

Disruption of Visual Awareness during the Attentional Blink Is Reflected by Selective Disruption of Late-stage Neural Processing

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Abstract

■ Any information represented in the brain holds the potential to influence behavior. It is therefore of broad interest to determine the extent and quality of neural processing of stimulus input that occurs with and without awareness. The attentional blink is a useful tool for dissociating neural and behavioral measures of perceptual visual processing across conditions of awareness. The extent of higher-order visual information beyond basic sensory signaling that is processed during the attentional blink remains controversial. To determine what neural processing at the level of visual-object categorization occurs in the absence of awareness, electrophysiological responses to images of faces and houses were recorded both within and outside the atten-

tional blink period during a rapid serial visual presentation stream. Electrophysiological results were sorted according to behavioral performance (correctly identified targets vs. missed targets) within these blink and nonblink periods. An early index of face-specific processing (the N170, 140- to 220-msec post-stimulus) was observed regardless of whether the participant demonstrated awareness of the stimulus, whereas a later face-specific effect with the same topographic distribution (500- to 700-msec poststimulus) was only seen for accurate behavioral discrimination of the stimulus content. The present findings suggest a multistage process of object-category processing, with only the later phase being associated with explicit visual awareness. ■

INTRODUCTION

An unresolved question in the field of visual cognitive neuroscience is the extent and quality of perceptual and higher-order processing that occurs in the absence of awareness. This question is of the broadest interest, because of the fact that any information encoded in the brain, whether an individual is aware of it or not, holds the potential to influence behavior. Thus, the investigation of visual processing, from basic sensory levels to more abstract and sophisticated levels of representation and how such processing does or does not unfold in the absence of awareness, remains an active area of cognitive neuroscience.

One major approach by which researchers have examined the extent of visual processing that occurs within versus outside awareness is the dissociation paradigm (Reingold & Merikle, 1988), which entails several key elements. First, for a particular visual process of interest (e.g., the discrimination of visual objects), images that invoke that process are presented to viewers, who then respond behaviorally in a manner that reflects conscious awareness of relevant image content (e.g., by performing an object-category discrimination task). Under these circumstances, experimenters manipulate the presentation of the images, such that, although they remain physically present, they are undetected or less accurately detected

by the participant. This reduced awareness is evident in a decrement in the relevant behavioral measure. In parallel, an implicit measure of that visual process, either neural (e.g., brain activity) or behavioral (e.g., behavioral priming), is examined under conditions of intact awareness versus disrupted awareness. If the implicit measure remains intact despite the observed behavioral decrement, it is inferred that the visual processing of interest is occurring in the absence of awareness.

In the hierarchy of human visual processing, the representation of object categories has been shown to be subserved, at least in part, by specialized neural modules in the occipital and temporal cortices. The specific function of human face processing represents one of the most well-studied visual-categorization processes, both in general and in the context of the dissociation paradigm. Face-specific processing has been shown to be subserved by functionally specific modules in ventral extrastriate visual cortex, most prominently the fusiform gyrus in the ventral temporal lobe, through intracranial recordings (Allison et al., 1994) and functional MRI (Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995). In addition, ERPs reflecting face-specific processing have been extracted from scalp-recorded EEG (Allison, Puce, Spencer, & McCarthy, 1999; Bentin, Allison, Puce, Perez, & McCarthy, 1996). These electrophysiological signals have been hypothesized to originate from the same cortical areas in the occipito-temporal sulcus and fusiform

gyrus (Bentin et al., 1996) and in the STS (Itier & Taylor, 2004). This ERP activity unfolds in time as an initial negative-polarity voltage deflection peaking at approximately 170-msec poststimulus, termed the N170, which is then often followed by a longer-lasting negative-polarity wave with the same topographic distribution, occurring from ~400 to 800 msec, depending on the task (Harris, Wu, & Woldorff, 2011; Philiastides & Sajda, 2006b). The relative timing of these two phases of activity, with the N170 being early and the following negativity occurring later, has led to the suggestion that the former is associated with predominantly feedforward visual signaling and the latter may arise from reentrant signaling from higher-order cortical regions. In support of this distinction, one study has separated these two phases of the face-specific negativity on the basis of their likely respective input signals, with the N170 correlating with preceding occipital signals and the later negativity correlating more so with preceding frontal and parietal activations (Philiastides & Sajda, 2006a). These two phases of face-specific activity (an initial stimulus-driven negative-polarity peak followed by a longer-latency, likely reentrant, negativity) together represent a useful multiphasic reflection of object-category-specific neural processing, which thereby provides implicit measures of this process that can be tracked across varying conditions of awareness.

There are multiple methods by which visual awareness of a physically present stimulus can be disrupted, each of which potentially acts through a unique mechanism (Kim & Blake, 2005). One method of disrupting visual awareness of particular interest, because of its proposed high-level mechanism of disruption, is the attentional blink (AB). In this paradigm, a viewer is asked to detect targets within a rapid serial visual presentation (RSVP) stream of target and distractor images, typically presented at ~8–11 stimuli per second. The effect manifests as reduced detection, indeed reduced reported awareness, of a target when it follows another detected target by several distractor images (stimulus lags) such that the relative SOA of the two targets is ~200–500 msec (Dux & Marois, 2009; Nieuwenstein, Potter, & Theeuwes, 2009; Raymond, Shapiro, & Arnell, 1992). Because detection/perception of the secondary target (T2) in these studies is reduced during this period following a detected preceding target (T1), it has been proposed that the effect arises from a deficit in attentional or other high-level cognitive resources during this period.

A number of studies employing electrophysiological measures of neural processing have supported a later or higher-level mechanism of disruption in the AB. For example, generic feedforward visual sensory processing of the T2 stimulus, indexed by the sensory-evoked P1 and N1 ERP responses, has been shown to be preserved during the AB (Sergent, Baillet, & Dehaene, 2005; Vogel, Luck, & Shapiro, 1998). Moreover, the later semantic-related N400 ERP component was reported to be equivalent at Lag 7 (nonblink) and Lag 3 (blink) trials (Rolke,

Heil, Streb, & Hennighausen, 2001; Luck, Vogel, & Shapiro, 1996), suggesting that processing up to the level of semantic analysis is preserved during the AB. This full high-level processing during the AB has been partially questioned, however, by a subsequent N400 study showing some disruption of semantic processing of T2 when task demands or perceptual load associated with T1 were increased (Giesbrecht, Sy, & Elliott, 2007), as well as by another study demonstrating an absence of the N400 in the case of missed targets as well as the absence of late syntactic incongruity effects during the AB period (Batterink, Karns, Yamada, & Neville, 2010). In fact, the only tested electrophysiological component that seems to consistently scale with behavioral measures of detection, at least in the absence of T1 task load manipulations, has been the P300 (Vogel et al., 1998), a longer-latency ERP response normally associated with the detection of target stimuli. Neuroimaging studies have theorized that frontal and parietal regions play a key role in the AB (Tombu et al., 2011; Marois, Chun, & Gore, 2000), in that their levels of activation appear to track with the attentional resource deficits observed during this effect. Relatedly, a study employing TMS has shown that stimulating the right parietal cortex reduces the magnitude of the AB effect (Cooper, Humphreys, Hulleman, Praamstra, & Georgeson, 2004), further implicating this region. Finally, corresponding scalp-recorded electrophysiological signals over frontal and parietal regions have been observed only in conditions of awareness in a masking context, which follow in time the occipital activations associated with low-level, feedforward visual signaling (Fahrenfort, Scholte, & Lamme, 2008). All of these findings, taken together, suggest that the AB acts to disrupt relatively late, high-level processing, while leaving generic feedforward visual signaling intact.

Despite the findings supporting a late-acting disruption mechanism in the AB that leaves low-level visual processing intact, the extent of object-category processing that occurs in the absence of awareness in the context of the AB remains unclear for two reasons. First, although there have been studies that have measured responses to faces and other objects during the AB, the comparison isolating object-category processing, that is, for example, a comparison between responses to faces as compared with other objects, has not been made. One recent study demonstrated multiple processing stages of the emotional content of facial expression, a conclusion founded on the observation of differential disruption of enhancement effects associated with emotional versus neutral faces (Luo, Feng, He, Wang, & Luo, 2010). This result may not necessarily speak to the processing of visual object category, however, as it has been suggested that the affective content of a face may be subserved by a separate, faster, subcortical pathway than the actual face-object processing (Hung et al., 2010). Second, studies that have shown preserved high-level visual processing during the AB have done so by comparing responses to images presented at Lag 3 (blink trials) with those presented at Lag 7 (nonblink

trials). A potential concern with this approach, however, is that the AB is not typically a total effect. Rather, it normally yields conditions of unawareness in only a subset of all Lag 3 trials—usually only around 10–40%—(Dux & Marois, 2009) thus potentially resulting in an inflated account of processing in the absence of awareness if one considers all Lag 3 trials as constituting “unawareness.” Accordingly, a likely better measure of the effect of the AB on a neural measure of a visual process is derived by comparing trials with the same lag but with different behavioral outcomes, such as comparing Lag 3 trials in which the AB was present (Lag 3 misses) with Lag 3 trials in which the AB was absent (Lag 3 hits). In this way, experimenters can avoid the possibility of an inflated account of processing in the absence of awareness driven by a majority of Lag 3 trials in which stimuli were actually visible.

The present study investigated the extent of face-specific processing that occurs in the absence of awareness as induced by the AB. The N170, a negative-polarity ERP effect over occipito-temporal scalp regions reflecting face object category-specific processing (Bentin et al., 1996), was tracked across conditions of awareness, with the aim of determining the extent of this process that occurs in the absence of awareness as well as the timing of the disruption exerted by the AB. Moreover, we employed explicit trial sorting and identification of conditions of unawareness to avoid the possibility of an inflated measure of visual processing being inferred during the absence of awareness. By comparing face-specific responses in the context of Lag 3 hits with those associated with Lag 3 misses, we aimed to demonstrate (1) whether any phase (early or late) of the electrophysiological index of face processing can be dissociated from awareness as disrupted by the AB; and (2) whether effects on the early phase of the face-specific negative-polarity ERP, presumably reflecting a more bottom-up process, and the later phase of the face-specific negative wave, perhaps reflecting a recurrent or reentrant neural process, could be further dissociated from one another as a function of awareness.

METHODS

Participants

Thirty-five healthy participants with normal or corrected-to-normal vision participated in the study. Data from nine of these participants were not included in the analyses because of excessive eye blinks or because of inadequate behavioral effects that precluded effective binning of data (less than five sums of a given behavioral trial type over the entire experimental session for a participant), leaving data from 26 participants (mean age = 23.3 years, $SD = 3.3$ years; 16 men; two left-handed). All participants used their right hand to make the responses required for the task. Informed consent was obtained for each participant in accordance with a standard protocol approved by the Duke University Internal Review Board. Participants

were compensated \$15/hr for their participation in the study.

Stimuli and Task

Participants were seated with their eyes 70 cm from the center of a 19-in. CRT stimulus presentation monitor with a 60-Hz refresh rate. During the experimental session, participants completed 14 runs of a dual target detection/categorization task (Figure 1), with each run lasting 4 min, for ~60 trials per run. The stimulus set consisted of 2.9°-diameter circular cropped face and house images that were centrally presented in an RSVP stream. Most of these images were grayscale nontarget stimuli, with infrequent images that were red- or green-tinted and served as targets. Participants were asked to detect, as reflected by a button press, the red- or green-tinted face and house targets occurring among grayscale face and house distracters. On each trial, 13 images (faces and houses, equiprobably randomly selected) were presented at a rate of ~11 per second, with each image having a duration of 33 msec and with interimage blank buffer periods of 50 msec (Presentation software package, Neurobehavioral Systems, Albany, CA). Following the presentation stream for each trial, participants were asked to indicate whether a green image was presented and, if so, whether it was a face or a house and then to indicate the same for any detected red-tinted images. It should be noted that the order of red- and green-tinted targets within the presentation stream itself was randomized (see below). Four trial types of randomized order and equal distribution were included (Figure 1): single-target trials (i.e., containing only a “T2”), Lag 1 dual-target trials (containing a “T2” immediately following the T1 on the next image stimulus), Lag 3 dual-target trials, and Lag 7 dual-target trials (containing a T2 following a T1 either three or seven stimuli later, respectively). Every trial contained a color-tinted target (red or green), which occurred 10 images into the stream, and served as the only target in single-target trials and as the secondary target (T2) in dual-target trials. On single-target trials, it was also used as a face-specific neural-response localizer image (using the face-minus-house ERP subtraction). On dual-target trials, the occurrence of the T1 varied in position to form the various dual-target trial types of different lags.

Behavioral performance was measured for each run, and percent hue saturation of targets was titrated accordingly (in 5% increments between 5% and 60%) to ensure a minimum performance of ~90% detection for single-target trials. Possible AB trials were defined as dual-target trials in which a T2 followed a T1 by a lag of three images (SOA of 249 msec). Non-AB trials were defined as dual-target trials wherein a T2 followed T1 by a lag of one image (SOA of 83 msec) or by seven images (SOA of 581 msec). It is important to note that the various trial types were presented in randomized order and were equally likely to occur, as were the face and house targets, regardless of whether they were the T1 or T2

Figure 1. Stimuli and task: Every trial was composed of the same number of randomly selected faces and houses embedded in an RSVP context. Each image in the stream was presented for 33 msec, followed by a 50-msec blank buffer period. Targets (images of a red or green tint) to which electrophysiological responses were ultimately time-locked always occurred at a lag of 10 images following the onset of the trial. In single-target trials, this was the only color-tinted image presented. In Lag 1, Lag 3, and Lag 7 trials, a primary target (T1) was presented at a specific lag before a T2. Participants were asked to report both the presence and object-category identity of the green- and red-tinted targets following each trial.

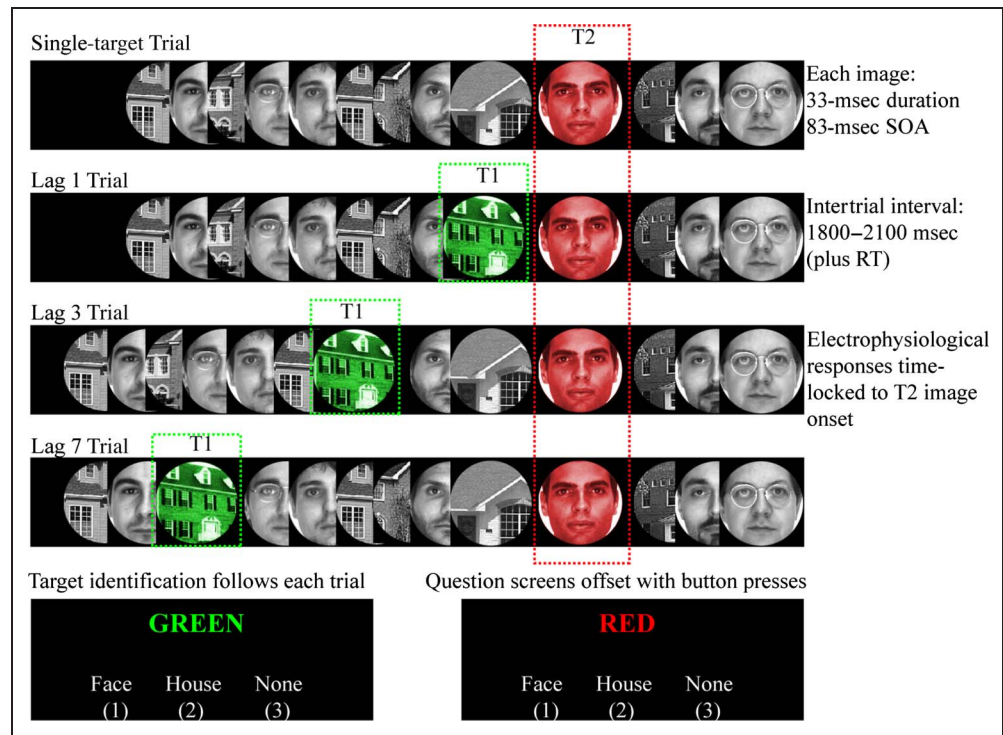


image. However, to disambiguate participants' responses to targets, dual-target trials always contained one green target and one red target that could occur in either order (green first or red first). This provided certainty in determining which targets participants were detecting versus failing to detect, given the possibility of presenting two targets of the same object category in a trial. Participants were verbally surveyed following the experiment, and none reported noticing a pattern in the order of color-tinted targets presented.

Data Analysis

Behavioral

Behavioral performance was compared for the different trial types, both at the level of target detection (wherein participants indicated the presence of a color-tinted target, regardless of whether their categorization was correct or not) as well as at the level of face–house discrimination (for the detected-target trials). In addition to target detection rate for the detection/categorization task, d-prime scores based on signal detection theory (Macmillan & Creelman, 1997) were calculated to quantify the amount of object information that participants acquired in the AB (Lag 3) and non-AB (Lag 7) trial types.

EEG Acquisition and ERP Data Analysis

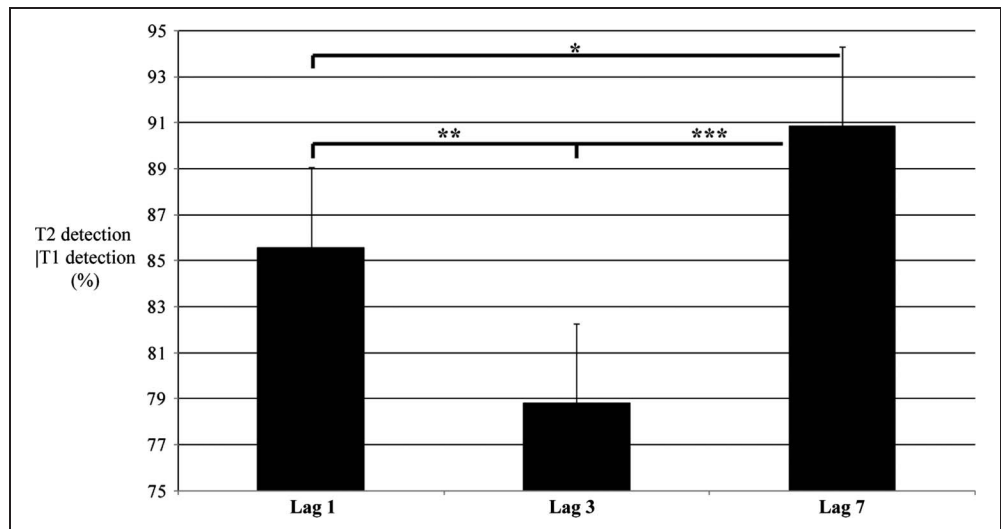
The EEG was recorded continuously from a custom 64-channel cap (Electrocap, Inc., Eaton, OH) with extended

inferior occipital coverage (Woldorff et al., 2002), using a right mastoid reference, a bandpass filter of .01–100 Hz, a sampling rate of 500 Hz, and a gain of 1,000 (Neuroscan Amplifier system, Charlotte, NC). Eye movements were monitored with a closed-circuit video camera as well as with two vertical EOG channels below the eyes referenced to prefrontal electrodes (Fp1 and Fp2) and a horizontal EOG channel measuring differential activity between the left and right outer canthi. Artifact rejection was performed offline to remove trials contaminated by blinks, muscle activity, drift, or eye movement.

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 moving-average filter, which at our 500-Hz sample rate attenuates external electrical noise with frequencies at and above ~56 Hz. The ERP averages were subsequently algebraically rereferenced to the average of all the electrodes (common reference) and baseline corrected relative to the 100-msec preceding stimulus onset.

Face-selective ERP effects were extracted by contrasting the ERP evoked by the face image stimuli with those evoked by the house image stimuli for the same trial type (lag and behavioral condition). Comparisons of face-specific effects across different awareness outcomes were achieved by comparing averages of trials within the Lag 3 condition as a function of behavior. Specifically, trials in which participants were considered “aware” were those in which the T2 stimulus was both detected and correctly identified (a hit). In contrast, trials of “unawareness” were identified as those in which participants indicated

Figure 2. Behavioral AB effect: The behavioral decrement in T2 detection, given the detection of the prior T1 as a function of the different item lags, is shown. Lag 3 trials showed the lowest rate of T2 detection in the context of T1 detection, Lag 1 trials showed some sparing, and Lag 7 trials showed the greatest T2 performance (* $p < .05$; ** $p < .01$; *** $p < .001$).



that they saw no second target, although one was present (a complete miss). In addition, we analyzed responses for incorrect categorization trials (or incorrect trials) in which participants indicated the presence of a target image but misidentified it. Because the comparison of hits with misses represents the clearest cut distinction between conditions of awareness and unawareness, our discussion will focus on this comparison. However,

it should be noted that the same pattern of results holds when comparing hits with misses or incorrect categorizations.

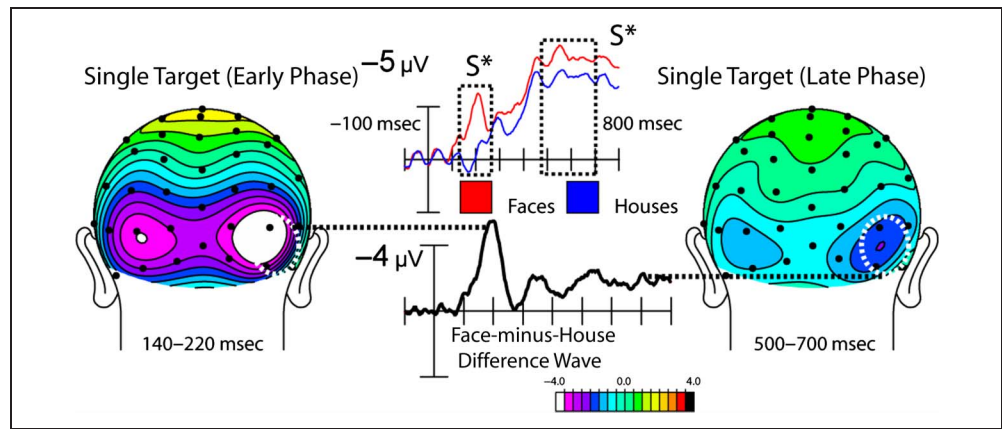
The ERPs were statistically analyzed using a within-subject two-factor (Trial type \times Face-minus-house) repeated-measures ANOVA on the mean amplitude of the face-specific activity. Effect latencies and durations were determined using successive 10-msec moving

Table 1. Statistical Tests of Mean ERP Amplitudes to Faces and Houses at the Different Lag Conditions

Comparison	Early Phase (140–220 msec)		Late Phase (500–700 msec)	
	<i>F</i> (1, 25)	<i>p</i>	<i>F</i> (1, 25)	<i>p</i>
Single target: Face vs. house	118.7	<.0001	27.2	<.0001
L7: Face vs. house	52	<.0001	2.78	.11
L3: Face vs. house	41.9	<.0001	0.01	.94
Face-minus-house diff. waves: L7 vs. L3	<0.01	.95	1.61	.22
L7 hits: Face vs. House	116.5	<.0001	14.3	<.001
L3 hits: Face vs. house	56.7	<.0001	9.1	<.01
Face-minus-house diff. waves: L7 hits vs. L3 hits	2.5	.13	<0.01	.95
L3 misses: Face vs. house	12.87	<.01	0.62	.44
Face-minus-house diff. waves: L3 hits vs. L3 misses	0.43	.52	4.26	<.05
L3 incorrect: Face vs. house	9.35	<.01	0.47	.50
Face-minus-house diff. waves: L3 misses vs. incorrect	0.03	.86	0.01	.92
Face-minus-house diff. waves: L3 hits vs. incorrect	0.65	.43	4.55	<.05

Activity measures were taken from the average of three right-hemisphere scalp sites surrounding the standard 10–20 system site T02. L3 = Lag; L7 = Lag 7; diff. = difference.

Figure 3. Face-specific activity localizer. Single-target trials: For single-target trials, in which a face or house occurred in the target slot, a significantly greater negative-polarity voltage deflection was observed in response to faces relative to houses, providing a straightforward localizer condition for face-selective activity. This face-selective ERP activity was most prominent at temporal occipital scalp sites and during the time window of 140- to 220-msec poststimulus, reflecting the hallmark N170 response. The same pattern was seen with a similar topographic distribution during the later poststimulus time window of 500–700 msec.



windows across the 800 msec following the onset of the stimulus. All face-specific effects, at both early and late latencies, were examined over the average of the three right temporal–occipital electrode sites in our 64-channel

custom cap (TO2, TI2, and C6p) nearest to the standard 10–20 system scalp site TO2, consistent with the typical distributional peak of the negative-polarity face-specific ERP effects.

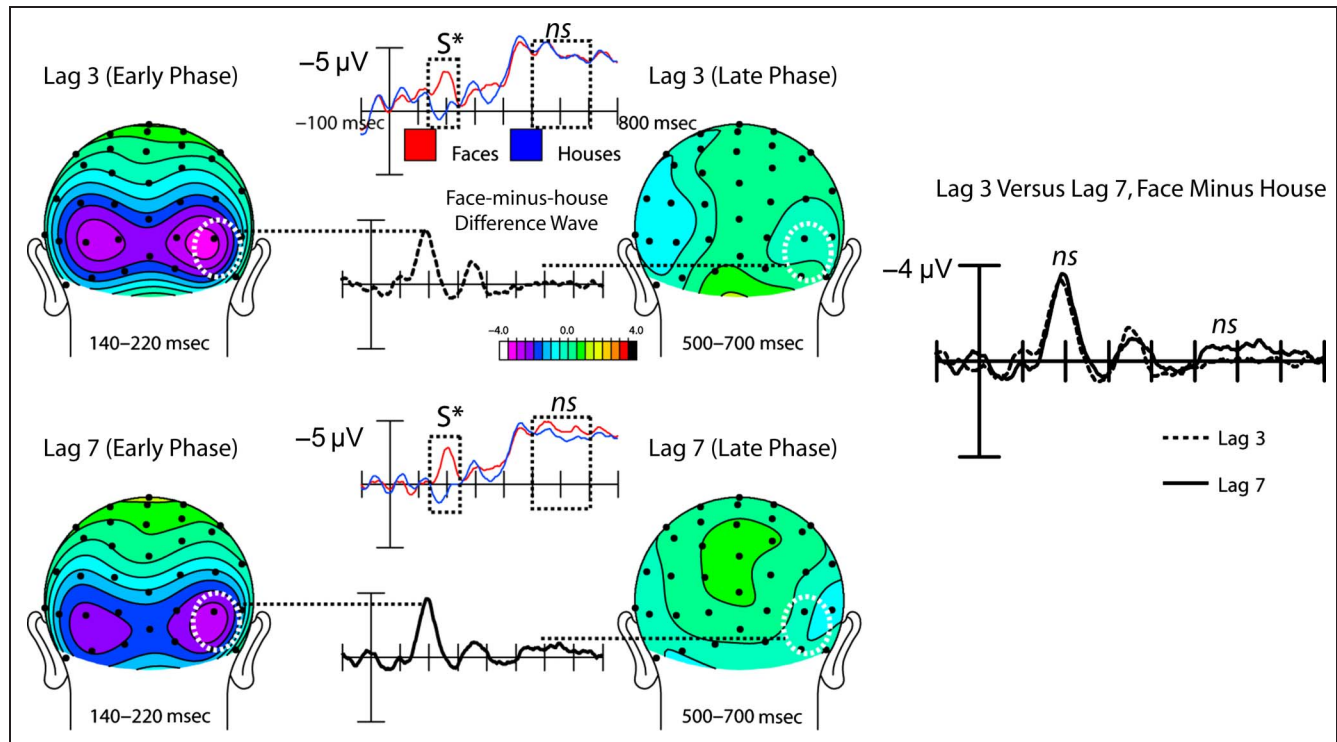


Figure 4. Intact face-specific processing in Lag 3 trials as compared with Lag 7 trials, collapsed across behavior: The traditional analysis (comparison of Lag 3 and Lag 7 trials) of electrophysiological data revealed that there was no difference in the face-specific amplitude enhancement. The face-specific enhancement, in both Lag 3 (top) and Lag 7 (bottom) trials, was observed as a bilateral negative-polarity amplitude enhancement with an occipito-temporal scalp distribution. This response’s temporal and scalp distributions were consistent with the face-specific N170. The superimposed face-minus-house difference waves showed no difference in the face-specific response between Lag 3 (dashed line) and Lag 7 (solid line) trials across the entire averaged epoch, although there was a trend for a larger late-phase response in Lag 7 trials.

RESULTS

Behavior

As noted above, the target-detection task difficulty was titrated by varying the percent hue saturation of the red and green targets within each run, with the goal of having a detection rate of around 90%. As per this goal, the mean detection rate turned out to be 92.3% for single-target trials, which was achieved using a mean hue saturation of $32\% \pm 12.5\%$ across all participants. The T1 detection rates for dual-target trials were similar to the rates for single-target trials, with a mean of 93.2% across participants. Detection rates did not differ for the face versus the house targets for single-target trials (92.2% and 92.4%, respectively), T1s (93.8% and 92.5%, respectively), or T2s of any lag (all p s > .05). There was a significant effect of trial type on T2 detection given a T1 detection ($F(2, 50) = 12.6, p < .001$). This overall effect was driven by a reduction in T2 detection in Lag 3 trials relative to both Lag 1 and Lag 7 trials ($t(25) = 3.0, p = .01$ and $t(25) = -4.2, p < .001$, respectively). Specifically, detection rates for Lag 1, Lag 3, and Lag 7 T2s, given a detected T1, were 85.6%, 78.8%, and 90.8%, respectively (Figure 2). This pattern of detection performance is consistent with that typically observed for the AB. Further examination of detection trials revealed that correct categorization of T2s significantly decreased in Lag 3

trials relative to Lag 7 trials. Specifically, for those T2s that were detected in Lag 7 and Lag 3 trials, pairwise comparisons of d -prime values across faces and houses revealed a significant decrease in discrimination performance from Lag 7 trials to Lag 3 trials from 1.44 for Lag 7 trials to 0.92 for Lag 3 trials ($t(25) = 5.3, p < .0001$).

Electrophysiology

Examination of single-target trials as a face-minus-house localizer revealed a biphasic face-specific negativity during the time windows of 140–220 and 500–700 msec (Table 1; Figure 3). Subsequent tests were restricted to these time windows and this scalp region. Some of these tests examined the effect of trial types for lags inside versus outside the AB window (Lag 7 vs. Lag 3), as per traditional AB analyses. In addition, however, and more importantly, aware versus unaware conditions were investigated by comparing the face-specific effect within Lag 3 trials as a function of behavior as disrupted by the AB (Lag 3 correctly identified T2 stimuli versus Lag 3 completely missed T2 stimuli).

Analyses examined the presence and absence of the face-specific electrophysiological effect in both the early and late neural latencies across trial types and behavior. The presence and absence of face-specific effects within

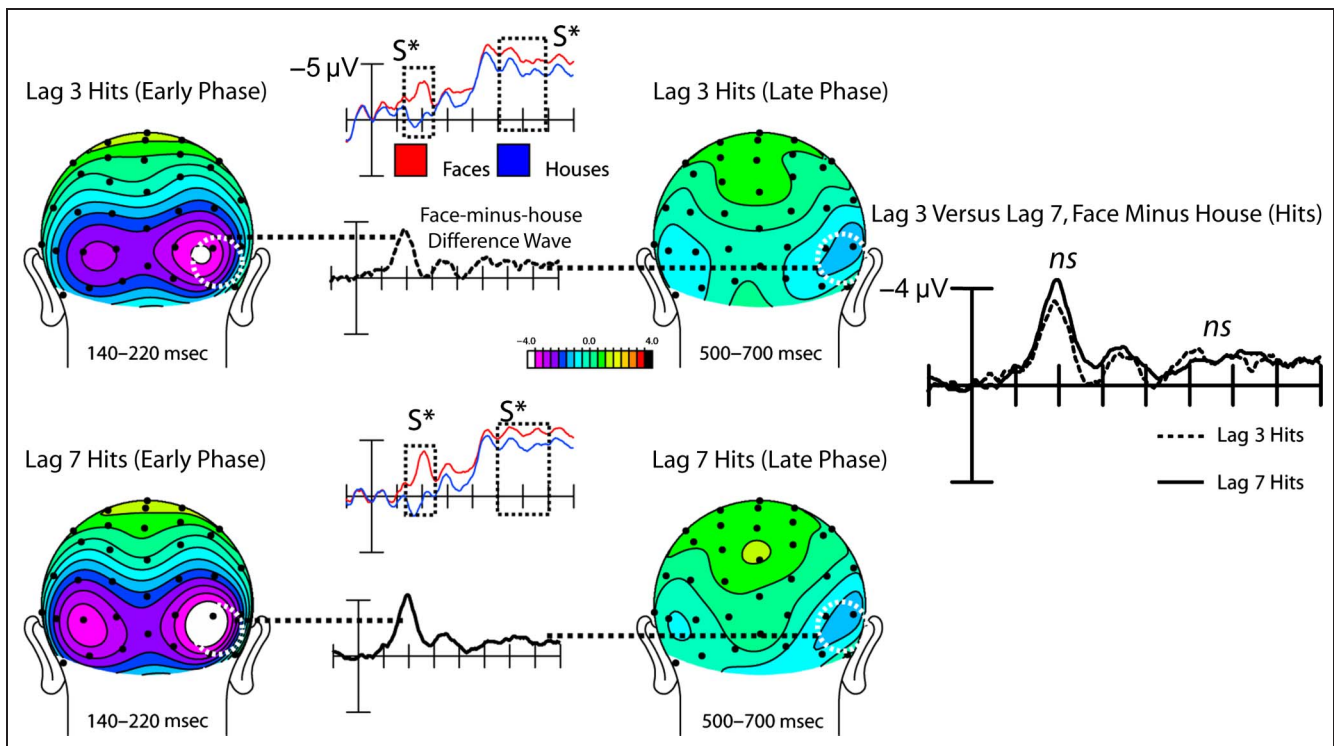


Figure 5. Hits only: Intact N170 and late face-specific activity in Lag 3 trials compared with Lag 7 trials. In the context of accurate behavior (correct identification of T2 or hits), there was no difference across Lag 3 (top) and Lag 7 (bottom) in the face-specific negativity-wave activations, which were present as the initial N170 peak and then as a later negativity. The superimposed face-minus-house difference waves showed no difference in the face-specific response between Lag 3 hits (dashed line) and Lag 7 hits (solid line) across the entire averaged epoch. Within each of these conditions of hits, for both lags, a significant face-specific activation was observed at both the early (140–220 msec) and late (500–700 msec) stages.

each condition were determined by examining mean amplitude differences between face-evoked potentials and house-evoked potentials within lag types and behavior.

As per the traditional Lag 3 versus Lag 7 AB analysis, face-specific effects across these lag presentation conditions were first compared, collapsing across all behaviors within each lag. A face-specific enhancement was present in the early phase of 140–200 msec but absent in the late phase of 500–700 msec (see Table 1; Figure 4) for both lag conditions, although trending toward significance in the case of Lag 7 trials. No significant difference in the face-specific amplitude enhancement was observed between Lag 7 and Lag 3 trials in either the early or late time windows, when collapsed across all behaviors. When comparisons were restricted to accurate behavior (hits) only, however, the face-specific activity was present in both early and late phases for Lag 3 and Lag 7 trials (Table 1; Figure 5). In addition, this face-specific activation for hits did not differ between Lag 3 and Lag 7 hits (Figure 5). The presence of this late-phase face-specific negativity only in the case of accurate behavior suggests that it is related to behavioral performance. As an additional consideration, the apparent lack of a face-specific negativity at this late processing phase even in Lag 7 when collapsed across all behaviors may be because of the fact that, although there were significantly more misses in the case of Lag 3 targets (the AB effect), there

remained a substantial number of Lag 7 trials in which targets were detected but incorrectly categorized. The absence of a significant late negativity in the case of Lag 7 trials when all behaviors were collapsed is therefore likely because of a dilution of the effect from these incorrect trials, as this activation appears to be highly influenced by behavioral performance.

To more specifically isolate the face-specific activity in the presence and absence of awareness, Lag 3 trials associated with the correct identification of T2 stimuli (hits) and Lag 3 trials associated with an effective AB (completely missed T2s) were examined. In the case of hits, the face-specific effect was present in both the early and late phases, as previously stated (Table 1; Figure 5). In the case of misses, the face-specific N170 was present, but the late-phase face-specific negativity was absent (Table 1; Figure 6). Finally, the face-minus-house difference waves for Lag 3 hits and Lag 3 misses differed only at the late phase. Specifically, the N170 did not significantly differ across conditions of awareness and was not disrupted by the AB (Figure 6). In sharp contrast, the late-phase face-specific effect was present only in the case of accurate behavior and not in cases of unawareness for these trials. In summary, a dissociation between early and late phases of the face-specific negativity was observed as a function of awareness, as modulated by the AB. It should be noted that the same dissociation was observed when comparing hits

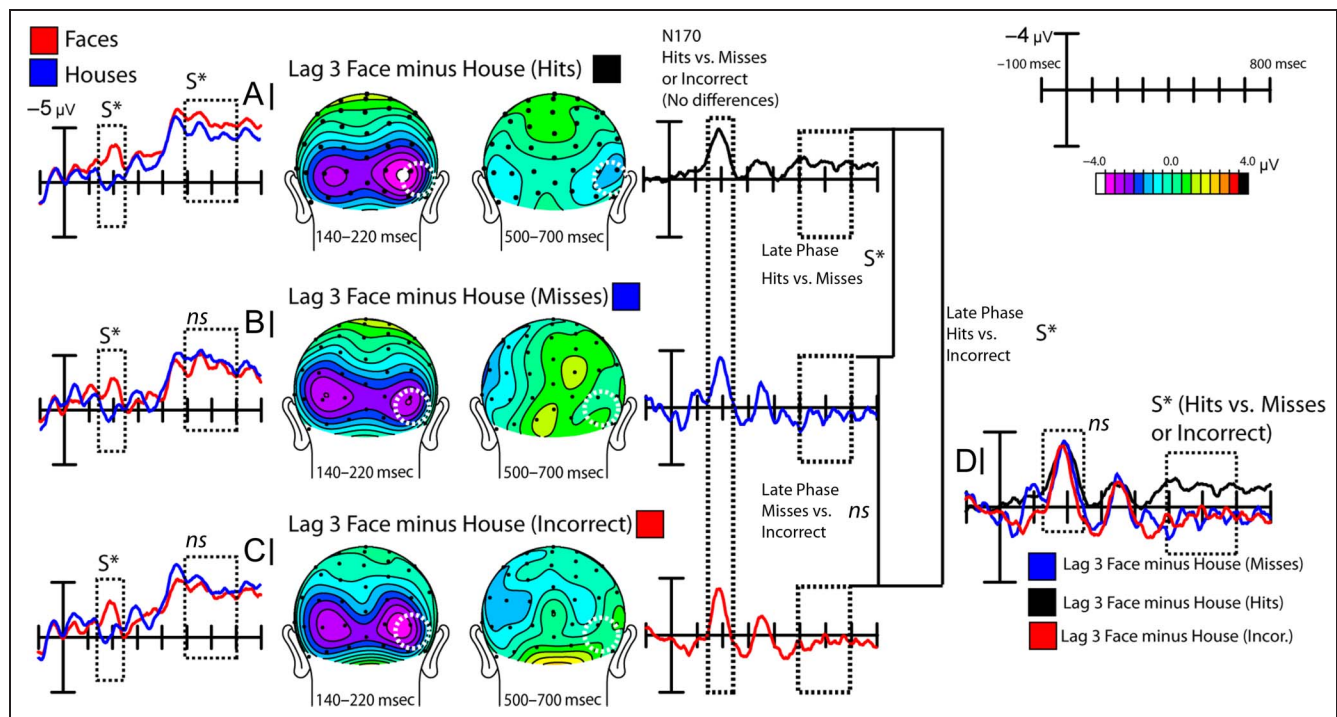


Figure 6. Hits versus misses in Lag 3 (AB window) show intact N170 but disrupted late face-specific activity: The AB did not affect the early face-specific negativity (the N170 face-minus-house difference wave). During the period of 140–220 msec following the onset of the T2 stimulus, accurately identified faces and houses elicited a robust N170 (A), as did completely missed and miscategorized T2 stimuli (B and C, respectively), with none of these differing in amplitude. A dissociation between hits and misses/miscategorizations, however, was observed for the late phase of the face-specific negativity. Specifically, the late face-specific negativity was robustly present for the Lag 3 hits but was absent for both misses and miscategorizations (D).

and incorrect categorizations within Lag 3, with the late face-specific negativity being eliminated and the earlier-latency face-specific N170 activity not differing between hits, complete misses, and incorrect categorizations (see Table 1; Figure 6).

DISCUSSION

An Attentional Blink for Faces and Houses

This study was designed to provide clearly specified conditions of awareness and unawareness necessary to directly investigate the extent of face-specific processing that occurs within and without awareness as manipulated by the AB. First, faces and houses as T2s were equally affected by their lag relative to detected T1s. Specifically, the detection of face targets and house targets following a detected T1 was similarly reduced in the case of Lag 3 trials, less so but also similarly in Lag 1 trials, and not at all in Lag 7 trials, relative to single-target trials. By uncovering a behavioral decrement equal in magnitude for face and house detection in this study, electrophysiological responses to faces versus houses between and within Lag 3 and Lag 7 trials could be appropriately compared, and thus, the face-specific responses could be suitably extracted. Moreover, responses on trials in which the AB occurred (Lag 3 misses) could be compared with physically identical trials in which the AB did not occur (Lag 3 hits). This in turn allowed for a comparison at the level of object category (faces vs. houses), extracted as a function of the behaviorally manifested awareness within Lag 3 trials. Thus, these conditions and analysis techniques were able to directly and precisely address the question of whether face-specific processing occurs in the absence of awareness as manipulated by the AB. Ultimately, it was found that early indices of face-specific processing were present regardless of the level of awareness, whereas the late phase of the face-specific electrophysiological activity was disrupted in conditions of blink-induced unawareness.

Lag 3 versus Lag 7 Trials

In a traditional comparison of face-specific neural activations between lags—that is, one made between Lag 7 and Lag 3 trials regardless of the behavioral responses—no significant difference in face-specific activity was observed in any time window. Furthermore, neither of these two trial types (i.e., T2s in Lag 7 or Lag 3, again collapsed across behavior) elicited face-specific activity that differed significantly from that in single-target trials. Considered alone, this would seem to suggest that face-specific processing, and thus, category-level discrimination in the brain, occurs in the absence of awareness, completely unaffected by the AB. This finding would be in agreement with several studies that made an analogous between-

lag comparison in an AB paradigm when investigating other higher-level visual or cognitive processes. For example, using a semantic priming paradigm in which participants were given a prime word before the onset of the RSVP stream, it has been shown that, if the T2 was semantically incongruous with the prime, the semantics-related N400 ERP was observed both for Lag 3 and Lag 7 trials (Vogel et al., 1998; Luck et al., 1996). Although a key part of this finding was replicated by another group, thus supporting the presence of semantic processing during Lag 3 trials, it was also shown that a reduction of the N400 component in Lag 3 trials occurred under conditions of increased T1 task demands (Giesbrecht et al., 2007). Similarly, in another study employing an RSVP stream, reduction of the N400 component was observed in cases of induced task switching, further suggesting that these high-level cognitive effects are susceptible to attentional resource constraints (Vachon & Jolicoeur, 2011). In addition, even in the case of affective content, which is thought to be processed during the AB, amplitude enhancements of visual-evoked potentials otherwise accompanying affective stimulus content were reduced and delayed as attentional resources were degraded in AB trials (Luo et al., 2010). All of these findings, taken together, suggest that, when the AB effect is enhanced or trials in which it was effective in suppressing awareness are isolated, decreases in neural measures of higher-level visual processing may indeed be observed.

Lag 3 Hits versus Lag 3 Misses

Although various types of visual processes have been reported to occur during the AB, from basic feedforward visual sensory processing to the affective content of faces and the semantic content of words, there remains some controversy surrounding several of these higher-level neural indices of visual processing, as noted above. These controversies may be because of differences in task load across experiments (as per Giesbrecht et al., 2007) as well as data-sorting issues that differentially isolate trials of unawareness from those of awareness. In studies investigating the effect of the AB on neural responses, Lag 3 responses have tended to be directly compared with Lag 7 responses, with Lag 3 trials being ostensibly identified as AB trials and Lag 7 ones being viewed as outside the AB window. To more accurately examine the relationship between these neural responses and awareness, however, it must be appreciated that Lag 3 trials do not invariably, or even typically, lead to conditions of unawareness. Indeed, the typical decrement in the detection of T2s following detected T1s for Lag 3 versus Lag 7 trials is between 10% and 40% (Dux & Marois, 2009). This means that 60–90% of Lag 3 trials typically consist of instances in which the participant was actually aware of the stimulus. Furthermore, if the neural signal of interest does in fact scale with the level of awareness, then there may be only a relatively small decrease from Lag 7 to Lag 3 in the relevant neural

response, which may in turn be taken as an evidence of preserved perceptual processing in the absence of awareness.

Accordingly, sorting and comparing the trials of accurate categorization and complete misses within Lag 3 trials provides a more directed and precise analysis of face-specific activations as a function of behaviorally manifested awareness. In doing so for the current experiment, full preservation of early neural indices of face-specific processing coded by the N170 was observed, thus dissociating this early brain-activity measure from awareness. A dissociation between the early and late phases of the face-specific negativity was observed, however, with the late phase being eliminated in conditions of unawareness as induced by the AB. This in turn suggests that the timing of disruption exerted by the AB lies between processing at the level of the N170 and the later face-specific activity observed beginning at 500-msec poststimulus. This would be consistent with research supporting global reentrant processing, which may here be reflected as this long-latency category-specific brain activity, as a necessary condition for the emergence of awareness. This result also suggests that the AB may be disrupting higher-level neural processes, such as in frontal cortex, that may normally provide or engender such a feedback signal to extrastriate visual areas and, ultimately, early visual cortical regions (Tomblu et al., 2011; Camprodon, Zohary, Brodbeck, & Pascual-Leone, 2010; Del Cul, Dehaene, Reyes, Bravo, & Slachevsky, 2009; Bullier, 2001; Di Lollo, Enns, & Rensink, 2000). That is, the present results suggest that the N170 is mainly driven by feedforward processing propagating through the ventral visual stream leading up to the initial face-specific module, which is not subject to the disruptive effects of the AB. In contrast, the much-later second phase of the face-specific negativity, likely driven by reentrant visual processing signals originating from later higher-level feedback processes to the posterior sensory-processing regions, seems to be significantly disrupted during the AB. This interpretation is supported by the timing of the disruption observed here as well as by previous studies employing covariational modeling to evidence the preponderance of early occipital signal input to the N170 but later parietal signal input to the late face-specific negativity (Philiastides & Sajda, 2006a). This is not to say that the face-specific N170 does not depend on any reentrant signaling at all, such as possible local reentrance within lower-level visual circuits that has been implicated in awareness and the intactness of early face-specific responses (Boehler, Schoenfeld, Heinze, & Hopf, 2008; Reiss & Hoffman, 2007; Harris, Ku, & Woldorff, in press). Instead, the current findings suggest that the net feedforward signal comprising the early phase of the face-selective negative-wave activity (i.e., the N170), composed of a combination of purely feedforward signaling and signals arising from lower-level local/rapid reentrant loops, is left intact by the AB. In clear contrast, the current results show that, on trials in which perceptual awareness is disrupted by the AB, there is a strong

attenuation, if not elimination, of the late face-selective cortical activity, and thus of any longer-latency reentry activity from higher brain regions.

The present experiment offers a set of findings that can potentially reconcile otherwise contradictory findings in the literature. The preponderance of studies investigating neural measures during the AB do so by either comparing brain response associated with Lag 3 trials with those associated with Lag 7 trials (as in Vogel et al., 1998), as noted above, or by increasing the task load associated with T1s such that a greater magnitude blink is observed and comparing Lag 3 low-load with Lag 3 high-load trials (Giesbrecht et al., 2007). This approach is in contrast to directly examining responses to missed targets relative to accurately perceived ones for the same lag. Such an approach, as currently implemented, was able to reveal the novel finding that the late-phase face-specific activity scales closely with behavioral measures of awareness, whereas the early N170 face-specific activity does not.

The above-described dissociation between the early and late phases of face-specific processing was also made possible by the high temporal resolution provided by electrophysiological measures that are otherwise unavailable using hemodynamic measures. For example, in a study employing a variant of visual masking, enhanced face-specific activity was observed in masked conditions in the right fusiform gyrus (Morris, Pelphrey, & McCarthy, 2007). However, the effect was reduced relative to unmasked conditions, and thus, it might have reflected the initial stages of face-specific processing being preserved but with a reduction or absence of a late face-specific enhancement, a distinction that could not be made with the fMRI recordings. In contrast, the high temporal resolution of ERPs employed here was able to delineate the time course of the processing and to disentangle the strikingly different pattern of effects for the early and late phases of face-specific activity as a function of awareness. Overall, the current study demonstrates that the late, but not the early, neural index of face-specific processing is subject to the disruptive effects of the AB. Such results are consistent with studies suggesting that visual awareness arises, at least in part, from late, reentrant processing (Dux, Visser, Goodhew, & Lipp, 2010; Fahrenfort, Scholte, & Lamme, 2007) as well as with studies demonstrating direct modulation of visual awareness through TMS disruption of these late signals (Camprodon et al., 2010; Bullier, 2001).

Finally, in addition to providing a novel context for face-specific processing as it relates to awareness disrupted by the AB, the current findings help to refine the nature of the attentional gating invoked during the AB. Specifically, the perseverance of the N170 during the AB is in direct contrast to studies clearly showing strong gating of this effect by spatial attention (Crist, Wu, Karp, & Woldorff, 2008). In the Crist et al. (2008) study, for example, it was found that strongly focused

spatial visual attention away from targets strongly attenuated the P1 response associated with them as well as the downstream face-specific negativity, essentially gating the N170. This modulation of the N170 by spatial attention has since been observed in several other contexts by other authors (Feng, Martinez, Pitts, Luo, & Hillyard, 2012; Carlson & Reinke, 2010). Attentional gating of visual perceptual processing as seen in a spatial attention context would have severely attenuated the presently extracted N170 as well as the earlier feedforward extrastriate signals coded by the visual P1 (Crist et al., 2008). However, the current study necessitated focal spatial attention on the relevant visual stream at all times, and in this way, spatial attention effects were not invoked. The current results, in conjunction with many others citing intact sensory signals during the AB (Luo et al., 2010; Giesbrecht et al., 2007; Sergent et al., 2005; Vogel et al., 1998), therefore reinforce the distinction that exists between the effects of visuospatial attentional gating and other types of attentional gating, such as that observed in the AB. This latter type of gating, presently invoked, is likely more because of attentional capacity limitations that come into play while processing the content of a detected T1 stimulus.

Conclusions

This study reports several important findings. First, it demonstrates that faces, a stimulus type that has been suggested as being relatively resistant to the effects of the AB, especially when containing emotion or being familiar (Miyazawa & Iwasaki, 2010; Maratos, Mogg, & Bradley, 2008; Raymond & Jackson, 2006), are in fact susceptible as objects whose conscious perception can be disrupted during the AB. More importantly, for our present goals, the results show that the early phases of face-specific processing, as reflected by the N170 ERP component, are fully intact during conditions of unawareness. In addition, with this more precise isolation of distinct levels of awareness as achieved by comparing Lag 3 trials in which participants completely missed T2 images with Lag 3 trials in which they detected and correctly categorized T2s, a dissociation between the early and late phases of face-specific activity was revealed. In particular, the late phase of face-specific processing was closely associated with awareness, whereas a fully intact early phase of category-specific activity (the N170) was elicited regardless of whether the participant was aware of the image. Thus, the present results not only reveal brain activation patterns related to conscious visual perception but also underscore the importance of truly distinguishing awareness variations through more precise data-sorting procedures. Finally, the present results serve to further distinguish the effects of the AB from those of spatial attention, with the disruption of the AB occurring later than the low-level attenuation of feedforward sensory signals.

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