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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 identification occurs in the absence of awareness, electrophysiological responses to images of faces and houses were recorded both within and outside of the attentional blink period during a rapid serial visual presentation (RSVP) stream. Electrophysiological results were sorted according to behavioral performance (correctly identified targets versus missed targets) within these blink and non-blink periods. An early index of face-specific processing (the N170, 140–220 ms post-stimulus) was observed regardless of whether the subject demonstrated awareness of the stimulus, whereas a later face-specific effect with the same topographic distribution (500–700 ms post-stimulus) was only seen for accurate behavioral discrimination of the stimulus content. The present findings suggest a multi-stage process of object-category processing, with only the later phase being associated with explicit visual awareness.

Keywords

Object processing; Consciousness; Perception; High-level vision; Event related potentials; Attention; Visual

INTRODUCTION

An as yet 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, due to the fact that any information encoded in the brain, whether an individual is aware of it or not, holds the potential to influence behavior.

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Thus, the investigation of visual processing, from basic sensory levels to more abstract and sophisticated levels of representation, and how it 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 of 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 in the brain), 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 subject. 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, event-related potentials (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 occipitotemporal sulcus and fusiform gyrus (Bentin, et al., 1996) and in the superior temporal sulcus (Itier & Taylor, 2004). This ERP activity unfolds in time as an initial negative-polarity voltage deflection peaking at approximately 170 ms post-stimulus, termed the N170, which is then often followed by a longer-lasting negative-polarity wave with the same topographic distribution, occurring from ~400–800 ms, depending upon 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 feed-forward 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 provide 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, due to 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 of ~200–500 ms (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 time 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 time period.

A number of studies employing electrophysiological measures of neural processing have supported a later or higher-level mechanism of disruption in the attentional blink. For example, generic feed-forward 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 attentional blink (Sergent, Baillet, & Dehaene, 2005; Vogel, Luck, & Shapiro, 1998). Moreover, the later semantic-related N400 ERP component was reported to be equivalent at Lag 7 (non-blink) and Lag 3 (blink) trials (Luck, Vogel, & Shapiro, 1996; Rolke, Heil, Streb, & Hennighausen, 2001), suggesting processing up to the level of semantic analysis is preserved during the attentional blink. This full high-level processing during the AB has been partially questioned, however, by a subsequent N400 study showing some disruption of semantic processing T2 when task demands or perceptual load associated with T1 were increased (Giesbrecht, Sy, & Elliott, 2007), as well as 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 attentional blink 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 attentional blink (Marois, Chun, & Gore, 2000; Tombu et al., 2011), in that their levels of activation appear to track with the attentional resource deficits observed during this effect. Relatedly, a study employing transcranial magnetic stimulation (TMS) has shown that stimulating the right parietal cortex reduces the magnitude of the attentional blink 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, feed-forward visual signaling (Fahrenfort, Scholte, & Lamme, 2008). All of these findings taken together suggest that the

attentional blink acts to disrupt relatively late, high-level processing, while leaving generic feed-forward visual signaling intact.

Despite the findings supporting late-acting disruption mechanism in the attentional blink 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 attentional blink remains unclear for two reasons. First, although there have been studies that have measured responses to faces and other objects during the attentional blink, the comparison isolating *object-category* processing, that is, for example, a comparison between responses to faces as compared to 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 attentional blink have done so by comparing responses to images presented at Lag 3 (blink trials) to those presented at Lag 7 (non-blink trials). A potential concern with this approach, however, is that the attentional blink 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 when considering all Lag 3 trials as constituting ‘unawareness.’ Accordingly, a likely better measure of the effect of the attentional blink on a neural measure of a visual process will be derived by comparing trials with the same lag but with different behavioral outcomes, such as comparing Lag 3 trials in which the attentional blink was present (Lag 3 misses) to Lag 3 trials in which it 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 attentional blink. The N170, a negative-polarity ERP effect over occipitotemporal 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 attentional blink. 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 to 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 attentional blink; and (2) whether or not 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.

MATERIALS AND 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 due to excessive eye blinks, or due to 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 subject), leaving data from 26 participants (mean age of 23.3 ± 3.3 years; 16 male; two left-handed). All participants used their right hand to make the responses required for the task. Informed consent was obtained for each subject in accordance with a standard protocol approved by the Duke University Internal Review Board. Participants were compensated \$15/hour for their participation in the study.

Stimuli and task

Participants were seated with their eyes 70 cm from the center of a 19-inch 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 minutes, for a total of ~60 trials per run. The stimulus set consisted of 2.9°-diameter circular cropped face and house images that were centrally presented in a rapid serial visual presentation (RSVP) stream. Most of these images were grayscale non-target stimuli, with infrequent images that were red or green-tinted and served as targets. Subjects 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 ms, and with inter-image blank buffer periods of 50 ms (Presentation software package, Neurobehavioral Systems, Albany, CA). Following the presentation stream for each trial, subjects indicated whether a green image was presented, and, if so, whether it was a face or a house, and then to indicate the same thing 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 3 or 7 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 3 images (SOA of 249 ms). Non-AB trials were defined as dual target trials wherein a T2 followed T1 by a lag of 1 image

(SOA of 83 ms) or by 7 images (SOA of 581 ms). 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 image. However, in order to disambiguate subjects' 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 subjects were detecting versus failing to detect, given the possibility of presenting two targets of the same object category in a trial. Subjects 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 subjects 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 attentional blink (Lag 3) and non-attentional blink (Lag 7) trial types.

EEG Acquisition and ERP Data Analysis—The electroencephalogram (EEG) was recorded continuously from a custom 64-channel cap (Electrocap, Inc.) with extended inferior occipital coverage (Woldorff et al., 2002), using a right mastoid reference, a bandpass filter of .01–100Hz, sampling rate of 500 Hz, and gain of 1000 (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 was 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 re-referenced to the average of all the electrodes (common reference) and baseline corrected relative to the 100 ms 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 subjects 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 subjects indicated that they saw no second target, even though one was present (a *complete miss*). In addition, we analyzed

responses for *incorrect categorization* trials (or *incorrect* trials) in which subjects indicated the presence of a target image, but misidentified it. Because the comparison of hits to misses represents the clearest cut distinction between conditions of awareness and unawareness, our discussion will focus on this comparison. However, it should be noted, as seen in Table 1 and Figure 6, that the same pattern of results holds when comparing hits to misses or incorrect categorizations.

The ERPs were statistically analyzed using a within-subjects two-factor (trial type by face-minus-house) repeated-measures analysis of variance (ANOVA) on the mean amplitude of the face-specific activity. Effect latencies and durations were determined using overlapping 10-ms moving windows across the 800 ms 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 standard 10–20 system scalp site TO2, consistent with the typical distributional peak of the negative-polarity face-specific ERP effects.

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 subjects. The T1 detection rates for dual-target trials were similar to the rates for single-target trials, with a mean of 93.2% across subjects. Detection rates did not differ for the face versus the house targets for single-target trials (92.2% and 92.4%, respectively), T1's (93.8% and 92.5%, respectively), or T2's of any lag (all $p > .05$). 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, Lag3, and Lag 7 T2's, 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 attentional blink. Further examination of detection trials revealed that correct categorization of T2's significantly decreased in Lag 3 trials relative to Lag 7 trials. Specifically, for those T2's that were detected in Lag 7 and Lag 3 trials, pair-wise 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 ms and 500–700 ms (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 attentional blink window (Lag 7 versus 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 attentional blink (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 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 attentional blink 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 ms, but absent in the late phase of 500–700 ms (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 behavior. 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 behavior may be due to the fact that although there were significantly more misses in the case of Lag 3 targets (the attentional blink 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 behavior was collapsed is therefore likely due to 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 correct identification of T2 stimuli (hits) and Lag 3 trials associated with an effective attentional blink (completely missed T2's) 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 attentional blink (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 sum, a dissociation between early and late phases of the face-specific negativity was observed as a function of awareness, as modulated by the attentional blink. It should be noted that the same dissociation was observed when comparing hits and incorrect categorizations within Lag 3, with the late face-specific

negativity being eliminated and the earlier-latency faces-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

The present 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 attentional blink. First, faces and houses as T2's were equally affected by their lag relative to detected T1's. 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 the present 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 suitably extracted. Moreover, responses on trials in which the attentional blink occurred (Lag 3 misses) could be compared to physically identical trials in which the attentional blink did not occur (Lag 3 hits). This in turn allowed for a comparison at the level of object category (faces versus 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 or not face-specific processing occurs in the absence of awareness as manipulated by the attentional blink. 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., T2's in Lag 7 or in 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 attentional blink. This finding would be in agreement with several studies that made an analogous between-lag comparison in an attentional blink paradigm when investigating other higher-level visual or cognitive processes. For example, using a semantic priming paradigm in which subjects 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 (Luck, et al., 1996; Vogel, et al., 1998). 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 attentional blink, amplitude enhancements of visual-evoked potentials otherwise accompanying affective stimulus content were reduced and delayed as attentional resources were degraded in attentional blink trials (Luo, et al., 2010). All of these findings taken together suggest that, when the attentional blink 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 attentional blink, from basic feed-forward 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 due to differences in task load across experiments (as per Giesbrecht et al., 2007), as well as to data-sorting issues that differentially isolate trials of unawareness from those of awareness. In studies investigating the effect of the attentional blink on neural responses, Lag 3 responses have tended to be directly compared to Lag 7 one, with Lag 3 trials being ostensibly identified as attentional blink trials and Lag 7 ones being viewed as outside the AB window. In order 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 detection of T2's following detected T1's 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 subject 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 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 attentional blink. This in turn suggests that the timing of disruption exerted by the attentional blink lies between processing at the level of the N170 and the later face-specific activity observed beginning at 500 ms post-stimulus. 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 attentional blink may be disrupting higher-level neural processes, such as in frontal cortex, that may normally provide or engender such a feed-back

signal to extrastriate visual areas and ultimately early visual cortical regions (Bullier, 2001; Camprodon, Zohary, Brodbeck, & Pascual-Leone, 2010; Del Cul, Dehaene, Reyes, Bravo, & Slachevsky, 2009; Di Lollo, Enns, & Rensink, 2000; Tombu, et al., 2011). That is, the present results suggest that the N170 is mainly driven by feed-forward 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 attentional blink. 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 attentional blink. 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, including local reentrance within the lower level visual circuits. Instead, the current findings suggest that the net feed-forward signal comprising the early phase of the face-selective negative-wave activity (i.e., the N170), composed of a combination of purely feed-forward signaling and signals arising from lower-level local/rapid reentrant loops, is left intact by the attentional blink. In clear contrast, the current results show that on trials in which perceptual awareness is disrupted by the attention blink, there is a strong attenuation, if not elimination, of the *late* face-selective cortical activity.

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 attentional blink do so by either comparing brain response associated with Lag 3 trials to those associated with Lag 7 trials (as in (Vogel, et al., 1998)), as noted above, or by increasing the task load associated with T1's such that a greater magnitude blink is observed and comparing Lag 3 low-load to 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 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 is 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 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 early,

neural index of face-specific processing is subject to the disruptive effects of the attentional blink. 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 (Bullier, 2001; Camprodon, et al., 2010).

Finally, in addition to providing a novel context for face-specific processing as it relates to awareness disrupted by the attentional blink, the current findings help to refine the nature of the attentional gating invoked during the attentional blink. Specifically, the perseverance of the N170 during the attentional blink 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 (Carlson & Reinke, 2010; Feng, Martinez, Pitts, Luo, & Hillyard, 2012). Attentional gating of visual perceptual processing as seen in a spatial attention context would have severely attenuated the presently-extracted N170, as well as earlier feed-forward 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 attentional blink (Giesbrecht, et al., 2007; Luo, et al., 2010; Sergent, et al., 2005; Vogel, et al., 1998), therefore reinforce the distinction that exists between the effects of visuo-spatial attentional gating, and other types of attentional gating, such as that observed in the attentional blink. This latter type of gating, presently invoked, is likely more due to attentional capacity limitations that come into play while processing the content of a detected T1 stimulus.

Conclusions

The present 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 attentional blink, especially when containing emotion or being familiar (Maratos, Mogg, & Bradley, 2008; Miyazawa & Iwasaki, 2010; Raymond & Jackson, 2006), are in fact susceptible as objects whose conscious perception can be disrupted during the attentional blink. 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 subjects completely missed T2 images to Lag 3 trials in which they detected and correctly categorized T2's, 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 or not the subject was aware of the image. Thus, the present results not only reveal brain activation patterns related to conscious visual perception, but they 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 attentional blink from those of spatial attention, with the disruption of the attentional blink occurring later than low-level attenuation of feed-forward sensory signals.

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Figure 1. Stimuli and task

Every trial was comprised of the same number of randomly selected faces and houses embedded in a rapid serial visual presentation (RSVP) context. Each image in the stream was presented for 33 ms, followed by a 50 ms 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 prior to a T2. Subjects were asked to report both the presence and object-category identity of the green and red tinted targets following each trial.

Figure 2. Behavioral Attentional Blink effect

The behavioral decrement in T2 detection given 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, whereas Lag 1 trials showed some sparing, and Lag 7 trials showed the greatest T2 performance. ($p < .05$; $p < .01$; $p < .001$)

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 140–220 ms post-stimulus, reflecting the hallmark N170 response. The same pattern was seen with a similar topographic distribution during the later post-stimulus time window of 500–700 ms.

Figure 4. Intact face-specific processing in Lag 3 trials as compared to Lag 7 trials, collapsed across behavior

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 (upper panel) and Lag 7 (lower panel) 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 response in the later phase.

Figure 5. Hits only: Intact N170 and late face-specific activity in Lag 3 trials compared to Lag 7 trials

In the context of accurate behavior (correct identification of T2, or hits), there was no difference across Lag 3 (upper panel) and Lag 7 (lower panel) 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 ms) and late (500–700 ms) stages.

Figure 6. Hits versus misses in Lag 3 (AB window) show intact N170 but disrupted late face-specific activity

The attentional blink did not affect the early face-specific negativity (the N170 face-minus-house difference wave). During the time period of 140–220 ms following the onset of the T2 stimulus, accurately identified faces and houses elicited a robust N170 (panel A), as did completely missed and miscategorized T2 stimuli (panels 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 (panel D).

Table 1

Statistical tests of mean ERP amplitudes to faces and houses at the different lag conditions. Activity measures were taken from the average of three right-hemisphere scalp site surrounding standard 10–20 system site T02. L3 and L7 = Lag 3 and Lag 7, respectively.

Comparison	Early phase (140–220 ms)		Late phase (500–700 ms)	
	F(1, 25)	<i>p</i>	F(1, 25)	<i>p</i>
Single target: Face v. House	118.7	<.0001*	27.2	<.0001*
L7: Face v. House	52	<.0001*	2.78	.11
L3: Face v. House	41.9	<.0001*	.01	.94
Face minus House diff. waves: L7 v. L3	<.01	.95	1.61	.22
L7 Hits: Face v. House	116.5	<.0001*	14.3	<.001*
L3 Hits: Face v. House	56.7	<.0001*	9.1	<.01*
Face minus House diff. waves: L7 Hits v. L3 Hits	2.5	.13	<.01	.95
L3 Misses: Face v. House	12.87	<.01*	.62	.44
Face minus House diff. waves: L3 Hits v. L3 Misses	.43	.52	4.26	<.05*
L3 Incorrect: Face v. House	9.35	<.01*	.47	.50
Face minus House diff. waves: L3 Misses v. Incorrect	.03	.86	.01	.92
Face minus House diff. waves: L3 Hits v. Incorrect	.65	.43	4.55	<.05*