Visual Object-Category Processing With and Without Awareness

by

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Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Psychology and Neuroscience in the Graduate School of Duke University

2012
ABSTRACT

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Abstract

Any information represented in the brain, whether an individual is aware of it or not, holds the potential to affect behavior. The extent of visual perceptual processing that occurs in the absence of awareness is therefore a question of broad import and interest to the field of cognitive neuroscience. A useful approach for examining the extent and quality of visual processing that occurs in the absence of awareness is the dissociation paradigm. In this approach, experimenters track implicit measures of the visual process of interest across conditions of awareness modulated by visual presentation manipulations. Object-category discrimination by the visual system represents a relatively sophisticated level of representation that may or may not occur in the absence of awareness. Here, electrophysiological measures (scalp-recorded event-related potentials, or ERPs) of object-category discrimination by the brain (the face-specific N170 ERP component and the longer-latency face-specific negativity) were tracked across conditions of visual awareness as manipulated by multiple presentation paradigms (sandwich masking, object-substitution masking, the attentional blink, and motion-induced blindness). In addition, where possible, other related comparisons examining lower-level visual processes and higher-level attentional processes were employed to help delineate the specific level and mechanism by which awareness was disrupted in each case. The experiments implicated a unique set of mechanisms of reducing awareness for each method, while providing insight into the complex relationships between the various phases of visual processing in the human brain and awareness. Ultimately it was observed
that neural indices of face-specific processing are differentially susceptible to disruption exerted by these various methods, and that there do in fact exist conditions in which awareness can be disrupted while leaving various facets and phases of face-specific processing intact. These findings help to establish object-category discrimination as a process that can occur in the absence of visual awareness, and contributes to our understanding of the neural factors that influence and determine behavior.
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1 Visual object-category processing with and without awareness: principles, findings and current studies

1.1 Introduction and overview

1.1.1 Vision: hierarchical representation and reentrant signaling

Human vision is perhaps the most well-studied and understood facet of cognitive neuroscience to date. Research spanning more than a century has extensively described the hierarchical structure of the visual system and its functional dynamics. Visual perception has been shown to be mediated by a system of highly interconnected sensory-processing modules, each tuned to specific and relevant visual features (Hubel & Wiesel, 1962; Shipp & Zeki, 1989). Moreover, each of these modules occupies a step in a feed-forward hierarchical cascade of neural processing contributing to a holistic and behaviorally relevant representation of a given visual object. In addition, more recent research suggests that higher-level aspects of vision related to the emergence of conscious awareness are mediated by recurrent processes, wherein signals are propagated from higher to lower-level visual representation modules following the initial feed-forward sweep, resulting in the final stages of visual perception characterized by subjective awareness (Di Lollo, Enns, & Rensink, 2000). What is as yet unclear is the extent and quality of visual processing that can occur in the absence of a viewer’s awareness, especially relative to that which occurs with awareness.

This question has broad implications in multiple fields. In its most general sense, it speaks to some of the oldest and most elusive philosophical questions of mind: namely that of the nature of perceptual experience. For example, knowledge that visual
information is processed to a high level of sophistication by the brain outside of awareness may necessitate a revision of the very definition of qualia as a subjective unit of perceptual experience. As an increasing amount of perceptual information is demonstrated to be processed by the brain, a definition of qualia requiring subjective knowledge of the percept becomes increasingly restrictive and irrelevant. In addition, the fact that information that is processed outside of awareness still has the potential to influence subsequent behavior broadens the scope of interest in this question to include a variety of fields in psychology and cognitive neuroscience. Researchers examining decision-making, emotion, executive and cognitive control, perception, and how these faculties relate to unconscious processing would benefit greatly from a comprehensive understanding of the extent to which the visual world is processed with and without awareness. Finally, in a clinical setting, where localized brain damage due to stroke, head trauma, or other focal lesions leads to specific deficits in visual awareness, knowledge of perceptual processes that normally occur in the absence of awareness will be useful in providing more accurate and comprehensive diagnoses of cognitive deficits and their neural underpinnings.

1.1.2 Dissociation paradigm

Visual processing in the absence of awareness can be studied using what is known as a dissociation paradigm, wherein a stimulus of which the viewer is essentially unaware (evident in a behavioral inability to report/discriminate the stimulus) is still processed to some extent. With the approach of the dissociation paradigm, such unconscious processing is evident in another measure that does not necessarily require the subject’s
explicit report (for example, as in priming or in measures of brain activity) (Reingold & Merikle, 1988). As generally applied, when the degree of processing reflected by the implicit measure of a given visual process remains intact while the explicit conscious measure of the same process is significantly reduced (a condition of lessened awareness), it is inferred that this visual process is occurring to some extent in the absence of the viewer’s awareness. It is because of this dissociation between the two measures (one direct/explicit, one indirect/implicit) of the same visual process that perceptual processing in the absence of awareness can be inferred.

1.1.3 Face (object category)-specific processing

Behavioral and psychophysical studies have provided much insight into visual processes in the absence of awareness, and technological advancements have allowed the dissociation paradigm to be applied to concurrent neural measures of visual processing. Tracking behavioral and neural indices of face-specific processing is an emblematic instantiation of this type of research, and a fruitful avenue by which to understand a particularly sophisticated and relevant visual process and how it relates to conscious awareness. While there is a rich literature on face-specific processing within awareness, whether or not such object-category level discrimination can occur in the absence of awareness remains a highly controversial issue. In general, this appears to be due to a failure to examine unconscious face-specific processing through the use of valid measures and multiple methodologies. Given the current state of the field and previous findings, a comprehensive account of the type and extent of visual processing that occurs in the absence of awareness, as well as the various mechanisms by which visual
presentation protocols can attenuate visual awareness, remains elusive. It will therefore prove ideal to track neural measures of multiple levels of visual processing in the context of awareness and unawareness, and to do so using multiple methods of disrupting awareness. Ultimately, such a line of research will lead to a multi-level model of visual perceptual processing, how each relates to the emergence of conscious awareness, and the various mechanisms by which this high-level cognitive faculty can be interrupted.

1.2 Human vision

The human visual system is comprised of a network of interconnected and functionally specialized modules that exist in a hierarchical structure, in which visual signals are propagated in a feed-forward, bottom-up, simple-to-complex fashion, as well as in a top-down modulatory fashion, with higher level areas feeding activity back into the lower-level areas (Grill-Spector & Malach, 2004). The resultant dynamics of the visual system is hence one of reverberating activity, in which it is thought that an initial feed-forward/ bottom-up sweep of activity builds a representation of the visual image, followed by recurrent top-down processes whence higher level phenomena such as awareness emerge.

1.2.1 Hierarchical representational structure

In the case of initial feed-forward signaling, the visual system has been demonstrated to be comprised of a hierarchically organized series of modules, each of which exhibits selective tuning for progressively more complex aspects of the visual environment (Figure 1). The hierarchical configuration has been tested and supported through a multitude of research studies spanning several decades and utilizing a variety of
measures. Beginning with studies of response properties of intracranially recorded neurons in primary visual cortex of macaques (Hubel & Wiesel, 1968), it has been demonstrated that as the visual signal is propagated through visual cortex, its representation is determined through the integration of inputs from lower levels, and the increasingly selective tuning of neuronal populations in these later stages reflects this. For example, following processing in area V1, which exhibits selectivity for line orientation, cells in V2 respond to figure contours, even if they are illusory (Peterhans & Vonderheydt, 1991). Whereas V1 and V2 show responses to any visual stimulus, subsequent visual cortical regions are more selective, with cells in V4, for example, responding maximally to stimuli with particular color or shape (Gallant, Braun, & Vanessen, 1993; Schein & Desimone, 1990). Areas later in the visual stream are selective for ever more complex aspects of visual stimulation, such as motion and its associated qualities of direction (Tootell et al., 1995) and coherence (Rees, Friston, & Koch, 2000) in dorsal extrastriate regions, and object identity in the case of ventral extrastriate visual regions (Perrett, Hietanen, Oram, & Benson, 1992), functional processes that are of primary interest here.
The visual system operates through a hierarchical processing structure, wherein low levels of representation are characterized by a narrow receptive field (retinotopically organized) and a broad sensitivity (responsive to a wide variety of visual stimuli), and high levels of representation are characterized by broad receptive fields (no longer spatially or retinotopically organized) and a narrower sensitivity (a greater degree of complexity and specificity in maximal responsiveness).

### 1.2.2 Reentrant signaling

In addition to the hierarchically processed feed-forward visual signal, visual perception is also dependent upon recurrent activity made possible by bidirectional connections between the various levels of the system. The extent of these bidirectional connections and their prevalence has been well-documented and supports a great deal of “top-down” communication in addition to feed-forward processing (Shipp & Zeki, 1989; Vanessen, Felleman, Deyoe, Olavarria, & Knierim, 1990). Specifically, activity from
higher levels can feed back onto lower levels of the visual system and modulate activity patterns there and in subsequent feed-forward sweeps through the system (Figure 2). This mechanism has been implicated in a variety of top-down processes, as well as emergent perceptual processes associated with conscious awareness. For example, the allocation of covert attention to a specific spatial location (a top-down process) has been shown to enhance visual cortical responses at both early and late stages of visual processing. (Crist, Wu, Karp, & Woldorff, 2008; Heinze & Mangun, 1995; Johannes, Munte, Heinze, & Mangun, 1995; Mangun, 1995; Peelen, Heslenfeld, & Theeuwes, 2004). Also, studies employing transcranial magnetic stimulation to disrupt various stages of visual processing have suggested that recurrent visual cortical processing plays a causal role in a viewer’s ability to detect and categorize visual stimuli (Bullier, 2001; Camprodon, Zohary, Brodbeck, & Pascual-Leone, 2010), suggesting a necessary role of such feedback processes in the emergence of visual awareness. Most directly, in the case of the study employing transcranial magnetic stimulation applied over the occipital pole (corresponding to cortical region V1) (Camprodon, et al., 2010), it was shown that identification of briefly presented natural images (photographs) was impaired when activity was disrupted at 100 ms and 220 ms post-stimulus and, importantly, not intermediate latencies. While it is well-established that the effect observed at the 100 ms latency is likely due to the disruption of the feed-forward volley of activity associated with the target image, the effect observed for the 220 ms latency is likely due to disruption of the activity mediated by feedback projections to V1, or reentrant processing associated with the target.
In addition to a hierarchical organization, the visual system is characterized by a high degree of interconnectedness between regions, facilitating reentrant processing and top-down influences from high levels of representation to low. This reentrant activity has been implicated in various top-down processes, such as selective focusing of spatial attention, as well as the emergence of visual awareness.

In sum, it is likely that the highest levels of visual processing, i.e., the emergence of visual awareness, arise from both essential feed-forward signals propagated through increasingly complex levels of representation in a hierarchically organized manner, as well as feedback processes which back-propagate the elaborated visual signal to earlier visual areas. Further, and more specifically, it has been hypothesized that the initial feed-forward sweep of activity through visual cortex represents a provisional hypothesis as to the nature of the stimulus, while the consistency of the feedback reentrant activity with
representations existing in early visual areas as it reenters either confirms or disconfirms that hypothesis, thus determining the emergent percept (Reiss & Hoffman, 2007). While this is an attractive model of the mechanisms through which visual awareness might emerge, one aspect of this account— that of the degree and quality of neural visual processing that occurs in the absence of awareness—remains unanswered. That is, to what degree are specific levels of visual processing and the emergence of awareness related?

1.3 Studying visual processes and awareness: the dissociation paradigm

1.3.1 General principles

The degree to which any cognitive or perceptual process proceeds in the absence of awareness can be explored by creating conditions in which stimuli invoking that process cannot be explicitly reported by the subject, and yet other evidence suggests processing is occurring. Dissociation paradigms are most often used to this end and embody the intuitive logic behind such an examination. These paradigms seek to establish that stimuli of which the subject is unaware (unawareness being evident from an explicit behavioral measure) still exert an influence at a neural, cognitive or behavioral level (as in priming, for example) (Holender, 1986; Merikle & Cheesman, 1987; Merikle & Reingold, 1988).

In a dissociation paradigm, several essential steps are taken to investigate a given visual perceptual process and how it relates to awareness. First, a particular visual process is chosen, along with a set of visual stimuli that invoke that process. Second, two measures of that process are selected, one of which is behaviorally explicit (“did you see it?” or “what did you see?”) and necessitates the viewer’s awareness of the stimuli, the
other of which is an implicit measure of the same process (Figure 3). Third, the visual
presentation parameters of the stimuli are manipulated such that a decrement in the
explicit behavioral measure is observed, thus creating at least two conditions of
differential awareness (intact and disrupted). Fourth, the second measure is examined
under the behaviorally established conditions of awareness versus unawareness (or
disrupted awareness) (Figure 4). If this implicit measure is shown to be intact, or to suffer
a lesser decrement than the direct measure across awareness conditions, it is inferred that
some visual perceptual processing of the nature being examined has taken place even
when the subject’s behavior indicates they are unaware of the images. Thus, as generally
applied, such a dissociation paradigm is typically referred to as the “relative sensitivity”
approach, as the crux of any interpretation lies with the relative decrement observed in
the explicit and implicit measures of the same perceptual process (Merikle & Reingold,
Figure 3. Direct and indirect measures of visual processing levels

The dissociation paradigm is founded on the assumption that a given visual perceptual process (a level of visual representation) can be measured directly (in a manner requiring explicit report by the viewer), and indirectly, or implicitly (in a manner that does not necessarily require the explicit report of the viewer).
In the dissociation paradigm, images invoking a given visual process are presented in a such a way that differential conditions of explicit behavioral performance are created, namely such that viewers experience a significant decrement in their ability to explicitly report the relevant content of the images. The implicit measure of the visual perceptual process is then taken in conditions of intact awareness (accurate explicit performance / report) and disrupted unawareness (decreased explicit performance). If the implicit measure remains intact in the context of decreased explicit performance, it is inferred that this visual process is occurring in the absence of awareness.

1.3.2 Design and analysis: a hypothetical experiment

1.3.2.1 Probing the process of interest

When implementing the dissociation paradigm, there are several concerns that guide the implementation of any study and are well-illustrated by a hypothetical example experiment wherein an experimenter seeks to demonstrate that the color of an image can be processed in the absence of awareness. Once the visual process in question is
established, the task (explicit and implicit measures) must be carefully chosen so as to maximize validity of any interpretation. Specifically, the explicit behavioral measure, as well as the implicit measure, must map onto the cognitive process being probed. Therefore, the explicit behavior which will ultimately establish conditions of awareness and unawareness must entail a color judgment made by the subject. This can take the form of a color-detection task wherein the subject is to detect targets of a certain hue in a stream of distracters, or a forced choice discrimination task, wherein the subject is asked to evaluate the color of a target, whether they had the impression of seeing it or not. Although at their core, these two measures probe the same color-discrimination ability, they potentially measure two different aspects of visual awareness. In a detection task, the subjectivity of the viewer is probed more so than in a forced-choice task, which is more of an objective measure of their behavioral ability, regardless of their perception of it (Wiens, 2006). Each metric has unique advantages, with detection reflecting the subjective state of awareness, and forced-choice accounting for response biases and overly conservative reporting criteria. It is therefore ideal to employ a combination of measures that probe awareness in a more comprehensive manner than with any of the measures alone. In this particular example, asking the subject to state, on a trial-by-trial basis: 1) whether there was a target, 2) their confidence level, and 3) the color of the target regardless of their impression of seeing it, gives the experimenter the most complete account of the subject’s explicit ability to detect and discriminate the parameter of interest.
The implicit measure would also entail color discrimination while not necessarily requiring an explicit response. One example could be to observe a color after-effect when the subject is asked to name the color of a later image. To judge whether or not color processing occurs in the absence of awareness, the experimenter would then examine the perseverance of color after-effects in conditions of awareness and unawareness. If the subjects experience color after-effects to the same extent regardless of their state of awareness as indicated by their explicit performance, then it can be inferred that perceptual processing of color occurs in the absence of awareness.

1.3.2.2 Degrading only the viewer’s awareness

In addition to probing the cognitive process of interest and employing valid measures, the manner in which the experimenter chooses to attenuate awareness is vital to the interpretation and validity of findings. Put more directly, there are a great many ways in which an image can be made present but invisible, and how an experimenter achieves this is the crux of any argument made for or against visual processing in the absence of awareness (Kim & Blake, 2005). Any particular manipulation of image presentation that disrupts awareness does so through a unique mechanism, and at a certain level of the visual processing hierarchy. For example, in order to render an image present- but-invisible, experimenters can degrade the feed-forward signal induced by the image, the recurrent processing associated with the image processing, or both. What is important is that the method of producing a decrement in the viewer’s explicit behavioral measure does not do so in a manner that invalidates interpretations involving the idea of awareness. For example, while it is very straightforward to manipulate awareness of
visual stimuli by asking the subject to close their eyes during half of the experiment, such a decrement is only achieved by cutting off visual processing altogether, and therefore reveals little of interest concerning awareness.

The above, admittedly oversimplified, example of what can be wrong with a visual presentation protocol is illustrative of an inherent tradeoff in implementing the dissociation paradigm. Specifically, experimenters must adequately decrease the subject’s behavioral performance to maintain the validity of their conditions, while at the same time maintaining the physical integrity of the target stimulus input signal invoking the visual process of interest. This “physical integrity” comprises the target image’s duration, spatial frequency content, contrast, orientation, and luminance. Simply, all of the low-level properties of the target image giving rise to a unique feed-forward signal must be identical, or closely maintained, across conditions of awareness and unawareness. Therefore, the following discussion of how experimenters attenuate visual awareness will only address those methods that hold target images physically intact, yet still manage to achieve a decrement in behavior indicative of a lack of awareness.

1.3.2.3 Valid sorting and analysis of data

Finally, purported conditions of awareness and unawareness must be identified as such in accordance with the presentation manipulation and resulting fluctuations in the explicit behavioral measure. Specifically, experimenters must decide how the implicit measure will probe the visual process. Their options are to examine the implicit measure in terms of the physical manipulation (e.g., all masked trials represent conditions of unawareness) or in terms of the subject’s behavioral decrement in the explicit measure as
a function of the physical manipulation (all masked trials in which the subject performed at chance levels, or failed to detect the targets, represent conditions of unawareness). The fact is that some methods of disrupting visual awareness are not absolute, and some but not all trials in the disruption condition will reflect unawareness. This makes it essential that differential conditions of awareness are established through adequate measures of the subject’s performance in the explicit behavioral task. This principle is illustrated in the hypothetical experiment mentioned above examining color after-effects in the absence of awareness. If the experimenters chose a method of disruption, such as object-substitution masking, that yields a 15-30 percent decrement in detection performance, the importance of sorting data according to behavior becomes clear. More specifically, if color after-effects require awareness, the experimenters will observe this only if they examine those trials in which subjects failed to detect targets. In this case, examining the data according to the physical presentation manipulation, that is, collapsing trials in a condition in which over half reflect awareness, experimenters would arrive at a wholly different conclusion. In particular they will report observing color after-effects without awareness, but the effect would have been driven by contamination of their “unawareness” condition by trials in which the subject was actually quite aware.

1.4 Present but invisible images: methods of disrupting awareness

Given the criterion that the target image have a consistent physical strength across conditions of awareness, some common methods for validly producing a behavioral decrement in target detection/discrimination are continuous flash suppression, various
forms of visual masking, the attentional blink, and motion-induced blindness. Each of these methods has contributed uniquely to behavioral accounts of visual perceptual processing in the absence of awareness. In addition, both behavioral and neural measures have been applied to delineate the unique mechanisms through which each of these methods disrupts visual awareness, although some remain as yet to be determined.

**1.4.1 Continuous flash suppression**

In interocular suppression, unique input streams are presented to each eye and verged into one using a stereoscope, resulting in fluctuating perceptual dominance of each input. This effect can manifest during passive viewing of a binocularly rivalrous stimulus wherein awareness of each possible image fluctuates, or it can be exogenously driven as in continuous flash suppression (CFS). In CFS, the experimenter renders input to one eye highly salient by introducing rapid changes in its pattern, thus suppressing less salient or static input from the other eye in a temporally controlled and durable manner (Tsuchiya, Koch, Gilroy, & Blake, 2006)(Figure 5). Behavioral data has suggested that the mechanism by which this phenomenon emerges is indeed one of suppression, wherein the input to one eye achieves perceptual dominance through greater salience, higher contrast, or by adaptation to the other image. Knowledge of the functional dynamics of early visual processing, along with modeling and simulation studies, have allowed experimenters to better characterize this mechanism, showing that it most likely acts at a neuroanatomical level prior to extrastriate cortical regions where images from the eyes are already integrated. Although the mechanism mediating this effect in the case of continuous flash suppression is in principle shared by other forms of bistable perception
wherein inhibitory influence in primary visual cortex from one eye suppresses output originating in the other eye to extrastriate regions (Lumer, 1998a, 1998b), CFS is unique in that its dynamics can be driven by stimulus presentation parameters, and is not so unpredictable as in simple interocular suppression.

**Continuous flash suppression (CFS)**

**Figure 5. Continuous flash suppression (CFS)**

In continuous flash suppression, disparate visual input is presented to each eye. When one of the inputs is a flickering (~10 Hz) pattern mask, the salience of this input suppresses the input (target) of the other eye.

### 1.4.2 Masking

In visual masking, when a scrambled, non-object mask image is presented immediately following a brief target in the same physical position (so-called backward masking) (Figure 6), detection and discrimination of that target can be completely suppressed, as evidenced in behavioral measures. Initial theories of the mechanism mediating this effect cited the mask input as somehow “beating” the target signal to levels of visual representation and awareness, thereby blocking/disrupting the ability of the viewer to perceive the target. Thus for nearly three decades, the dominant theoretical account of visual masking invoked an inhibitory mechanism in a dual-channel
information processing model, wherein sustained slower channels charged with the processing of object features associated with the target are inhibited by faster transient channels involved in coarse pattern processing associated with the mask (Breitmeyer & Ogmen, 2000; Ogmen, Breitmeyer, & Melvin, 2003). However, with the advent of neural measures of high temporal resolution sensitive to multiple stages of visual processing, this idea has since been replaced by theories of reentrant signal disruption. Specifically, it has been proposed that the feed-forward visual signal acts as a sort of provisional hypothesis as to the identity of the image, only to be confirmed through reentrant processing from later areas of representation to early visual areas, which is necessary for visual awareness to occur. In the case of visual masking, it would appear that this reentrant process of confirmation fails, as the original image representation has been replaced in early areas by the signal associated with the mask, thus suppressing the viewer’s perception of the target (Reiss & Hoffman, 2007). This has been supported by the development of a new variant of masking through object substitution (Enns & DiLollo, 1997), wherein no masking image per se physically replaces the target image at the same location (Figure 7). Also supporting the explanation of masking as mediated by the disruption of reentrant visual processes is electrophysiological data (Fahrenfort, Scholte, & Lamme, 2007), showing that early indices of figure-ground segmentation remain intact, while reentrant processes associated with this process and subsequent behavioral report are disrupted by backward masking.
Backward masking

Target briefly (~17-50 ms) presented in foveated/attended location

Mask presented in same location suppresses target awareness Duration > 100 ms

Percept

Figure 6. Backward masking

In visual backward masking, the perception of a briefly presented target image is suppressed when it is immediately followed by a competing non-target mask.

Object substitution masking (OSM)

Target briefly (~17-50 ms) presented in unfoveated/unattended location

Delayed offset of target cue suppresses target awareness Duration > 100 ms

Percept

Figure 7. Object-substitution masking (OSM)

In object-substitution masking, the perception of a briefly presented target within an array of distracters is suppressed when a surrounding cue (four dots in this case) remains for a delay period following the offset of the target and distracter array.

1.4.3 Attentional blink

In the attentional blink (AB), a viewer must detect and discriminate visual targets embedded in a rapid serial visual presentation stream (RSVP). In the context of an RSVP with a presentation rate of ~9-12 Hz, it has been shown that the detection and processing of a secondary target (T2) is significantly reduced if it follows a detected primary target
(T1) by a lag of ~2-3 images or around 150-400 milliseconds (Raymond, Shapiro, & Arnell, 1992)(Figure 8). In the case of the attentional blink (AB), behavioral studies have suggested consolidation of the primary target (T1) as causing an unavailability of cognitive resources in the processing of a relevant secondary target at a certain lag in the ongoing RSVP stream, thus resulting in decreased awareness of the secondary target (Chun & Potter, 1995; Jolicoeur & Dell' Acqua, 1998; Shapiro, Raymond, & Arnell, 1994). While this depletion of consolidation resources resulting in a processing bottleneck at a relatively high level of processing has been cited as the mechanism of this phenomenon, evidence against such a bottleneck is strong (Awh et al., 2004; Olivers, Spalek, Kawahara, & Di Lollo, 2009; Visser, Bischof, & Di Lollo, 1999) and has pointed more to a loss of perceptual control during target identification (Di Lollo, Kawahara, Ghorashi, & Enns, 2005; Kawahara, Kumada, & Di Lollo, 2006). Neural evidence derived from event-related potentials (ERPs) supports this high level mechanism, showing that early extrastriate visual processing, as well as more abstract levels of semantic processing, is intact across conditions of awareness as manipulated by the attentional blink (Vogel, Luck, & Shapiro, 1998) and that the effect of the attentional blink on electrophysiological indices of various levels of processing is comparable to that of fluctuations in top-down allocation of attention (Luo, Feng, He, Wang, & Luo, 2010). Thus, regardless of the precise mechanism by which the attentional blink exerts its disruption of perceptual processing, it appears that its influence is top-down, originating from a relatively high cognitive level not unlike that which endogenously deploys attentional resources.
In the attentional blink, detection of targets embedded in a rapid serial visual presentation (RSVP) is potentially disrupted, depending upon the delay between targets. At the rate of around 9-12 stimuli per second, if a target occurs immediately (Lag 1) or substantially (Lag 7) after a detected target, there is little to no observed decrease in detection performance. However, if a target follows a detected target within 2-3 images (Lag 3), there is a marked decrease in detection performance for the second target.

### 1.4.4 Motion-induced blindness

In motion-induced blindness, static parafoveally presented targets fluctuate in and out of visual awareness when superimposed on a globally moving array of distracters (Bonneh, Cooperman, & Sagi, 2001)(Figure 9). A wide variety of possible mechanisms have been proposed for this phenomenon, based on various behavioral studies. These include broad ideas of competition between the two visual stimuli (target and masking distracter array)(Bonneh, et al., 2001), along with ideas of depth ordering and surface completion of the mask (Graf, Adams, & Lages, 2002), static targets as perceptual scotomas (New & Scholl, 2008), perceptual filling-in (Hsu, Yeh, & Kramer, 2006) and the adaptive suppression of motion streaks in the human visual system (Wallis & Arnold, 2009). Theories invoking the idea of competition have since been supported by hemodynamic findings of a slow oscillation of relative activity levels between the MST complex associated with processing of motion stimuli and areas of V4 associated with
processing the static target. Specifically, it was found that when targets were visible, activity was higher in areas corresponding to the target and when targets were perceptually invisible, levels of activity were relatively higher in areas processing the motion of the mask (Donner, Sagi, Bonneh, & Heeger, 2008; Scholvinck & Rees, 2010).

While the temporal resolution of this particular neuroimaging method does not allow the determination of the shift in activity from one region to the other to be a cause or side-effect of the observed perceptual shifts, it does lend support to one of the proposed mechanisms by which motion-induced blindness acts to disrupt awareness of visual targets.

![Figure 9. Motion-induced blindness (MIB)](image)

In motion-induced blindness, visual awareness of an ever-present parafoveal target fluctuates when that target is superimposed on a globally moving array of distracters.

In sum, there is a wide variety of methods by which to render a physically present image perceptually invisible. Provided that the physical integrity of the target is maintained, four useful ways of achieving this are through continuous flash suppression,
various forms of masking, the attentional blink, and motion-induced blindness. Each of these appears to act through unique mechanisms to achieve the phenomenological perceptual disappearance of a physically intact visual stimulus, which behavioral and neural evidence may indicate is nevertheless processed to some level of sophistication by the visual system.

1.5 Findings

Modern noninvasive neuroimaging techniques have allowed experimenters to more completely examine the structural and functional properties of the human visual system and its organization. This has in turn provided well-defined indices of functional neural activity relatable to specific visual processes, allowing these to be used as implicit measures of visual processing in a dissociation paradigm. Specifically, high spatial resolution functional magnetic resonance imaging (fMRI) measures have led to the functional mapping of much of the visual cortex, using specialized stimuli that invoke levels of processing in a focused manner, from low-level psychical characteristics such as orientation and color (S. Engel, Zhang, & Wandell, 1997; S. A. Engel, 1994; S. A. Engel, Glover, & Wandell, 1997), to higher levels of visual representations, such as objects (Kanwisher, McDermott, & Chun, 1997) and words (Baker et al., 2007). In addition, high temporal resolution measures of brain activity, such as event-related potentials (ERPs), allow experimenters to delineate a cascade of neural visual processing stages and events that lead up to and/or follow the process of interest. From early sensory signals manifested as the visual evoked P1-N1 complex (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002) to high levels of analysis requiring the formation of sophisticated
representations of more abstract characteristics such as semantic content and incongruity, as indexed by the N400 (Curran, Tucker, Kutas, & Posner, 1993; Harvey & Marsh, 1983; Shappell, Pritchard, Brandt, & Barratt, 1986), processing of various visual input signals has been electrophysiologically characterized and studied. In this way, measuring neural processing at multiple levels of complexity in the visual processing hierarchy has become an accessible and more direct manner by which to probe visual perceptual processes and how they relate to awareness.

A wide variety of visual processes such as these, each occurring at different levels of the visual processing hierarchy, have been demonstrated to proceed during conditions of decreased visual awareness as achieved through the various methods outlined above. Low levels of visual processing, such as the extraction of basic visual features of line orientation (Montaser-Kouhsari, Moradi, Zandvakili, & Esteky, 2004) and motion direction (Hofstoetter, Koch, & Kiper, 2004), to the binding of low-level visual features based on Gestalt principles of good continuation and common region (Mitroff & Scholl, 2005), have been shown to proceed in the absence of awareness. While such low-level visual processing in the absence of awareness is not surprising, higher-level processes such as the grouping of cues leading to the illusory Muller-Lyer percept (Moore & Egeth, 1997), affective processing of emotive faces (Murphy & Zajonc, 1993), and the semantic content of invisible words (Luck, Vogel, & Shapiro, 1996; Vogel, et al., 1998) have also been shown to proceed outside of awareness. These findings and their implications regarding visual object processing in the absence of awareness are considered in greater detail below.
1.6 Face-specific effects reflect visual object-category processing

The identification of object-category content by the visual system represents a relatively high level of representation (Figure 10), and has been extensively studied. Evidence of face-specific processing as a proxy for the identification of stimulus object category content has been shown using multiple measures. Adaptation effects, wherein repeated exposure to a stimulus results in subsequently speeded behavioral responses or decreased neural responses, have been used to demonstrate processing of image contents. Behaviorally, it has been demonstrated that visual adaptation effects can occur at the level of face identity as well as at lower level physical properties (Dehaan, Bauer, & Greve, 1992), indicating such configural processing by the visual system. Neuroimaging studies have also provided compelling evidence of face-specific processing within awareness (Figures 11 and 12). Perhaps the most well-studied example of such high-level processing is the consistently extracted face-specific enhancement of neural activity in a ventral occipital area specialized for object processing known as the fusiform gyrus. For example, the perception of human faces closely correlates with greater hemodynamic responses (Andrews & Schluppeck, 2004; Kanwisher, 2000; Kanwisher & Yovel, 2006; Puce, Allison, Asgari, Gore, & McCarthy, 1996) (Figure 11) in this extrastriate cortical region, resulting in its demarcation as the “fusiform face area (FFA) (Kanwisher, et al., 1997).” These findings are corroborated by corresponding event-related potential (ERP) (Allison, Mccarthy, Nobre, Puce, & Belger, 1994; Allison, Puce, Spencer, & McCarthy, 1999; Bentin, Allison, Puce, Perez, & McCarthy, 1996) (Figure 12) and event-related
magnetoencephalographic (MEG) measures (Liu, Higuchi, Marantz, & Kanwisher, 2000). These latter two measures of functional brain activity, EEG and MEG, both with particularly high temporal resolution, have succeeded in characterizing the well-studied N170 component, and its MEG analog, the M170 (Bentin, 1998; Bentin, et al., 1996) as reflecting face-specific processing. The N170 is a negative-polarity voltage deflection of greater amplitude in response to faces relative to images of other object categories, an effect which peaks spatially over ventrolateral occipital cortex, particularly on the right. It typically peaks at approximately 170 milliseconds after stimulus onset, although it also tends to be followed by a second phase of negative-polarity face-specific activity of greater duration but similar topographic distribution around ~100 milliseconds later (Jemel, Schuller, & Goffaux, 2010).
Figure 10. Face-specific processing in the human visual system
Face-specific processing represents a specific level of visual analysis that reflects object-category discrimination, and can be measured both behaviorally and neurally.

Figure 11. Hemodynamic correlates of face processing
Face-specific processing has been associated with enhancements of hemodynamic activations in the fusiform gyrus, as well as the right superior temporal sulcus.
Figure 12. Electrophysiological correlates of face processing

Face-specific processing is manifested electrophysiologically as a greater amplitude, negative-polarity response to faces relative to other object categories (houses in this case) peaking 170 ms poststimulus. This response typically exhibits a bilateral, occipitotemporal scalp distribution, consistent with a dipole source modeled in bilateral ventral extrastriate visual regions, namely, the fusiform gyrus.

An added advantage of highly temporally resolved measures such as ERPs in investigating this process is their ability to disentangle constituent processes that may otherwise be conflated in a more sluggish measure such as fMRI. Specifically, face-specific effects seem to be mediated by both feed-forward mechanisms as well as reentrant processes, as has been suggested by electrophysiological studies tracking face-specific responses across attentional conditions (Luo, et al., 2010), as well as across conditions of performance indicating a decrease in awareness (Morris, Pelphrey, & McCarthy, 2007; Reiss & Hoffman, 2007). Although the multi-stage nature of face-
specific and object-category level processing is well-established, the relationship between this level of analysis and visual awareness remains elusive, due to limitations described below.

1.7 Face processing in the absence of awareness: an unanswered question

At first glance, whether or not face-specific processing and, by extension, object-category processing, occurs in the absence of awareness has been extensively investigated using the dissociation paradigm. A number of studies have purported to present images of faces and other object categories invoking this process of discrimination between object category in conditions of awareness and unawareness as established through the various methods listed above. However, upon closer examination, it becomes evident that this question has neither adequately nor thoroughly been addressed through a sufficiently strict implementation of the dissociation paradigm, and this has led to continuing controversy regarding the extent to which face-specific processing occurs in the absence of awareness. Specifically, it would appear that three issues surrounding claims of face-specific processing in the absence of awareness perpetuate controversy. First, in many studies that appear to be examining this question, direct probing of face-specific processing is not achieved. Second, in studies claiming a lack of face processing in the absence of awareness, the interpretation is based upon problematic experimental design. Specifically, the manipulation of the stimulus employed to the end of disrupting awareness in these studies actually degrades the low-level physical integrity of the target, precluding any interpretation speaking to the
awareness of the viewer. Third, studies asserting intact processing of faces outside of awareness utilize analyses that fail to prevent contamination of the set of purportedly ‘unaware’ trials by instances in which the subject may have in fact been aware of the stimuli, resulting in an inflated estimate of face-specific processing in conditions of unawareness.

1.7.1 An un-probed visual process

Studies employing variants of interocular suppression (Jiang & He, 2006; Vizueta et al., 2007; Williams, Morris, McGlone, Abbott, & Mattingley, 2004), and masking (Kiss & Eimer, 2008; Pessoa, 2005; Pessoa, Japee, & Ungerleider, 2005; Whalen et al., 1998; Wiens, 2006), as well as other methods (Murphy & Zajonc, 1993), have determined that face processing does occur, at least to some degree, in the absence of awareness. For example, one study examined the well-studied enhancement of visual-evoked responses to faces with negative affective content (fearful or angry) using continuous flash suppression. This study found that, even in the case that subjects were unable to report the affective content of a presented face, the amplitude of visual-evoked potentials in response to fearful and angry faces remained significantly greater than those to neutral faces, despite the degraded awareness of the viewer. Specifically, an amplitude enhancement was observed at both early stages of visual cortical processing, manifested as a greater P1 response, as well as later stages of face processing, at the level of the N170 (from 160-220 ms poststimulus) (Jiang et al., 2009; Vizueta, et al., 2007). In addition, bilateral increases in amygdala activation have been observed using hemodynamic measures in response to the same fearful face stimuli under interocular
suppression conditions, further supporting the dissociation of face processing from visual awareness (Williams, et al., 2004). In the context of visual masking methods, similar face processing in the absence of awareness has been observed using ERPs. For example, using a backward masking paradigm, wherein brief targets followed by scrambled masks are less visible than longer duration targets, a sustained positivity over fronto-central electrode sites in response to fearful target faces relative to neutral ones was present regardless of subjects’ level of face content identification performance (Kiss & Eimer, 2008). In addition, behavioral dissociations between subjects’ report of affective content of backward masked target faces and objective measures of their performance derived from signal detection theory demonstrate a great deal of affective information is available even in strongly masked target faces (Pessoa, 2005; Pessoa, et al., 2005). Backward masking has also revealed an enhancement of amygdala activity in response to fearful target faces relative to neutral ones using hemodynamic measures, further supporting the processing of face content in the absence of awareness (Whalen, et al., 1998). Also, a study simply reducing the duration of affective face stimuli to achieve minimal subjective visibility showed a behavioral effect of affective priming (Murphy & Zajonc, 1993). Specifically, even in the case that viewers were unable to see the briefly presented faces, their appraisal of a later novel and affectively neutral target was shown to be influenced by the affective content of the invisible face. Despite the broad scope of measures and awareness-disrupting presentation methods, all of these studies taken together would support the idea that an appreciable degree of face content is processed independent of awareness.
While it may be tempting to accept these conclusions to support the processing of object category per se outside of awareness, it is essential to note what precisely these studies initially set out to investigate, what they actually found, and the generalizability of their conclusions. More specifically, the studies described above focused on demonstrating that the emotional content of a face stimulus is processed in the absence of awareness. This is manifested as enhanced visual neural responses during perceptual suppression, or as enhanced activity in the amygdala. At no point in these studies, however, are responses to purportedly suppressed face stimuli compared to those associated with other object categories. The key comparison in these studies is invariably between responses to emotional faces and responses to neutral faces within and outside of awareness. This is true of both the behavioral measure establishing conditions of awareness (an affective discrimination task) and the implicit measure of the same process (amplitude enhancements of scalp ERP components or increased amygdala activation). Because these studies do not directly probe category-specific processing, and because the fast and largely automatic processing of the affective content of faces does not necessarily require the categorical processing of the face as an object (Hung et al., 2010), these studies would not seem to be adequate grounds upon which to base claims of object-category processing in the absence of awareness. So, although these studies provide compelling support for the affective primacy hypothesis that emotional content can be processed outside of awareness and prior to higher level visual information, the question as to whether or not category specific processing mediated by the visual
pathway and devoid of emotional content occurs in the absence of awareness remains open.

This general issue of internal validity is also well-illustrated in a number of face priming studies claiming either that face-specific processing is or is not happening in the absence of awareness. In face priming studies investigating the extent of face processing that occurs in the absence of awareness, face prime images are presented under conditions of reduced visibility, usually masked. A second target face to which the subject must respond is then presented under fully visible conditions. Face priming is manifested as an effect of reduced reaction times and neural responses to the target face following masked faces relative to other images. Several studies employing electrophysiological measures have shown reduced visual-evoked potentials following masked matching faces relative to unmatching faces (Henson, Mouchlianitis, Matthews, & Kouider, 2008). These findings have been corroborated by hemodynamic measures showing corresponding reductions in activity in face-specific regions of the brain in the same conditions (Kouider, Eger, Dolan, & Henson, 2009). However, a number of studies employing masked face priming as an index of face processing in the absence of awareness have purported to show the opposite, specifically that face processing is not occurring under masked conditions. Several studies (Jemel, Pisani, Calabria, Crommelinck, & Bruyer, 2003; Martens, Schweinberger, Kiefer, & Burton, 2006; Trenner, Schweinberger, Jentzsch, & Sommer, 2004) have demonstrated that priming effects at low levels of visual processing (P1 effects with a latency of ~80-120 ms post-stimulus) occur in the absence of awareness, but that these effects are not manifested at
the level of face processing (140-240 ms post-stimulus) in masked conditions. Simply, the absence of a reduced response to a face previously presented under unaware conditions (an effect of adaptation) suggests that the face was not processed to completion during the “unaware” presentation. However, whether the studies yielded a positive or negative result, there is a general issue of validity surrounding each of these studies that renders the question of category-specific processing in the absence of awareness difficult to address. In each of these studies, the comparison necessary to address this issue, which is responses to faces following masked primes of faces and objects of other categories, is never made. In these studies comparisons are either made between responses in which the prime was the same or a different face, therefore probing face familiarity, or between responses to faces preceded by a face or scrambled object, thus probing the nature of the image as an object and not a category. In addition, in studies of face priming, conditions of awareness and subsequent measures of face processing are indirect, as they are in reference to the visible target faces and not directly to the prime presented under differential conditions of visibility. This indirectness raises the possibility that the presence or absence of adaptation effects reflect not the processing of the masked prime, but rather the degradation of an iconic memory trace associated with the prime (Martens, et al., 2006). Although these studies contribute much to the understanding of face familiarity and image processing in the absence of awareness, the probing of behavior and neural responses associated prime images of faces and non-face objects, and necessary to address the question of categorical processing in the absence of awareness are not present.
1.7.2 Degrading images instead of awareness

Another common problem is illustrated by studies claiming a lack of face-specific processing in conditions that are identified as unawareness when in actuality they are conditions of degraded physical integrity of the target (i.e., face) stimuli. For example, one group claimed the stepwise emergence of the face-specific N170 component as a function of increasing awareness (Jemel et al., 2003). Here, the stimulus manipulation employed to achieve a behavioral “awareness” effect was the parametric degradation of image contrast. Naturally, this degradation did result in a behavioral decrement in categorization performance that would otherwise be interpreted as a decrease in target visibility or awareness. However, this manipulation of such a low-level visual property represents less a decrease in the awareness of the viewer and more a decrease in the actual face-ness of the visual image stimulus input. In addition, decreasing the duration of a target image to achieve awareness is also an example of a physical manipulation of the image and not necessarily the awareness of the viewer. This finding was also supported by data showing that as the duration of a masked face image is decreased and the image is increasingly scrambled, behavioral performance as well as neural indices of face-specific processing decrease (Grill-Spector, Kushnir, Hendler, & Malach, 2000). What these studies have in common is the degradation of the physical integrity of target stimuli to achieve “unawareness.” The result, however, is the inability to make clear claims about awareness and how it relates to the processing of object-category. Simply, extracting a correlation between the level of “awareness” and face-specific processing in these cases is not surprising, but to describe such a result in terms of awareness and unawareness at
all is misleading, as this result simply reflects the dependence of face-specific processing on the physical face-ness of an image. These studies in turn underscore the importance of changing not the image presented, but rather the context in which it is presented to achieve differential conditions of awareness as reflected in behavior. Furthermore, the aforementioned methods of disrupting awareness account for this issue by holding physical properties of the target images intact across conditions.

1.7.3 Inflating implicit measures: contamination by awareness

Finally, in the case of some studies asserting that face processing occurs in the absence of awareness, possible contamination of the ‘unaware’ condition with trials in which the subject may be aware remains problematic. Here, the problem lies in the way trials are binned in the analysis stage to explore implicit measures rather than the visual presentation protocol. For example, in a study employing a variant of masking known as sandwich masking, wherein the target image is embedded in time between masking images occurring both before and after, the results showed enhanced hemodynamic activation in right fusiform gyrus in response to masked face images (Morris, et al., 2007). While the comparison examined in this study speaks to object-category processing outside of awareness (responses to faces compared to those associated with images of sporting goods equipment), the manner in which data was examined may not be as valid. More specifically, although the manipulation effectively diminished awareness as evident in decrements to chance levels in both detection and categorization of stimuli, the manner in which investigators tracked an implicit measure of face processing is questionable. As is common practice, masked trials were collapsed regardless of behavior into a condition
called “unawareness.” This means that in this particular instance, the nearly ten percent of trials in which the subject managed to detect the images in the masked condition may be driving the face-specific activity observed in that condition. Furthermore, because no direct comparison is made between the effect size of masked and unmasked trials, the possibility of a markedly smaller effect in “subliminal” conditions being driven by a small number of trials in which the viewer was aware of the images is left open.

Another example of this problem is evident in studies of semantic processing outside of awareness during the attentional blink. In a series of highly impactful studies (Luck, et al., 1996; Vogel, et al., 1998), it was shown that the N400, an ERP component reflecting semantic incongruity detection, was present during the attentional blink and, by extension, that word meanings are therefore accessed in the absence of awareness. Upon closer examination of the analytical methods, however, this interpretation became problematic due to an inflation of the N400 by contamination of “unaware” trials with awareness and this problem is well-illustrated by a later study coming to very different conclusions (Giesbrecht, Sy, & Elliott, 2007). Specifically, the attentional blink is not an all-or-none awareness-disrupting phenomenon resulting in chance performance as might be seen in visual masking. Rather, a decrement in detection on the order of ~10-30 percent is typical. In the study citing intact N400 enhancements to semantically incongruent words during the attentional blink, trials at the relevant lag were collapsed, regardless of behavior (personal communication, Luck, 2010), meaning that between 70 and 90 percent of trials in the “unaware” condition were trials in which the subject was in fact aware of the targets. Therefore, whether or not the N400 is associated with
awareness, this result is unsurprising. This, combined with the later attentional blink study that cited possible elimination of the N400 effect when only misses were considered (therefore better isolating unawareness) (Giesbrecht, et al., 2007)), underscores the importance of taking into account the possible incomplete elimination of awareness and thus the necessity for sorting data in a manner that isolates images of which the viewer was truly unaware.

In sum, the literature concerning the extent of object-category processing in the absence of awareness is rich, but limited by three factors. First, many studies that would seem to probe face-specific processing as a proxy for object-category processing are actually probing different faculties entirely, as in the case of affective priming. Second, studies that demonstrate that face-specific processing ceases in the absence of awareness by degrading the physical integrity of the target stimuli are not actually assessing viewer’s awareness of the images. Third, a number of otherwise interesting and sound studies have observed face-specific processing in the absence of awareness in what amounts to a possible false positive, as the effect was likely driven by contamination of the “unaware” condition by trials in which the viewers were actually aware of the images.

1.8 Current studies: applying principles

Considering the limitations of the previous studies that have sought to examine the relationship between face-specific processing and awareness, the question as to whether such processing occurs outside of awareness at all, as well as its extent, remains open. Given the criteria for a validly implemented dissociation paradigm, a well-informed design for future study is possible and will possess several qualities. First, both the
explicit and implicit measure must probe awareness and object-category discrimination ability. This is straightforward for the implicit measure, as neural indices of face-specific processing would be most appropriate. In the case of the explicit behavioral measure, a dual detection and categorization task, or a forced choice categorization task, would be most appropriate, as these most directly map onto the process being probed. In addition they can provide data on a subjective level in the case of a detection task, while also providing data on an objective level, as in a forced choice task (Wiens, 2006). Second, the method by which experimenters attenuate awareness must preserve the physical integrity of the target stimuli, in this case, images of faces and other object categories. Degrading the contrast or decreasing presentation duration of target images does not attenuate awareness of the viewer per se, but rather the strength of the input, precluding any generalization from behavioral effects to the construct of awareness. Therefore, the methods outlined above (continuous flash suppression, various forms of masking, the attentional blink, and motion-induced blindness) are most valid to this end (Figure 13), although it should be noted that the proposed mechanism of continuous flash suppression may render it less informative in the way of object-category processing, as it disrupts signaling prior to such a module. Third, to ensure that accounts of processing outside of awareness are not inflated by contamination of the unaware condition with trials in which the viewer was actually aware, trials identified as “unaware” should comprise only chance performance overall or should only include incorrect responses. Simply, if the method of attenuating awareness yields an incomplete effect, and the implicit measure scales with awareness, collapsing the data will result in an inflated account of the implicit
measure outside of awareness. Therefore, experimenters must be mindful of the robustness of the method being used and sort behavioral data speaking to awareness accordingly.

Such a multi-methodological approach will lead to a rich data set speaking to the relationship between object category processing and awareness, as well as to the mechanisms of awareness disruption. Given the proposed hypotheses that visual...
awareness may be mediated by reentrant processing (Bullier, 2001; Camprodon, et al., 2010; Fahrenfort, Scholte, & Lamme, 2008) and that face-specific processing is a multistage process mediated by feed-forward and reentrant signaling (Jemel, et al., 2010; Luo, et al., 2010), several predictions can be made, and previous findings can be explained. Specifically, if electrophysiological measures of high temporal resolution are employed, it will be possible to examine how each stage of face-specific processing (those associated with feed-forward signaling and those associated with reentrant processing) relates to awareness.

For example, in the case of continuous flash suppression, disruption of awareness appears to occur at a relatively early level of visual processing, as described above (Lumer, 1998a, 1998b). Accordingly, it would not be surprising to see attenuation of face-specific processing that correlates with a decrement in awareness. While this does not seem to be entirely consistent with some recent findings, it is important to note that previous results speak more to affective processing (Jiang, et al., 2009) and the identification of highly ecologically significant content of faces (Jiang, Costello, Fang, Huang, & He, 2006) and not necessarily to the identification of object category. If the comparison is made between responses to faces and other object categories, rather than between affectively loaded faces and neutral faces, it may indeed be the case that object-category is not being processed outside of awareness, at least as manipulated by interocular suppression. It would therefore not be surprising to observe an elimination of both feed-forward and reentrant indices of face-specific processing.
While this result would be compelling, it will be important to take into account the fact that every method of disrupting visual awareness, as stated above, acts through different mechanisms. It is therefore useful to examine the same question of face-specific processing using the other methods outlined in the current paper. In visual backward masking and object-substitution masking, it has been proposed that target perception suppression occurs because of a mismatch between the representation being “carried” by reentrant visual processes and the representation of the mask image which has since replaced the target in early visual areas (Di Lollo, et al., 2000; Fahrenfort, et al., 2007). Assuming this is the correct mechanism, it can be hypothesized that such masking will disrupt reentrant processing associated with later phases of face-specific activity, while feed-forward sweeps of face-specific activity at earlier phases will be preserved. This would implicate the reentrant process as correlated with awareness and behavioral performance, but demonstrate that some degree of object-category processing is nevertheless still occurring, manifested as early neural responses. This is consistent with previous studies that have claimed face processing without awareness but also builds upon their interpretations. For example, as discussed in the masking study showing fusiform gyrus activity in response to faces in masked conditions (Morris, et al., 2007), it is possible that the activity observed is not equivalent to full processing of faces, but rather early phase activity that is independent of awareness occurring in the absence of reentrant processing. Given the sluggishness of responses measured by fMRI, it is not possible with this method to differentiate between the presence and absence of reentrant processing across masking conditions. Accordingly, the employment of
electrophysiological measures that can disentangle these constituent processes will likely prove very useful.

The awareness-disruption effects of the attentional blink may well act through mechanisms at the highest levels of visual processing. Specifically, it has been shown that sensory processing is preserved in the context of disrupted awareness in the attentional blink (Vogel, et al., 1998). Given the controversy surrounding the perseverance of high level indices of visual processing (the N400, for example (Giesbrecht, et al., 2007; Luck, et al., 1996)), the attentional blink represents a prudent avenue by which to track face processing, which in level and time of processing falls in between the early sensory processing and that of semantic analysis. Given present findings of a correlation between behavior and neural indices of high-level visual processes during the attentional blink, a pattern of findings similar to those found in masking would be predicted. Specifically, it would be hypothesized that when subjects do not detect targets during the attentional blink, feed-forward face-specific activity will be preserved, while reentrant processing associated with awareness will be disrupted.

Finally, the use of motion-induced blindness would serve a double purpose in such a research endeavor. First, it seems likely to act through a relatively high level of disruption, given the variety and complexity of processes that have been shown intact during blindness episodes, from the production of afterimages (Hofstoetter, et al., 2004) to the updating of object representations based on Gestalt principles (Mitroff & Scholl, 2005). Second, as a relatively new method of disrupting visual awareness, by studying the persistence of feed-forward and reentrant visual processes within and outside of
blindness episodes, the specific mechanism of interference can be better illuminated.

While a great deal has been learned through hemodynamic measures, uncovering an oscillating asymmetry of activity in dorsal and ventral visual areas (Donner, et al., 2008), the use of electrophysiological measures will potentially allow the tracking of feed-forward and reentrant processing, possibly providing support for theories positing reentrance as a necessary condition for awareness.

1.9 Overview

Although certain aspects of the human visual system have been well-studied in terms of structure and function, there is a great deal that is as yet unknown about how specific visual processes relate to the more elusive construct of conscious awareness. This question can be examined through the dissociation paradigm wherein two measures of the process of interest, one of which necessitates awareness and one of which is an implicit measure, are tracked during conditions of awareness and unawareness. If the implicit measure remains intact in the context of a decrement of the explicit measure indicative of disrupted awareness, the process is said to occur in the absence of awareness. This paradigm can be employed to investigate the extent of face-specific processing in the visual system indicative of object-category discrimination. Although various studies have investigated face-specific processing and visual processing outside of awareness, less has been done to integrate these areas of research into a research program implementing a principled dissociation paradigm using a variety of measures and disruption methods.

This is due to three fundamental problems: 1) various studies purporting to probe face-specific processing and awareness in actuality were probing rather different processes
and constructs; 2) findings of a lack of face-processing in the absence of awareness were founded on degradations of the low-level physical properties of the stimulus, and not of the awareness of the viewer; 3) some studies showing face-processing without awareness were inflating implicit measures by allowing trials of awareness to contaminate allegedly “unaware” conditions. By employing a variety of awareness disrupting paradigms in conjunction with highly temporally resolved electrophysiological measures capable of disentangling feed-forward and reentrant visual processes, the question of whether the brain can tell the difference between visual objects at a categorical level even when a viewer’s behavior cannot, can be more definitively addressed.
2 Sandwich masking eliminates both visual awareness of faces and face-specific activity through a feed-forward mechanism\(^1\)

2.1 Introduction

The degree to which any cognitive or perceptual process proceeds in the absence of awareness can be explored by creating conditions in which stimuli invoking that process cannot be explicitly reported but are still possibly processed by the subject. The demonstration of such processes often use so-called dissociation paradigms, which seek to establish that stimuli of which the subject is unaware (evident in an explicit behavioral measure) still exert an influence at a neural, cognitive or behavioral level (as in priming, for example) (Merikle & Cheesman, 1987; Reingold & Merikle, 1988). As generally applied, when the relative sensitivity of the two measures (an explicit behavioral measure and an implicit behavioral or neural measure) related to the same perceptual process changes across conditions of awareness, perceptual processing in the absence of awareness is implied.

For example, it has been shown that the affective valence of a visually masked image of an emotional face, even though not perceived as assessed by explicit report, can still influence decisions about other stimuli (e.g., concurrent or succeeding neutral ones). This behavioral demonstration of affective priming (Murphy & Zajonc, 1993), as well as corroborating electrophysiological findings (Vizueta, et al., 2007), suggests at least

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partial emotional processing outside of awareness. More broadly, a dissociation such as this helps to delineate the type and extent of visual processing that can occur outside of awareness (Holender, 1986; Reingold & Merikle, 1988). Such logic has also been used to provide evidence that visual feature extraction, such as line orientation (Montaser-Kouhsari, et al., 2004), the binding of low level visual features based on Gestalt principles of good continuation or common region (Mitroff & Scholl, 2005), and the grouping of visual cues to form the Muller-Lyer illusion (Moore & Egeth, 1997) can occur in the absence of explicit awareness. However, while these previous findings are compelling, it has not been demonstrated, behaviorally or neurally, that visual processing at the level of specific object-category discrimination occurs outside of awareness. Moreover, the neural mechanisms by which such higher level visual processing does or does not reach conscious awareness are not at all clear.

Neuroimaging studies have provided compelling evidence of visual-object category processing of stimuli within awareness. For example, the perception of human faces closely correlates with greater hemodynamic responses in the ventral occipital area known as the fusiform face area (FFA) (Andrews & Schluppeck, 2004; Kanwisher, 2000; Kanwisher & Yovel, 2006; McCarthy, Puce, Gore, & Allison, 1997). This finding is corroborated by corresponding event-related potential (ERP) (Allison, Mccarthy, et al., 1994; Allison, et al., 1999; Bentin, et al., 1996; McCarthy, Puce, Belger, & Allison, 1999; Puce, et al., 1996; Puce, Allison, & McCarthy, 1999) and event-related magnetoencephalographic (MEG) measures (Liu, et al., 2000). These latter two measures of high temporal resolution, EEG and MEG, have succeeded in characterizing the well-
studied N170 component, and its MEG analog, the M170 (Bentin, 1998; Bentin, et al., 1996) as reflecting face-specific processing. The N170 is a negative-polarity ERP response to images of faces relative to images of other object categories. It typically peaks first at approximately 170 milliseconds after stimulus onset, and is often followed by an extended negative-polarity ERP wave with a similar topographic distribution over the next several hundred milliseconds that tends to be closely tied to behavior (i.e., delayed for longer face-categorization response times) (Philiastides & Sajda, 2006b). Such a dual-phase spatiotemporal profile of visual evoked potentials in response to objects (Fahrenfort, et al., 2008) and faces in particular (Jemel, et al., 2010; Luo, et al., 2010) has been characterized in several studies and supports an account of feed-forward signal propagation followed by reentrant processing of the same polarity and topographic distribution. The face-specific N170 exhibits a bilateral, although typically somewhat right-weighted, occipitotemporal scalp distribution (Bentin, 1998; Bentin, et al., 1996). By tracking the intactness of the N170, along with the later recurrent face-specific ERP activity phase, in conditions of awareness and unawareness of visual object stimuli, it is possible to evaluate whether this type of object category level processing occurs in the brain in the absence of awareness.

The extent to which visual processing of faces occurs in the absence of awareness remains controversial. One particularly rich body of literature concerns the phenomenon of face priming in which behavioral or neuronal responses to a face are modulated by pre-exposure to the same face (Jemel, Pisani, et al., 2003). Studies of face priming have provided conflicting indirect evidence either for or against face-specific processing in the
absence of awareness. On the one hand, priming effects manifested by higher accuracy, shorter response times, and above-chance face-name associations were observed in studies using sandwich masking for faces that were presented but undetected according to verbal report (Schweinberger, Klos, & Sommer, 1995). In addition, several electrophysiological studies have shown reduced visual ERP responses at both early and late time windows to masked faces when they are preceded by the same face (Henson, et al., 2008). Similar masked face priming effects have been localized to face-specific regions within the occipital complex using functional magnetic resonance imaging (Kouider, et al., 2009). These effects suggest that some level of face processing at the level of identity continues uninterrupted by masking, and is dissociable from awareness.

On the other hand, other studies using sandwich-masking procedures have also shown that early visual-evoked potentials to a masked face exhibit adaptation effects while later indices of face familiarity do not, suggesting a higher-level processing interruption by masking (Jemel, Calabra, Delvenne, Crommelinck, & Bruyer, 2003; Martens, et al., 2006; Trenner, et al., 2004).

Although studies of masked face priming have been useful in examining the extent of face processing in both behavioral and neural terms, there are still several limitations of the literature with respect to the question of face-specific processing being investigated in the present study. For example, while adaptation effects are sensitive and valid as indices for the level of target processing, they are somewhat indirect, as they relate to a later probe and not necessarily to the target of interest. In fact, some studies assert that observing a reduction of adaptation effects at high levels may not necessarily reflect the
effect of decreased awareness, but rather of the persistence, or lack thereof, of a “fast-decaying iconic memory trace” (Martens, et al., 2006). In addition, previous studies of face priming have focused on face processing at the level of familiarity and not at the level of object category. Accordingly, the level of object categorization processing (e.g., faces versus other objects) that can be achieved within and outside of awareness still remains unclear.

Other studies have examined the processing of face targets directly in various conditions of identification and categorization performance, which presumably reflect various levels of awareness. For example, the amplitude of the face-specific N170 component to face images of parametrically degraded contrast was found to be positively correlated with the level of participants’ subjective awareness of the face images (Jemel, Schuller, et al., 2003). In the case of masking approaches, some degree of face-specific hemodynamic activity in the right fusiform gyrus has been reported to be present in a backward masking experiment (Morris, et al., 2007), while in an object-substitution masking paradigm containing parafoveal face and house targets presented at unpredicted locations, face-specific electrophysiological indices were reported absent (Reiss & Hoffman, 2007). Indeed, different studies use different paradigms to render a visual stimulus invisible, each of which presumably suppresses visual processing at a unique stage of processing (Kim & Blake, 2005). Therefore, the discrepancies among studies may be due to the wide-ranging quality and nature of stimulus exposure to the visual system.
The present study aimed to address some of these issues concerning face processing in the absence of awareness through an electrophysiological approach employing event-related potential (ERP) measures of brain activity. By using a variant of visual masking wherein target stimuli are both preceded and followed by non-object visual masks (i.e., sandwich masking), we investigated how the face-sensitive ERP component, the N170 (Bentin, 1998; Bentin, et al., 1996), would vary with masking-induced modulations of perceptual awareness. The design of the present study afforded several advantages. First, sandwich masking robustly reduces perceptual awareness while keeping the physical qualities and exposure duration of the masked images themselves the same as those of the unmasked stimuli. Second, because of the efficacy of sandwich masking, it is possible to use stimuli that are presented foveally and that are always spatially attended, thus dissociating the effects of awareness of interest here from previously observed effects of visuospatial attention (Crist, et al., 2008). Third, using the face-specific N170 effect as a neuronal signature of category-specific processing provides clear insight into the underlying neural substrates of conscious vs. unconscious perceptual processing of object category. Fourth, the use of an electrophysiological measure with high temporal resolution affords the ability to decompose the visual processes leading up to and presumably contributing to face perception. Fifth, and finally, the inclusion of blank-images trials provided an important visual stimulation control condition for investigating the underlying mechanisms of sandwich masking by providing electrophysiological indices of image vs. no-image processing in both masked and unmasked conditions.
2.2 Methods

2.2.1 Participants

Two separate experiments were performed, in which thirty-four healthy adults with normal or corrected-to-normal vision participated. Data from eight participants were excluded from analyses due to excessive eye movements, leaving data from 12 participants (mean age of 20±1.5 years, 6 males) and 14 participants (mean age of 25±6.9 years, 7 males) from the first and second experiments, respectively. All participants used their right hand to perform the task (two participants were left handed). Informed consent was obtained for each subject according to protocols approved by the Duke University Internal Review Board (IRB). All participants were recruited through local advertisements at Duke University campus and were compensated for their participation in accordance with stipulations outlined by the IRB.

2.2.2 Stimuli and task

Participants were seated with their eyes 60 cm from the center of a 19-inch CRT stimulus presentation monitor with a 60 Hz refresh rate. During each session, participants completed two blocks of runs, each with a different task. The stimulus set consisted of 6.6° x 8.8° grayscale face and house images, along with scrambled non-object masks produced by the “liquefication” function in Adobe Photoshop, which imparts a set of masking random swirls to images. In each trial, a first mask (100 ms duration), an object image (17 ms duration), and then a second mask (100 ms duration) were presented sequentially, with varied intervals between these images that robustly modulated the perceptual awareness of the object images. More specifically, in the unmasked condition
the interval between the masks and object images was 100 ms (distal masking); while in the masked condition it was 0 ms (proximal masking). The inter-trial interval (ITI) was randomly jittered between 500 and 800 ms. Four trial types -- masked faces and houses and unmasked faces and houses -- occurred with equal frequency and with a randomized order within each run.

In the first experiment, participants performed either a color-detection task or a two-alternative forced choice (2AFC) task in each run, with these runs separated into two different task blocks. In the color-detection task (Figure 14A & 14B), participants were instructed to identify, with a button press, rare target masks (20% of trials) that were either slightly magenta- or cyan-tinted (the rest being grayscale). For the color detection task, subjects completed six runs of 100 trials each, evenly and randomly distributed among trial types (masked and unmasked faces and houses). In the 2AFC task, participants were instructed to categorize, with a button press, the object images as being either a face or a house (Figure 1C & 1D, note that none of the masks in the 2AFC runs were colored). In the second experiment, a “blank-image” trial type was added to the color detection task, in which a blank image of background color was presented between the two masks, a trial type that provided a baseline measure for assessment of low-level visual processing of the object images. Thus, in this second experiment, trials could randomly include a face, a house, or a blank image in between the masks. Aside from the introduction of the blank image to the color detection task block, task instructions (for color-detection and categorization tasks) were identical across experimental groups, the
only difference being the number of trials in the color detection task (120 randomized trials evenly distributed between masked and unmasked faces, houses, and blank images).

**Figure 14. Stimuli and task**

In each trial five consecutive images were presented in quick succession at fixation. The target image (i.e., faces, houses, or blank) was always presented in the third temporal position and was either immediately preceded and followed by non-object scrambled masks (masked/subliminal condition) or preceded and followed by non-object scrambled masks with a 100 ms period between images (unmasked/supraliminal condition). In the color-detection task, participants were required to make a speeded response to the infrequent color-tinted masks (A & B). In the two-alternative forced choice categorization task (C & D), participants were required to identify target object stimuli, masked or unmasked, as being either a face or a house.

### 2.2.4 Data analysis

#### 2.2.4.1 Behavioral

In addition to accuracy and reaction time data for the color-detection task, d-prime scores based on signal detection theory (Macmillan & Creelman, 1997) were calculated to quantify the amount of object information participants acquired in the subliminal vs. supraliminal condition during the 2-AFC task (see relevant Results sections).
2.2.4.2 EEG and ERP data

The electroencephalogram (EEG) was recorded continuously from a custom 64-channel cap (Electrocap, Inc., Eaton, OH) with a right mastoid reference, using 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 zoom-lens video camera, 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 heavily attenuates signal noise with frequencies at and above ~56 Hz. The ERP averages were subsequently algebraically re-referenced to the average of all electrodes (common reference). In addition, we conducted analyses employing an average mastoid reference, a commonly used referencing scheme. All electrophysiological data were time-locked to the onset of the object image in each trial (faces, houses, and, in the case of the color detection task in the second experiment, blank images). These time-locked electrophysiological responses were then averaged according to condition and stimulus type to extract comparisons of interest as described below. Face-selective ERP effects were extracted by contrasting the ERP evoked by the face image stimuli with those evoked by the house image stimuli, separately for the different perceptual conditions. Object-specific ERP effects were extracted by contrasting
the ERP evoked by faces and houses (collapsed) with those evoked by the blank-image trials added to the color detection task in the second experiment. The ERPs were statistically analyzed using repeated-measures analyses of variance (Object Category by left versus right Electrode Site [left versus right]) of mean amplitudes within specific latency windows (6 ms wide, from 0 to 636 ms poststimulus) for the corresponding electrodes over left and right occipitotemporal scalp sites (TO1 and TO2). A separate analysis with the same factors was performed at over two more medial and posterior scalp sites (O1 and O2), which are sensitive to early visual sensory ERP responses, to examine mean amplitude differences in masked and unmasked conditions in response to objects (face and houses, collapsed) versus blank-image trials. Observed mean amplitude effect between conditions were considered significant if the p-value was less than .05 for at least 6 consecutive time bins of 6 ms, assessed between 0 and 636 ms poststimulusly. The onset of the component was identified as the first of these 6 consecutive time bins.

2.3 Results

2.3.1 Behavior

In the color-detection task, the mean accuracy and reaction time values were 96.7 ± 1.8 percent and 399 ± 7.8 milliseconds, respectively. This high level of performance indicates that participants were in fact closely attending to the visual stimulus stream, as instructed.

A significant decrement of visual awareness in the subliminal masking condition as compared to the supraliminal one was revealed by behavioral measures of participants’ percepts about the objects (i.e., the ability to discriminate between faces and houses).
Mean discrimination accuracy approached ceiling at 94.5% for the supraliminal trials, but was 54.3% for the subliminal ones (very close to chance level performance of 50%). The mean d-prime score for the supraliminal condition was $3.7 \pm 1.14$, whereas the mean subliminal one was over an order of magnitude lower ($0.31 \pm 1$), resulting in a highly significant difference in discrimination sensitivity between the conditions ($t_{25}=-19.0$; $p<.00001$). These behavioral results provide evidence of robust attenuation of awareness of the image objects in the subliminal masking condition, despite sustained focal attention toward the stimuli.

2.3.2 Electrophysiology

All statistics and plots below are with respect to the ERP data measures relative to a common reference. Parallel analyses employing an average mastoid reference yielded the same pattern of effects.

2.3.2.1 Face/house N170 difference (data from both experiments 1 and 2)

Results from the electrophysiological data, for both the color-mask-detection and the 2AFC tasks in both experiments, indicated that early face-selective neural processing was present in the supraliminal conditions but eliminated in the subliminal masked conditions. In particular, hallmark face-selective N170 ERP activity -- namely, a significant negative-polarity difference between faces and houses, peaking at around 170 ms and having an occipitotemporal scalp distribution -- was observed for the supraliminal trials but not for the subliminal ones (Figure 15). For the supraliminal condition in the color-detection task (Figure 15A), a significant face-specific N170 effect was observed between 132-246 ms poststimulus ($F_{1,25}=58.16$, $p<0.001$), followed by a second phase of
similarly distributed, longer-latency, negative polarity, face-selective activity between 512-590 ms ($F_{1, 25}=8.19, p=.0088$). Likewise, for the supraliminal conditions in the forced-choice categorization task (Figure 15C), a similar set of biphasic face-selective effects was observed in the poststimulus intervals of 138-264 and 500-585 ms ($F_{1, 25}=32.7, p<.0001$ and $F_{1, 25}=33.16, p<.0001$, respectively). These face-specific ERP effects did not differ significantly between the color-detection and categorization tasks.

Figure 15. Face selective ERP effects in the subliminal vs. supraliminal condition
Plotted here are the waveforms time-locked to the onset of the object image stimulus and the corresponding topographical distribution maps of the face-minus-house contrast for (A) the supraliminal condition in the color detection task, (B) the subliminal condition in the color detection task, (C) the supraliminal condition in the forced-choice categorization task, and (D) the subliminal condition in the forced-choice categorization task. For both tasks, a bilateral, right lateralized, negative-polarity difference between faces and houses was observed in the supraliminal conditions, but not in the subliminal conditions.
In summary, we observed normal face-selective neural activity with intact perceptual awareness and accurate discrimination of the object image content in the distal sandwich-masking conditions (i.e., trials with the brief blank interval between the masks and object images). In contrast, both the face-selective neural activity and the perceptual awareness of the visual stimulus content was eliminated by the proximal masking (i.e., trials with no blank interval between the masks and the object image stimulus), despite the stimulus images being displayed with the same duration.

2.3.2.2 Object-specific P1 difference (data from experiment 2 only)

In addition to the modulation of the face-specific N170 responses, the effects of the masking on earlier low-level visual processing were of interest. In Experiment 2, to investigate possible contributing mechanisms of the sandwich-masking paradigm being employed here, responses on trials with face and house images were collapsed and compared to responses on the trials with a blank target image (essentially providing a ‘something versus nothing’ comparison), separately for the masked and unmasked conditions. In the supraliminal (unmasked) condition, we observed a robust positive-polarity ERP response (Figure 16A) over bilateral medial posterior scalp in the sensory-ERP component latency range of 100 ms post-stimulus (66-138 ms, (F1, 13=48.16, p<.0001)). This positivity exhibited a similar scalp distribution and onset latency to that of the visual evoked P1 effect generally thought to originate from early extrastriate low-level visual processing areas in occipital cortex (Clark, V.P. & Hillyard, S.A., 1996; Woldorff, M.G. et al., 1997; Di Russo et al., 2002). In contrast, for the subliminal
(masked) conditions, the same component (faces and houses collapsed vs. blank images), although reaching significance (F_{1,13}=9.48, p=.01), was drastically reduced in both amplitude and duration (84-114 ms post-stimulus) (Figure 16B). These results suggest that in the subliminal condition, early visual sensory processing, although present, was so heavily attenuated as to be almost eliminated by the sandwich masking.

Figure 16. Sensory-related ERP effects in the subliminal vs. supraliminal condition

The early sensory evoked ERP effects were extracted by contrasting the responses to trials with object stimuli (faces and houses) with the responses to trials with blank images, separately for the two masking contexts (N = 14). (A) In the supraliminal condition, we observed a robust positive-polarity ERP over bilateral occipital region peaking at 100 ms, a response highly consistent with the well-studied sensory evoked P1 effect elicited by the object stimuli. (B) In the subliminal condition, a much weaker (~five times smaller) sensory evoked P1 effect was observed at this latency.

2.4 Discussion

The present study shows that visual awareness of faces, as measured by object-category discrimination ability, was eliminated in conditions of immediately temporally adjacent masks. When visual awareness of faces was abolished through visual sandwich
masking, the face-specific N170 effect was also eliminated. This is not to say that the N170 can or should be equated to the awareness process, but rather that the masking as employed here disrupted both the N170 and the emergence of awareness. Moreover, and more specifically, the present results suggest that sandwich masking reduces awareness by disrupting the visual signal at processing stages prior to face-specific processing and prior to the emergence of awareness.

Discordant findings regarding the extent of face-specific processing that can occur within and outside visual awareness seem to have arisen from three issues in terms of design and interpretation. First, in many studies, the experimental designs did not allow for a direct measure for face-specific categorical processing. Second, in some studies reporting a lack of face processing in the absence of awareness, the interpretation is based upon physical manipulation of the target image itself (i.e., degrading the contrast of a face image until viewers no longer categorize it as one). Third, studies asserting intact processing of faces without awareness often define and sort “aware” and unaware” trials in a way that risks contaminating the ‘unaware’ condition with trials by instances in which the subject may have in fact been aware of the stimuli. For example, if the method employed to disrupt visual awareness is not robust enough to yield chance performance, or no awareness, trials deemed “unaware” based only on the presentation manipulation will contain some trials in which there was some awareness. This in turn may lead to an inflated estimate of the extent of face-specific processing outside of awareness.

The extent to which the content of faces is processed in the absence of awareness is of broad interest, and has led to a number of cases of indirect evidence supporting
unconscious face-related processing. However, the indirect nature of these studies, especially vis-à-vis face-specific processing, tends to limit the interpretability of these findings concerning such specificity. For example, several previous studies have reported that the emotional content of a face stimulus is processed in the absence of awareness (Jiang & He, 2006; Kiss & Eimer, 2008; Murphy & Zajonc, 1993; Pessoa, 2005; Pessoa, et al., 2005; Vizueta, et al., 2007; Whalen, et al., 1998; Wiens, 2006; Williams, et al., 2004). This is manifested as enhanced (higher amplitude) visual-evoked potentials responses during perceptual suppression, or as enhanced hemodynamic activity in the amygdala. In these studies, however, the responses to purportedly suppressed face stimuli are not compared to those associated with other object categories. This is true of both the behavioral measure establishing conditions of awareness (an affective discrimination task) and the implicit measure of the same process (modulation of scalp ERP components or of amygdala activation). Because these studies do not directly probe category-specific processing, and because the fast and presumably automatic processing of the affective content of faces does not necessarily require the categorical processing of the face as an object (Hung, et al., 2010), these studies would not seem to be adequate grounds upon which to base claims of object-category processing in the absence of awareness.

This general issue of internal validity is also instantiated in a number of studies claiming that face-specific processing is not occurring in the absence of awareness. For example, in face priming studies, reaction times and neural responses to faces that were previously presented under masked conditions are modulated, providing evidence that processing of the face had occurred in the absence of awareness. On the other hand,
several studies (Jemel, Pisani, et al., 2003; Martens, et al., 2006; Trenner, et al., 2004) have demonstrated that priming effects at low levels of visual processing occur in the masked absence of awareness conditions, but that such priming effects are not manifested at the level of face processing in these conditions. Simply put, the absence of a reduced face-specific response to a face previously presented under unaware conditions (an effect of adaptation) suggests that the face was not processed to the level of identity during the “unaware” presentation. In each of these studies, relevant comparisons are made not at the categorical level, but at the level of face familiarity, which, while highly interesting, does not necessarily address face-object-specific processing in the absence of awareness.

Another common issue related to some studies reporting a lack of face-specific processing during unawareness is that the conditions identified as unaware are actually conditions of degraded physical integrity of the target (i.e., face) stimuli. For example, one group reported the stepwise emergence of the face-specific N170 component as a function of increasing awareness of the face images (Jemel, Schuller, et al., 2003). In that study, however, parametric degradation of image contrast was employed to extract behavioral curves of increasing categorization performance. This manipulation of such a low-level visual property, however, would seem to represent less a decrease in the awareness of the viewer and more a decrease in the actual face-ness of the visual image stimulus input. This finding was also supported by data showing that as the duration of a masked face image is decreased and the image is increasingly scrambled, behavioral performance as well as neural indices of face-specific processing decrease (Grill-Spector, et al., 2000). What these studies have in common is the direct manipulation of the
physical integrity of target stimuli to reduce categorization performance, as reflected behaviorally or by the brain. Such results, although of considerable interest, would seem to be less about perceptual processing outside of awareness, and more about how physical stimulus integrity relates to the object-related processing.

Finally, in the case of studies asserting that face processing occurs in the absence of awareness, it is important to consider possible contamination of the ‘unaware’ condition with trials of which the subject may actually be aware. Here, the issue lies in the way trials are binned to explore implicit measures, rather than being derived from the visual presentation protocol. For example, in a study employing sandwich masking, the results showed hemodynamic activation in right fusiform gyrus in the masked condition in response to face images relative to images of other objects (Morris, et al., 2007). While the comparison examined in this study was directed toward assessing object-category processing outside of awareness, the manner in which data was examined may be important to consider. More specifically, the manipulation did effectively diminish awareness as evident in decrements to chance levels in both detection and categorization of stimuli. As is common practice, however, masked trials were collapsed regardless of behavior into a condition called “unawareness.” This means that, in this particular instance, the ten percent of trials in which the subject managed to detect the images in the masked condition could have been driving the face-specific activity observed in that condition. Furthermore, because no direct comparison was made between the effect size of masked and unmasked trials, the possibility of a markedly smaller effect in “subliminal” conditions being driven by a small number of trials in which the viewer was
aware of the images is left open. This problem has previously been articulated by Kouider and colleagues (2004), who asserted that partial awareness of a target stimulus in experiments investigating semantic priming can lead to its illusory reconstruction at the probe stage, thus perpetuating the controversy surrounding unconscious semantic priming (Kouider & Dupoux, 2004).

The present study sought to mitigate these issues in several ways. First, all relevant electrophysiological data were time-locked to the onset of the object images, and the contrasts were made between responses to the face images versus to the house images, thus explicitly differing at the categorical level. Second, the physical integrity of the target images themselves was preserved while fully inducing elimination of visual awareness. Thus, the “face-ness” of the face image stimuli themselves was not compromised. Finally, the conditions upon which interpretations are based in the current study reflect robust and unambiguous disruption of visual awareness. The distinction between awareness and unawareness was bolstered by the drastic behavioral performance difference between the distally masked (supraliminal) and proximally masked (subliminal) conditions. More specifically, in the distally masked (i.e., supraliminal) condition the face/house discrimination performance indicated that the physical characteristics of the target images were readily and easily identified, whereas in the proximally masked (subliminal) condition task performance was essentially at chance. Because the physical qualities of the target stimuli were held constant (i.e., identical images presented for identical durations of 17 ms), this perceptual decrement can only be attributed to the masking-related interaction processes in the brain. Furthermore, such
robust masking made it possible to examine electrophysiological data according to trial type and not necessarily according to behavioral performance. Examining only misses and hits in a less robust paradigm is subject to a certain degree of ambiguity in that any extracted face/house differences in the masked condition may reflect later processes associated with behavioral responses (Summerfield, Egner, Mangels, & Hirsch, 2006) and not the stimuli which are of primary interest here.

Concerning the electrophysiological findings, the addition of a blank-image condition allowed us to assess the possible mechanisms through which sandwich masking disrupts awareness. By comparing electrophysiological responses to objects versus blanks across the masking conditions, we observed that there was strong attenuation in the subliminal masking conditions of the feed-forward visual signal reflected in the P1 component at 100 ms, which has been associated by source analysis and neuroimaging linkages with the initial feed-forward activity in extrastriate regions of visual cortex (Clark & Hillyard, 1996; Di Russo, et al., 2002; Heinze et al., 1994; Woldorff et al., 1997). This result suggests that the disruption by sandwich masking techniques such as that used here occurs at or before the level of the feed-forward signal through extrastriate visual cortex. This in turn suggests that under such circumstances insufficient visual information is unable to reach the hierarchically later stages of visual processing, such as those associated with face detection/discrimination, resulting in the observed decrement in both categorization ability and the face-specific N170 neural response. Thus, the current results suggest that the effects of sandwich masking derive from an early signal-
disruption mechanism, which leads to the visual object image content never reaching awareness, as well as never eliciting electrophysiological measures of that content.

The present results are in contrast to functional accounts of backward masking and object substitution masking which propose that unawareness is accomplished through disrupting, longer latency, reentrant processing to early visual areas (Fahrenfort, et al., 2007; Reiss & Hoffman, 2007). Our findings suggest masking as employed here disrupts awareness through an early stage of disruption not unlike the race model of sustained (mask) and transient (target) channels proposed by other groups (Breitmeyer & Ogmen, 2000; Ogmen, et al., 2003). However, this seems likely due to the inclusion of a forward mask and its disruptive effect on the feed-forward signal. In examining the raw electrophysiological data comparing masked objects (faces and houses) with masked blank images, it appears that the visual-evoked potential (VEP) associated with the target was integrated with the larger and dominant VEP initiated by the forward mask in the subliminal masking conditions. This may have in turn resulted in a low visual target signal-to-noise ratio and the inability to extract the target image content in those conditions (Keysers & Perrett, 2002), a mechanism comparable to those observed as decrements in higher-order categorization performance for lag 1 secondary targets embedded in a rapid serial visual presentation (RSVP) stream (Akyurek & Hommel, 2005). In sum, and taking into account previous findings concerning the mechanisms of backward masking, it would appear that while it is possible that the backward mask disrupts reentrant visual processing of a signal associated with the target, the forward
mask, because of its relative strength and temporal proximity, may disrupt the feed-forward signal before reaching such reentrant stages, as suggested by our results.

A possible caveat of the present study is that it employed only two inter-stimulus intervals (0 and 100 ms) for the masked and unmasked conditions, respectively. Although this resulted in very clear-cut conditions of awareness as measured behaviorally, these conditions represent the two extremes over a possibly wide spectrum of intermediate levels of awareness. A parametric approach that varies the ISI between masks and object images across intermediate d-prime values could also be a useful way for assessing the association between awareness and the neural indices of face-specific processing.

2.5 Overview

In summary, our results show that, in the context of unawareness as achieved with sandwich masking, neural indices of face-specific processing are closely associated with behavioral measures of image discriminability, being eliminated when image discriminability and awareness are also eliminated. In addition, our electrophysiological findings indicate that sandwich masking also induces heavy attenuation of early lower-level visual processing, prior to the stage at which robust object-category-specific processing activity is typically elicited. The results thus suggest that the effects of sandwich masking, a widely used approach in the study of visual processing and conscious awareness, derive from an early disruption mechanism of the feed-forward pathways in or prior to extrastriate visual cortical areas, and thus also considerably prior to entry into the higher-level object-discrimination processing. Moreover, the present
findings underscore the importance of taking into consideration the mechanisms by which a given stimulation or task approach may actually accomplish an observed disruption in awareness.
3 The temporal cascade of visual and attentional processing stages during object-substitution masking and its relationship to perceptual awareness

3.1 Introduction

The extent and quality of visual processing that occurs in the absence of awareness is of the broadest import to cognitive neuroscientists, as information coded in the brain, regardless of its emergence as a conscious percept, holds the potential to influence behavior. Knowledge of such information that is impervious to decrements in perceptual awareness therefore contributes to the growing body of neural measures that can possibly explain or predict subsequent behavior. In order to establish such a disconnect between a given perceptual process and awareness, experimenters can track an implicit neural measure of that process across conditions of relevant explicit behavioral performance. Specifically, an explicit behavioral measure reflecting the relevant process serves as an index of the viewer’s awareness, and presentation manipulations of relevant images are implemented to disrupt this measure. A second implicit (e.g. neural activation) measure of the same process is then tracked across these behavioral conditions that reflect distinct levels of visual awareness. If the neural measure remains present during conditions of behavioral unawareness, it is said that the perceptual process it reflects occurs in the absence of awareness (Holender, 1986; Reingold & Merikle, 1988).

The degree to which object-category information is coded in the brain in the absence of awareness is of particular interest, being an especially sophisticated visual process of significant importance for adaptive behavior. Brain activity measures reflecting object-
category processing, such as the face-specific N170 event-related potential (ERP) component, provide an effective way to examine the relationship between such neural processing and awareness. The N170 is a negative-polarity voltage deflection over occipito-temporal scalp areas that is larger in amplitude in response to faces than to images of other category (Bentin, et al., 1996). This response peaks at about 170 milliseconds following the onset of the object image, and is often followed by another negative-polarity response at a longer latency (~400-800 ms) with a similar distribution on the scalp, which is presumably due to some sort of reentrant, or feedback, processing (Harris, Wu, & Woldorff, 2011; Philiastides & Sajda, 2006a). The N170 and later negativity are traceable to sources in ventral visual cortical regions associated with high-level object-category processing and identification in the fusiform gyrus (Kanwisher, et al., 1997) and the superior temporal sulcus (STS), and anatomically later regions in the lateral occipital cortex (Grill-Spector et al., 1998; Puce, et al., 1996). Tracking the presence or absence of this response across behavioral conditions of awareness therefore reveals the extent of this neural process that occurs in the absence of awareness.

In order to create conditions of awareness and unawareness, across which experimenters can compare a neural measure of a specific visual perceptual process, a manipulation of the target stimulus presentation is employed. Object substitution masking (OSM) is a useful way to attenuate awareness robustly, while at the same time maintaining the integrity of low-level stimulus processing coded in the generic feed-forward visual signal. In OSM, a visual array, composed of a parafoveal visual target and a number of distracters, is briefly presented, with the target item being indicated by a
proximal, but spatially distinct cue, typically several dots surrounding its edges. The effect of masking is observed as a behavioral decrement in target detection and discrimination when the offset of the cue is delayed relative to that of the other images in the array, which all offset simultaneously (Enns & DiLollo, 1997; Giesbrecht & Di Lollo, 1998). Initially, it was hypothesized that this striking masking effect occurs because spatially unattended targets are coded with low resolution as their corresponding feed-forward signal propagates along the visual pathway, and therefore are susceptible to substitution by the persisting mask information that stays on the screen (Enns & DiLollo, 1997). More recently, it has been proposed that object-substitution masking may attenuate awareness through the disruption of reentrant processing (Di Lollo, et al., 2000; Reiss & Hoffman, 2007; Weidner, Shah, & Fink, 2006). This mechanism is plausible, and favored relative to a feed-forward mechanism, for several reasons. First, the mask and the target image are not spatially coincident, making disruption through a feed-forward mechanism, as appears to be the case in sandwich masking (Harris, et al., 2011), unlikely, as the visual signals associated with the target and mask in OSM are coded as retinally distinct representations. Second, the observation that OSM works as a function of cue offset relative to the array implicates more than the brevity of the array or presence of a mask in the behavioral effects observed. It has been proposed that the delayed offset of the cue results in a mismatch between the initial feed-forward representation of the target location and the signal that exists in early visual areas during a later reentrant phase of processing (Di Lollo, et al., 2000; Reiss & Hoffman, 2007). Specifically, in conditions of simultaneous cue offset relative to the rest of the array, the provisional hypothesis
regarding the nature of the target represented by the initial feed-forward sweep encounters no competition when the reentrant signal returns to early visual areas. On the other hand, in the case of a delayed offset, the only commonality between the initial feed-forward signal and the sensory signal that exists in early areas is the cue, which is then substituted in place of the target, resulting in decreased awareness of the target. This proposed mechanism is consistent with a growing body of empirical literature that supports the possibility that reentrant visual signaling from functionally late regions back to earlier ones, such as V1, is a necessary condition for visual stimuli to enter subjective awareness (Bouvier & Treisman, 2010; Camprodon, et al., 2010; Dux, Visser, Goodhew, & Lipp, 2010; Fahrenfort, et al., 2008). The OSM paradigm therefore provides a useful method for creating visual unawareness while ensuring that the generic feed-forward visual signal is left intact.

In addition to enabling conditions to study the presence or absence of face-specific processing in the context of unawareness, applying high temporal resolution electrophysiological measures such as EEG to OSM can provide a particularly rich data set delineating the temporal cascade of visual and cognitive events either leading up to, or not leading up to, awareness. A series of electrophysiological events reflecting specific visual processing steps (both feed-forward and reentrant) leading up to the emergence of perceptual awareness has been implicated in the context of other masking methods, with some evidence suggesting later reentrant processing (160 ms and after) as being essential for the emergence of awareness (Fahrenfort, et al., 2008).
The current study sought to examine face-specific processing in the absence of awareness during OSM and introduced new conditions and comparisons to the additional ends of 1) directly examining the timing with which OSM disrupts generic visual signaling; and 2) the consequences of this mechanism regarding neural correlates of later visual attentional and working memory processes. To examine the timing of disruption in OSM, a third “blank” (background matched, surrounded by target cue) was introduced. Specifically, by collapsing neural responses to objects (faces and other target object images) and comparing them to those associated with empty space, the effect of OSM can be tracked across behavioral conditions of awareness (delayed offset hits versus misses). Thus, early extrastriate processing, and later reentrant stages of visual signaling associated with the presence or absence of a target can be examined across conditions of awareness to determine the timing with which OSM exerts its disruption on generic target-related visual sensory processing coded in the P1 ERP response, and on later positive polarity response of the same scalp distribution reflecting associated reentrant processing (Di Russo, et al., 2002).

In a similar vein, electrophysiological components, associated with attentional allocation and visual short-term memory, are also of interest in the context of object-substitution masking. Specifically, the nature and design of object-substitution masking, in conjunction with the use of neural measures with high temporal resolution such as EEG, allows for the investigation of different facets of the cascade of attentive and visual processes that typically lead to awareness. For example, lateralized responses associated with shifts of visuo-spatial attention and discrimination processes in the context of
unpredicted target locations can be very effectively assessed with ERPs. In particular, the negative-polarity posterior contralateral response (N2pc component) to targets reflecting the allocation of visual attention to a specific lateralized location (Luck & Hillyard, 1994b) can be easily probed in this context. Further, the presence and absence of this component can be examined across conditions of awareness as manipulated by object-substitution masking conditions, and the implications of such variations vis-à-vis the mechanism of disruption considered. Similarly, a longer latency component, the so-called sustained posterior contralateral negativity (SPCN), can be extracted by the same subtraction (contralateral versus ipsilateral targets), an activation that appears to reflect working memory maintenance of a lateralized target during a subsequent discrimination (Jolicoeur, 2006; Robitaille, Jolicaeur, Dell'Acqua, & Sessa, 2007), and examined across conditions of awareness. As per visual processing in the absence of awareness, the modulation of these effects may be explanatory in the perseverance, or lack thereof, of object-category specific processing outside of awareness.

In the current study, we use these various neural indices to investigate the temporal cascade of these attentional and visual cognitive processes during object-substitution masking. We in particular make some specific predictions concerning these processing stages and their relationship to the awareness disruption that can be affected OSM. As far as generic visual processing, the index of which is extracted by comparing trials in which a target was present to those in which it was blank, it is likely that successful masking by object substitution (yielding a miss) will only affect reentrant stages. This would manifest as a disruption of early reentrant visual signaling to V1 in the case of misses relative to
hits in the masked condition, at a latency substantially later than the feed-forward visual signaling (~80-120 ms and after). This mechanism of disruption would then ramify to other neural indices of interest. For example, the face-specific N170 which arises from feed-forward and prior, low-level reentrant visual signals would likely be disrupted in the case of misses and not in the case of hits. Similarly, it is believed that the N2pc and SPCN are mediated by high-level reentrant signaling and would thus be disrupted in miss trials and perhaps not for correct detections (i.e. hits), in which case attention would be successfully allocated to the location of interest, and the target discriminated (Prime, Pluchino, Eimer, Dell'Acqua, & Jolicoeur, 2011; Schankin & Wascher, 2007).

3.2 Methods

3.2.1 Participants

Thirty-four subjects participated, of which 7 were excluded due to excessive eye movements, (i.e., where the trial rejection rate was more than 25%). This left 27 subjects (6 female, 2 left-handed) with a mean age of 23.8 ± 5.4 years in the final analysis. All subjects were recruited through local advertisements and signed up to participate through the Center for Cognitive Neuroscience’s study participation website (participate.mind.duke.edu). Informed consent was obtained for every subject for their paid participation in accordance with stipulations outlined by the Duke University Medical Center IRB.

3.2.2 Stimuli and task

Participants were seated 70 cm from a 19-inch CRT stimulus presentation monitor with a refresh rate of 60 Hz. They completed 15 experimental runs comprised of 120
trials each. These trials were subdivided into two masking conditions (masked and unmasked), and three target conditions (face, house, or “blank”) within each run, for a total of 300 trials of each type per subject. The stimulus set consisted of distracters and targets, all of which were 2.9° diameter circular cropped images presented parafoveally. For each trial, an array of 15 scrambled non-object distracters, plus one target identified by a surrounding four-dot cue, was presented for one frame (17 ms), after which the array offset (Figure 17). Target images (40 faces, 40 houses, and blank) occurred in one of four target locations (upper left, upper right, lower left, lower right) randomly, with equal probability in each experimental run. Masked and unmasked trials were randomly intermixed within each run. Masking by object substitution was induced by delaying the offset of the four-dot cue surrounding the target by 500 ms relative to the offset of the target/distracter array. Participants were asked to detect and discriminate the cued target images among an array of scrambled image non-object distracters, indicating the target object as a face, a house, or empty space surrounded by the cue.
Figure 17. Stimuli and task

Subjects were asked to complete a three-alternative forced choice task for every trial, indicating whether the target image (surrounded by a 4-dot cue) was a face, house, or empty space. In 50% of the trials, the offset of the 4-dot cue was delayed relative to the rest of the array by 500ms, establishing the masked condition.

3.2.3 Data acquisition and analysis

3.2.3.1 Behavioral

Behavioral performance at the level of target detection (indicating that an object was presented when either a face or house was present) and categorization (correctly identifying the category of the target image as a face or house) was compared across
delay conditions (simultaneous offset versus delayed offset). The masking effect of delaying the offset of the target cues was measured in terms of detection performance, which was the percentage of target images (faces and houses) detected versus those incorrectly classified as blanks.

3.2.3.2 EEG acquisition

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

3.2.3.3 ERP data analysis

The artifact-free data were time-locked-averaged selectively for the different stimulus types. These averages were then low-pass filtered offline using a nine-point running average filter, which at our 500 Hz sample rate attenuates external electrical noise at and above ~56 Hz. The ERP averages were subsequently algebraically re-referenced to the average of all electrodes (common reference) and baseline corrected relative to the 200 ms preceding stimulus array onset. Because of the lateralized presentation of the target images, and to capitalize on the likely lateralized distribution of the visual-evoked
potentials, the channels were flipped along the midline for trials in which targets occurred in the left versus the right visual field, and then collapsed together in a contralateral versus ipsilateral (to the target) manner. This ultimately mimicked right-sided target presentation for all trials. For plotting and statistical analysis purposes, all visual-evoked potentials are therefore examined on the contralateral, or left, scalp locations. Face-selective effects were extracted in each masking condition, as well as within each behavioral outcome (correct, detected, undetected), by contrasting the face-evoked ERP with the house-evoked ERP at scalp electrode site TO1, which, based on the aforementioned analyses, corresponds to the typical temporal-occipital scalp site at which this effect is observed, and contralateral to target presentation. Generic visual processing associated with the target was extracted by contrasting the object-evoked (faces and houses) with the blank-evoked ERP (empty space surrounded by target cue) at scalp electrode sites TO1 and O1, consistent with late, possibly reentrant, N1 and P1 topographic distributions, respectively. Lateralized attentional and working memory components (N2pc and SPCN, respectively) were extracted by subtracting object-specific activity occurring ipsilateral to the side of the target (i.e., thus ipsilateral to the direction of the required shift of attention) from the activity contralateral to such a shift focusing on scalp electrode site TO1, as these effects are typically seen with a temporal-occipital distribution. Finally, and importantly, conditions of awareness and unawareness were established through behavioral measures within the masked condition. Specifically, delayed offset trials in which subjects correctly identified present targets were considered trials of awareness, whereas delayed offset trials in which subjects indicated “no target”
when one was in fact presented were considered trials of unawareness. Selectively binning the masked trials in this way facilitates the comparison of electrophysiological components across psychological conditions while maintaining identical visual stimulation. In addition, it avoids the issue of inflating the account of processing that occurs in the absence of awareness when all masked trials are considered regardless of the efficacy of masking.

The ERP effects were statistically analyzed using within-subjects two-factor repeated-measures analysis of variance (ANOVA), depending upon the contrast being examined (trial type by face-minus-house effect for face-specific processing across awareness conditions; trial type by object-minus-blank effect for generic visual processing; and trial type by contralateral-minus-ipsilateral object activity for the N2pc and SPCN effects). Effect latencies and durations were determined using consecutive 50 ms (0-50; 50-100, etc.) moving windows, and then refined using 10 ms wide windows on the first and last of 2 or more consecutively significant 50 ms windows.

3.3 Results

3.3.1 Behavior

Behavioral measures of accuracy showed a significant and robust decrease in detection performance (from 85 to 59 percent) in the case of delayed cue offset relative to the target/distracter array relative to simultaneous offset (t_{26} = 5.7, p < .0001). This effect did not vary in magnitude according to stimulus type (face versus house), indicating that object-substitution masking was equally effective in decreasing awareness of both faces and houses. These distinct behavioral effects provide the requisite conditions of
awareness and unawareness to track electrophysiological indices of relevant cognitive processes across conditions of awareness.

3.3.2 Electrophysiology

3.3.2.1 Face-specific effect

Face-specific activity was significantly reduced from 200-750 ms post-stimulus when the offset of target cue was delayed relative to that of the target/distracter array, as revealed by a comparison of the mean amplitude of the face-specific (face minus house) effect across masking conditions ($F_{1, 26} = 13.2, p < .01$; Figure 18C). The face-specific amplitude enhancement was still present in the masked condition (Figure 18B), as shown by a comparison of the mean amplitude of visual–evoked responses to faces and houses, but was confined to narrower time windows (200-350 ms and 700-850 ms post-stimulus), and was reduced in amplitude ($F_{1, 26} = 6.8, p < .05$ and $F_{1, 26}, p < .05$, respectively; Figure 18C). In the case of unmasked trials, the same comparison yields a more striking ($F_{1, 26} = 27.2, p < .001$) and long-lasting (180-950 ms) face-specific electrophysiological effect (Figure 18A). However, when examining only trials with accurate behavior (detected and correctly identified face and house targets), the face-specific activation did not differ across masking conditions. Specifically, no difference in the amplitude of face-specific activity was extracted across the post-stimulus time window of 200-750 ms between masked and unmasked hits ($F_{1, 26} = .01, p = .91$; Figure 18D, E &F). This suggests that any difference between masked and unmasked trials with regard to face-specific activity was driven by the effectiveness of the masking. Specifically, masking by object-substitution seemed to occur on a subset of delayed-cue-offset trials, which are more
numerous, and the associated neural responses more dominant, in this masked condition than in the unmasked condition.

To examine face-specific processing in the case of unawareness, behavioral conditions of awareness (correctly identified target) and unawareness (indicated by a “blank” behavioral response despite a target being present) were compared within the delayed cue offset condition, effectively providing a comparison of neural measures when masking worked versus when it did not work, under identical stimulus conditions. Comparisons of the extracted face-specific activity difference waves across masked hits and misses revealed a significant difference during the time window of 170-450 between hits and misses ($F_{1, 26} = 4.9, p < .05$; Figure 18H). This difference was driven by an apparent presence of face-specific amplitude enhancements in the case of hits, present from 180-850 ms post-stimulus ($F_{1, 26} = 11.1, p < .01$; Figure 18E), and an absence of such an effect at all time windows during the same interval (180-850 ms) for misses ($F_{1, 26} = .09, p = .77$; Figure 18G). In sum, when masking by object-substitution was effective (i.e., when the subject reported seeing no target even though one was presented), all electrophysiological indices of face-specific processing were eliminated.
Figure 18. Face-specific activity in masked and unmasked trials
Robust face-specific processing was observed for the unmasked trial type at early and late stages (A & C). In the case of masked trials collapsed across all behavior, significant but smaller face-specific responses were also extracted at early and late stages (B & C). Subsequent comparisons isolating awareness and unawareness in the masked condition revealed that, in the case of accurate behavior, face-specific responses were present at early and late stages, and did not differ from those associated with accurate behavior in the unmasked condition (D, E & F). However, in the case of unawareness (masked trials in which subjects failed to detect presented targets), elimination of the face-specific negativity at both early and late stages was observed (G & H).
3.3.2.2 Object-specific processing

In order to examine the extent of generic, target-related visual processing that occurs in the absence of awareness during object-substitution masking, visual-evoked potentials in response to objects (faces and houses) were compared to those in response to “blank” target trials across behavioral conditions (hits and misses). Difference waves (object-present minus blank, occurring in the target location) were compared across behavioral conditions indicating the level of awareness (hits versus misses). Differential visual-evoked potentials (objects versus blanks) were analyzed at two scalp sites and two time windows between hits and misses within the masked condition. Specifically, a difference between hits and misses was observed in a negative-polarity enhancement in response to objects versus blanks over posterior occipital scalp regions (TO1) between 190 and 350 ms post-stimulus ($F_{1, 26} = 14.9, p < .001$). This extracted target-specific effect was present for hits ($F_{1, 26} = 18.27, p < .001$) but not misses ($F_{1, 26} = 0.42, p > .05$). In addition, longer-latency (400-700 ms post-stimulus) object-specific effects extracted in the same way (object minus blank) were seen over scalp topographies corresponding to the early extrastriate P1 effect (peaking at occipital channel O1), and differed across conditions of awareness ($F_{1, 26} = 7.63, p < .05$). This effect was driven by a presence of this positive-polarity voltage enhancement in the case of hits ($F_{1, 26} = 18.41, p < .001$) and an absence of such an enhancement in the case of misses ($F_{1, 26} = 1.12, p = .3$) over the same time period (Figure 19). The timing and distribution of these effects, corresponding to early extrastriate sources, supports the idea that object-substitution masking disrupts processing at longer-lateness reentrant processing to earlier visual cortical areas.
Figure 19. Generic visual processing for masked hits and misses
A significant decrease in object-specific (faces and houses collapsed minus empty space) activity in the case of masked misses relative to masked hits was observed over posterior occipital scalp regions beginning at latency of 190 ms post-stimulus (A). Another reduction in object-specific activation was seen at longer latency (400-700 ms) over more superior occipital sites in the case of masked misses versus masked hits.

3.3.2.3 Masked hits versus misses: Attentional shifting and visual memory activity

Following the disruption described above, successful object-substitution masking (the subject responding “no target” even when one was presented), ramified as a disruption of attentional shifting and visual working memory activity associated with the target location. Specifically, a significant decrease in contralateral vs. ipsilateral object-specific activity manifested as negative-polarity posterior (channel TO1) voltage deflections.
contralateral to the target, and reflecting visuo-spatial attentional allocation and working memory/discrimination processes was observed. This difference in lateralized negative-polarity object-specific effects was seen across conditions of awareness over the time window of 200-350 ms (F1, 26 = 14.23, p < .001) and later over the same scalp sites between 750 and 1000 ms post-stimulus (F1, 26 = 6.38, p < .05). This was due to the lack of this amplitude enhancement in the case of misses during both time periods (F1, 26 = .14, p = .71; F1, 26 = .04, p = .84, respectively), and its presence in the case of hits (F1, 26 = 13.76, p < .01; F1, 26 = 10.16, p < .01 for early and late effects, respectively; Figure 20). This pattern of electrophysiological results suggests that, cognitively, and as a result of successful object-substitution masking, the subject failed to successfully shift attention to the target location (evident in the elimination of the N2pc component) and make the subsequent discrimination (seen in the lack of a later SPCN). Based on the proposed mechanism of this form of masking (disruption of reentrant processing to early visual areas), it makes sense that subsequent reentrant signals, such as the N2pc and SPCN would also be reduced in the case of misses.
3.4 Discussion

The design of the present study affords several advantages vis-à-vis examining specific visual and cognitive processes in the absence of awareness. The parameters of the present experiment (in terms of timing, eccentricity of targets, and number of distracters) allowed for a robust behavioral effect of diminished detection in the masked
condition, while at the same time maintaining high performance in the unmasked condition. While a behavioral effect of this magnitude has been observed in the past, it has typically been in the context of relatively simple stimuli, such as geometric shapes and line drawings. The susceptibility of highly salient photographic stimuli, as those presently used, has been historically markedly less, especially in the case of faces which are detected and recognized faster and at greater visual eccentricities than other stimuli (Hershler, Golan, Bentin, & Hochstein, 2010). Implementing a design with such a robust behavioral effect allowed for an effective trial sorting analysis of high level object-category neural processing. In addition, the manner in which awareness was operationalized here was especially conservative, and prevented possible false positives with regard to neural indices of specific processes. Specifically, a target here was not considered to be outside of unawareness simply because the offset of target cues was delayed. Because object-substitution masking is not necessarily a total effect, which would yield chance performance or complete unawareness on every masked trial, data were sorted according to behavior to more selectively reflect this decrement within the masked condition. Moreover, this approach was facilitated because of the added blank target type and the “no target” response option. Thus, trials were only considered “aware” if subjects were able to correctly identify a target being present, while trials were only considered “unaware” if an object (face or house) was present as a target and subjects indicated that they had not seen one. Such sorting according to behavior allowed analyses to avoid inadvertently inflating the extent of a given process in the absence of awareness, in the case of neural measures scaling with awareness. This method is in contrast to
previous studies that have compared responses across masking conditions when investigating semantic processing as well as face-specific processing (Reiss & Hoffman, 2006, 2007). More specifically, the additional conditions included here (null or blank image targets, along with a three-alternative forced choice task) enabled a clear isolation of aware versus unaware conditions.

With regard to neural indices of perceptual processes, the present study helps lay out the cascade of visual, attentive and cognitive events following the onset of a masked trial that leads to either awareness or unawareness of a target stimulus. In particular, the initial feed-forward sweep of activity associated with the target array is intact during OSM, and the disruption likely begins with aberrations of reentrant processing to primary visual cortex, a theory proposed by several groups (Di Lollo, et al., 2000; Dux, et al., 2010). The current data support this view, in that image-specific activity (object target versus blank target) only differed between conditions of awareness (hits versus misses in the case of delayed cue offset) after a latency allowing for intact feed-forward visual processing (~190 ms). What was particularly interesting about the modulation of object-category specific processing as indexed by the N170 here is the fact that it occurred as a function of masking condition, but only when trials of behavior indicating a lack of awareness were isolated. This is in contrast to previous studies of face-specific processing during OSM, as well as higher level semantic processing in the same context (Reiss & Hoffman, 2006, 2007). What these previous studies showed was strong disruption of event-related potential measures of these processes in the case of delayed cue offset (masked conditions) and not unmasked conditions. This divergence across
conditions is presently supported, but in the context of the further distinction between awareness and unawareness that is achieved through electrophysiological data sorting for identical stimuli but according to behavior. Thus, the present results are compatible with previous studies of face processing in the context of object-substitution masking, but also underline the variable efficacy of OSM in disrupting awareness. In turn, these results demonstrate that it is not simply the delayed offset of the cue that disrupts face-specific processing, but a number of events related to that delay that either result or do not result in successful disruption of reentrant processing.

The perseveration of face-specific processing, as well as generic visual signaling, occurring in the case of trials in the masked condition (i.e., delayed offset) that were correctly detected, raises the question of what is making the difference when it comes to the delayed offset of a target cue resulting in the disruption versus no disruption of these neural visual processes and ultimately visual awareness. The unique properties of OSM, as a paradigm that requires unpredicted target locations and shifts of visuo-spatial attention to these locations for successful detection suggests a central role of attention. This has been investigated most directly in the case of a study examining the N2pc and SPCN components in OSM in the case of masked versus unmasked trials, as well as in cases of accurate versus inaccurate behavior in masked trials (Prime, et al., 2011). Specifically, this study reported a lack of an N2pc in the case of unmasked trials, which they attributed to the diffuse allocation of attention not requiring a shift with the onset of a trial. In addition, this group observed an N2pc in all delayed offset conditions, regardless of behavior, as well as an SPCN that scaled with behavior in the masked
condition (absent for misses). The present results are thus at odds with these findings. Specifically, the current study finds no difference in the N2pc component between the masking conditions when limited to trials with accurate behavior. The fact that it was just as present for unmasked-condition hits as it was for masked-condition hits suggests that the shift of attention to the target location was, in both cases, necessary for successful detection and identification. These differences with Prime et al. might be explained by paradigmatic differences in visual presentation. In particular, the brevity of target stimulation in the present study (a single frame constituting 17 ms), may have required a more focused attentional deployment and better formation of a visual short-term memory trace. Also, the more conservative criteria for awareness in the current study may account for the disruption of both the N2pc and SPCN in the case of misses in the delayed offset condition here. Specifically, whereas Prime et al. showed that incorrect behavior was nevertheless accompanied by an N2pc, this incorrect behavior constituted both target detection and misidentification. In the present context of a three-alternative forced choice task in which “no-target present” was a response option, misses constituted instances of a target being present, but misidentified as “blank.” This lack of detection may in turn be due to a failure to successfully shift attention to the target location in time to detect the presence of an object, which would therefore explain this difference in observation. The subsequent observation of a disrupted visual short-term memory component (the SPCN) is also therefore not surprising, as low-level information necessary for discrimination would have been unavailable.
Given that the trials in which OSM was effective in attenuating awareness were physically identical to those in which it was not, factors other than the visual parameters of presentation likely contributed to variations in the efficacy of OSM. The apparent modulation of attentional components (N2pc) following the onset of trials in which masking resulted in unawareness suggests that fluctuations in the deployment of attentional resources, as well as the global attentive state of the subject just prior to the onset of the trial, may be involved. In addition to disrupting reentrant processing to early areas, OSM may be enhanced in efficacy by trial-to-trial fluctuations in global attentional states during the interval preceding masked trial onset. For example, greater power in alpha-band oscillatory activity over occipital and parietal regions may predict inadequate attentional resources and subsequent behavior on masked trials. Although the current data set is not adequate to definitively comment on such a prediction, this inverse relationship between alpha power and attentional performance has been observed in the context of simple allocation of visual attention to a lateralized location (Gomez, Vazquez, Vaquero, Lopez-Mendoza, & Cardoso, 1998), as well as during lapses of performance in a sustained visuo-motor tracking task (Peiris, Jones, Davidson, Carroll, & Bones, 2006). Finally, the phase of alpha oscillations just prior to the onset of a trial in a metacontrast masking study effectively predicted awareness, with onsets near “troughs” being more associated with misses (Mathewson, Gratton, Fabiani, Beck, & Ro, 2009).

Despite the advantages of the current study, there persists some ambiguity in identifying the exact temporal locus of disruption exerted by OSM. Specifically, in the comparison of target-present versus target-absent trials, it was not possible to observe an
intact P1 that does not differ across conditions of awareness, which would be an index of intact feed-forward visual signaling originating in early extrastriate regions (Clark & Hillyard, 1996). This is likely due to the number of distracters included in the target array, the associated signal of which would drive most of the visual P1, and which, along with the distracters, is subtracted away when thus isolating object-specific target activity. As a result, the present study relies upon the timing of the divergence of the visual signals associated with this generic processing across behavioral conditions of awareness, which remains compatible with the lower temporal limit and reentrant mechanism of disruption exerted by OSM, albeit being observed later than would be expected.

### 3.5 Overview

The present electrophysiological study of object-substitution masking yielded a rich data set speaking to levels of visual processing that occur in the absence of awareness, as well as the role of attention in the efficacy of the masking. It was observed that face-specific processing at early and late stages is disrupted in cases of unawareness in masked conditions, and that the timing of disruption of generic visual processing was consistent with a reentrant mechanism for the disruption. In addition, post-stimulus attentional effects, as well as indices of visual short-term memory, were disrupted in the case of unawareness and may reflect a failure to successfully shift visuospatial attention to target locations and subsequently to discern target content on those trials.
The attentional blink disrupts late, but not early, object-category neural processing

4.1 Introduction

An as yet unresolved question in the field of visual cognitive neuroscience is the extent and quality of sensory and perceptual 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. 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 has been via what is known as a dissociation paradigm (Reingold & Merikle, 1988). The dissociation paradigm in vision entails several key elements. First, for a particular visual process of interest, visual images invoking that process are presented to viewers, who then respond behaviorally in a manner that reflects the conscious influence or awareness of that process - such as by discriminating object categories. Under these circumstances, experimenters manipulate the presentation of the images, such that they remain physically present, yet are undetected, or less accurately detected, by the subject. This reduced awareness is evident in a decrement in the relevant behavioral responses. In parallel, an implicit measure of that visual process, either neural or otherwise, is examined under conditions of intact awareness versus disrupted awareness. If the implicit measure remains intact despite the
observed behavioral decrement, it is concluded 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 lateral occipital cortex. 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 a particular functionally specific module in lateral visual cortex, located in the fusiform gyri and inferior temporal regions of ventral extrastriate visual cortex. Activity associated with this module has been observed as an amplitude enhancement of visual-evoked potentials in response to faces relative to a variety of other object categories peaking at ~200 ms post-stimulus, as measured intracranially (Allison et al., 1994). The further identification of the “fusiform face area” or FFA was originally driven by observations of increased hemodynamic activity in the right fusiform gyrus following the perception of a face relative to images of other objects (Kanwisher, et al., 1997; Puce, Allison, Gore, & Mccarthy, 1995). Subsequent studies have extracted scalp-recorded event-related potentials (ERPs) reflecting such face-specific processing (Allison, et al., 1999; Bentin, et al., 1996), as well as magnetoencephalographic indices of the same process (Liu, et al., 2000). These signals have been hypothesized to originate from related cortical areas in the occipitotemporal sulcus and fusiform gyrus (Bentin, et al., 1996) and in the superior temporal sulcus (Itier & Taylor, 2004), depending somewhat on the level
of face processing being examined (faces relative to other objects, eye-specific processing or face identity, for example).

With regard to object category discrimination, the most relevant neural index has been extracted by comparing responses to images of faces to those associated with images of other object categories. The N170, a negative-polarity ERP wave observed over occipitotemporal scalp regions, is derived from this sort of comparison and it thought to reflect such face-specific processing (Bentin, et al., 1996). This face-specific electrophysiological activity unfolds in time as an initial negative-polarity ERP deflection peaking at approximately 170 ms post-stimulus, which is then often followed by a long-lasting negative-polarity wave with the same topographic distribution, occurring from ~400-800 ms, depending upon the task (Harris, et al., 2011; Philiastides & Sajda, 2006b). These two phases of face-specific activity (an initial negative-polarity peak followed by a longer-latency, more long-lasting negativity) together represent a useful multiphasic reflection of object-category neural processing, which can be tracked as implicit measures of this process across conditions of awareness.

A hallmark of the considerable body of literature concerning visual processing in the absence of awareness is the wide variety of methods by which experimenters can render a physically present image to be perceptually suppressed (Kim & Blake, 2005). Importantly, each of the methods would seem to exert its disruptive influence through different mechanisms, and at potentially different stages of visual processing. For example, sandwich masking, in which disruptive mask images precede and follow a briefly presented target in time, appears to act through a disruption of the feed-forward
signal (Harris, et al., 2011). Another form of masking called object-substitution masking, in which the mask surrounds the target as a cue and acts to disrupt awareness through the timing of its offset relative to the target, has been proposed to act through the later disruption of reentrant visual processing (Di Lollo, et al., 2000; Reiss & Hoffman, 2006, 2007). For the purposes of investigating relatively sophisticated levels of visual processing, such as the object-category discrimination coded in the aforementioned N170 and later negativity, and how they relate to awareness, a mechanism of disruption preserving generic feed-forward processing while achieving robust behavioral effects is ideal.

One method of disrupting visual awareness that is 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 distracter 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 lagging distracter images such that the relative SOA of the two targets is of ~200-500 ms (Dux & Marois, 2009; Nieuwenstein, Potter, & Theeuwes, 2009; Raymond, et al., 1992). Because detection / perception of the secondary target (T2) is reduced when the primary target (T1) was detected several stimuli and several hundred milliseconds previously, it was speculated that the effect arose from a deficit in attentional or other high-level cognitive resources during that intervening time period. However, the exact level of processing at which the AB exerts its disruptive effect is still not clear. A number of studies employing
electrophysiological measures of neural processing have supported a late or high-level mechanism of disruption in the attentional blink. For example, it has been demonstrated that generic feed-forward visual sensory processing to the T2, indexed by the sensory-evoked P1 and N1 responses, is preserved during the attentional blink (Sergent, Baillet, & Dehaene, 2005; Vogel, et al., 1998). Moreover, even the later semantic-related N400 ERP component was reported to be equivalent at Lag 7 (non-blink) and Lag 3 (blink) trials (Luck, et al., 1996; Rolke, Heil, Streb, & Hennighausen, 2001), suggesting processing all the way up to the level of semantic analysis is preserved even during the reduced awareness seen during an attentional blink. This full high-level processing during the AB has been partially questioned, however, by a subsequent study showing disruption of semantic processing of T2 when task demands or perceptual load associated with T1 were increased (Giesbrecht, et al., 2007). 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, an ERP response normally associated with oddball stimuli or correct target detection (Vogel, et al., 1998).

Finally, electrophysiological and neuroimaging studies have suggested that the bottleneck limiting information processing and resulting in the attentional blink, as well as other effects disrupting visual awareness, can be localized to areas in and around the prefrontal cortex, as well as a fronto-parietal network, all of which are areas that follow feed-forward visual cortical processing areas in terms of the cascade of events ultimately leading to perception (Fahrenfort, et al., 2008; Marois, Chun, & Gore, 2000; Tombu et al., 2011). In addition, a study employing transcranial magnetic stimulation has shown
that stimulating the right parietal cortex reduces the magnitude of the attentional blink
effect (Cooper, Humphreys, Hulleman, Praamstra, & Georgeson, 2004), further
implicating these regions. All of these findings suggest that the attentional blink acts to
disrupt late, possibly reentrant processing, while leaving generic feed-forward visual
signaling intact. This property makes it an appealing method by which to disrupt
awareness, as visual signaling during the attentional blink may reach higher-level ventral
visual cortical areas subserving object-category discrimination, but still not reach
conscious awareness.

Despite the findings supporting late-acting disruption mechanism in the attentional
blink, which 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 a number of studies have measured
responses to faces and other objects during the attentional blink, the comparison isolating
object-category processing, that is, a comparison between responses to faces and other
objects has not been made. For example, 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, et al., 2010). While this demonstrates intact
emotional processing in the absence of awareness, it does not necessarily speak to the
processing of visual object category, as various studies have suggested that the affective
content of a face may be subserved by a separate, faster pathway than face-specific
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 issue with this approach, however, is that the attentional blink is not necessarily a total effect, normally yielding conditions of unawareness in only a subset of all Lag 3 trials. More specifically, the behavioral decrement typically observed in Lag 3 (versus, for example, Lag 7 trials) is on the order of a ~10-40% decrease in T2 detection (Dux & Marois, 2009), meaning that only ~10-40% of Lag 3 trials are likely to constitute conditions of unawareness. This potentially results in an inflated account of processing in the absence of awareness. Accordingly, a probably better measure of the effect of the attentional blink on a neural measure of a visual process is derived by comparing trials with the same lag but with different behavioral results, 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 actually having been visible.

The present study investigated the extent of face-specific processing that occurs in the absence of awareness as induced by the attentional blink. To this end, neural responses to face images were compared to those of another object category. In addition, we employed trial sorting and identification of conditions of unawareness to avoid the above-mentioned possibility of an inflated measure of visual processing in the absence of awareness. Several patterns of results with regard to face-specific processing were possible. 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.

### 4.2 Methods

#### 4.2.1 Participants

Thirty-five healthy participants with normal or corrected-to-normal vision participated in the study. Data from 9 of these participants were not included in the analyses due to excessive eye blinks, technical issues, or inadequate behavioral effects precluding proper binning of data (less than five sums of a given behavioral trial type over the entire experimental session), leaving data from 26 (mean age of $23.3 \pm 3.3$ years; 16 male). All participants used their right hand to make the responses required for the task (two participants were left handed). Informed consent was obtained for each subject in accordance with the standards of the Duke University Internal Review Board. Participants were compensated $15/hour for their participation in the study.

#### 4.2.2 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 21),
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, most of which were grayscale nontarget stimuli, with infrequent ones that were red or green-tinted and served as targets. Subjects were asked to detect via button press green or red-tinted face and house targets occurring among grayscale face and house distracters in a centrally presented rapid serial visual presentation (RSVP) stream. 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 interimage 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 to then do the same for red-tinted images. Four trial types of randomized order and equal distribution were included: 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 the secondary target (T2) in dual target trials. On single-target trials it was also used as a 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 (Figure 21).
Figure 21. 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 relative to T2. Subjects were asked to report both the presence and object-category identity of the green and red tinted targets following each trial.

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 attentional blink 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-attentional blink 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 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 one that could occur in either order. 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 targets presented.

4.2.3 Data Analysis

4.2.3.1 Behavior

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, 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 participants acquired in the attentional-blink and non-attentional-blink trial types.

4.2.3.2 EEG acquisition and ERP data analysis

The electroencephalogram (EEG) was recorded continuously from a custom 64-channel cap (Electrocap, Inc.) with a right mastoid reference, using 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 electrodes (common reference) and baseline corrected
relative to the 166 ms preceding stimulus onset (two periods of the RSVP driving
stimulus rate). 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
types. Trials within each lag trial type were subsequently sorted according to behavior
(e.g., detected and correct; undetected) to examine the effect of the attentional blink on
face-specific processing. The ERPs were statistically analyzed using a within-subjects
two-factor (trial type by face-minus-house effect) repeated-measures analysis of variance
(ANOVA) on the mean amplitude of the face-specific activity enhancement. 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 were
examined over right temporal occipital electrode sites (averaged across scalp sites TO2,
TI2 and C6p), consistent with these locations typically being around the distributional
peak of the negative-polarity face-specific ERP wave, at both early and late latencies.
4.3 Results

4.3.1 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 ± 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 of face and house targets did not differ 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 (F2, 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 (t25= 3.0; p=.01 and t25=-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 22). This pattern of detection performance is consistent with that typically observed for the attentional blink.
Figure 22. Behavioral attentional blink effect
The behavioral decrement in T2 detection given T1 detection typical of the attentional blink 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)

4.3.2 Electrophysiology
Omnibus statistical tests of the face-specific mean amplitude enhancement over temporal occipital sites revealed a significant effect of trial type across the poststimulus time window of 140-700 ms (F2, 50= 4.3, p<.05). Further examination of single target trials revealed a biphasic face-specific negativity during the time windows of 140-220 ms (F1, 25=118.7, p<.0001) and 500-700 ms (F1, 25=27.2, p<.0001). Subsequent tests were restricted to these time windows (across 10 ms time windows) and this scalp region, which examined the effect of trial types for lags inside versus outside the attentional blink window (Lag 7 versus Lag 3), as well as those more precisely probing visual awareness as disrupted by the attentional blink (Lag 3 hits versus Lag 3 misses).
Subsequent analyses examined the presence and absence of the face-specific effect at early and late neural latencies across trial types and behavior. These effects were analyzed by comparing the face-specific difference waves (face minus house) associated with one lag versus another (Lag 7 versus Lag 3) or associated with one behavior versus another within a lag (Lag 3 hits versus misses). No significant difference in the face-specific amplitude enhancement was observed between Lag 7 and Lag 3 trials across either the early or late time windows, collapsed across all behavior ($F_{1, 25}=0.00, p=0.95$ for 140-220 ms; $F_{1, 25}=1.61, p=0.22$ for 500-700 ms; Figure 23). Within each trial type, collapsing all behavioral responses in this way revealed a face-specific enhancement present in the early phase of 140-200 ms ($F_{1, 25}=52.0, p<0.0001$ for Lag 7 and $F_{1, 25}=41.9, p<0.0001$ for Lag 3), but absent in the late phase ($F_{1, 25}=2.78, p=0.11$ for Lag 7 and $F_{1, 25}=0.01, p=0.94$ for Lag 3) for both lag conditions, although trending toward significance in the case of Lag 7 trials. Considering the hit rates for these two lags, this pattern seemed likely to be driven by an asymmetry in the number of trials in which subjects missed the T2 stimulus across these two trial types (~200 of ~3500 trials in the case of Lag 7; ~800 of ~3500 trials in the case of Lag 3), which in turn suggested a relationship between the presence of face-specific activations at a late phase and behavioral performance. When comparisons were restricted to accurate behavior (hits) only, the face-specific enhancement did not differ across lag (Lag 3 versus Lag 7: $F_{1, 25}=2.5, p=0.13$ for 140-220 ms; $F_{1, 25}=0.00, p=0.95$ for 500-700 ms; Figure 24). Further comparisons within lag type showed that the face-specific negativity was present at both the early and late phase for both Lag 7 ($F_{1, 25}=116.5, p<0.0001$, and $F_{1, 25}=14.3, p<0.001$) and Lag 3 ($F_{1, 25}=56.7,$
p < .0001 and F1, 25 = 9.1, p < .01). These findings suggest that the late phase of the face-specific activation is related to behavioral performance. As an additional consideration, the apparent lack of a face-specific negativity at this late phase in Lag 7 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 the late negativity in the case of Lag 7 trials when all behavior was collapsed is likely due to the influence of these incorrect trials, as this activation is highly influenced by behavioral performance. The role of behavior and the effect of the attentional blink on this late phase of face-specific activity were therefore further examined.

Figure 23. 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 reveals that there is no difference in the face-specific amplitude enhancement. The face-specific enhancement, in both Lag 3 (upper panel) and Lag 7 (lower panel) trials, is observed as a bilateral negative-polarity amplitude enhancement with an occipito-temporal scalp distribution. This response’s temporal and scalp distributions are consistent with the
face-specific N170. The superimposed face minus house difference waves show no difference in the face-specific response between Lag 3 (dashed line) and Lag 7 (solid line) trials across the entire averaged epoch.

Figure 24. 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), there is no difference across Lag 3 (upper panel) and Lag 7 (lower panel) in the face-specific negativity, which is present as the initial N170 peak, and then as a later negativity. The superimposed face minus house difference waves show no difference in the face-specific response between Lag 3 (dashed line) and Lag 7 (solid line) hits across the entire averaged epoch. Within each of these conditions, a significant face-specific activation is observed at early (140-220 ms) and late (500-700 ms) stages.

To more specifically isolate the face-specific activity in the presence and absence of awareness, the face minus house difference waves associated with Lag 3 trials were examined as a function of behavior. These analyses revealed a dissociation between the early and late phases of face-specific activity for Lag 3 compared to Lag 3 misses. Specifically, during the initial N170 phase of activity (140-220 ms poststimulus) no
significant difference in the face-specific enhancement was observed between Lag 3 hits and misses (Figure 25) ($F_{1, 25} = .43$, $p = .52$). This result suggests that, regardless of the level of awareness during the attentional blink, the early face-specific processing is not disrupted. However, a significant difference in the face-specific effect was observed at the late phase activity between Lag 3 hits and misses (500-700 ms poststimulus, comprised of consecutive 10 ms time windows, all of which were also individually significant) ($F_{1, 25} = 4.3$, $p < .05$). This effect was driven by a lack of a face-specific amplitude enhancement for Lag 3 misses during this late phase of processing (500-700 ms) ($F_{1, 25} = .62$, $p = .44$) versus the presence of the face-specific effect in the case of hits ($F_{1, 25} = 9.1$, $p < .01$), shown by directly comparing the mean amplitude of face and house responses in the case of hits and misses. Overall, it is evident that the earlier index of face-specific processing represented by the N170 effect was unrelated to fluctuations in behavioral performance during the Lag 3 trials associated with the attentional blink. However, 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 extracted between conditions of awareness, as modulated by the attentional blink.
Figure 25. Hits versus misses in Lag 3 (AB window) show intact N170 but disrupted late face-specific activity

Comparison of Lag 3 trials in which the attentional blink was present (T2 missed, upper panel) to Lag 3 trials in which the blink was absent (T2 detected and correctly identified, lower panel) reveals no difference in the early N170 phase of the face-specific negativity. In sharp contrast, a later face-specific negativity is present in the case of accurate behavior but absent in the case of trials in which there was a behaviorally manifested attentional blink (Lag 3 misses). Correspondingly, the superimposed face minus house difference waves show no difference in the early N170 face-specific response, but reveal a dissociation in the late face-specific negativity between Lag 3 misses (dashed line) and Lag 3 hits (solid line), with the face-specific negativity being present at the later phase (500-700 ms) for hits, but absent for misses.

4.4 Discussion

4.4.1 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 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 neutral face and house detection in the present study, electrophysiological responses to faces and houses across Lag 7 and Lag 3 trials could be compared, as is normally done, and as discussed below. 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 directly 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.

4.4.2 Lag 3 versus lag 7 trials

In a traditional comparison of neural activations across Lag conditions -- that is, one made between Lag 7 and Lag 3 trials that collapses all behavior within lag -- no significant difference in face-specific activity was observed at any time window. Furthermore, neither of these two trial types (i.e., Lag 7 and Lag 3 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, but investigating other visual or cognitive processes. For example, using this sort of comparison, visual processing at the level of the semantic content of words has been reported to be preserved during Lag 3 trials. Specifically, in a seminal study employing a semantic priming paradigm, wherein subjects were given a prime word before the onset of the RSVP stream, it was shown that if the T2 was semantically incongruous with the prime, the semantics-related N400 ERP was observed (Luck, et al., 1996; Vogel, et al., 1998). Although this finding was replicated by another group, thereby also supporting 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). This latter study thus suggested that when the behavioral attentional blink effect is enhanced by increasing the T1 task load, a reduction in high-level neural visual processing may be observed (Giesbrecht, et al., 2007). Similarly, a reduction of the N400 component was observed in cases of induced task switching in a similar RSVP setting, further suggesting that these high-level cognitive effects are susceptible to attentional resource constraints (Vachon & Jolicœur, 2011). In addition, it has been shown that the affective content of faces can be processed during attentional blink trials. However, in one experiment, amplitude enhancements of visual-evoked potentials otherwise characteristic of affective stimulus content were reduced and delayed as attentional resources were degraded in Lag 2 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 is
was effective in suppressing awareness are isolated, decreases in neural measures of higher level visual processing may indeed be observed.

4.4.3 Lag 3 hits versus lag 3 misses

Although a wide variety of visual processes are thought 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. These controversies may be due to differences in task load across experiments, 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 data is typically compared to Lag 7 data, 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 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 Lag 3 T2’s following detected T1’s is between 10 and 30% (Dux & Marois, 2009). This means that typically 70-90% of Lag 3 trials 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 such a small decrease from Lag 7 to Lag 3 in the relevant neural response may seem convincing as evidence of preserved perceptual processing in the absence of awareness.
Accordingly, sorting and comparing the trials of detection and non-detection within Lag 3 trials provides a substantially more directed 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 shown, thus dissociating this measure from awareness. A dissociation between early and late phases of the face-specific negativity was observed, however, with the late phase being eliminated in conditions of unawareness as achieved through 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 peak and the later face-specific activity observed beginning at 460 ms post-stimulus. This would be consistent with research supporting 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 such a feed-back signal to extrastriate visual areas and ultimately early visual cortical regions (Bullier, 2001; Camprodon, et al., 2010; Di Lollo, et al., 2000; Tombu, et al., 2011). That is, the present results suggest that the N170 is mainly driven by feed-forward processing (and perhaps some early reentrant activity) propagating through the ventral visual stream prior to any face-specific module, and is therefore not subject to the disruptive effects of the attentional blink, which likely acts to disrupt activity at a functionally later stage. In contrast, the late phase of the face-specific negativity seems more likely to be driven by
reentrant visual processing signals originating from later higher-level processes that are indeed actually disrupted during the attentional blink.

The present experiment offers a set of findings that can potentially reconcile some otherwise contradictory findings in the literature. In addition to the core question concerning the extent to which category-specific information is processed and discriminated in the brain in the absence of awareness, the present study differs from several previous related ones in the manner in which neural data are examined. 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)), 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). In the current study we took a more conservative and direct approach to establishing trials of awareness and unawareness by comparing Lag 3 trials in which T2 behavior was completely correct (detection and correct categorization) to Lag 3 trials in which T2’s were completely missed (no detection). Such an approach in turn revealed the unique finding that late-phase face-specific activity scales with behavioral measures of awareness while the early N170 peak does not.

The above-described dissociation between early and late phases of face-specific processing was made possible by the high temporal resolution provided by electrophysiological measures that is otherwise unavailable in the context of 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, et al., 2007). However, the effect was reduced and thus could 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 fMRI recordings. More specifically, if it is the case that the early face-specific N170 is dissociable from awareness (i.e., it is elicited regardless of manifested awareness), and the late face-specific negativity mediated by reentrant processing is associated with (i.e., varies with) awareness, then neuroimaging results showing a present but somewhat reduced face-specific response in masked conditions may reflect the overall net reduction of face processing activity, but collapsed over time. In contrast, the high temporal resolution of ERPs employed in the current study 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 early face-specific activity can occur in the absence of awareness as modulated by the attention blink, but that late, presumably recurrent, activity from higher-level brain regions feeding back into the ventral visual stream would seem to vary according to awareness of the stimulus input. Such results are thus consistent with theories of visual awareness arising from reentrant processing (Dux, et al., 2010; Fahrenfort, et al., 2007) and as suggested by studies directly acting on this type of processing and subsequent awareness using TMS (Bullier, 2001; Camprodon, et al., 2010).
4.5 Overview

The present study reports several important findings. First, it demonstrates that faces, a stimulus type otherwise considered resistant to the effects of the attentional blink, especially when target faces contain emotion or are 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 main goals here, however, it shows that the early phases of face-specific processing are intact in conditions of unawareness. As with previous research showing extensive visual processing at the level of semantic content during the attentional blink window, directly comparing electrophysiological indices of face processing associated with Lag 3 trials to those associated with Lag 7 trials revealed substantial face processing during the attentional blink window, and thus intact object-category-specific discrimination processes in the brain. However, when the variation in awareness was more precisely isolated by comparing Lag 3 trials in which subjects 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 extracted. In particular, the results demonstrated that the late phase of face-specific processing, presumably reflecting a recurrent brain activation process, was closely associated with awareness, whereas a fully intact early phase of category-specific activity (the N170) was elicited regardless of the behavioral manifested awareness level. Thus, the present results not only reveal brain activation patterns related to conscious visual perception, but they also underscore the importance of isolating the construct of awareness through more
precise data-sorting procedures. Moreover, it reconciles otherwise disparate neuroimaging findings by providing a more temporally resolved account of object processing, including its relationship to conscious awareness.
5 Object-category processing during motion-induced blindness as revealed by electrophysiological recordings

5.1 Introduction

The extent of visual processing that occurs outside of awareness is an unresolved issue of broad importance to the field of cognitive neuroscience. Research examining this question is predicated on the notion that any information that is represented in the brain, whether an individual is aware of it or not, holds the potential to affect subsequent behavior in a relevant way. Identifying the information coded in the brain with or without explicit awareness therefore enhances our understanding of what determines or influences behavior.

The predominant method of identifying perceptual processes that occur in the absence of awareness is through a method known as the dissociation paradigm, which is comprised of several essential components (Reingold & Merkle, 1988). In particular, once a perceptual process of interest is identified, two measures of this process are obtained as a viewer is presented with images invoking this process. An explicit measure is derived from the viewer’s behavioral output or report regarding the content of the images, which serves as an index of their level of awareness. A second measure is typically implicit in nature and reflects the processing of the image content of which the viewer may not be aware, as in the case of behavioral priming or neural responses. Through any number of possible manipulations of the presentation parameters of relevant images (e.g., motion-induced blindness, as described below), conditions are
created in which images are present but not visible to the viewer, which is reflected in a
marked decrease of the explicit measure (Kim & Blake, 2005). The implicit measure is
then probed in these conditions of reduced awareness versus those with full awareness. If
the implicit measure of the perceptual process is shown to be intact, regardless of the
viewer’s ability to report relevant image content, then it is inferred that this process is
occurring in the absence of awareness (Holender, 1986; Reingold & Merikle, 1988).

Discrimination of object category by the visual system is evident through multiple
measures, behavioral and neural, and thus provides explicit and implicit indices that can
be used to examine its relationship with visual awareness. One of the most well-studied
and readily measured processes reflecting such categorical discrimination is face-specific
processing. This process has been most directly (intracranially) observed as enhanced
neural responses to images of faces relative to any other object category observed in
functional modules of the ventral extrastriate and temporal cortices in human and non-
human primates (Allison, Ginter, et al., 1994; Harries & Perrett, 1991; Perrett, et al.,
1992). Using functional MRI this face-specific response has been further localized in
normal human observers to areas in the fusiform gyrus and lateral occipital cortex
(Kanwisher, et al., 1997; Puce, et al., 1995), as well as the occipitotemporal sulcus
through intracranial recordings in patients (Puce, McCarthy, Bentin, & Allison, 1997). In
the context of scalp-recorded electrophysiological measures, face-specific processing has
been recorded as a negative-polarity amplitude enhancement over lateral-inferior
temporal-occipital regions, peaking at ~170 ms after stimulus onset (Bentin, et al., 1996),
and then recurring with a similar scalp distribution at longer latencies (~300-800 ms,
depending upon viewer behavior (i.e., enhanced when relevant to task, delayed when reaction times are slowed))(Harris, et al., 2011; Philiastides, Ratcliff, & Sajda, 2006). These high temporal resolution event-related potential measures of this process are especially useful indices of this relatively high-level of object category discrimination that may not require an explicit report of image content, and thus can serve as an informative implicit measure of this process.

Of the wide array of possible manipulations available to the end of disrupting visual awareness of target images, motion-induced blindness is of particular interest. In motion-induced blindness (MIB), parafoveally presented static targets are superimposed on a globally moving array of distracters. While maintaining fixation at a central location and covertly attending these ever-present targets, viewers periodically lose and regain awareness of the targets (Bonneh, et al., 2001). This striking perceptual phenomenon provides a novel and robust manner by which to attenuate visual awareness experimentally and serves as an appealing method by which to examine face-processing in the absence of awareness. To this end, experimenters use motion-induced blindness to gauge the extent of target-associated processing that occurs in the absence of awareness by probing target-specific processing within and outside of motion-induced-blindness episodes (Kim & Blake, 2005).

Several lines of research have indicated that a range of visual processes are uninterrupted by MIB and, by extension, that MIB acts through a high-level mechanism to disrupt visual awareness. For example, the formation of negative afterimages, a process mediated by a relatively low level of visual processing, is uninterrupted by MIB,
that is, whether the disappearance of a target occurs within or outside MIB episodes (Hofstoetter, et al., 2004). Similarly, orientation-specific aftereffects persist following exposure to a Gabor patch of a given angle, regardless of whether it was presented during or outside of motion-induced blindness (Montaser-Kouhsari, et al., 2004; Rajimehr, 2004). Also, higher-level processes of object representation and updating have been demonstrated to occur during MIB. For example, one experiment showed that the sudden physical offset of a perceptually suppressed target “breaks” the blindness episode, making the viewer aware of this transient change. This in turn suggested that changes in the gross physical properties of the target (i.e., its presence or absence) were being processed during MIB episodes, despite the objects being invisible to the subject (Mitroff & Scholl, 2004). This group also showed that if two previously disparate objects are linked with a line during a blindness episode, they tend to re-emerge simultaneously as one object, indicating that their object-based representation was updated during MIB (Mitroff & Scholl, 2005).

In addition to studies focusing on the visual processes that occur during MIB, research examining the more general dynamics of MIB has supported a mechanism of disruption that acts relatively late in terms of visual processing stages. For example, research investigating the temporal dynamics of MIB has uncovered patterns of disruption consistent with a high-level mechanism. Specifically, MIB episodes associated with specific static targets are shown to be enhanced (to occur more frequently and for greater durations) when those targets are covertly attended (O. Carter, Luedeman, Mitroff, & Nakayama, 2009). In addition, the manner in which the visual system
accounts for the static target location during blindness episodes is similar to the high-
level mechanisms of perceptual filling-in observed for the retinal blindspot or scotomas
(Hsu, et al., 2006). For example, super-imposing a stationary grid over a static target and
moving array results in the target being replaced by the stationary pattern, in what
amounts to a perceptual filling-in effect based upon context (New & Scholl, 2008). In
general, evidence has suggested a rivalrous relationship between the static target and
array of moving distracter stimuli that is manifested in the temporal properties of MIB
(O. L. Carter & Pettigrew, 2003). This relationship is also evident via hemodynamic
measures that show a competitive relationship between ventral and dorsal visual regions
associated with the static target and motion array, respectively, which track the perceptual
state of the subject in their respective levels of activity (Donner, et al., 2008; Scholvinck
& Rees, 2010).

By combining the robust but as-yet unexplained effect of motion-induced blindness
with high temporal resolution measures of face-specific neural processing afforded by
EEG, the present study sought to examine the extent and nature of object-category
processing that can occur during motion-induced blindness. In addition, the possible
mechanism of the disruption that is exerted by MIB was examined. In line with several
previous studies, these processes were probed by examining responses associated with
the perceptual onset of a static target following a blindness episode. Specifically, two
conditions were employed: one in which the disappearance and reappearance of target
images was physical in nature (a static or “no-motion” condition), and the other in which
target objects only disappeared and reappeared perceptually (motion-induced blindness
condition). Face-specific neural responses were then tracked across these actual and perceptual onset conditions to gauge the extent of object-category processing in the brain during MIB, the assumption being that a lack of face-specific activity following a perceptual onset (following an MIB episode) reflects that face-processing was intact during the MIB. In addition, activity preceding the perceptual onset of a present image was compared to that preceding the re-onset of a physically disappeared image, to extract an electrophysiological difference between perceptual “reentrance” and perceptual “entrance.” This comparison effectively extracts activity reflecting the emergence of awareness of a physically present image of which the viewer was previously unaware, which in turn speaks to the mechanism underlying MIB.

5.2 Methods

5.2.1 Participants

Twenty-six neurologically intact participants with normal or corrected-to-normal vision participated in the study. Before beginning the EEG portion of the study, each subject underwent a behavioral screening procedure to establish a minimal level of susceptibility to the motion-induced blindness effect (described below). Four subjects were excluded on the basis of inadequate behavioral effects. Two additional subjects were excluded due to excessive eye blink artifacts in the acquired EEG data (trial rejection rate due to blink artifacts greater than 25%). This left 20 participants with sufficient behavioral effects and viable EEG data for the final analysis (mean age 22.8 ± 2.4 years, 8 female, all right-handed). All participants completed informed consent
procedures as approved by the Duke University IRB, and were paid for the duration of
their participation, even if only for the screening task.

5.2.2 Stimuli and task

Prior to the EEG session, subjects were screened so as to only include those with a
sufficiently robust motion-induced blindness (MIB) effect. Subjects were seated with
their eyes 70 cm from the center of a 19-inch CRT stimulus presentation monitor with a
60 Hz refresh rate and were asked to covertly attend a parafoveal static yellow disc
(visual angle of 3.37°; eccentricity of 7.46°, located in the upper left quadrant of the
screen). This target was superimposed on a full-screen array of blue cross distracters on a
black background, which rotated clockwise as a single surface with its origin at central
fixation, at a speed of 15 rounds (360° rotation) per minute (Psychtoolbox, MATLAB).
Subjects were asked to press a response button when the target disappeared, and to
release this button when it reappeared. If subjects experienced MIB episodes at a rate of
at least 5 disappearances per minute, and of a mean duration of at least 100 milliseconds,
they then proceeded to participate in the full experimental session.

After applying the EEG cap, the experimental session began. This differed from the
screening task in several ways. Static targets were selected randomly and equiprobably
from a set of 80 grayscale circular cropped faces and houses, each of the same size and
eccentricity as the static targets utilized in the screening task. The background array of
distracters was adjusted to include black crosses over a grey background, rendering all
visual elements in the display greyscale. Two run types were included: a “static” type in
which there was no motion of the distracter array, and another in which the distracter
array rotated with the same parameters as in the screening task (Figure 26), alternating between clockwise and counter-clockwise rotation on each run. Regardless of the run type, subjects were instructed to covertly attend to location of the static target, and to push a response key as quickly as possible upon the reappearance of the target after a disappearance period. In the case of static runs, the target would physically disappear for a duration that was randomly jittered between 1200 and 1800 ms, and then reappear. Following the button press, a new image (face or house) would be presented at the target location and the sequence would repeat. In the case of the motion condition, the target image only perceptually disappeared (due to MIB) and, following the button press indicating reappearance, would switch (after a random period between 800 and 1200 ms) to another selected image that remained onscreen until the subsequent button press. This approach enabled disambiguation of physical disappearances in which motion induced blindness could not occur (during the static condition) and perceptual disappearances in which the target never physically disappeared (during the motion condition). Regardless of the run type, subjects were instructed in an identical manner, namely to press the button upon the reappearance of an image that had previously disappeared. Subjects completed 16 experimental runs, each of which ran for 4 minutes, with the majority (12) being of the motion run type (in order to obtain comparable numbers of trials across conditions). Button presses were recorded throughout both run types to assess reaction time in the case of the static condition (relative to the actual reappearance of an actual target), as well as the susceptibility of faces and houses to MIB during the motion condition.
Figure 26. Stimuli and task

Subjects performed the same task for two types of experimental runs. In the static condition (A), randomly selected face and house targets appeared parafoveally (upper left quadrant) for a variable period of time prior to disappearing and then reappearing, at which point subjects were instructed to press a response key as quickly as possible. In the motion condition (B), parafoveal targets superimposed on a coherently rotating array of distracters would perceptually disappear due to MIB (but would never actually physically disappear), with subjects being given the same instructions as in the static condition.

5.2.3 EEG acquisition and analysis

Electroencephalographic (EEG) data was continuously recorded during static and motion run types from a 64-channel custom cap (Electrocap, Inc., Eaton, OH) with a right-mastoid reference, using a bandpass filter of .01-100 Hz, a sampling rate of 500 Hz,
and a gain of 1000 (Neuroscan Inc., Charlotte, NC). Eye movements and blinks were monitored using two horizontal electro-oculogram (EOG) channels referenced to one another and placed on the outer canthi, and two vertical EOG channels placed below the eyes and referenced to frontal electrodes Fp1 and Fp2. Subject behavior was also monitored using a closed circuit video camera.

Following the experimental session, acquired data was analyzed offline using Linux-based ERPSS data analysis software (Univ of Calif at San Diego, La Jolla, CA). Extracted epochs containing eye blinks, eye movements, muscle activity, and slow drift artifacts were rejected offline prior to selective averaging. Artifact-free data were time-locked averaged selectively for the different stimulus types, both to the onset of the stimuli, as well as to button presses indicating the reappearance of images (following physical disappearances in the case of the static condition, and following MIB-induced perceptual disappearances in the motion condition. Averages were low-pass filtered offline using a nine-point running average filter, attenuating external electrical noise of ~56 Hz frequency content and higher. Event-related potential (ERP) averages were algebraically re-referenced to the average of all electrodes (common reference) and baseline corrected to the 200 ms preceding stimulus onset in the case of image-locked responses, and to the period of -1000 to -900 ms preceding the button press in the case of response-locked trials. Face-selective effects were extracted by comparing responses to faces to those associated with houses within each condition.

In order to examine the extent of face-specific processing that occurred during motion-induced blindness, ERP activity time-locked to the button presses in response to
the reappearance of a face was compared to the corresponding activity associated with the reappearance of a house for the static (physical onset) and motion (perceptual onset) conditions. The extent to which the face-specific effect for these reappearances differed between the static and motion conditions was used to infer the extent of face-specific processing that occurs during MIB. Specifically, in the case of the static condition, a face or house stimulus reappeared after having actually disappeared, meaning that no face-specific processing was possibly occurring during the intervening period. In the case of the motion condition, the targets were always present during the preceding MIB episode, but the extent of face-specific processing during that episode is unknown. Accordingly, if the face-specific ERP responses for the reappearances were identical for perceptual onsets after an MIB as for actual physical onsets, it would suggest that during the preceding MIB no face-specific processing had been ongoing, similar to how there would have been no face-specific processing prior to an actual physical onset because there had been no image present. If however, the extracted face-specific activity surrounding the reappearance button press differed significantly between physical and perceptual onsets of targets, it would not only differentiate the neural processes triggered by those onset events, but it would also differentiate between the ongoing object-related processes preceding those onset events. In particular, if no face-specific activity was observed surrounding a button press in the post-MIB reappearance condition, it would suggest that face-specific processing had been uninterrupted during the preceding MIB, thereby dissociating face-specific processing activity from awareness during the MIB. Finally, to examine more general differences between perceptual and physical onsets, the response-
locked data was collapsed across image type (i.e., collapsed across faces and houses), and
compared between the static and motion conditions. This comparison was made for
assessing whether activity patterns for an image of any type (i.e., not specific to any
object category) differed for perceptual versus physical onsets, which would also speak to
the mechanism by which MIB disrupts awareness.

5.3 Results

5.3.1 Behavior

In the static condition, whether a disappearing/reappearing stimulus was a face or
house had no bearing on the reaction time of the subjects. Specifically, subjects were able
to respond to faces and houses with equal reaction time, as the mean RT across stimulus
type (403 ms for faces and 409 ms for houses) did not differ ($t_{19} = .96$, $p = .34$). In addition,
results showed that motion-induced blindness was equally effective in diminishing
subjects’ awareness of faces and houses. In particular, an average of ~10 blindness
episodes per stimulus type (10.0 ± 4.1 for faces; 9.9 ± 3.5 for houses) per run was
observed, with no difference in the mean number of episodes across stimulus type
($t_{19} = .13$, $p = .9$).

5.3.2 Electrophysiology

Electrophysiological data time-locked to the onset of face and house targets
(appearance of a new object in the static condition and switching to a new object in the
motion condition) showed robust face-specific processing in both the static and motion
condition. In both the static and motion conditions, face-specific activity elicited by a
new image was characterized by a higher-amplitude negative polarity response to faces
relative to houses across the post-stimulus time window of 150-800 ms over the relevant ventro-lateral temporal-occipital scalp area (F1, 19=21.6, p<.001 for the static condition; F1, 19=30.2, p<.0001 in the motion condition; site T01/T02; Figure 27). This extracted face-specific activity did not differ between the static and motion conditions (F1, 19=1.0, p=.33; Figure 27). This result thus demonstrates that, despite the apparent physical differences across the static and motion condition (actual visual offsets occurring in the static but not in the motion condition, as well as constant rotational motion of a distracter array only in the motion condition only), stimulus-locked face-specific processing was present and equally robust in both conditions.
Face-specific activations were extracted over right temporal-occipital scalp sites in response to new-image target onsets in the static (A) and motion (B) conditions during the post-stimulus time window of 150-800 ms. These responses did not differ across conditions.

To investigate the extent of face-specific processing that occurs during motion-induced blindness, response-locked face-specific activity associated with the reappearance of target images was compared across the static and motion condition. This face-specific activity differed significantly between the static and motion conditions during the time period surrounding the button press indicating reappearance (-150 to
+300 ms) ($F_{1,19}=24.1, p<.001$; Figure 28). This effect was driven by the presence of a face-specific ERP activity in the static condition ($F_{1,19}=20.6, p<.001$) and an absence of this activity in the motion condition ($F_{1,19}=0.1, p=.93$) during the same time period. For the static condition, where this activity was observed, this button-press-locked response would reflect the convolution of the stimulus-onset-driven face-specific negativity with the response time distribution associated with the button press. If the strictly perceptual onset had actually triggered a comparable face-specific response, a similar activation pattern would be expected in the response-locked averages for the motion condition. Because no discernible face-specific processing was observed for these perceptual onsets, it suggests that face-specific processing had continued uninterrupted during motion-induced blindness, and that the perceptual onset marked only reentrance of the target into awareness and not the coming online of face-specific processing anew.
Physical reappearances of faces and houses (static condition) triggered face-specific activations visible in the response-locked averages temporally surrounding the button press (A). In the case of the purely perceptual onsets of faces and houses (motion condition) following motion-induced blindness episodes, there was no face-specific activation.

Additional analyses collapsing across the face and house object types further examined activity preceding button press responses in the static and motion conditions.

This analysis sought to uncover differences in activity preceding the emergence of
awareness of an image that had been continuously present (motion condition) to activity preceding the awareness of a physically reappearing image (static condition). This comparison uncovered a significant positive-polarity voltage deflection over parietal scalp sites during the 700 ms preceding a button press in the motion condition, but not in the static condition ($F_{1,19}=48.3, p<.0001$; Figure 29). In the present context, this establishes such activation as distinguishing two types of perceptual reappearances: one in which the object was present but not within awareness, for which this response was present (following MIB), and another in which no object was present and for which no such response was observed.

Figure 29. Perceptual versus physical target onsets
Comparisons of perceptual (A) and physical (B) onsets of targets time-locked to the button press, regardless of object category, revealed a positive-polarity voltage deflection over parietal scalp regions during the 700 ms leading up to the button press in the case of perceptual onsets but not physical onsets.
5.4 Discussion

The present results suggest that face-specific processing continues relatively intact during motion-induced blindness, and that MIB therefore disrupts visual awareness through a higher-level mechanism that acts functionally late in terms of visual processing stages. With regard to object-category processing, face-specific electrophysiological effects were present in the case of physical onsets, but not in the case of strictly perceptual onsets following MIB episodes. This means that although the disappearance of the targets was perceptually equivalent during the two conditions, the neural processing related to the appearance and reappearance in the motion condition was rather unlike that for targets that appear or reappear following a complete lack of prior ongoing visual processing (actual disappearance and reappearance in the static condition). This perseverance of visual neural processing in the absence of awareness is consistent with studies employing motion-induced blindness that demonstrate intact lower-level visual perceptual processes during MIB. The present study adds a level of visual perceptual complexity to the processes that are thought to occur during motion-induced blindness based on behavioral studies, which have included orientation-specific processing (Kouhsari, Moradi, Zand-Vakili, & Esteki, 2002) and the formation of negative afterimages at lower levels (Hofstoetter, et al., 2004), as well as the unified nature of an object formed during MIB (Mitroff & Scholl, 2005), and the state of an object following its disappearance during MIB (Mitroff & Scholl, 2004).

The intactness of object-specific processing during motion-induced blindness is not surprising in light of some proposed mechanisms of MIB. In particular, it has been
proposed that MIB occurs as a result of competing representations of the distracter array and the static target within the visual system (Bonneh, et al., 2001). This is in turn manifested as alternating dominance of the mask display and the static target in terms of what is consciously perceived. This account has been supported by neuroimaging studies tracking the relative levels of activity in ventral and dorsal visual regions during and outside of motion-induced blindness episodes. These studies have found that, during episodes of motion-induced blindness, areas coding for the static target objects in ventral visual regions (V4, for example) show a lower level of activity relative to when the targets are visible. In addition, dorsal motion-processing regions show greater activation during blindness episodes than during target visibility (Donner, et al., 2008; Scholvinck & Rees, 2010). The present study speaks to the ramifications of the dynamics observed during MIB by measuring the neural correlates of the perceptual events immediately following blindness episodes. Specifically, the perceptual onset, relative to a physical onset, was characterized by a significant increase in parietal activity during the 700 milliseconds leading to the button press indicating reappearance. This signal could reflect a higher-level process of attentional capture by the perceptual reemergence process (of a target that was continuously present), which would not be observed in the case of a physically absent target, and may accompany its re-entrance into visual awareness. It makes sense that such an effect would only be seen in the perceptual onset condition, as such attentional switching could cause the static target to regain perceptual dominance in a competitive context that simply does not exist in the static condition.
The functional significance of this parietal signal is not clear, although other findings suggest a possible role of this area in the emergence of awareness. For example, the topographic distribution of the current effect is similar to that observed in studies examining the sequence of scalp-recorded voltage events leading, versus not leading, to the emergence of visual awareness. In particular, parietal activation following initial occipital visual components has been reported to correlate with awareness measures, and leading this activation to be interpreted as reflecting a global reentrant signal from high-level parietal regions back to occipital cortex mediating the emergence of awareness (Fahrenfort, et al., 2007, 2008). If the present parietal effect reflects such reentrant activity, it is possible that the competition between representations of the moving distracter arrays and the static targets results in suppression of this more global reentrant process during MIB, which would leave face-specific processing occurring prior to this activation uninterrupted. On the other hand, another study showed that when the left inferior parietal cortex was transiently disrupted using transcranial magnetic stimulation (TMS), it facilitated a switch to the alternate perceptual state. In particular, such disruption shortened blindness episodes when applied at their onset, while also shortening intervals of target awareness when applied at the onset of the awareness (Funk & Pettigrew, 2003). This attentional switch account seems more likely in the present study, as this parietal effect was not accompanied or followed by a re-instantiation of face-specific processing, as would be expected in the case of a global reentrant process.

The present results offer a compelling addition to the body of literature concerning motion-induced blindness, as well as to that concerning visual processing the absence of
awareness more generally. It must be noted, however, that the interpretation of these results is somewhat constrained by the assumption that the response time distribution in the case of perceptual onsets is comparable to that of the physical onsets. This assumption is necessary because of the indeterminate nature of the timing of perceptual target onsets in the motion condition, of which the only marker is the button press executed as quickly as possible by the subjects. However, it seems rather unlikely that the total absence of a face-specific effect in the post-MIB case and the presence of a parietal positivity for any object just prior to the button press in that condition are both simply artifacts attributable to differences in RT distributions. With regard to face-specific processing, if it were actually present in the motion condition, the RT distribution would have to be so spread out relative to that of the static condition as to effectively wash out this effect, which seems unlikely. In addition, the observed parietal effect reflecting perceptual onset of a present image is simply not present in the case of static onsets, and cannot be explained by a difference resulting from the convolution of an RT distribution with the same stimulus-locked voltage deflections. Specifically, the parietal difference resulted solely from its presence in the motion condition and complete absence in the static condition. Thus, it seems rather unlikely that there was such a variable RT distribution in the MIB condition that it would wash out a face-specific effect in that comparison, but would result in an enhanced effect in another comparison.

5.5 Overview

Motion-induced blindness represents a useful tool in disrupting visual awareness while at the same time maintaining low-level visual stimulation. A variety of behavioral
studies have demonstrated that a great deal of visual perceptual processes occurs during MIB, and others have proposed high-level mechanisms of competition to account for the effect. The present study adds to the understanding of MIB and visual processing in the absence of awareness in two ways. First, it shows that although salient images of faces and other objects are susceptible to the effects of MIB, neural activity reflecting object-category discrimination is unaffected. Second, it extracts a pattern of activity just prior to the perceptual onset of an image (following MIB) that suggests disruption of a process possibly originating in parietal cortex, and reflecting an attentional capture by a present target that reestablishes its dominance in an MIB setting, as a possible high-level mechanism mediating MIB.
6 General discussion

6.1 Introduction

The question of the extent and quality of visual perceptual processing that occurs in the absence of awareness holds broad implications for the field of cognitive neuroscience. Studying visual perceptual processing that occurs in the absence of awareness often takes the form of a dissociation paradigm, to which present technology and knowledge of visual processes are particularly amenable. In this approach, explicit behavioral measures reflecting conscious awareness and implicit measures of the underlying perceptual process are probed in parallel across conditions of visual awareness. If the implicit measure, be it behavioral, as in the case of priming, or neural, as is the case for the face-specific negativity probed here, remains unchanged regardless of the level of awareness indicated by the explicit measure, then it is inferred that this process is occurring in the absence of awareness (Holender, 1986; Reingold & Merikle, 1988).

The present research employed electrophysiological measures of scalp-recorded dendritic field potentials, reflecting the summed electrical activity of neuronal populations responding to a specific event. In the context of such event-related potentials (ERPs), object-category specific activity was extracted by comparing neural responses to sets of images that differ at the categorical level. Face-specific processing reflects such processing and is manifested as a multiphasic negative-polarity amplitude enhancement over occipito-temporal scalp regions, peaking at about 170 ms post-stimulus (Bentin, et al., 1996), followed by a longer latency negativity of the same scalp distribution (Philiastides & Sajda, 2006b). This neural marker therefore served as the implicit index
of object-category processing by the visual system that was tracked across distinct conditions of awareness.

A hallmark of this field of research is the variety of ways in which experimenters can manipulate visual presentation of relevant images to disrupt visual awareness (Kim & Blake, 2005). Every method of disrupting visual awareness, from various types of masking to the attentional blink and motion-induced blindness, potentially acts through unique mechanisms and with different temporal dynamics. The present research program employed a multi-methodological approach to disrupting awareness of visually presented object images, face and non-face images in particular. In addition, the use of the high temporal-resolution electrophysiological measures of EEG allowed for a close examination of the temporal cascade of the neural activity leading up to and following this higher-level visual process, including the preceding lower-level visual processing and higher-level attentional processes invoked in these paradigms. Regarding the core question of whether or not object-category processing can occur in the absence of awareness, present results indicate that it can. However, whether or not such processing occurs, and which facets, depends upon the method employed to the end of establishing conditions of unawareness. Ultimately, the present results speak not only to the extent of face-specific processing that can occur in the absence of awareness, but also to the various ways by which awareness can be disrupted and the mechanisms that underlie these.
6.2 Sandwich masking reveals dependence of face-specific processing on intact feed-forward signaling

In the context of sandwich masking, a robust, practically all-or-none, behavioral effect on awareness was obtained between the masked and unmasked trial types, which allowed a direct comparison between these conditions. The contrast between these conditions revealed a complete elimination of face-specific processing in the masked condition, as reflected by the face-specific N170 and later negativity. In addition, by introducing a blank “no-stim” target type, it was possible to track the integrity of the feed-forward visual signaling across masking conditions, which was also demonstrated to be eliminated in the case of masked trials. This result thus implicates a low-level mechanism of disruption exerted by sandwich masking (Figure 30) and underscores the importance of investigating the specific mechanism of disruption for each awareness-disrupting paradigm in endeavoring to account for observed changes in higher-level visual processes.
It was observed that early neural indices of feed-forward extrastriate visual signaling were disrupted in the case of sandwich masking. It appears that this mechanism of disruption ramified as a complete elimination of face-specific processing.

**6.3 Object-substitution masking disrupts face-specific processing through a reentrant mechanism just prior to the initial encoding of face information**

The second approach employed here for disrupting the awareness of presented visual images was object-substitution masking (OSM), in which the delayed offset of a four-dot cue impedes detection of a briefly presented target within those four dots. In this case, it was demonstrated that face-specific processing at both early and late stages was eliminated in the case of unawareness. This inference was based in particular on the comparison of masking-condition trials in which the masking was effective in suppressing awareness versus trials in that same condition in which the masking was not effective. In addition to face-specific processing being eliminated when OSM was
behaviorally effective, longer-latency visual and attentional-shifting effects were also eliminated as a function of awareness within the masked condition. For example, the N2pc, a negative-polarity lateralized ERP wave that reflects the shifting of visuospatial attention to a laterally presented target (Luck & Hillyard, 1994a), was shown to be present in the case of accurate behavior, but absent in the case of unawareness. In addition, a later, similarly extracted, sustained posterior contralateral negativity (SPCN) reflecting visual working memory (Robitaille, et al., 2007) was also eliminated in the case of unawareness. The lack of these attention-related waves in the case of image unawareness indicates a possible failure to shift to the target location in time to encode the initial target information, and subsequently to discern the nature of the target.

The effect of OSM on generic visual processing was examined by including a blank “no-target” condition. The use of this condition revealed that the difference between effective and ineffective masking (reflecting unawareness and awareness, respectively) was seen after initial feed-forward visual signaling, but with the same topographic scalp distribution as early visual evoked potential responses. These results thus suggested that low-level reentrant processing was disrupted by effective object-substitution masking as has been suggested before (Di Lollo, et al., 2000; Dux, et al., 2010). In light of the aforementioned results, it is likely that such a disruption of early reentrant processing ramifies as a disruption of all face-specific processing, as well as other later visual and attentional processes (Figure 31).
In the case of object-substitution masking, no disruption in generic visual signaling was observed prior to a latency of 190 ms post-stimulus. This indicates that early feed-forward signaling was likely left intact. This mechanism yielded disruption of both early and late indices of face-specific processing, reflected by elimination of both the N170 and following longer-latency negativity. It is therefore likely that the early stage of face-specific processing represents a globally feed-forward process, while receiving inputs that arise from earlier reentrant visual signaling.

6.4 The attentional blink disrupts late, but not early, face-specific processing

In the case of the attentional blink, in which detection of a secondary target within a stream of rapidly presented distracters is disrupted by a detected target occurring several hundred milliseconds prior (Raymond, et al., 1992), only the later phase of the face-specific negativity was disrupted. Specifically, when trials in which subjects failed to detect a target were isolated, the early N170 was shown to be identical to that associated with accurate behavior across all conditions, whereas the later phase was shown to have been eliminated.
Although the exact mechanism by which the attentional blink that imposes the above-described effects cannot be inferred from this study alone, one key possibility is that it is through a higher-level mechanism involving a global reentrant signaling process in which parietal cortex may be involved. This speculation is supported by studies investigating the possibility of a unified bottleneck of processing in frontal and parietal areas (Tombu, et al., 2011), as well as those showing modulation of the behavioral attentional blink effect in the context of rTMS applied to the right parietal cortex (Cooper, et al., 2004). In sum, such results point to intact early visual processing, including early face-specific processing, but disrupted later processing (longer-latency negativity) that potentially relies on input from higher-level areas (Figure 32).

Figure 32. The attentional blink disrupts late, but not early, indices of face-specific processing

In the case of the attentional blink, it was observed that, in the case of unawareness during lag 3 trials, the N170 was present to the same extent as in any other condition of full awareness. The longer-latency, later face-specific negativity, however, was eliminated in these trials. This indicated that the attentional blink is likely disrupting visual signaling at a relatively high level of processing that only affects late visual signaling.
6.5 Motion-induced blindness does not disrupt face-specific processing

In the case of motion-induced blindness (MIB), wherein covertly attended static targets perceptually vanish when superimposed on a globally moving array of distracters, results suggested that face-specific processing was uninterrupted during blindness episodes. Specifically, it was shown that the perceptual onset of a physically present image (following an MIB episode) did not trigger any face-specific signaling at what could be interpreted as an early or late stage. Given that face-specific signals are observed to resolve after several hundred milliseconds, this indirectly suggests that face-specific processing was not interrupted at any point during MIB. This raised the question as to what made the difference between the perceptual onset of a continuously present object and that of an object that had actually disappeared and was physically reappearing. Further analyses showed a parietally-distributed positive-polarity ERP during the 700 ms leading up to the perceptual onset of a continually present object following an MIB, but not the onset of a physically reappearing object. This suggested that MIB was disrupting a more global process associated with a physically present object, the awareness of which had temporarily lapsed. This parietal activation may reflect a process of attentional switching between the motion mask and static target that precedes the re-emergence of awareness and that does not exist in the case of an actually disappeared target in which such a rivalrous relationship between the target and motion array would not exist (Figure 33).
Figure 33. Motion-induced blindness does not affect face-specific processing
Strictly perceptual onsets of faces and houses did not trigger any face-specific activations, suggesting that this processing was occurring for the duration of the motion-induced blindness episodes. In addition, activity differentiating a perceptual onset from a physical onset, leading up to a button press, was extracted over anterior occipital/posterior parietal areas. This suggests, albeit indirectly, that re-emergence of awareness following MIB episodes may be mediated by a higher-level attentional switch process, which facilitates the perceptual dominance of the static target, and which is not present for actual reappearances.

6.6 Future directions

6.6.1 Predicting unawareness versus awareness

The present set of results inspires several new lines of research driven by a number of remaining questions. For example, in the case of the attentional blink and object-substitution masking, the perceptual effect yielded by the manipulation of presentation parameters was partial (as is almost always the case in these paradigms), meaning that only a subset of “lag 3” or “masked” trials were characterized by unawareness. This raises the question as to why these methods of disrupting visual awareness vary in their effectiveness from trial-to-trial. This phenomenology suggests that factors other than the
physical nature of the visual stimulation are determining, or at least influencing, whether or not a subject will be aware versus unaware of a target. Given that both of these studies have implications for the availability of attentional resources, with the attentional blink presumably acting through a high-level bottleneck and object-substitution masking disrupting visuo-spatial attentional effects (the N2pc), it would be appropriate to investigate the more global attentional state of subjects prior to the onset of relevant trials. It has been demonstrated, for example, that higher levels of alpha band oscillatory activity over occipital and parietal areas is correlated with decrements in subsequent behaviors that necessitate visual attention (Gomez, et al., 1998; Mathewson, et al., 2009). Therefore, if in these paradigms, pre-trial intervals were selectively averaged in accordance with subsequent behavior (attentional blink lag 3 trials or masked trials that effectively disrupted awareness versus those that do not), it is reasonable to hypothesize that these intervals will be characterized by higher alpha-band power or phase synchrony. In fact, preliminary analyses of this type in the case of object-substitution masking suggest such a pattern of findings, albeit in a trend that did not reach significance in the present data (mean amplitude in 7.5-12.5 Hz frequency range for the 800 milliseconds preceding a hit was 0.93 microvolts, whereas during the same interval leading up to a miss trial, this value was 1.18 microvolts; \( t_{26} = 1.73, p=0.09 \) (Figure 34).
6.6.2 Object-category processing and perceptual decisions

In addition to raising questions regarding the predictability of awareness versus unawareness, the current study employing the attentional blink brings into question the relationship between face-specific electrophysiological effects and behavior. Specifically, it was found that the late face-specific negativity scaled with awareness in the attentional blink, whereas the earlier N170 face-specific effect was unaffected. It would therefore be of interest to introduce conditions in which the physical nature of images is not informative, and decisions are based solely on other factors. A study of the sort employing hemodynamic measures has uncovered patterns of activity that are highly influenced by viewers’ decisions in the face of ambiguous or weak stimulation.
Specifically, it has been shown that the fusiform gyrus exhibits enhanced responses to images of houses that viewers classify (incorrectly) as faces (Summerfield, et al., 2006). Due to the relative sluggishness of hemodynamic measures, it is unknown whether the early and late electrophysiological phases of such object-category specific activity are more associated with the content of perceptual decisions. Such a study employing high temporal resolution electrophysiological measures of the ramifications of perceptual decisions is currently underway, extending work completed as the senior thesis project of undergraduate Solange Ku under the supervision of the author of this dissertation.

Specifically, sandwich masking was used as in Chapter 2, but a third target stimulus type was included (in addition to faces and houses) that was ambiguous in content (scrambled images), thereby creating a condition of impoverished certainty as to the nature of the target (Figure 35). This, coupled with a two-alternative forced choice task (face or house) allowed for neural responses associated with trials that had identical but ambiguous image content and differed only in the behavioral response to be compared. Preliminary findings in this perceptual decisions study show both pre- and post-stimulus activity patterns that mirror the decision made by the subjects in the face of the image ambiguity (Figure 36). In addition to extracting face-specific activations to non-face images, this study appears to be uncovering pre- and post-stimulus correlates of mistaking one object-category for another, suggesting that the pre-stimulus state of relevant brain regions can ramify into the eventual perceptual decision made by a viewer (Figure 37). These and future findings in this line of research will aid in pinning down the relationship that exists
between neural mechanisms underlying visual perceptual processing and behavior, regardless of physical visual stimulation.

**Figure 35. Perceptual decisions stimuli and task**
In a sandwich masking paradigm, subjects completed a two-alternative (face/house) forced-choice task in the context of three possible target types (face/house/scrambled non-object).

**Figure 36. Neural indices of perceptual decisions**
In the case of unmasked scrambled images, a face-response-specific negativity of the same topographic distribution as a stimulus-driven face-specific enhancement was observed. It was of a broader temporal distribution than a visually-evoked face-specific negativity, and began earlier.

In the case of unmasked faces, the behavior of subjects had a profound influence on pre- and post-stimulus activity. Specifically, faces mistaken for houses evoked post-stimulus responses that were indistinguishable from those associated with actual houses. In addition, faces mistaken for houses were preceded by greater positive-polarity activity over temporal-occipital scalp regions (i.e., opposite from the negative-polarity activity associated with face-specific processing).

6.6.3 Directly investigating mechanisms

A final line of research that could fruitfully follow from the present findings would employ electrical or magnetic stimulation techniques to further investigate the mechanisms underlying the various approaches used to attenuate awareness. In a similar vein to a study probing the efficacy and level of disruption of the attentional blink (Cooper, et al., 2004), studies employing transcranial magnetic stimulation (TMS) to brain areas and at time windows thought to mediate these effects could be used to either potentiate or disrupt their influence, which would manifest as differences in behavior.
reflecting the efficacy of disruption. For example, in the case of the attentional blink, stimulating/potentiating activations in the right parietal cortex using repeated TMS has been shown to attenuate the attentional blink effect, suggesting that this region is instrumental in its mechanism (Cooper, et al., 2004). In the case of object-substitution masking, studies employing transient disruption through rTMS have shown that the effect of OSM can be reduced in the case of transient disruption of activity in areas V5/MT+ and V1 (Hirose et al., 2007).

It will be useful to more directly examine the roles of these regions by differentially potentiating and disrupting activity with the goal of modulating the effect of OSM, with stimulation parameters not unlike those used in a study examining the role of the timing of disruption (Camprodon, et al., 2010). In this way, differential roles for feed-forward and reentrant stages of processes could be examined, and the roles of motion and V1 areas better refined. Finally, in the case of motion-induced blindness, TMS has uncovered hemispheric asymmetry and competition with regard to potentiating and disrupting episodes of MIB. Specifically, it was shown that disruptive TMS applied to the left posterior parietal cortex facilitated subsequent perceptual switches by shortening MIB episodes when applied with the onset of blindness, as well as shortening perceptual awareness when applied immediately after an MIB episode. The opposite pattern was extracted with the same stimulation patterns when applied to the right posterior parietal cortex. Ultimately, these findings suggested that 1) inferior parietal cortex mediates perceptual switch processes in MIB and 2) that there exists a competitive interhemispheric relationship in MIB (Funk & Pettigrew, 2003). It would be of interest to
examine the relationship between those previously extracted parietal effects and the present parietal effect (implicated in the strictly perceptual onset). In particular, potentiating a perceptual/attentional switch process by disrupting this activity may prolong MIB episodes and further suggest this area as mediating the effect. In addition, more selectively disrupting the dorsal versus ventral visual streams may render static targets to be more or less resistant to the effect. Such a finding would support the idea that stimulus competition and subsequent alternating dominance in ventral and dorsal signaling plays an important role in the phenomenology of MIB.

6.7 Conclusion

The cascade of neural events leading to visual awareness is characterized by initial feed-forward signaling that builds a representation of a visual stimulus, followed by multi-level reentrant processing that refines this representation and facilitates the emergence of awareness. The present series of experiments demonstrates that the various methods for disrupting visual awareness act through unique mechanisms at different levels of the visual and cognitive processing sequence. In addition, the present work shows that the different facets and phases of face-specific processing (e.g., early and late) are differentially susceptible to disruption exerted by these various methods, and that there exist conditions in which awareness can be eliminated while leaving these neural processes intact. Taken together, this research 1) indicates that a relatively sophisticated level of visual perceptual processing- the discrimination of object-category- can occur in the absence of awareness and 2) provides a more comprehensive account of how the emergent property of visual perception can be disrupted.
Works Cited


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Biography

Joseph Allen Harris was born in St. Paul, Minnesota on September 10th, 1984. He entered Duke University as an undergraduate in 2003, studied abroad at L’Université de Paris VII Jussieu from 2005-2006, and graduated with honors, earning a Bachelor of Science degree in Psychology with a Neuroscience concentration, and with French studies as a second major in 2007. He attended Duke University for graduate school, entering through the Interdisciplinary Program in Cognitive Neuroscience in 2007, and ultimately affiliating with the department of Psychology and Neuroscience. He earned his Master of Arts degree through the department of Psychology and Neuroscience in the fall of 2010.

Published works


Academic awards and honors

2007  Finalist, Zener Award for Outstanding Theses for Graduation with Distinction, Duke University dept. of Psychology and Neuroscience

2007  National Science Foundation GFRP Honorable Mention

2008  National Science Foundation GRFP Honorable Mention

2011  Fellow, Preparing Future Faculty (PFF) mentorship program

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