grand average waves revealed P1 (75–130 ms) and N1 (130–210 ms) potentials in occipital, temporal and parietal sites. In addition, P2 (210–300 ms), N2 (210–320 ms) and P3 (320–550 ms) potentials were observed in all electrode sites. The peak amplitudes and latencies of the potentials were statistically analysed with type (masked versus unmasked) \times attention (global versus local) \times consistency \times lobe \times hemisphere ANOVAs. For the P1 and N1 components, the factor lobe included three levels (occipital, temporal, and parietal); for the analyses of the P2, N2 and P3 all the four lobes were included. Greenhouse-Geisser corrections were applied to the P -values when the degrees of freedom were >1. Here we summarize and focus on those findings which are relevant to the current topic and that have the stimulus type (masked versus unmasked), attention or consistency as a factor.

P1 amplitudes showed a type \times attention \times hemisphere interaction [$F(1,11) = 7.11, P < 0.05$] but further statistical tests did not show any reliable source for this interaction. The type \times attention interaction [$F(1,11) = 8.43, P < 0.02$] for latencies was due to 5 ms longer P1 latencies to unmasked than to masked stimuli in the local attention condition [$F(1,11) = 7.50, P < 0.02$]. The attention \times lobe interaction [$F(2,22) = 12.20, P < 0.001$] shows that in the global condition P1 latencies were shorter in occipital and temporal sites as compared with parietal sites [$F(2,22) = 6.83, P < 0.02$], whereas such a difference was not statistically significant in the local condition.

N1 amplitudes were stronger to unmasked (-8.5μ V) than to masked (-6.3μ V) stimuli [$F(1,11) = 20.84, P < 0.01$], particularly at occipital and temporal electrodes [$F(2,22) = 9.16, P < 0.01$]. N1 latencies were faster to masked (173 ms) than to unmasked (180 ms) stimuli [$F(1,11) = 23.17, P < 0.01$].

P2 amplitudes were more positive to masked (0.4μ V) than to unmasked stimuli (3.6μ V) [$F(1,11) = 102.14, P < 0.001$], with the greatest difference at occipital and temporal electrodes [$F(3,33) = 35.26, P < 0.001$]. The attention \times lobe interaction [$F(3,33) = 5.85, P < 0.02$] suggests that attention to local form (2.6μ V) was characterized by stronger positivity than attention to global form (1.8μ V) in frontal sites, whereas in occipital sites attention to global form (3.0μ V) was characterized by stronger positivity than attention to local form (1.8μ V). The type \times attention \times hemisphere interaction [$F(1,11) = 6.67, P < 0.05$] seems primarily to be due to amplitudes being more negative over the right hemisphere (-0.2μ V) than over the left (0.7μ V) for the unmasked stimuli in the local attention condition. The type \times consistency \times hemisphere [$F(1,11) = 22.47, P < 0.01$] interaction was due to a stronger consistency effect for unmasked stimuli over the left hemisphere as compared with that over the right hemisphere [$F(1,11) = 6.15, P < 0.05$]; the consistency effect was manifested as larger negativity to consistent stimuli as compared with inconsistent stimuli. The type \times attention \times consistency \times lobe interaction [$F(3,33) = 3.73, P < 0.05$] suggests that the consistency effect was the largest in temporal sites for unmasked stimuli in the local attention condition. Note that there is no evidence of a consistency effect for unmasked stimuli in the global attention condition. P2 latencies were faster for unmasked (236 ms) than masked (243 ms) stimuli [$F(1,11) = 8.70, P < 0.02$].

N2 amplitudes were more negative to unmasked (-2.7μ V) than to masked (0.9μ V) stimuli [$F(1,11) = 79.33, P < 0.001$], with the largest difference at occipital and temporal sites [$F(3,33) = 13.02, P < 0.01$]. ERPs in the local attention condition were more negative than those in the global condition in occipital electrodes [$F(3,33) = 5.20, P < 0.05$] and over the right hemisphere [$F(1,11) = 10.65, P < 0.01$]. The type \times attention \times hemisphere interaction [$F(1,11) = 5.80, P < 0.05$] was due to larger difference between masked and unmasked stimuli in the local attention (4.4μ V) than in the global attention condition (2.4μ V) over the right hemisphere [$F(1,11) = 8.32, P < 0.02$]. The consistency effect was larger in the local than in the global attention condition [$F(1,11) = 5.57, P < 0.05$]. The type \times consistency \times hemisphere interaction [$F(1,11) = 10.08, P < 0.01$] was due to larger consistency effect for unmasked stimuli over the left hemisphere (0.7μ V) than the right hemisphere (-0.1μ V) [$F(1,11) = 6.55, P < 0.05$]. Further statistical analyses of the Type \times consistency \times lobe interaction [$F(3,33) = 5.44, P < 0.02$] did not find any reliable source for it; the same holds true for the four-way interaction for latencies [$F(3,33) = 4.09, P < 0.02$].

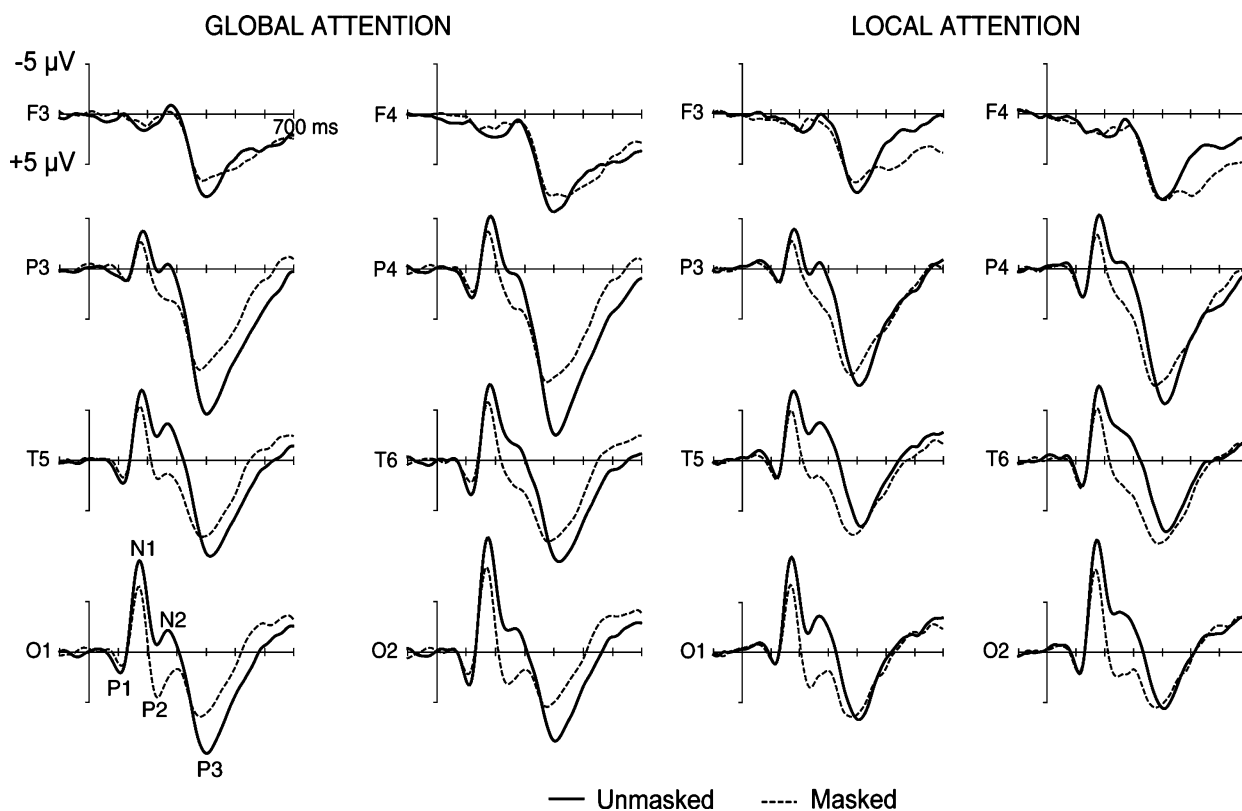


Figure 2. Grand average ERPs to unmasked and masked stimuli in the global and local attention conditions (Experiment 1).

P3 amplitudes were more positive to unmasked ($10.7 \mu\text{V}$) than to masked ($9.2 \mu\text{V}$) stimuli [$F(1,11) = 7.79$, $P < 0.02$], with the largest difference at parietal sites ($15.1 \mu\text{V}$ versus $11.8 \mu\text{V}$) [$F(3,33) = 16.44$, $P < 0.001$]. Most importantly, the type \times attention [$F(1,11) = 7.79$, $P < 0.02$] and type \times attention \times consistency [$F(1,11) = 6.83$, $P < 0.05$] interactions suggest that the amplitude difference between unmasked and masked stimuli was larger in the global attention condition ($11.7 \mu\text{V}$ versus $9.0 \mu\text{V}$) than in the local one ($9.7 \mu\text{V}$ versus $9.3 \mu\text{V}$), particularly for consistent stimuli. In addition, the difference favouring the global condition was the largest at parietal sites, as indicated by the type \times attention \times lobe interaction [$F(3,33) = 6.49$, $P < 0.02$]. P3 latencies were shorter in response to masked stimuli (396 ms) than to unmasked stimuli (415 ms) [$F(1,11) = 7.80$, $P < 0.02$]. This effect was modified by type \times lobe [$F(3,33) = 14.20$, $P < 0.001$] and type \times attention \times consistency \times hemisphere [$F(1,11) = 5.30$, $P < 0.05$] interactions, suggesting that the latencies for masked stimuli were shorter than for unmasked ones over the occipital, temporal and parietal sites, but not over the frontal sites and not for consistent stimuli over the right hemisphere in the local attention condition.

Discussion

The results revealed that visual awareness was reflected in ERPs as an early negative enhancement (VAN) in the N1–N2 time range, particularly in occipital and posterior temporal sites. VAN was robust in both attention conditions, suggesting that it emerges independent of the scope of attention. Only the later portion of VAN (in P2–N2 time window) was modified by attention over the right hemisphere. This finding is similar to recent findings in our laboratory, showing that manipulation of selective attention does not have any effect on the early part of VAN but it modifies only the later part of VAN after 200 ms from stimulus onset (Koivisto *et al.*, 2005). VAN was followed by a positive enhancement in P3 latency range, peaking at parietal sites. The manipulation of attention had the strongest influence on the positivity: the positive enhancement of ERPs to recognized stimuli, as compared with those to unrecognized stimuli, was present only in the global attention condition. In addition, attention modulated the ERPs in the P1,

P2 and N2 time windows. Some of these effects of attention were not related to awareness, suggesting that stimuli which failed to exceed the subjective threshold were nevertheless unconsciously perceived. However, the consistency of the global and local form modified ERPs only in aware (unmasked) conditions after 210 ms.

In Experiment 1 we kept the stimulus-mask stimulus-onset asynchrony (SOA) constant but varied the spatial overlap so that in the masked (nonconscious) condition the stimulus and the mask overlapped whereas in the unmasked (conscious) condition they did not. As a result, the observers' phenomenal experience (i.e. visual awareness) varied between the masked and unmasked condition. Whereas in the unmasked condition they had a subjective visual experience of only the mask, in the unmasked condition they were subjectively aware of both the stimulus and the mask. [The fact that the observers did not recognize the orientation of the corner in the masked global attention condition suggests that they could not consciously detect the appearance of the stimulus, because the orientation of the global corner could have been easily recognized on the basis of detecting something (i.e. the vertical line of the stimulus) either on the left or the right.] This phenomenal difference between the conditions is not a disadvantage in our experiment since the very aim was to manipulate visual awareness of the stimulus. A potential disadvantage in the masking procedure of Experiment 1 may lie in the lack of spatial overlap between the stimulus and mask in the unmasked, conscious condition. The stimulus and the mask stimulated different areas of the retina, and therefore, different regions in retinotopic areas in visual cortex (e.g. V1) in the unmasked condition, which might be responsible for the electrophysiological differences between masked and unmasked conditions.

Experiment 2

In order to rule out that the spatial nonoverlap between the stimulus and mask was responsible for the electrophysiological differences observed between consciously recognized and unrecognized stimuli in the previous experiment, we used two types of masking in Experiment 2. On the one hand, we kept the SOA constant and varied

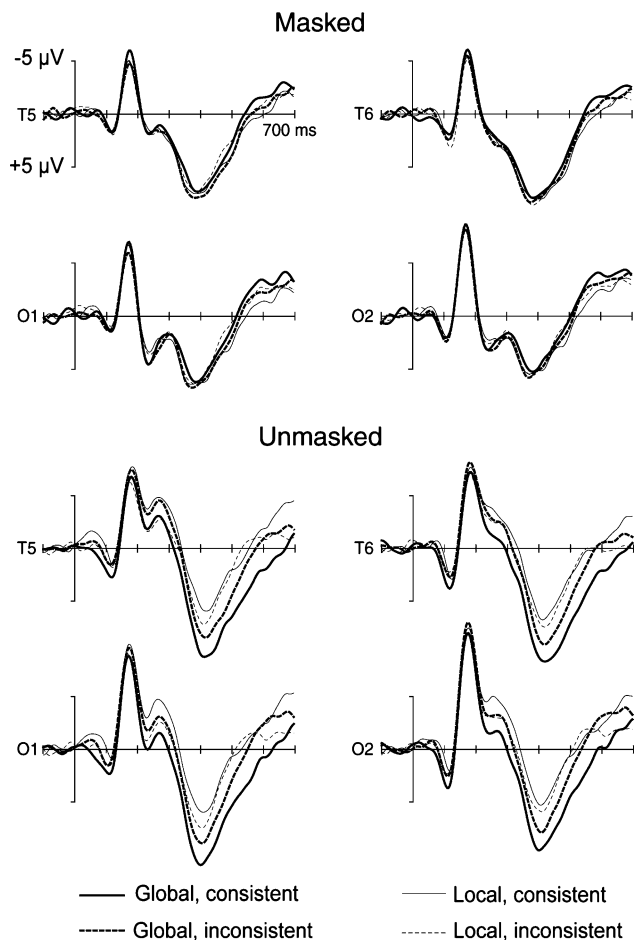


Figure 3. Grand average ERPs to masked and unmasked stimuli as a function of attention and consistency in occipital and posterior temporal electrodes (Experiment 1).

the spatial overlap between the stimulus and mask in the same way as we did in Experiment 1. On the other hand, we kept the spatial overlap between the stimulus and mask constant and manipulated the SOA between the stimulus and mask to make observers nonconscious (at a short SOA) or conscious (at a long SOA) of the stimulus. Assuming that the mask elicits its own electrophysiological response that is summed to the response elicited by the stimulus, this traditional masking procedure has the disadvantage that the difference in the onsets of the mask between conscious and nonconscious trials may contribute differently to the ERPs in conscious and nonconscious conditions.

If the electrophysiological correlates of consciousness observed in Experiment 1 were in fact due to the physical difference between masked (spatial overlap between the stimulus and mask) and unmasked (spatial nonoverlap) conditions, then they should not appear in the spatial overlap mask condition manipulating only the SOA (Experiment 2). And if the electrophysiological correlates of consciousness in the spatial overlap mask condition (SOA manipulation) will not be replicated in the spatial nonoverlap mask condition, then they are probably due to the different electrophysiological responses elicited by the masks at short and long SOAs. However, if the same set of electrophysiological correlates of awareness appear in both types of masking, then it is justified to hold that they are independent of the possible effects of spatial overlap and SOA.

Materials and Methods

Participants

The participants were sixteen right-handed (Oldfield, 1971), healthy students (four males), 20–28 years old, with normal or corrected to normal vision from the University of Turku. They sat in a comfortable

chair in a dimly lit room and completed two conditions (global and local attention) presented in a counterbalanced order. Four of the participants were rejected from the main analyses of the experiment because they either performed too well or too poorly, so that it was not possible to compute ERPs for each type of trials. The experiment was undertaken with the understanding and written consent of each participant.

Stimuli and Procedure

The target stimuli and the masks were the same as in Experiment 1. Each trial began by a fixation cross appearing at the center of the screen for 1000 ms, followed by the stimulus for 33 ms and then followed by one of three types of mask for 50 ms. (i) The immediate spatial mask overlapped spatially with the stimulus (SOA = 33 ms). (ii) The immediate nonspatial mask did not overlap spatially with the stimulus (SOA = 33 ms). (iii) The delayed spatial mask overlapped spatially with the stimulus (SOA = 188 ms). The interstimulus interval was 3 s, during which the participants responded to the orientation of the global or local shape of the stimulus. The different stimulus-mask combinations allowed us to compare two masking procedures. One of the procedures was identical to that in Experiment 1: the stimulus and the mask were presented at the same short SOA both in the masked (immediate spatial mask) and in the unmasked (immediate nonspatial mask) condition, but in the unmasked condition the stimuli were visible. In the other masking procedure, the stimulus and the mask overlapped spatially but in the unmasked condition (delayed spatial mask) the mask followed the stimulus at a longer SOA, making the stimulus visible. The masked trials and the immediate nonspatial and delayed spatial mask trials were presented in random order within each stimulus block.

The global and local attention conditions were conducted in two blocks, with the order of the conditions counterbalanced across the participants. There were 128 masked trials (immediate spatial mask) and 192 unmasked trials (immediate nonspatial mask and delayed spatial mask) in each attention condition. The participants held a response box on their lap and used the index, middle and ring fingers of the right or the left hand (counterbalanced across the participants) for pressing one of three buttons. The left button corresponded to 'left' answers, the right button to 'right' answers. A 'pass' button was located between the left and right buttons. The participants were asked to press the left or the right button immediately when they subjectively perceived a left or a right corner. They were not allowed to guess but to press the pass button when could not recognize or see the corner.

EEG Recording

EEG was recorded using tin electrodes attached to an electrocap (Electro-Cap International, Inc., USA) with international 10/20 system sites F1, F2, F3, F4, F7, F8, Fz, P3, P4, Pz, C3, C4, Cz, T3, T4, T5, T6, O1 and O2. An electrode below the left eye was used for monitoring blinks and vertical eye movements, and an electrode placed 1.5 cm to the right of the right eye was used for monitoring lateral eye movements. The nose was used as a reference and an electrode between Fz and Cz as ground. Electrode impedances were kept below 5 k Ω . EEG was amplified (SynAmps Model 5083) by using a band-pass of 0.1–100 Hz. The sampling rate was 500 Hz. The ERP components were analysed with the NeuroScan equipment. Baseline correction was performed to the activity in the –100 to 0 ms preceding the onset of the target. All epochs involving voltage peaks >70 μ V in the EEG or the EOG electrodes were rejected offline.

Results

Performance

The accuracy rates and RTs in different conditions are presented in Table 2. As compared with the corresponding trials in Experiment 1, the performance level was equally high in the immediate nonspatial mask trials (90% correct) and slightly better in the masked trials (15% correct; 84% were 'pass' responses). The 6 ms longer stimulus duration and SOA in Experiment 2 is likely to explain the latter finding. A 2 (attention: global, local) \times 2 (consistency: consistent, inconsistent) \times 2 (masking: immediate nonspatial, delayed spatial) ANOVA was conducted on accuracy scores in the unmasked (conscious) conditions. This analysis

Table 2

The response times (RT), the percentage of correct recognition and the percentage of pass-responses in different mask conditions as a function of attention (global versus local) and consistency in Experiment 2 (standard deviations in parentheses)

Attention	Consistency	Immediate nonspatial mask			Delayed spatial mask			Immediate spatial mask		
		RT (ms)	Correct	Pass	RT (ms)	Correct	Pass	RT (ms)	Correct	Pass
Global	Consistent	593 (89)	97 (4)	3 (4)	627 (141)	94 (15)	5 (12)	-	22 (26)	77 (27)
	Inconsistent	654 (138)	92 (8)	7 (8)	655 (176)	91 (13)	8 (12)	-	26 (29)	73 (30)
Local	Consistent	756 (128)	90 (12)	10 (12)	868 (188)	69 (27)	29 (24)	-	7 (10)	92 (10)
	Inconsistent	879 (125)	82 (20)	13 (13)	858 (128)	79 (20)	19 (17)	-	6 (4)	93 (6)

revealed a significant main effect for attention [$F(1,11) = 11.59$, $P < 0.01$], showing that the accuracy level was higher in the global (94%) than the local (80%) condition. The main effect for masking [$F(1,11) = 5.01$, $P < 0.05$] showed more accurate responses in immediate nonspatial masking (90%) than in delayed spatial masking (83%). In addition, the mask \times consistency interaction [$F(1,11) = 7.99$, $P < 0.02$] indicated that the consistency effect was stronger in the immediate nonspatial masking than in the delayed spatial masking condition. Attention \times masking [$F(1,11) = 15.03$, $P < 0.01$] and attention \times consistency \times masking [$F(1,11) = 5.40$, $P < 0.05$] interactions suggested that delayed spatial masking was more effective than immediate nonspatial masking in the local condition, particularly for consistent targets.

Response times were analysed with an attention \times consistency \times masking ANOVA on correct responses to consciously recognized targets. Responses were faster in the global (632 ms) than in the local (840 ms) condition [$F(1,11) = 38.32$, $P < 0.001$]. The main effect for consistency was significant [$F(1,11) = 27.08$, $P < 0.001$], indicating faster responses to consistent (711 ms) than to inconsistent (762 ms) targets. The consistency effect was stronger after immediate nonspatial masking than after delayed spatial masking [$F(1,11) = 15.68$, $P < 0.01$]. In immediate nonspatial masking, the consistency effect (93 ms) was highly significant [$F(1,11) = 132.15$, $P < 0.001$], whereas this effect was not present in delayed spatial masking (9 ms) ($F < 1$). The consistency effect was particularly strong in the local attention condition in immediate nonspatial masking, as indicated by the attention \times consistency \times masking interaction [$F(1,11) = 18.19$, $P < 0.01$].

The analyses of response times and accuracy rates showed that the global form of the stimulus was easier to recognize than the local form. In addition, the delayed spatial masking procedure interfered more strongly with performance than the immediate nonspatial masking procedure, particularly with responding to the local shape of the stimulus. Also the consistency effect was smaller in the delayed spatial than the immediate nonspatial masking procedure; this effect was due to increase of RTs and errors to consistent targets in the delayed mask condition. Thus, in delayed spatial masking the spatial overlap between the stimulus and the mask at 188 ms SOA interrupted the processing of stimuli, particularly in the more difficult local attention condition. In general, the consistency effect was stronger after immediate nonspatial masking in Experiment 2 than in Experiment 1. These experiments differed in two ways. First, the stimulus durations and the SOAs in Experiment 2 were longer than those in Experiment 1. Second, Experiment 2 included more variable masking conditions, which may have altered the processing strategy of the participants. We were unable to determine which of these differences was responsible for the greater sensitivity of Experiment 2 to consistency.

ERPs

ERPs were averaged separately for unrecognized masked trials (pass response) and correctly recognized immediate nonspatial mask and delayed spatial mask trials in the two attention conditions (Fig. 4). Consistency effects were not analysed as the main purpose was to replicate the awareness-related effects. P1 (75–130 ms), N1 (130–210 ms), P2 (190–260 ms), N2 (210–320 ms) and P3 (320–550 ms) peak amplitudes and latencies were identified. Type (masked versus immediate nonspatial mask versus delayed spatial mask) \times attention (global versus local) \times lobe \times hemisphere ANOVAs were conducted on peak amplitudes and latencies. For the P1 and N1 components, the factor lobe

included three levels (occipital, temporal and parietal); for P2, N2 and P3 all the four lobes were included. Greenhouse-Geisser corrections were applied to the P -values when the degrees of freedom were greater than 1. Here we summarize and focus only on those findings that have the stimulus type as a factor and are relevant to the current topic.

P1 peak amplitudes and latencies did not show any effects involving type as a factor. It is important to note that in contrast to the other masking conditions, the mask in the delayed spatial mask condition had not yet appeared in this time window. In spite of that, there seems to be no difference between the ERPs in different the masking conditions, suggesting that the presence of the mask did not modify early ERPs.

The analysis of N1 amplitudes showed that ERPs to immediate nonspatial mask ($-6.8 \mu\text{V}$) and delayed spatial mask ($-7.9 \mu\text{V}$) trials were more negative than those to masked trials ($-4.9 \mu\text{V}$) [$F(2,22) = 9.08$, $P < 0.01$]. This effect was modified by a type \times lobe interaction [$F(4,44) = 11.84$, $P < 0.001$]. Separate analyses of the lobes showed no effect for stimulus type over the parietal lobes. The effect of stimulus type was significant over the occipital lobes [$F(2,22) = 10.79$, $P < 0.01$], indicating that N1 amplitudes to both types of unmasked stimuli were more negative than those to masked stimuli, while the unmasked stimulus types did not differ from each other. The effect of stimulus type was significant also over the temporal lobes [$F(2,22) = 16.62$, $P < 0.001$], showing that N1 amplitudes to both types of unmasked stimuli were more negative than those to masked stimuli, and that delayed spatial mask trials elicited more negative amplitudes than immediate nonspatial mask trials. The analysis of N1 peak latencies revealed that the latencies to delayed spatial mask stimuli peaked about 10 ms later than those to other types of stimuli [$F(2,22) = 9.75$, $P < 0.01$], particularly over the left hemisphere in the local attention condition, as suggested by the attention \times type \times hemisphere interaction [$F(2,22) = 5.56$, $P < 0.02$].

The analysis of P2 amplitudes showed a main effect for Type [$F(2,22) = 9.86$, $P < 0.01$] and a type \times lobe interaction [$F(6,66) = 20.30$, $P < 0.001$]. Separate analyses of the lobes showed significant effects for type over all the four lobes ($F_s > 4.77$). In the frontal electrodes, responses to delayed spatial mask stimuli were more positive than those to the other types of stimuli. Over the other sites, both types of unmasked stimuli elicited more negative responses than masked stimuli. The delayed spatial mask stimuli elicited more negative responses than the immediate nonspatial mask stimuli over the temporal and occipital lobes.

N2 amplitudes differed between the stimulus types [$F(2,22) = 6.02$, $P < 0.05$] and this effect was modified by a type \times lobe interaction [$F(6,66) = 16.09$, $P < 0.001$]. Over the temporal [$F(2,22) = 12.38$, $P < 0.01$] and occipital [$F(2,22) = 11.45$, $P < 0.01$] lobes, both types of unmasked stimuli elicited larger negative responses than masked stimuli. There was no effect for stimulus type in the parietal electrodes. In frontal electrodes all the stimulus types differed from each other [$F(2,22) = 13.29$, $P < 0.001$]; masked stimuli were associated with the most negative responses and delayed nonspatial mask stimuli with the most positive responses. The N2 peak latencies were the longest for masked stimuli and shortest for delayed spatial mask stimuli [$F(2,22) = 19.91$, $P < 0.001$]. However, the type \times lobe interaction [$F(6,66) = 5.23$, $P < 0.02$] suggests that in the frontal electrodes the delayed spatial mask stimuli had the longest latencies.

The analysis of P3 peak amplitudes revealed a main effect for type [$F(2,22) = 11.29$, $P < 0.001$] and a type \times lobe interaction [$F(6,66) = 15.89$, $P < 0.001$], suggesting that particularly over the parietal lobes [$F(2,22) = 4.85$, $P < 0.025$] immediate nonspatial mask (16.5 μV) and delayed spatial mask (17.4 μV) stimuli were associated

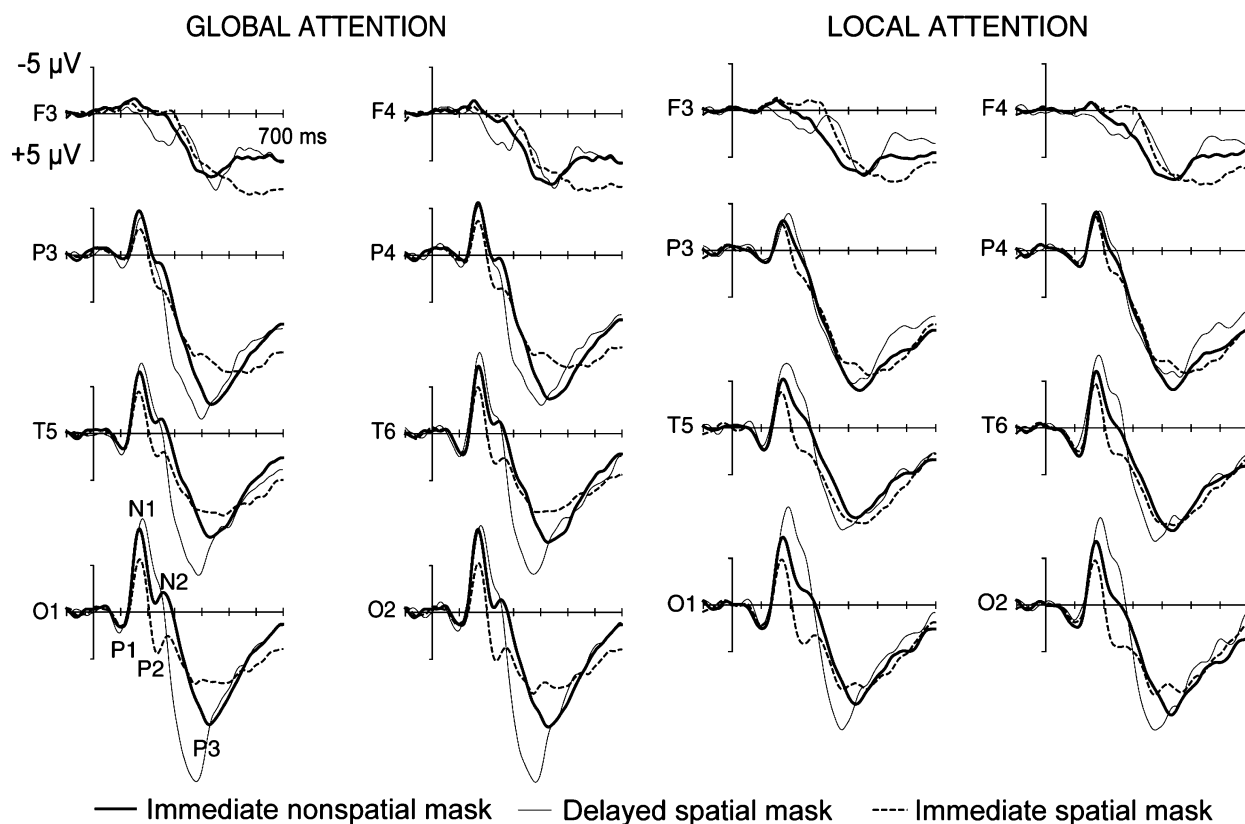


Figure 4. Grand average ERPs in different masking conditions in the global and local attention conditions (Experiment 2).

with larger positivity than masked stimuli (14.1 μV). The attention \times type \times lobe interaction [$F(6,66) = 2.49$, $P < 0.05$, uncorrected P -value] suggests that in the global attention condition, the immediate nonspatial and the delayed spatial mask stimuli were associated with larger positivity than masked stimuli over the parietal lobes [$F(2,22) = 8.35$, $P < 0.01$]. These effects were not statistically significant in the local attention condition. The P3 peak latencies were shorter in response to the delayed spatial mask stimuli, as compared with the other types of stimuli [$F(2,22) = 10.91$, $P < 0.01$], particularly over the occipital lobes [$F(6,66) = 10.39$, $P < 0.001$]. Here it is important to note that there was no difference in the P3 time window between ERPs to immediate nonspatial mask stimuli and ERPs to delayed spatial mask stimuli in the parietal electrodes in which the positive enhancement of ERPs to consciously recognized stimuli was the greatest in both experiments. The positive enhancement in parietal sites is therefore independent of the masking procedure. However, in occipital sites, the relatively early P3 peaks in the delayed spatial mask condition may have been partly produced by summation of the P1 evoked by the delayed mask.

In sum, conscious perception was associated with enhancement of negativity in the N1-N2 latency range at occipital and posterior temporal sites (VAN). This effect was observed in both masking conditions and the manipulation of attention did not have any effect on it. Figure 5 shows the scalp distribution of the VAN effect in the global and local attention conditions as a function of the masking condition, computed (NeuroScan Edit 4.1.1) from the difference waves (immediate nonspatial mask minus immediate spatial mask condition, delayed spatial mask minus immediate spatial mask condition). The occipito-temporal scalp distribution of VAN fits well with the idea that activation of the ventral stream from V1 to inferior temporal lobe is necessary for visual awareness (Bar *et al.*, 2001; Beck *et al.*, 2001; Kanwisher, 2001).

Subgroup

By combining the data from global and local conditions, it was possible to identify a subgroup of six participants who were able to recognize

a sufficient number of the stimuli in the masked condition (on average 88 stimuli, range 32-154), so that it was possible to compute ERPs for both consciously recognized and unrecognized targets in the immediate spatial masking condition (SOA = 33 ms). Thus, in this subset of data, conscious and nonconscious trials do not differ physically in any way, allowing us to further test whether or not the electrophysiological correlates of consciousness (early negativity and later positivity) were due to physical differences between masked and unmasked trials. However, it should be noted that the conscious experience of the masked stimuli at the short SOA cannot be expected to be equally strong or clear as compared with the experience in the unmasked conditions in which the conscious visual experience lasts for a longer time because of the lack of efficient masking.

As can be seen in Figure 6, the ERPs to consciously recognized stimuli show enhanced negativity in posterior electrodes around the N1 latency range, as compared with unrecognized stimuli. This observation was confirmed by a type (recognized, unrecognized) \times lobe (parietal, posterior temporal, occipital) \times hemisphere ANOVA on N1 peak amplitudes. It showed a significant main effect for type [$F(1,5) = 19.34$, $P < 0.01$], showing stronger negativity to recognized (-5.9 μV) than unrecognized stimuli (-3.4 μV). Corresponding analyses of the N1 peak latencies and the P1, P2 and N2 peak amplitudes and latencies did not show any effects involving type as a factor. The P3 peak amplitudes did not differ between recognized and unrecognized stimuli, but the peak latencies showed a nonsignificant tendency for longer latencies to unrecognized stimuli than to recognized stimuli at parietal and frontal sites [type \times lobe interaction: $F(3,15) = 3.18$, $P = 0.069$].

Discussion

Experiment 2 replicated the main findings of Experiment 1. The comparison of the masked trial and the two types of unmasked trials showed that in both attentional conditions visual awareness was associated with enhancement of negativity in N1-N2 latency range (VAN), most prominently at occipital and posterior temporal sites. The

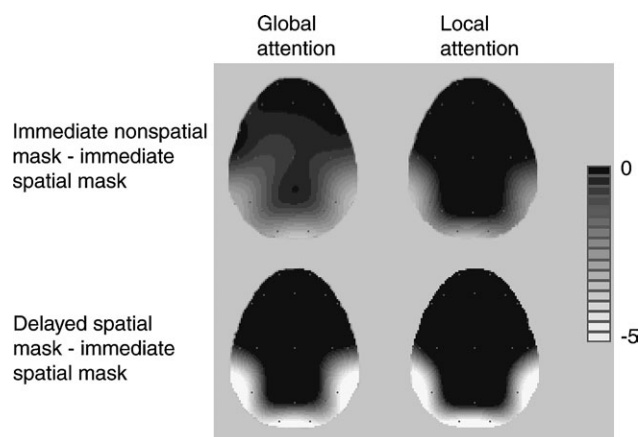


Figure 5. The scalp distribution of the VAN, calculated 180 ms after the onset of the stimulus, as a function of attention (global versus local) and the masking condition (immediate nonspatial mask versus delayed spatial mask) in Experiment 2. The white areas at occipital and posterior temporal sites show the presence of the negative difference (VAN) between ERPs to consciously recognized and unrecognized stimuli.

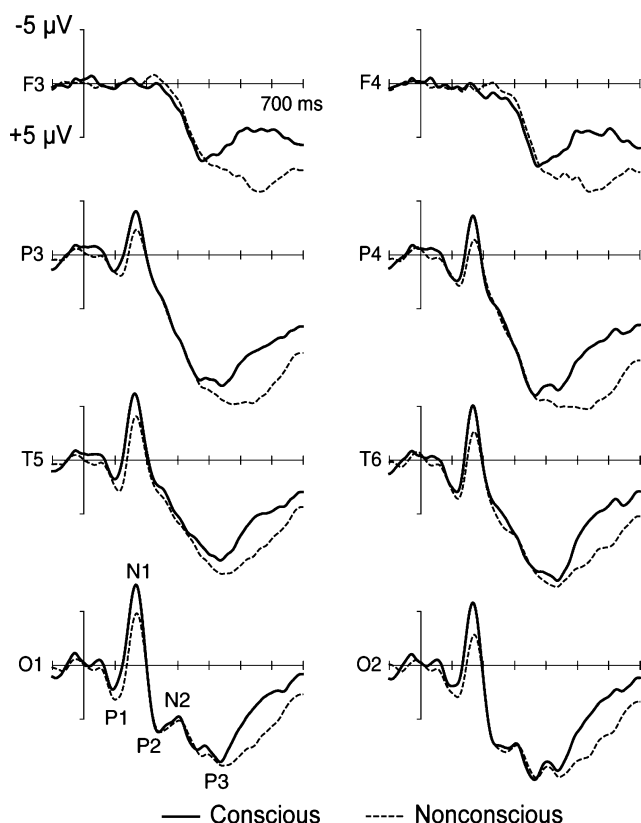


Figure 6. Grand average ERPs to conscious and nonconscious stimuli in the immediate spatial mask condition (SOA = 33 ms) (Experiment 2).

VAN was followed by an increase of positivity to consciously recognized stimuli in the P3 latency range in the global attention condition.

The early negative enhancement was larger in the delayed spatial mask condition than in the immediate nonspatial mask condition. This finding cannot be easily explained by the summation of the electrophysiological responses of the mask to the ERPs. In the delayed spatial mask condition the mask was displayed 188 ms after the onset of the stimulus, that is, around the time of the N1 peak when the negative enhancement was already present. Thus the stimuli were completely

unmasked until that point. In the immediate nonspatial mask condition, the mask had already appeared after 33 ms SOA. Here one would expect the N1 potential generated by the mask to summate to the ERPs elicited by the stimuli, which would lead to stronger negativity in the immediate nonspatial than in the delayed spatial mask condition — but we observed the opposite pattern.

Because the interference-free time of target exposure was shorter in the immediate nonspatial condition, we suggest that the mask may have induced metacontrast masking in the nonspatial condition, making the stimulus less clearly visible as compared with the delayed spatial mask condition. We carried out a control experiment without EEG recording to test the subjective visibility of the stimuli in each masking condition by presenting two blocks of 72 trials with the same apparatus and stimulus durations as in the actual experiment for eight independent participants. In one of the blocks, the task was to evaluate the relative duration of the stimulus on a scale from 0 (very short) to 9 (very long). In the other block, the task was to evaluate the sharpness of the stimulus on a scale from 0 (very low) to 9 (very high). After each trial, the evaluation was indicated by pressing the corresponding number in a numpad. The order of the blocks was counterbalanced. Although the stimulus duration was constant across the masking conditions, the results showed that its perceived duration varied as a function of masking [$F(2,14) = 50.72, P < 0.001$]. The duration in the delayed spatial masking (5.8) was perceived as longer than that in the immediate nonspatial masking (4.2) ($P < 0.01$), while the perceived duration in the masked condition was the shortest (1.6) ($P < 0.001$). Also the perceived sharpness of the stimulus varied as a function of masking [$F(2,14) = 6.68, P < 0.05$]; the masked stimuli (2.8) were rated to be less sharp than the stimuli in the immediate nonspatial masking (5.4) ($P < 0.05$) and in the delayed spatial masking (5.6) ($P < 0.05$). Assuming that the early negativity correlates with visual awareness (Koivisto and Revonsuo, 2003; Wilenius-Emet *et al.*, 2004), the finding that the early negativity (VAN) was larger in the delayed spatial masking than in the immediate nonspatial masking can be explained by the subjectively longer and sharper visual experience in the delayed spatial masking. This suggests a direct correlation between the magnitude of VAN and the contents of visual awareness.

Although the stimuli in the delayed spatial mask condition were rated to be more clearly visible than the stimuli in the immediate nonspatial mask condition, we found that response times were slower and accuracy was lower in the delayed condition, especially in the local attention condition. This finding suggests that the delayed mask interrupted postperceptual attentional processes that were not yet completed when the mask appeared. Thus, the delayed spatial mask and the immediate nonspatial mask induced different types of masking.

The fact that VAN was observed in both masking conditions suggests that it cannot be explained by the physical differences between masked and unmasked trials. This conclusion was more directly confirmed with the observation of VAN for the subgroup of participants for whom it was possible to compute ERPs for conscious and nonconscious trials while keeping the physical features of the target-mask stimuli identical at the short SOA. The VAN in this analysis was restricted to the N1 latency range, whereas it continued to N2 range in the analyses contrasting the masked and unmasked trials in the whole group. This difference can be explained by the short-lived and less clear subjective visual experience due to the overlap between the stimulus and the mask at the short SOA in the subgroup.

General Discussion

The earliest indication of aware perception was a negative amplitude shift at posterior sites 130–320 ms after the onset of the stimulus, peaking at ~260 ms (VAN). This effect was robust in both global and local attention conditions, suggesting that it emerges independent of the scope of attention. This negative effect is similar to those found in recent ERP studies on visual awareness using masking (Wilenius-Emet *et al.*, 2004; Koivisto *et al.*, 2005), binocular rivalry (Kaernbach *et al.*, 1999), change blindness (Koivisto and Revonsuo, 2003, 2005), contrast manipulation (Ojanen *et al.*, 2003) and neglect (Vuilleumier *et al.*,

2001). The fact that it appears in a large number of dissimilar experiments in which the subjective percept in visual consciousness has been dissociated from the unconscious processing of the physical stimulus suggests that VAN is a general electrophysiological marker of visual awareness. On the other hand, neither the present study nor any of the previous studies lend support for the finding that visual awareness would correlate with an early positive enhancement at ~100 ms (Pins and ffytche, 2003).

In Experiment 2, VAN was observed both with the nonspatial masking procedure which kept the SOA constant between masked and unmasked stimuli and with the more standard spatial masking procedure which kept the location of the stimulus and mask constant but manipulated the SOA. This pattern of results suggests that the nonspatial masking procedure, where the stimuli and the masks appeared in slightly different spatial positions in the unmasked condition, worked well, and the VAN response cannot be attributed, for example, to stimulation of different areas of the retina or to a need to separate the stimulus attentionally from the mask. That the VAN was not produced by the physical differences between the masked and unmasked trials was further supported by the analysis of the subgroup for whom the stimuli in the masked trials were near the subjective threshold so that conscious and nonconscious trials did not differ physically. Experiment 2 also suggests that the effect of the mask as a physical stimulus on the ERPs to the preceding stimulus is surprisingly small. The only clear effect was that the P3 in the delayed mask condition had a shorter latency than that in the immediate nonspatial mask condition over the occipital sites, which may be due to superimposition of the P1 evoked by the delayed mask and the P3 evoked by the stimulus. Because the mask is not attended to and it is repeated many times in the experiment, it is possible that repetition attenuation (Wiggs and Martin, 1998; Noguchi *et al.*, 2004) occurs for masks, so that neurons that are not critical for recognizing the target stimulus decrease their responses.

When the observers were attending to the global shape of the stimulus, the VAN was followed by a later positive difference in the P3 time window around 400 ms, peaking at parietal sites. This positive effect is similar to that found for aware change detection in change blindness paradigms (Niedeggen *et al.*, 2001; Turatto *et al.*, 2002; Koivisto and Revonsuo, 2003) and for changes in the visual content of awareness in binocular rivalry (Kaernbach *et al.*, 1999). This positivity was clearly present in the global attention condition, but only weak or nonexistent in the local attention condition. Because the observers were aware of the stimuli in the (unmasked) local attention conditions, the late positive difference cannot be a direct electrophysiological correlate of visual awareness. It must reflect further processes performed after the stimulus has reached visual awareness. The P3 potential is typically elicited by identity judgements, recognition and binary decisions (Donchin and Coles, 1988). Therefore the late positive difference in the P3 time window is more likely to be a correlate of the later stages of processing the perceived stimulus than an initial correlate of visual awareness. The late positive difference is not, however, a direct correlate of conscious decision-making either, because in that case the difference would have appeared in both attention conditions and its latency would have been slower in the local attention conditions, paralleling the response times which were strongly dependent on the manipulation of attention. One possibility is that the late positivity correlates with the confidence of the

observer's conscious decision which must have been lower in the more demanding local attention condition than in the global condition. The lack of the positivity effect in the subgroup showing VAN in the masked condition (Experiment 2) is also in line with the confidence explanation as for these observers the stimuli at the 33 ms SOA were near the subjective threshold, so that neither the subjective visual experience nor the confidence in the classification task could have been very strong. This issue could be resolved in further studies by including an independent confidence rating task after each trial. However, for the purpose of the present study, it is not important whether the late positive effect reflects confidence or not; the important point is that this effect was not present in the local attention condition although the subjects were aware of the stimuli — therefore the late positive difference cannot be a direct correlate of visual awareness.

Brain imaging studies (Lumer and Rees, 1999; Bar *et al.*, 2001; Beck *et al.*, 2001; Kanwisher, 2001; Rees and Lavie, 2001; Rees *et al.*, 2002) have indicated that the activation of the ventral visual stream, including the early visual area V1 (Rees and Heeger, 2003), and frontal and parietal areas correlate with awareness of visual stimuli. According to Lamme's model (2000, 2004), feed-forward activation along the ventral stream is fast (60–80 ms) and insufficient for aware visual perception. While feed-forward processing may be sufficient for nonconscious, implicit perception, recurrent backward processing from higher centres to earlier visual areas is required for aware perception. This model suggests that recurrent processing starts at ~100 ms from stimulus onset, at roughly the same time as the VAN starts to emerge. This local, restricted recurrent processing is assumed to correlate with subjective experience of seeing, phenomenal consciousness (see Block, 1996, 2001, 2005). This framework explains the effect of a backward mask by its interference with the local recurrent processing of the preceding stimulus, which makes the stimulus inaccessible to phenomenal consciousness. Lamme (2004) proposes that after the recurrent activation of visual areas, a further widespread, global recurrent interaction involving many brain regions (parietal and frontal attention areas) takes place. In the framework proposed by e.g. Lamme (2004), Block (2005) and Revonsuo (2005), this later interaction is regarded as the neural correlate of access (or reflective) consciousness, and it makes the information available to memory and report. In addition, Bar (2003) has reviewed evidence suggesting that feedback from prefrontal cortex to inferotemporal areas may occur very rapidly. If this is true, then prefrontal areas may have a relatively early contribution to recurrent processes. When interpreted according to this framework, VAN correlates with visual phenomenal consciousness, requiring the activation of the ventral stream plus local recurrent activation together with thalamo-cortical connections (Lamme, 2000, 2004; Revonsuo, 2005). The late positivity may correlate with some aspect of access or reflective consciousness (Block, 1996, 2001, 2005; Lamme, 2004; Revonsuo, 2005). In this form of consciousness, higher cognitive operations, such as evaluation, categorization or conscious report, are performed on an attentionally selected content of phenomenal consciousness.

Notes

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