

Neural processing stages during object-substitution masking and their relationship to perceptual awareness



Joseph A. Harris^{a,b,c,d}, Solange Ku^a, Marty G. Woldorff^{a,b,c,d,e,*}

^a Center for Cognitive Neuroscience, Duke University, Durham, NC, USA

^b Department of Psychology and Neuroscience, Duke University, Durham, NC, USA

^c Department of Neurology, University of Magdeburg, Magdeburg, Germany

^d Leibniz Institute for Neurobiology, Magdeburg, Germany

^e Department of Psychiatry, Duke University, Durham, NC, USA

ARTICLE INFO

Article history:

Received 29 January 2013

Received in revised form

27 May 2013

Accepted 30 May 2013

Available online 7 June 2013

Keywords:

Vision

Awareness

Perception

Attention

Substitution masking

Electrophysiology

ABSTRACT

The extent of visual perceptual processing that occurs in the absence of awareness is as yet unclear. Here we examined event-related-potential (ERP) indices of visual and cognitive processes as awareness was manipulated through object-substitution masking (OSM), an awareness-disrupting effect that has been hypothesized to result from the disruption of reentrant signaling to low-level visual cortical areas. In OSM, a visual stimulus array is briefly presented that includes a parafoveal visual target denoted by a cue, typically consisting of several surrounding dots. When the offset of the target-surrounding cue dots is delayed relative to the rest of the array, a striking reduction in the perception of the target image surrounded by the dots is observed. Using faces and houses as the target stimuli, we found that successful OSM reduced or eliminated all the measured electrophysiological indices of visual processing stages after 130 ms post-stimulus. More specifically, when targets were missed within the masked condition (i.e., on trials with effective OSM that disrupted awareness), we observed fully intact early feed-forward processing up through the visual extrastriate P1 ERP component peaking at 100 ms, followed by reduced low-level activity over the occipital pole 130–170 ms post-stimulus, reduced ERP indices of lateralized shifts of attention toward the parafoveal target, reduced object-generic visual processing, abolished object-category-specific (face-specific) processing, and reduced late visual short-term-memory processing activity. The results provide a comprehensive electrophysiological account of the neurocognitive underpinnings of effective OSM of visual-object images, including evidence for central roles of early reentrant signal disruption and insufficient visual attentional deployment.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

The extent and quality of visual processing that occurs in the absence of awareness is of the broadest import to cognitive neuroscientists, because information coded in the brain, regardless of its emergence as a conscious percept, holds the potential to influence behavior. Gaining an understanding of the perceptual information that is processed in the absence of awareness contributes much to understanding the neural factors, some of which a viewer is unaware, that explain and predict behavior. In order to establish such a disconnect between a given perceptual process and awareness, experimenters can isolate neural measures of that process as a function of conditions of awareness and unawareness of the relevant stimulus content. If the neural measure remains present during conditions of behavioral

unawareness, it can be inferred that the stage of perceptual processing it reflects occurs in the absence of awareness (Holender, 1986; Reingold & Merikle, 1988).

In order to create conditions of awareness and unawareness, across which the neural measures of a specific visual perceptual process could be compared, a manipulation of the target stimulus presentation typically needs to be employed. Object substitution masking (OSM) is a useful way to robustly reduce or eliminate awareness, while at the same time maintaining the integrity of low-level stimulus processing coded in the generic feed-forward visual signal. In OSM, a visual array composed of a parafoveal visual target and a number of distracters is briefly presented, with the target item being indicated by a proximal but spatially distinct cue, typically several dots surrounding its edges. When the offset of the surrounding cue dots is delayed relative to that of the rest of the array, the result is a striking reduction in the perception of the cue-surrounded image, reflected by a behavioral decrement both in target detection and discrimination (Enns & DiLollo, 1997; Giesbrecht & Di Lollo, 1998). Initially, it was hypothesized that this striking masking effect occurs because spatially unattended targets

* Corresponding author at: Duke University, Center for Cognitive Neuroscience, Box 90999, Durham, NC, USA. Tel.: +1 919 681 0604.

E-mail address: woldorff@duke.edu (M.G. Woldorff).

are coded with low resolution as their corresponding initial feed-forward signal propagates along the visual pathway, and therefore are susceptible to substitution by the persisting mask information that stays on the screen (Enns & DiLollo, 1997). More recently, it has been proposed that object-substitution masking may attenuate awareness through the disruption of reentrant processing to low-level visual processing brain regions (Di Lollo, Enns, & Rensink, 2000; Reiss & Hoffman, 2007; Weidner, Shah, & Fink, 2006).

This reentrant mechanism seems more plausible relative to a feed-forward mechanism for several reasons. First, the mask and the target image are not spatially coincident, making it unlikely that the disruption is through a feed-forward mechanism, as appears to be the case in other forms of masking, such as sandwich masking, for example (Harris, Wu, & Woldorff, 2011), given that the visual signals associated with the target and mask in OSM are coded from retinally distinct locations. Second, the observation that OSM works as a function of cue offset relative to that of the array implicates more than just the brevity of the array or the presence of a mask in the observed behavioral effects. It has been proposed that the delayed offset of the cue results in a mismatch between the initial feed-forward representation of the target location and the signal that exists in early visual areas during a hypothesized later reentrant phase of processing (Di Lollo et al., 2000; Reiss & Hoffman, 2007). The convolution of these two signals in the delayed offset condition, in which only the mask information remains consistent, is therefore hypothesized to result in the substitution of the four-dot cue for the target. Finally, neural study of the mechanisms of OSM using magnetoencephalographic (MEG) data and source modeling analyses has suggested early reentrant signaling to V1 as a necessary condition for awareness during OSM (Boehler, Schoenfeld, Heinze, & Hopf, 2008). Such a proposed mechanism is consistent with a growing body of empirical literature suggesting reentrant visual signaling to V1 more generally as an essential condition for visual awareness (Bouvier & Treisman, 2010; Camprodon, Zohary, Brodbeck, & Pascual-Leone, 2010; Dux, Visser, Goodhew, & Lipp, 2010; Fahrenfort, Scholte, & Lamme, 2008). The OSM paradigm, which may act through this mechanism, therefore provides a useful method for creating conditions of visual unawareness in which neural signals indicative of various visual processes can be probed.

The current study, by combining the high temporal resolution of event-related potentials (ERPs) with an OSM paradigm and an expanded set of conditions and analyses, sought to examine the full cascade of visual perceptual processing stages within versus outside of awareness. The specific goals were to examine (1) the timing with which OSM disrupts normal visual signaling; and (2) the fate of the neural underpinnings of object-specific (i.e., face-processing-specific) visual processes, attentional allocation processes, and working memory processes as a function of intact versus OSM-disrupted awareness.

As per the first goal – to examine the timing of disruption in OSM – we sought to capture the neural consequences of effective versus ineffective OSM in our event-related potential comparisons. This meant comparing visual-evoked potentials to the target and array in cases that resulted in unawareness to those that resulted in awareness despite masking. In addition, a third type of stimulus other than faces and non-faces was included as a trial type, namely a “blank” stimulus (matched for all other stimulus context factors). This allowed visual processing activity to be extracted similarly across conditions of awareness and unawareness. Specifically, by collapsing neural responses to objects (faces and other target object images) and comparing them to those associated with an absence of any image at all, the effect of OSM on basic visual target object processing could be tracked across behavioral conditions of awareness (delayed-dot-offset hits versus delayed-dot-offset misses). Thus, feed-forward extrastriate processing reflected in the early sensory-evoked P1 ERP component at 100 ms, and a later, likely reentrant stage of processing across various

identified parietal and occipital scalp regions, could be examined in cases of awareness versus unawareness (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002).

In addition to the timing of disruption exerted by OSM on basic visual processing, we aimed to directly examine the consequences of this disruption vis-à-vis specific visual processing stages. In particular, we also tracked across conditions of awareness the hallmark face-specific negative-polarity ERP waves (N170 difference wave and later face-specific negativity) reflecting object-category processing. The N170 is an enhanced negative-polarity voltage deflection over occipito-temporal scalp areas in response to images of faces than to images of other category (Bentin, Allison, Puce, Perez, & McCarthy, 1996). This face-specific response peaks at about 170–200 ms following the onset of the object image, and is often followed by another face-specific negative-polarity response at a longer latency (~400–800 ms) with a similar distribution on the scalp, with the latter presumably reflecting some sort of reentrant, or feedback, activity related to face processing (Harris, et al., 2011; Philastides & Sajda, 2006). Both the N170 and longer-latency face-specific negativity are traceable to sources in ventral visual cortical regions associated with high-level object-category processing in the fusiform gyrus in ventral occipital cortex (Kanwisher, McDermott, & Chun, 1997) and the superior temporal sulcus (STS) in the lateral occipital-temporal cortex (Grill-Spector et al., 1998; Puce, Allison, Asgari, Gore, & McCarthy, 1996). Tracking the presence or absence of these responses as a function of awareness can therefore reveal the extent of the underlying neural processes that occurs in the absence of awareness.

Lastly, electrophysiological components associated with attentional allocation and visual short-term memory were investigated. In terms of attentional allocation, the negative-polarity posterior contralateral response (N2pc) ERP component to lateralized targets (peak latency ~250 ms) can be extracted to examine the allocation of visual attention to a specific spatial location and item (Luck & Hillyard, 1994). Similarly, a longer latency component, the so-called sustained posterior contralateral negativity (SPCN) that has been associated with working memory processing and subsequent discrimination of a lateralized target (Jolicoeur, 2006; Robitaille, Jolicoeur, Dell'Acqua, & Sessa, 2007), can be extracted by the same subtraction (contralateral versus ipsilateral targets) and tracked across conditions of awareness. Taken together, the manner in which these indices of specific visual processing stages change as a function of awareness can reveal much regarding the consequences and neural underpinnings of OSM.

We made several specific predictions concerning these processing stages and their relationship to the awareness disruption exerted by OSM. As far as generic visual processing is concerned, we hypothesized that successful masking by object substitution (i.e., a “miss”) would affect early reentrant stages, in accordance with current theories citing the disruption of reentrant signaling to V1 as a primary mechanism of OSM. We thus hypothesized that, when comparing hits to misses within the masked condition, we would see no differences in processing up to the visual P1 ERP component that peaks at 100 ms, as this is a reflection of early striate and extrastriate feed-forward signaling (Clark & Hillyard, 1996). This would then be followed, however, by a reduction in a midline ERP component with a distribution over the occipital pole during a period immediately following the P1, consistent with a modulation of local reentrant input to low-level visual cortex (Boehler, et al., 2008; Clark & Hillyard, 1996). This mechanism of disruption would then likely ramify to other later neural indices of interest, assuming their integrity depends on this early recurrent signaling. Such processes would likely include the initial shift of visuo-spatial attention to the relevant target location coded by the N2pc, a negative-polarity voltage deflection contralateral to the shift of visual spatial attention (Woodman & Luck, 1999). More specifically, we hypothesized that, within the masked condition, we would see reduced attentional-shift-related N2pc activity in the case

of inaccurate behavior but normal/sufficient N2pc activity in the case of accurate behavior, which would speak to a role of attentional deployment in the observed behavioral decrements associated with OSM (Prime, Pluchino, Eimer, Dell'Acqua, & Jolicoeur, 2011; Schankin & Wascher, 2007; Woodman & Luck, 2003). Following this disruption, visual-evoked potentials reflecting later processing stages gated by attention would be accordingly disrupted in the case of misses relative to hits within the masked condition. These include object-generic processing extracted via a target-object minus blank target subtraction, object-category processing indexed by the face-specific N170 and later negativity, and the sustained posterior contralateral negativity (SPCN) indexing visual short-term-memory processing in the target discrimination task employed

2. Methods

2.1. Participants

Thirty-four subjects participated in the study, of which seven were excluded due to excessive eye movements and blinks (i.e., the trial rejection rate due to eye artifacts exceeded 25%). This thus yielded 27 participants (6 female, 2 left-handed) in the final analysis, with a mean age of 23.8 ± 5.4 years. Subjects were recruited through local advertisements, and informed consent was obtained for all subjects for their paid participation in accordance with a protocol approved by the Duke University Medical Center Institutional Review Board.

2.2. Stimuli and task

Participants were seated 70 cm from a 19-inch CRT stimulus presentation monitor with a refresh rate of 60 Hz and completed 15 experimental runs of 120 trials each. These trials were subdivided into two masking conditions (masked and unmasked) and three target conditions (face, house, or blank), for a total of 300 trials of each type per subject. The stimulus array items consisted of distracters and targets, all of which were 2.9° diameter, circularly cropped images presented parafoveally. For each trial, an array of 15 scrambled non-object distracters, plus

one target identified by a surrounding four-dot cue, was briefly presented (one frame = 17 ms), after which the array offset (Fig. 1). Target images (chosen from sets of 40 faces, 40 houses, and blanks) occurred in one of four target locations randomly (upper left, upper right, lower left, lower right), with equal probability in each experimental run. Masked and unmasked trials were randomly intermixed within each run. Masking by object substitution was induced by delaying the offset of the four-dot cue surrounding the target by 500 ms relative to the offset of the target/distracter array. For all trial types, participants were asked to detect and discriminate the cued target images among an array of scrambled image non-object distracters, by responding as to whether the target object, indicated by being surrounding by the dots cues, was a face, a house, or an empty space.

2.3. Data acquisition and analysis

2.3.1. Behavioral

Behavioral performance at the level of target detection (indicating that an object was presented when one actually was) and categorization (correctly identifying the category of the target image as a face or house) was compared across the dot-delay conditions (simultaneous offset versus delayed offset). The masking effect of delaying the offset of the surrounding dot cues was measured in terms of detection performance, which was the percentage of cued target images (faces and houses) detected versus those incorrectly classified as blanks. Categorization accuracy and reaction time in the case of detected targets were also measured for masked and unmasked conditions.

2.3.2. EEG acquisition

The continuous electroencephalogram (EEG) was recorded from a 64-channel, extended-coverage, custom cap (Electrocap, Inc.) using a right mastoid reference, with a bandpass filter of .01–100 Hz, sampling rate of 500 Hz, and a gain of 1000 (Neuroscan Amplifier system). Two vertical electro-oculogram (EOG) channels referenced to prefrontal electrodes (Fp1 and Fp2), along with two horizontal EOG channels referenced to one another, were used to monitor eye blinks and eye movements, respectively. Behavior and the global state of the participants were also monitored using a closed-circuit video camera. Artifact rejection was performed offline to remove trials contaminated by eye blinks, eye movements, muscle activity, or signal drift.

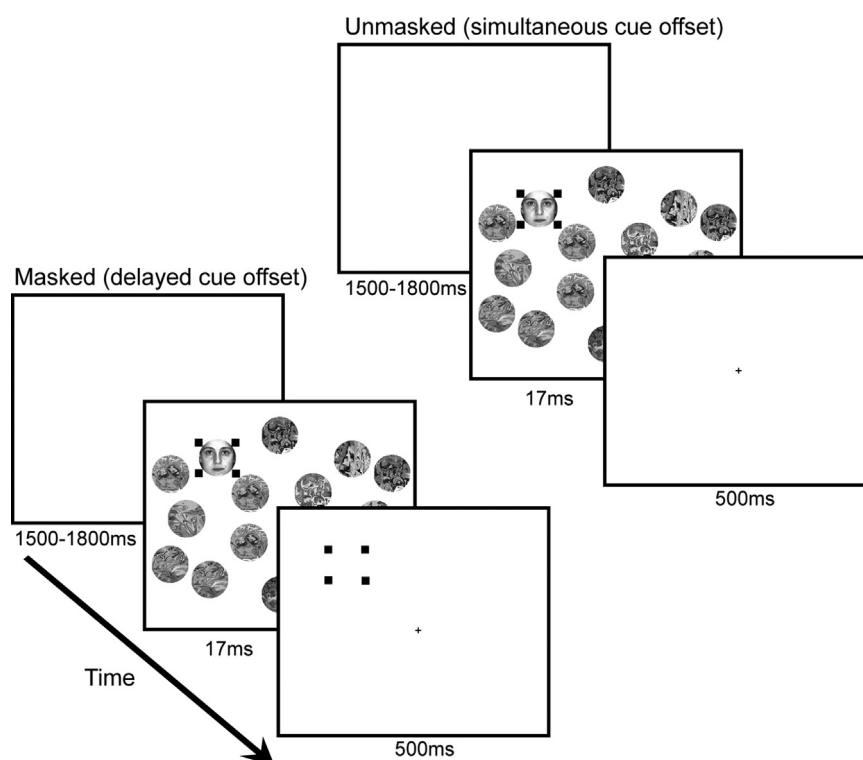


Fig. 1. Stimuli and task. Subjects were asked to complete a three-alternative forced choice task for every trial, indicating whether the target image (indicated by being surrounded by a 4-dot cue) was a face, house, or empty space. On half of the trials, the 4-dot cue offset at 17 ms with the rest of the array, which served as the unmasked-condition trials. On the other half of the trials, the offset of the 4-dot cue was delayed relative to the rest of the array by 500 ms, establishing the object-substitution masking condition.

2.3.3. ERP data analysis

The artifact-free data were time-locked-averaged selectively for the different stimulus types. These averages were then low-pass filtered offline using a nine-point running average filter, which at our 500 Hz sample rate heavily attenuates external electrical noise at and above ~ 56 Hz. The ERP averages were subsequently algebraically re-referenced to the average of all electrodes (common reference) and baseline corrected relative to the 200 ms preceding stimulus-array onset. Most importantly, conditions of awareness and unawareness were established through behavioral measures *within* the masked condition. Specifically, delayed-cue-offset trials in which subjects correctly identified present targets were considered trials of awareness, whereas delayed-cue-offset trials in which subjects indicated “no target” when one was in fact presented were considered trials of unawareness. Selectively binning the masked trials in this way enables the comparison of electrophysiological components between psychological conditions while maintaining identical visual stimulation. In addition, it avoids the problem of possibly inflating the estimation of processing that can occur in the absence of awareness if one instead were to consider all masked trials as unawareness trials regardless of the actual efficacy of masking. Thus, the electrophysiological results were focused mainly on differences between behavioral conditions *within* the masked (delayed-cue-offset) condition.

The naming convention for the electrode sites of our custom cap adheres generally to the standard 10–20 or 10–10 systems, with some descriptor modifications as necessary. For sites within a few millimeters of the standard sites, we have used the standard site names. For sites deviating more than a few millimeters but less than one centimeter from their closest 10–20 or 10–10 analogs, the traditional name is used, with a prime (') symbol added (e.g., O1'). Lastly, for those sites more than 1 cm from a standard site, a letter suffix is added indicating the direction of the relative offset with respect to the closest standard positions (“a” for slightly anterior, “p” for slightly posterior, “i” for slightly inferior, etc.). In addition, we have attempted to make the regions of interest clear in each case by placing white rectangles around those regions on our head figures.

Because of the lateralized presentation of the target images, and to be able to focus on the likely lateralized distribution of some of the key visual-evoked potentials, for some of the analyses the electrode locations were flipped along the midline for trials in which targets occurred in the left visual field, and then collapsed together with corresponding unflipped channels for targets occurring in the right visual field. This resulted in the corresponding topographic maps to have activity contralateral to the targets being plotted together on the left side of the scalp, and the ipsilateral responses on the right side. For referencing to effects of these contra-ipsi data, the relevant sites will be referred to in a left-right paired way (e.g., O1i/O2i), given that they were derived from sites on both the left and the right sides of the head.

Generic visual processing was first examined by extracting visual-evoked potentials to arrays containing an object target (face or house) and comparing them across behavioral performance (hits and misses) at our scalp electrode sites TO1/TO2 during the post-stimulus time window of 80–120 ms, consistent with the distribution of the visual sensory-evoked P1 (Clark & Hillyard, 1996), as well as at sites overlying the occipital pole (Inz, Oz, I1, I2, O1i, and O2i) immediately after to probe reentrant signaling to striate cortex. Following this, signals at lateral occipital sites (TO1/TO2, T11/T12, C5p/C6p) at a later time window were measured to assess signals that would be sensitive to object-related activity originating in the lateral occipital complex (LOC) (Grill-Spector et al., 1999).

To further isolate activity associated with the target, and not the distracters contained in the array, visual-evoked potentials associated with blank target trials were subtracted from those associated with face and house target trials, yielding an object-target minus no-object target subtraction. This effect was examined at scalp electrode sites T11/T12, TO1/TO2, and I1/I2 (lateral occipital sites) during an early time window (up to 300 ms) and our parieto-occipital scalp site O1'/O2' at a later time window (up to 700 ms). Face-selective effects were extracted in each masking condition (delayed and simultaneous offset of the four-dot cues), as well as within each behavioral outcome (correct, detected, and undetected), by contrasting the face-evoked ERP with the house-evoked ERP at scalp electrode site TO1/TO2. Based on the aforementioned analyses, this location corresponds to the typical temporal-occipital scalp sites at which this face-selective effect is most robustly observed, contralateral to the side of its presentation. Lateralized attentional and working memory components (N2pc and SPCN, respectively) were extracted by subtracting object-present activity occurring ipsilateral to the side of the target (i.e., thus ipsilateral to the direction of the required shift of attention) from the same activity contralateral to such a shift, focusing on the scalp region corresponding to electrodes O1'/O2', TO1/TO2, P3i/P4i, sites that are typically sensitive to such activity.

The ERP effects were statistically analyzed using different within-subjects, two-factor, repeated-measures analysis of variance (ANOVA), depending upon the contrast being examined. More specifically, for generic visual processing, the trial type (masked or unmasked; hits or misses within a masking condition) by object-minus-blank effects were extracted; for face-specific processing across awareness conditions, trial type by face-minus-house effects were examined; for the N2pc and SPCN effects, trial type by contralateral-minus-ipsilateral object activity was compared. Effect latencies and durations were determined using consecutive 50 ms (0–50; 50–100, etc.) latency windows, and then refined using 10 ms wide windows.

3. Results

3.1. Behavior

Behavioral measures of detection showed a significant and robust decrease in target-image detection performance (from 85 to 59 percent) in the case of delayed-cue offset trials relative to trials with simultaneous offset of the dot cues ($t_{26}=5.7$, $p<.0001$). This effect did not vary in magnitude according to object image type (face versus house), indicating that object-substitution masking was equally effective in decreasing awareness of both faces and houses. For correctly identified face and house targets, subjects were somewhat faster in categorizing faces relative to houses in the unmasked condition (mean RT for correctly identified unmasked targets was 678 ± 78 ms for faces and 708 ± 70 ms for houses; $t_{26}=3.6$, $p<.005$), but not for the correctly discriminated trials in the masked condition (mean RT for correctly identified masked targets was 687 ± 61 ms for faces and 695 ± 70 ms for houses; $t_{26}=.92$, $p=.37$).

3.2. Electrophysiology

3.2.1. Intact early extra-striate but disrupted reentrant striate visual signaling within the masked condition

To extract the precise timing with which object-substitution masking exerts its disruptive influence, two key comparisons were made. First, and most generally, visual-evoked potentials in response to targets, collapsed across faces and houses, were compared within the masked condition as a function of awareness level, as reflected by the behavioral response. Specifically, the ERPs to target images that were detected and correctly identified were compared with the ERPs to target images that were missed (i.e., where a “no-target” behavioral response had been given), all within the delayed offset condition. At the relevant electrode site (TO1/TO2), during the 80–120 ms post-stimulus time period associated with the visual P1 response, no significant difference in mean amplitude was observed between target hits and misses within the masked condition ($F_{1, 26}=.05$, $p=.82$; Fig. 2A–C)(Clark & Hillyard, 1996). Via the same hits versus misses comparison, the first extractable difference in generic visual-evoked potentials to the entire array as a function of awareness began at 130 ms post-stimulus and continued through 170 ms post-stimulus over the occipital pole (Inz, Oz, I1, I2, O1i, and O2i). This was observed as a reduced amplitude positivity in the case of misses relative to hits ($F_{1, 26}=5.22$; $p=.03$; Fig. 2D–F). Finally, a significant reduction in amplitude in a negative-polarity response was observed in the case of misses relative to hits with a broad lateral occipital distribution (TO1/TO2, T11/T12, C5p/C6p) contralateral to the target ($F_{1, 26}=20.5$, $p=.0001$; Fig. 2G–I). It should be noted that this pattern of results applied equally to faces and houses, which were equivalent *within* hits and misses, with the same pattern of differences observed *between* hits and misses (Supplementary Fig. S1), with the exception of the lateral occipital negativity (Fig. S1C). This negativity was present for faces and houses, but smaller for house hits than for face hits. In the case of misses it was equally small for faces and houses. (Supplementary Fig. S1).

3.2.2. Disrupted object-generic processing within the masked condition

In order to examine the extent of generic, target-related, visual processing that occurs in the absence of awareness during object-substitution masking, visual-evoked potentials in response to objects (collapsed across faces and houses) were compared to those in response to blank target trials across behavioral conditions, separately for hits and misses. Difference waves between trials with a target object image present versus not (i.e., blank-image trials) were then compared across behavioral measures

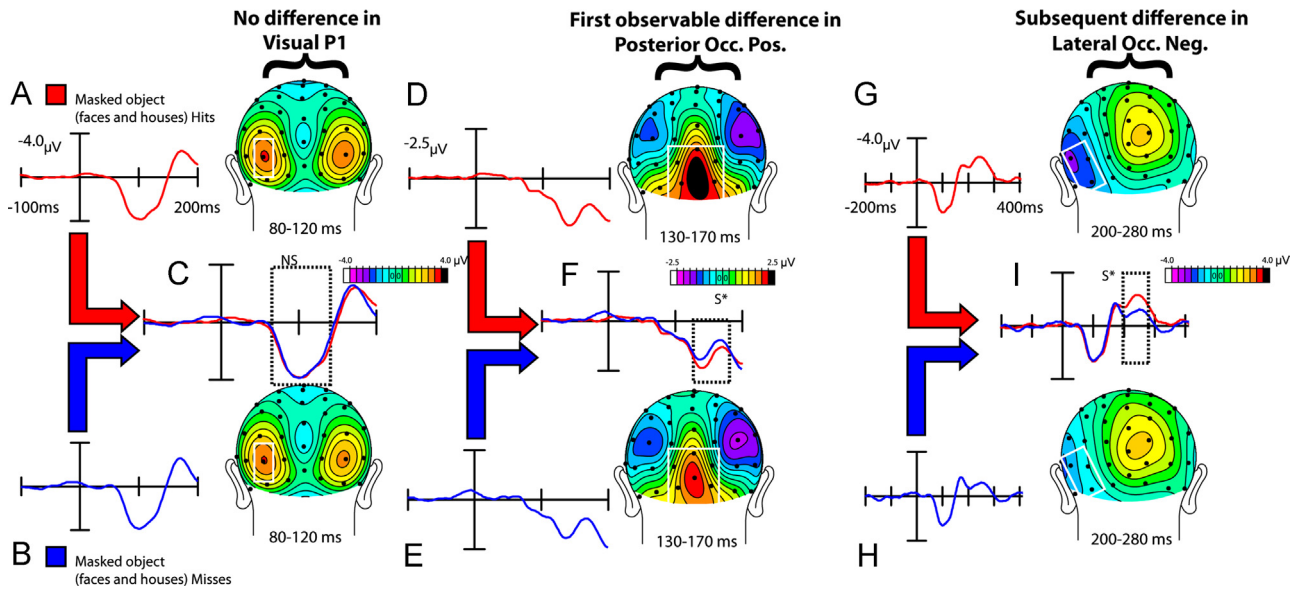


Fig. 2. Visual-evoked potentials to target/distracter array within the masked condition. The early sensory-evoked visual P1 component did not differ as a function of behavior within the masked condition. In the case of accurately detected targets (A), this component was observed over occipital sites during the 80–120 ms post-stimulus period. (B) shows the same for targets that would be undetected. (C) shows the overlaid traces for hits and misses, underscoring that no P1 difference was observed. (F) shows the same comparison, over occipital pole sites, during the post-stimulus time period of 130–170 ms. Here, a significant reduction in a positive amplitude response was observed in the case of misses (E) relative to hits (D). Finally, a late lateral occipital negativity was observed over the post-stimulus time window of 200–280 ms in the case of targets that would be correctly discriminated (G). This negativity was present, but significantly reduced in the case of targets that would be missed, suggesting a downstream consequence of early reentrant disruption with regard to generic visual processing (H&I).

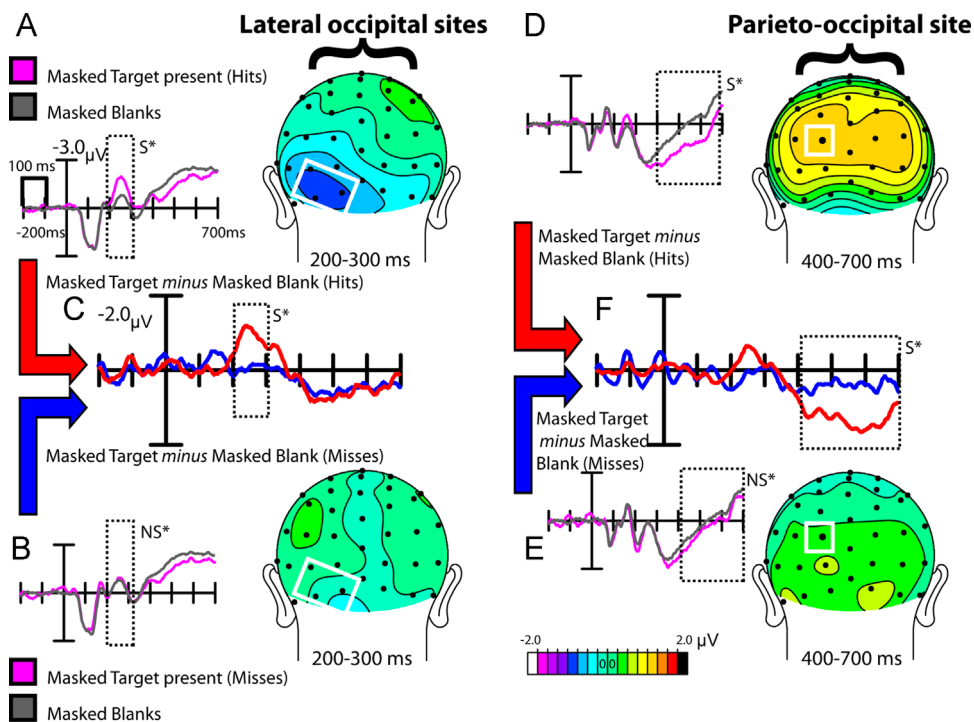


Fig. 3. Object-generic processing for masked-condition hits and misses. Significant decrease in visual-object-related activity (faces and houses collapsed minus empty space) in masked-condition miss trials relative to masked-condition hit trials was observed over lateral ventral occipital scalp regions beginning at a latency of 200 ms post-stimulus (A). Another reduction in visual-object-related activation was seen at a longer latency (400–700 ms) over somewhat more superior occipital sites in the case of masked-condition misses versus masked-condition hits (B).

reflecting the level of perceptual awareness (hits versus misses). Within the masked condition, differential visual-evoked potentials (objects versus blanks) were analyzed at two scalp regions typically sensitive to generic visual processing activity at early and later time windows (200–300 ms and 400–700 ms, respectively).

First, for the early time window, a difference between hits and misses was observed as a negative-polarity enhancement in response to objects versus blanks over posterior occipital scalp regions (T11/T12, TO1/TO2, and I1/I2) ($F_{1, 26} = 13.7$, $p < .005$; Fig. 3C). Specific comparisons showed that the extracted object-generic response (that is, activation in response to faces and

houses minus that associated with 'blank' trials) effect was present for hits ($F_{1, 26}=37.6, p < .0001$; Fig. 3A) but not misses ($F_{1, 26}=3.9, p > .05$; Fig. 3B). In addition, in the later time period (400–700 ms post-stimulus), an object-generic effect extracted in the same way (object minus blank) was seen that had a parieto-occipital scalp topography (O1'/O2') and that differed across conditions of awareness ($F_{1, 26}=7.63, p < .02$; Fig. 3F). This effect was driven by a presence of this positive-polarity voltage enhancement in the case of hits ($F_{1, 26}=18.4, p < .001$; Fig. 3D) and an absence of such an enhancement in the case of misses ($F_{1, 26}=1.12, p=.3$; Fig. 3E) over the same time period.

These results outline a cascade of visual processing that was present for cases in which masked targets were seen, and absent in cases of unawareness in which they were missed, extracted from physically identical stimulation. First, no differences were observed in the electrophysiological activity up through the visual extrastriate component P1 peaking at 100 ms. Rather, the first observed activity difference was a modulation in a midline posterior positivity over the occipital pole from 130–170 ms, with a distribution consistent with an effect on early local reentrant activity into low-level visual cortex (e.g., V1). Following this difference, there was also a reduction with unawareness of a lateralized posterior occipital negativity extracted through a target-object-present minus target-absent subtraction at ~200 ms post-stimulus, consistent with reduced signaling in the object-selective visual cortical region known as the lateral occipital complex (LOC) and associated with object processing (Grill-Spector et al., 1998). Finally, awareness trials were further characterized by a positive-polarity, bilateral occipital voltage response during the time window just prior to response execution, possibly reflecting late reentrant stages associated with the emergence of awareness (Fahrenfort et al., 2008), an effect that was also not observed on unaware trials.

3.2.3. Face-specific effect between and within masking conditions

The face-specific activity was first extracted for the different masking conditions, but collapsed across behavior (i.e., regardless of what the behavioral responses were), as per the approach that has commonly been applied in the field. In the case of the unmasked-condition trials (i.e., those with simultaneous cue offsets), this analysis showed that the face-minus-house comparison yielded a striking and long-lasting (180–950 ms) face-specific electrophysiological effect (sites TO1/TO2; $F_{1, 26}=27.2, p < .001$; Fig. 4A and C). In contrast, in the masked (delayed-cue-offset) condition, again collapsed across behavior, some face-specific activity was still present (Fig. 4B and C), but it was confined to narrower time windows (200–350 ms and 700–850 ms: $F_{1, 26}=6.8, p < .02$; 700–850 ms and $F_{1, 26}=5.9, p < .03$, respectively) and appeared substantially reduced in amplitude (Fig. 4C). Direct comparisons of the face-specific activities for the simultaneous-offset and delayed-offset conditions showed these to be significantly different across the 200–750 ms post-stimulus time window. ($F_{1, 26}=13.2, p < .01$; Fig. 4C).

Further examining these effects more specifically as a function of behavior, however, showed that on trials with accurate behavior (detected and correctly identified face and house targets), the face-specific activation did *not* differ between the delayed-offset ("masked") and the simultaneous-offset ("unmasked") conditions. Specifically, no difference in the amplitude of face-specific activity was observed across the entire post-stimulus time window of 200–750 ms between *hits* in the delayed-offset condition and *hits* in the simultaneous offset condition ($F_{1, 26}=.01, p=.91$; Fig. 4D–F).

To directly examine face-specific processing as a function of awareness, trials with behavioral responses indicating awareness (correctly identifying the target) and those indicating unawareness (giving a behavioral response reporting the perception of a "blank" even though a target was present) were compared *within* the

delayed-cue-offset condition. Such a contrast effectively provides a comparison of neural measures between trials with identical stimulus conditions that only differed at the level of perceptual report (i.e., when masking worked and led to a miss, versus when masking did not work and led to a correct discrimination of the target). Specifically, in the case of hits, the face-specific negativity was present from 180–850 ms post-stimulus ($F_{1, 26}=11.1, p < .01$; Fig. 4E and G), whereas for misses this effect was absent in all time windows during the same interval (180–850 ms) ($F_{1, 26}=.09, p=.77$; Fig. 4F and G). In addition, direct comparison of the extracted face-specific activity difference waves for hits versus misses in the masked condition revealed a significant difference during the time window of 180–450 between hits and misses ($F_{1, 26}=4.8, p < .04$; Fig. 4G). Thus, the relatively small face-specific activity observed in the delayed-offset ("masked") condition when collapsed across behavior appears to be derived from the averaging of miss trials, in which there was no face-selective activity, with hit trials, in which there was the full amount of face-selective activity (i.e., the same amount as for the hit trials in the unmasked condition).

3.2.4. Masked-condition hits versus misses: attentional shifting and visual-working-memory activity

In addition to the disruptions described above, successful object-substitution masking (the subject responding "no target" even when one was present) was reflected in aberrations of attentional shifting and visual-working-memory activity associated with the target location (Fig. 5). Specifically, on image-aware trials versus image-unaware trials during the delayed-cue-offset condition, a significant decrease in contralateral vs. ipsilateral target-related N2pc and SPNC activity was observed over posterior sites (O1'/O2', TO1/TO2, P3i/P4i). In the case of accurate behavior indicating awareness, a robust negative-polarity amplitude enhancement in response to contralateral relative to ipsilateral targets was seen at time windows consistent with the N2pc (180–400 ms) and later SPNC component (700–900 ms) ($F_{1, 26}=59.3, p < .0001$; $F_{1, 26}=35.3, p < .0001$ for early and late effects, respectively; Fig. 5A and B). These effects were also present in the case of misses during the same relevant time windows ($F_{1, 26}=40.5, p < .0001$, and $F_{1, 26}=14.3, p < .001$, for the N2pc and SPNC, respectively; Fig. 5C and D). In the case of misses, however, both of these effects were significantly reduced ms ($F_{1, 26}=14.5, p < .001$, and $F_{1, 26}=4.25, p < .05$, for the N2pc and SPNC time windows, respectively; Fig. 5E). Overall, these results indicate that in the context of object-substitution masking, immediately following the occurrence of the putative early reentrant mechanism, a reduced N2pc component is observed, followed by a later and even more dramatic reduction in the SPNC component.

It should also be noted that the N2pc and SPNC were fully present in the case of accurate behavior in the unmasked (simultaneous offset) condition. Amplitude differences between contralateral and ipsilateral targets that were correctly identified were extracted at the relevant region at an early (180–400 ms; $F_{1, 26}=60.0, p < .0001$) and late time window (700–900 ms; $F_{1, 26}=48.1, p < .0001$), corresponding to the N2pc and SPNC, respectively. These extracted differences were comparable to those extracted in the case of accurate behavior (i.e., hits) in the masked condition, although the N2pc was somewhat reduced in amplitude (mean N2pc amplitude comparison for hits in masked-condition versus hits in the unmasked-condition over the 180–400 ms latency window yielded $F_{1, 26}=15.2, p < .001$). In contrast, the SPNC had only a trend toward a significant difference between masked and unmasked conditions when the behavioral responses were accurate (the same comparison over 700–900 ms yielded $F_{1, 26}=3.74, p > .06$).

4. Discussion

The design of the present study afforded several advantages vis-à-vis examining specific visual and cognitive processes in the

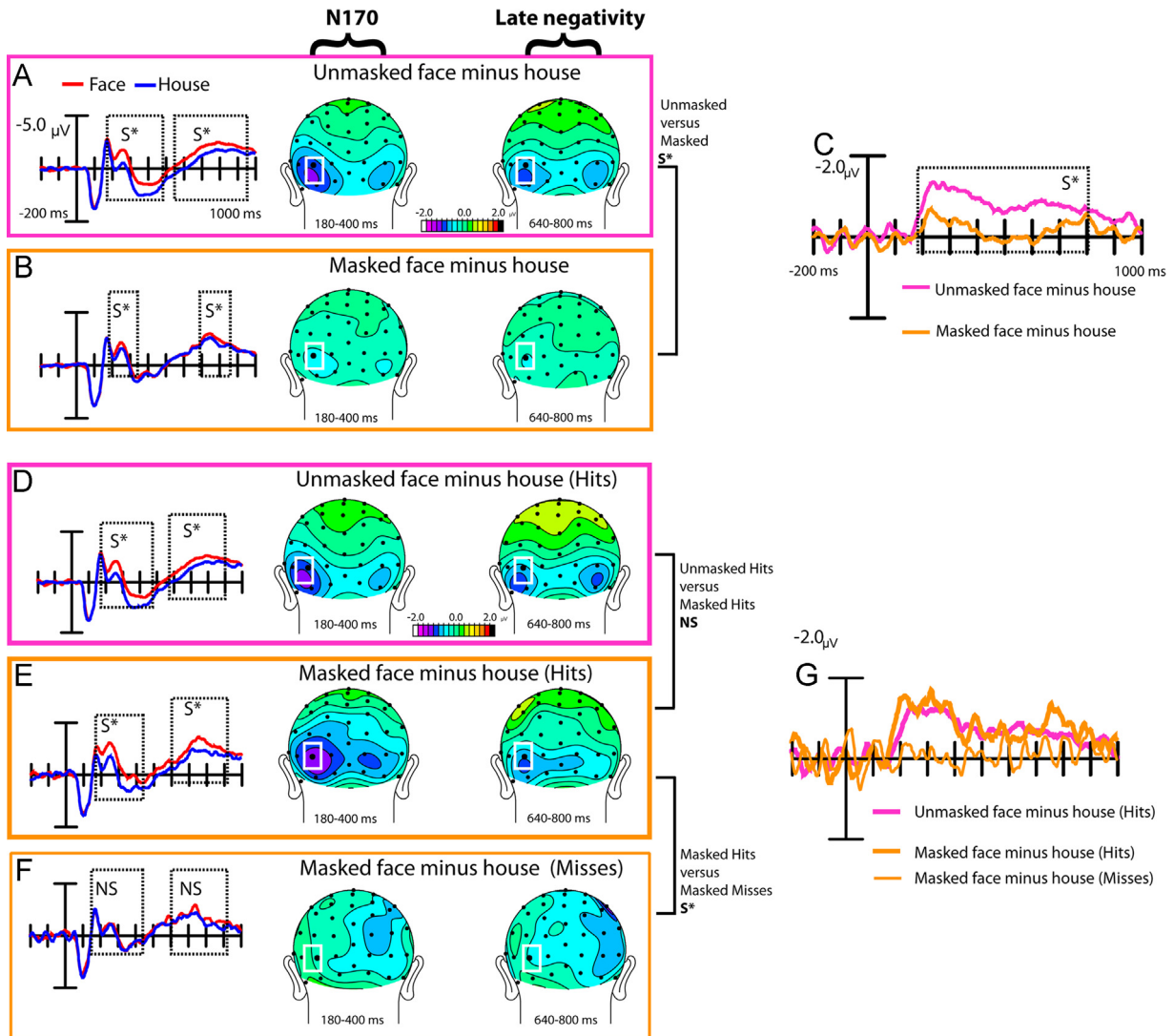


Fig. 4. Face-specific activity in masked and unmasked trials. Face-specific activity was present in both the unmasked (A) and masked (B) conditions, though significantly decreased in the case of masked-condition trials (C). Comparisons isolating awareness and unawareness in the masked condition revealed that in the case of accurate behavior face-specific responses were present at early and late stages in the masked (delayed-offset) condition, and did not differ from those associated with accurate behavior in the unmasked condition (D and E). However, in the case of unawareness (masked trials in which subjects failed to detect presented targets), the face-specific negativity at both early and late stages was eliminated (F and G).

absence of awareness. The parameters of the present experiment (in terms of timing, eccentricity of targets, and number of distracters) allowed for a robust behavioral effect of diminished detection in the masked (delayed-offset) condition, while at the same time maintaining high performance in the unmasked (simultaneous offset) condition. While an OSM behavioral effect of the magnitude seen here has been observed in the past, it has typically been in the context of relatively simple stimuli, such as geometric shapes and line drawings. The susceptibility of highly salient photographic stimuli, such as those used here, has historically been markedly less, especially in the case of faces, which often tend to be detected and recognized faster and at greater visual eccentricities than other stimuli (Hershler, Golan, Bentin, & Hochstein, 2010). Implementing an OSM design with such a robust behavioral effect allowed for an effective trial sorting analysis of high-level object-category neural processing, as there were comparable numbers of trials of hits and misses within the masked condition.

In addition, the manner in which awareness was operationalized here was especially conservative, thereby preventing possible false positives that can be generated with regard to neural indices of specific processes during the masked condition. Specifically, a target

here was not considered to be outside of unawareness simply because the offset of the dot cues around the target were delayed. Because object-substitution masking is not typically a total effect (i.e., which would be reflected by chance performance or complete unawareness on every masked-condition trial), data were sorted according to behavior to more selectively reflect this decrement *within* the masked condition. Moreover, this approach was facilitated because of the added blank target type and the “no target” response option. Thus, trials were only considered “aware” ones if subjects were able to correctly identify a target, while trials were only considered “unaware” if a target object (face or house) was actually present and subjects indicated that they had not seen one. Such sorting according to behavior allowed analyses to avoid inadvertently inflating the extent of a given process in the absence of awareness, which would occur in the case of the neural measures scaling with awareness. Overall, the additional conditions included here (blank target images), along with a three-alternative forced choice task, enabled a clear isolation of aware versus unaware trials with identical stimulus conditions.

With regard to neural indices of perceptual processes, the present study provides insight into the cascade of visual, attentional, and cognitive events following the onset of a masked trial that

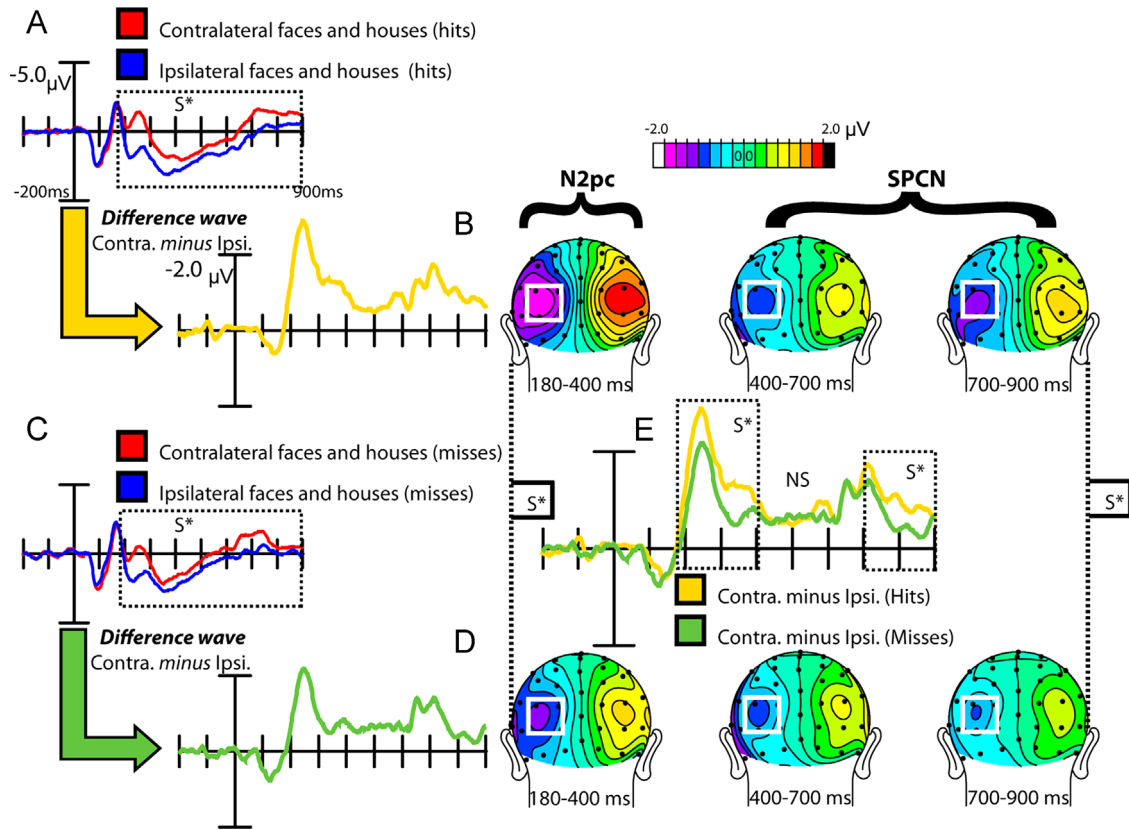


Fig. 5. Lateralized visual and attentional effects (N2pc and SPCN) within the masked condition. In the case of masked misses (C and D) relative to masked hits (A and B), significant reduction of the attentional-shift-related lateralized posterior negativity (N2pc; 180–400 ms) was observed through a contralateral minus ipsilateral subtraction (contralateral on the left side of the scalp), reflecting the presumed shift of visual attention toward the cued target. For the later (400–700 ms) sustained posterior contralateral negativity (SPCN) associated with visual working memory, a similar reduction in the case of misses was observed (E). The relevant difference waves (contralateral minus ipsilateral targets) in the case of masked-condition hits versus masked-condition misses are shown in (E).

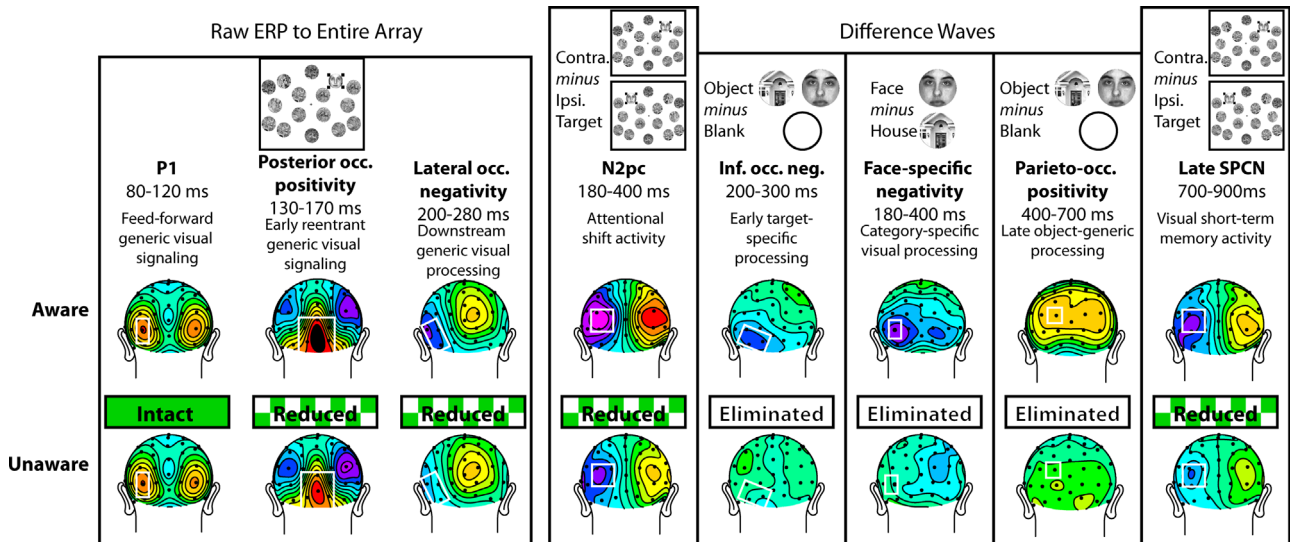


Fig. 6. Summary figure. Electrophysiological indices of various visual, perceptual, and cognitive processes as a function of awareness within object-substitution masking conditions are summarized. In cases of unawareness of the masked target, the first observed change is that of a reduced occipital pole response, with all temporally downstream effects being either reduced or eliminated altogether, ultimately culminating in a failure to detect the masked target. (See text for detailed discussion).

characterizes either awareness or unawareness of a target stimulus (summarized in Fig. 6). First, the initial feed-forward sweep of activity in striate and extrastriate activity (up to 130 ms) appears to be intact during OSM. Rather, the first observed disruption of visual activity for unaware trials was a modulation of activity over the occipital pole beginning at 130 ms post-stimulus, with a distribution consistent with

an aberration of local-reentrant processing to primary visual cortex (Boehler et al., 2008; Di Lollo et al., 2000; Dux et al., 2010). Relatedly, it has also been shown that awareness can be impaired by active disruption of reentrant signaling to V1 using TMS pulses to this scalp region, although at a later latency (Camprodon et al., 2010). The current data provide the first scalp-recorded event-related

potential evidence for this early local-reentrant mechanism, likely into V1, marking the precise time at which visual-evoked potentials associated with awareness and unawareness of targets diverge.

This low-level occipital modulation at 130 ms was then followed by a cascade of modulations for aware versus unaware trials (Fig. 6, continued). First, activity reflecting the attentional shifting to the lateralized target was markedly reduced for unaware trials, as reflected by a reduced N2pc component beginning at 180 ms. Concurrently, a lateralized negativity with a distribution similar to the previously characterized "visual awareness negativity" (VAN, present for images that were seen and not those unseen) (Rodríguez et al., 2012) was reduced here in cases of unawareness. However, as noted above, this response is likely a convolution of the VAN and face-specific negativity, both of which are reduced in cases of unawareness (Fig. S1). Also, object-generic processing was also reduced for unaware trials, likely reflecting reduced net feed-forward signaling to LOC, as well as perhaps due to the earlier aberration in lower-level reentrant signals. This differential processing also ramified into a complete elimination of any object-category-specific (i.e., here face-specific) activity during unaware trials. Later differences in the comparison of hits to misses in the masked condition (400–700 ms) suggests that such disruption may then ramify as a reduction/elimination in later, likely more global, reentrant signaling just prior to response execution (i.e., the elimination of the late occipital positivity in unaware versus aware trials here), which may reflect disruption of late stages of visual processing that may lead to or be associated with awareness (Fahrenfort et al., 2008). Finally, unaware versus aware trials also showed a marked reduction in late activity associated with visual short-term working-memory processing.

With regard to higher-level stages of visual processing, a particularly interesting aspect of the modulation of object-category specific processing as indexed by the N170 here is that it occurred as a function of the masking condition, but only when trials of behavior indicating a lack of awareness were isolated. This is in contrast to some previous studies of face-specific processing during OSM, as well as higher level semantic processing in the same context (Reiss & Hoffman, 2006, 2007). What these previous studies showed was disruption of ERP measures of these processes in the case of delayed-cue offset (masked) conditions relative to simultaneous-offset (unmasked) conditions. This divergence across perceptual conditions is presently supported, but in the context of the further distinction between awareness and unawareness that is achieved through electrophysiological data sorting within the masked condition according to trial types behaviorally defined reflecting unawareness versus awareness. Thus, the present results are compatible with previous studies of face processing during object-substitution masking, but also indicate the variable efficacy of OSM from trial to trial in disrupting awareness. In turn, these results demonstrate that it is not simply the delayed offset of the cue that disrupts face-specific processing, but a number of events related to the effects of that delay that either result or do not result in successful disruption of prior reentrant processing.

The intactness of face-specific processing, as well as of generic visual signaling, occurring in the case of trials in the masked condition (i.e., delayed offset) that were correctly discriminated, raises the question of what (other than disruption of early reentrant signaling) may be making the difference between misses and hits in the masked condition, thereby leading to OSM when it occurs, and thus leading to the modulations of various indices of visual and cognitive processes observed. The unique properties of OSM, as a paradigm that requires unpredictable target locations and visuo-spatial attention shifts to these locations for successful detection, suggests a central role of attention in the effects. This has been previously investigated most directly in a study examining the N2pc and SPCN components in OSM in the case of masked

versus unmasked trials, as well as in cases of accurate versus inaccurate behavior in masked trials (Prime et al., 2011). Specifically, that study, as one of their findings, reported a lack of an N2pc in the case of unmasked trials. Although this lack of an N2pc on such trials seems fairly surprising, this result was attributed to the possibility that the paradigm needed only a diffuse allocation of attention and did not require a shift with the onset of a trial. In addition, this group observed an N2pc in all delayed-offset (i.e., masked) conditions, regardless of behavior, as well as an SPCN that scaled with behavior in the masked condition (absent for misses). The present results are thus at odds with these findings. Specifically, the current study extracted a robust N2pc response in the case of accurate behavior in both unmasked and masked trials, but a significantly smaller one for misses in the masked condition, which would be more consistent with a previous report of a slight, but insignificant, difference in N2pc amplitude as a function of behavior (accurate vs. inaccurate) within the masked condition (Woodman & Luck, 2003). It seems likely that the N2pc does scale with performance in the masked trials, but that our especially conservative approach to data sorting (comparing the masked condition trials with accurate detection of a target to trials with complete misses of one) was able to extract the presently significant pattern of results. The fact that our N2pc was present for accurate trials in both the unmasked and masked conditions that the shift of attention to the target location was critical for successful detection and identification, regardless of offset condition. The differences with the Prime et al. study might be explained by paradigmatic differences in visual presentation. In particular, the brevity of target stimulation in the present study (a single frame of 17 ms) may have required a more focused attentional deployment here for detection and discrimination across trials. Also, the more conservative criteria for awareness in the current study may also account for the disruption of both the N2pc and SPCN in the case of misses in the delayed offset (i.e., masked) condition here. Specifically, whereas Prime et al. showed that incorrect behavior was nevertheless accompanied by an N2pc, this incorrect behavior may well have been comprised of both successful and unsuccessful target detection. In the present context of a three-alternative forced choice task in which "no-target present" was a response option, misses constituted instances of a target being present, but misidentified as "blank." This lack of detection of any image being present may in turn be due to a failure to successfully shift attention to the target location in time to detect the presence of an object, which might therefore explain this difference in results. The subsequent observation of a disrupted visual short-term memory component (the SPCN) is also therefore not surprising, as low-level information necessary for discrimination would not have been available in the case of misses, but maintenance of the target location indicated by the delayed-offset four-dot cue would likely continue (Robitaille, Grimault, & Joliceur, 2009). Lastly, the present results indicate a likely reliance of the N2pc and an adequate shift of attention to the target upon the integrity of the earlier-latency low-level reentrant signaling that appears to be disrupted in the case of effective masking by object-substitution.

Taken together, the present results support the unique niche of OSM as exerting its disruptive effects at a relatively low level reentrant mechanism, as well as implicating spatial attentional deployment as playing a central role in its efficacy in disrupting visual awareness. For example, OSM as manifested here appeared to disrupt visual processing at a lower or earlier level than in the attentional blink, where disruption of a more global reentrant process after a latency of 270 ms is likely (Sergent, Baillet, & Dehaene, 2005; Harris, McMahon, & Woldorff, in press). The role of attentional deployment in OSM appears critical as well, as the N2pc was reduced in the case of masked miss trials. This is consistent with

results from previous studies that investigated the effect of spatial attention on face-specific processing. More specifically, it has been shown that allocation of spatial attention away from a stream of objects strongly gates both the face-specific N170 and the later face-specific negativity (Carlson & Reinke, 2010; Crist, Wu, Karp, & Woldorff, 2008; Feng, Martinez, Pitts, Luo, & Hillyard, 2012).

5. Conclusions

The present electrophysiological study of object-substitution masking yielded a rich data set speaking to levels of visual processing that occur in the absence of awareness, as well as to the attentional and working-memory processes associated with the efficacy of the perceptual masking. In cases of unawareness in the masked (delayed-offset) conditions, it was observed that the early feed-forward striate and extrastriate signaling (up to 130 ms) was left intact, with the first disruption of processing manifesting as a modulation of apparent reentrant signaling to low-level visual cortex slightly later (130–170 ms). Following this effect, the first consequence of this disruption was a reduction in the N2pc, an index of the shifting of visual attention to a lateralized target, which was significantly reduced within the masking condition, but only on trials in which targets would go undetected. Concurrent with and following this attentional deployment stage, all subsequent electrophysiological indices of various levels of visual processing were then correspondingly also impaired as a function of awareness. These included generic visual processing signals over lateral occipital and parietal scalp regions, both object-related and face-specific signals over lateral occipital sites, and late visual short-term-memory processing activity coded by the SPCN. Overall, these results delineate the full sequence of visual events underlying the disruption of perceptual awareness when object-substitution masking is effective versus when it is not, and point to a central role of effective visuo-spatial attention in overcoming these potentially disruptive effects.

Acknowledgments

This work was funded by NIH Grant R01-MH060415 to M.G.W. The authors would like to thank Carsten N. Boehler and Jessica J. Green for their input during the design phase of this experiment, as well as Kenneth C. Roberts for his valuable input during the analysis stages of the study.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2013.05.023>.

References

- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8(6), 551–565.
- Boehler, C. N., Schoenfeld, M. A., Heinze, H. J., & Hopf, J. M. (2008). Rapid recurrent processing gates awareness in primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 105(25), 8742–8747, <http://dx.doi.org/10.1073/pnas.0801999105>.
- Bouvier, S., & Treisman, A. (2010). Visual feature binding requires reentry. *Psychological Science*, 21(2), 200–204, <http://dx.doi.org/10.1177/0956797609357858>.
- Camprodon, J. A., Zohary, E., Brodbeck, V., & Pascual-Leone, A. (2010). Two phases of V1 activity for visual recognition of natural images. *Journal of Cognitive Neuroscience*, 22(6), 1262–1269.
- Carlson, J. M., & Reinke, K. S. (2010). Spatial attention-related modulation of the N170 by backward masked fearful faces. *Brain and Cognition*, 73(1), 20–27, <http://dx.doi.org/10.1016/j.bandc.2010.01.007>.
- Clark, V. P., & Hillyard, S. A. (1996). Spatial selective attention affects early extrastriate but not striate components of the visual evoked potential. *Journal of Cognitive Neuroscience*, 8(5), 387–402.
- Crist, R. E., Wu, C. T., Karp, C., & Woldorff, M. G. (2008). Face processing is gated by visual spatial attention. *Frontiers in Human Neuroscience*, 1, <http://dx.doi.org/10.3389/Neuro.09.010.2007> Artn 10.
- Di Lollo, V., Enns, J. T., & Rensink, R. A. (2000). Competition for consciousness among visual events: The psychophysics of reentrant visual processes. *Journal of Experimental Psychology—General*, 129(4), 481–507, <http://dx.doi.org/10.1037//0096-3445.129.4.481>.
- Di Russo, F., Martinez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Human Brain Mapping*, 15(2), 95–111.
- Dux, P. E., Visser, T. A. W., Goodhew, S. C., & Lipp, O. V. (2010). Delayed reentrant processing impairs visual awareness: An object-substitution-masking study. *Psychological Science*, 21(9), 1242–1247, <http://dx.doi.org/10.1177/0956797610379866>.
- Enns, J. T., & DiLollo, V. (1997). Object substitution: A new form of masking in unattended visual locations. *Psychological Science*, 8(2), 135–139.
- Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. F. (2008). The spatiotemporal profile of cortical processing leading up to visual perception. *Journal of Vision*, 8(1)<http://dx.doi.org/10.1167/8.1.12> Artn 12.
- Feng, W. F., Martinez, A., Pitts, M., Luo, Y. J., & Hillyard, S. A. (2012). Spatial attention modulates early face processing. *Neuropsychologia*, 50(14), 3461–3468, <http://dx.doi.org/10.1016/j.neuropsychologia.2012.09.031>.
- Giesbrecht, B., & Di Lollo, V. (1998). Beyond the attentional blink: Visual masking by object substitution. *Journal of Experimental Psychology—Human Perception and Performance*, 24(5), 1454–1466.
- Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzhack, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*, 24(1), 187–203.
- Grill-Spector, K., Kushnir, T., Hendler, T., Edelman, S., Itzhack, Y., & Malach, R. (1998). A sequence of object-processing stages revealed by fMRI in the human occipital lobe. *Human Brain Mapping*, 6(4), 316–328.
- Harris, J. A., Wu, C. T., & Woldorff, M. G. (2011). Sandwich masking eliminates both visual awareness of faces and face-specific brain activity through a feedforward mechanism. *Journal of Vision*, 11(7).
- Harris, J. A., MaMahon, A. R., & Woldorff, M. G. Disruption of visual awareness during the attentional blink is reflected by late-state neural processing. *Journal of Cognitive Neuroscience*. in press.
- Hershler, O., Golan, T., Bentin, S., & Hochstein, S. (2010). The wide window of face detection. *Journal of Vision*, 10(10) <http://dx.doi.org/10.1167/10.10.21> Artn 21.
- Holender, D. (1986). Semantic activation without conscious identification in dichotic-listening, parafoveal vision, and visual masking—A survey and appraisal. *Behavioral and Brain Sciences*, 9(1), 1–23.
- Jolicoeur, P. (2006). Neurophysiology of visual attention and visual short-term memory: From N2pc to SPCN. *Psychophysiology*, 43 S3–S3.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 17(11), 4302–4311.
- Luck, S. J., & Hillyard, S. A. (1994). Spatial-filtering during visual-search—Evidence from human electrophysiology. *Journal of Experimental Psychology—Human Perception and Performance*, 20(5), 1000–1014, <http://dx.doi.org/10.1037//0096-1523.20.5.1000>.
- Philiastides, M. G., & Sajda, P. (2006). Causal influences in the human brain during face discrimination: A short-window directed transfer function approach. *IEEE Transactions on Biomedical Engineering*, 53(12), 2602–2605, <http://dx.doi.org/10.1109/Tbme.2006.885122>.
- Prime, D. J., Pluchino, P., Eimer, M., Dell'Acqua, R., & Jolicoeur, P. (2011). Object-substitution masking modulates spatial attention deployment and the encoding of information in visual short-term memory: Insights from occipito-parietal ERP components. *Psychophysiology*, 48(5), 687–696, <http://dx.doi.org/10.1111/j.1469-8986.2010.01133.x>.
- Puce, A., Allison, T., Asgari, M., Gore, J. C., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letterstrings, and textures: A functional magnetic resonance imaging study. *Journal of Neuroscience*, 16(16), 5205–5215.
- Reingold, E. M., & Merikle, P. M. (1988). Using direct and indirect measures to study perception without awareness. *Perception and Psychophysics*, 44(6), 563–575.
- Reiss, J. E., & Hoffman, J. E. (2006). Object substitution masking interferes with semantic processing: Evidence from event-related potentials. *Psychological Science*, 17(12), 1015–1020.
- Reiss, J. E., & Hoffman, J. E. (2007). Disruption of early face recognition processes by object substitution masking. *Visual Cognition*, 15(7), 789–798, <http://dx.doi.org/10.1080/13506280701307035>.
- Robitaille, N., Grimault, S., & Jolicoeur, P. (2009). Bilateral parietal and contralateral responses during maintenance of unilaterally encoded objects in visual short-term memory: Evidence from magnetoencephalography. *Psychophysiology*, 46(5), 1090–1099, <http://dx.doi.org/10.1111/j.1469-8986.2009.00837.x>.
- Robitaille, N., Jolicoeur, P., Dell'Acqua, R., & Sessa, P. (2007). Short-term consolidation of visual patterns interferes with visuo-spatial attention: Converging evidence from human electrophysiology. *Brain Research*, 1185, 158–169, <http://dx.doi.org/10.1016/j.brainres.2007.09.004>.
- Rodriguez, V., Thompson, R., Stokes, M., Brett, M., Alvarez, I., Valdes-Sosa, M., et al. (2012). Absence of face-specific cortical activity in the complete absence of awareness: Converging Evidence from functional magnetic resonance imaging and event-related potentials. *Journal of Cognitive Neuroscience*, 24(2), 396–415.

- Schankin, A., & Wascher, E. (2007). Electrophysiological correlates of stimulus processing in change blindness. *Experimental Brain Research*, 183(1), 95–105, <http://dx.doi.org/10.1007/s00221-007-1023-z>.
- Sergent, C., Baillet, S., & Dehaene, S. (2005). Timing of the brain events underlying access to consciousness during the attentional blink. *Nature Neuroscience*, 8(10), 1391–1400, <http://dx.doi.org/10.1038/Nn1549>.
- Weidner, R., Shah, N. J., & Fink, G. R. (2006). The neural basis of perceptual hypothesis generation and testing. *Journal of Cognitive Neuroscience*, 18(2), 258–266.
- Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature*, 400(6747), 867–869.
- Woodman, G. F., & Luck, S. J. (2003). Dissociations among attention, perception and awareness during object-substitution masking. *Psychological Science*, 14(6), 605–611.